

# **International Whaling Commission**

## **Reproduction in Whales, Dolphins and Porpoises**

**PROCEEDINGS OF THE CONFERENCE  
*CETACEAN REPRODUCTION: ESTIMATING  
PARAMETERS FOR STOCK ASSESSMENT  
AND MANAGEMENT***

**La Jolla, California  
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*This volume is dedicated to the memory of  
Masaharu Nishiwaki  
1915–1984  
A friend to marine mammals and to us all*

# Preface

In the Introduction to this volume, the editors describe the long planning involved in bringing about and determining the aims of the Symposium and Workshop which resulted in this the sixth Special Issue of the Reports of the International Whaling Commission. The Workshop may not have answered every question that those of us who attended might have hoped; indeed, in true scientific manner, it may well have raised as many new questions as it attempted to answer. However, perhaps its greatest success was in bringing into contact international workers from various, and sometimes sadly isolated, fields: mathematicians and field biologists; physiologists and modellers; workers on the great whales and the smaller cetaceans. The fruits of this contact can be seen in the quality of the revised papers presented in this volume and in the continuing collaboration between the attendees at the meeting.

G. P. DONOVAN  
*Scientific Editor,*  
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*17 March 1984*

## COVER PAINTING

An Atlantic spinner dolphin, *Stenella longirostris*, and calf. Airbrush painting by Kenneth S. Raymond, Southwest Fisheries Center, La Jolla, California, USA. Logo of the 1981 conference.

## Introduction

The charges to the Conference were specific and several:

(1) To examine the question of information content of cetacean ovaries, i.e. do ovarian scars represent a readable reproductive history of the individual female? This is of obvious potential importance to estimating fecundity and populational birth rates.

(2) To review the question of density dependence of reproductive rates, in other words do birth rates go up in an exploited population to yield a harvestable surplus?

(3) To survey new methods that may improve the gathering and interpretation of reproductive information in the assessment and management of cetacean populations.

(4) To review cetacean reproductive biology and modelling across the board and identify major information gaps and research needs.

The Conference had two parts, a three-day symposium followed by a five-day workshop. The Symposium consisted of invited and submitted papers in sessions dealing with reviews by taxa, problems and new approaches in methodology, case studies of populations, density-dependence, and behaviour, functional morphology and physiology. Participation in the Workshop was by invitation.

The meeting had its beginnings in the recommendations of a meeting of an FAO-ACMRR *ad hoc* advisory group on small cetaceans in 1974 in La Jolla (chaired by E. D. Mitchell). A preliminary plan and budget were drafted at a meeting of a research-planning subcommittee of the small-cetacean group (W. F. Perrin, R. L. Brownell, Jr, J. G. Mead and T. Kasuya) in Washington, D.C. in 1975. The initial plan was to convene a workshop meeting on ovarian scars in odontocetes. The plan quickly expanded to include the baleen whales and male reproductive processes and later was opened out to include a review of reproductive models and methods.

The Conference was funded by the Southwest Fisheries Center of the U.S. National Marine Fisheries Service, the International Whaling Commission and the U.S. Marine Mammal Commission.

Of the 58 papers delivered in the Symposium, 45 were

submitted for publication. Of these, four were rejected and seven were withdrawn (for various reasons). Four papers not presented in the symposium are included in this volume (Benirschke and Marsh; Collet and St. Girons; Perrin and Henderson; and Schneyer and Odell). The first three deal with topics discussed at length in the Workshop, and the fourth is thought to be sufficiently relevant to merit inclusion.

In compiling and editing this volume, we placed heavy emphasis on peer review. The submitted papers were each reviewed by at least two referees, who were given the option of remaining anonymous. Some of the papers received as many as five reviews and were very substantially revised before being accepted for publication.

We received a tremendous amount of help from a host of people during the long years that it took to organize the Conference and guide its proceedings to publication. Serving on the Organizing Committee at the Southwest Fisheries Center were William H. Brinkerhoff, Virginia L. Cass, Lisa Ferm, Larry J. Hansen, John R. Henderson, Aleta A. Hohn, Makoto Kimura, Mark S. Lowry, Ruth B. Miller, Albert C. Myrick, Jr, Charles W. Oliver, Thomas B. Shay, Sandra Shay, Priscilla A. Sloan and Drew Stanley. Other SWFC staff who encouraged and assisted the enterprise were Roy M. Allen, Izadore Barrett, John F. Carr, Merle Marrow, Kenneth S. Raymond, Benjamin F. Remington, Gary T. Sakagawa, Frances M. Tonsich, Lillian L. Vlymen, and Charles Wright. The following chaired sessions of the Symposium: John R. Beddington, Kurt Benirschke, Joseph R. Geraci, Daniel Goodman and Roger S. Payne. Helen Becker, Frances Begley, Cheryl Harless, Patricia Metcalf, Lorraine C. Prescott and Mary DeWitt patiently typed and re-typed parts of the volume. A very large part of the work attendant on organization, logistics and publication was carried out at the IWC headquarters in Cambridge, by Greg Donovan, Stella Bradley, Ray Gambell, Martin Harvey and Daphne Ransom. We owe special thanks to the 58 referees who reviewed the papers; their job was the hardest of all.

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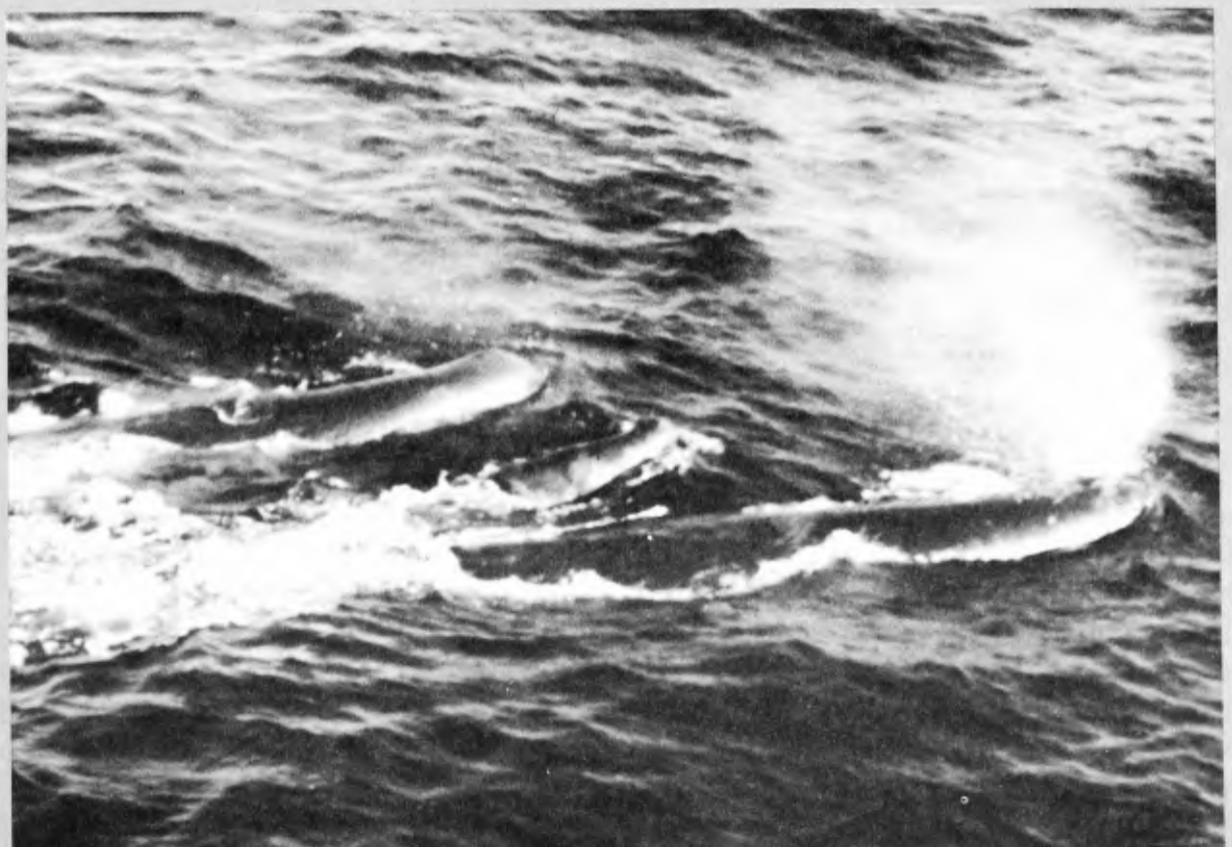
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# Report of the Workshop

Edited by

W. F. PERRIN AND G. P. DONOVAN



*Sperm Whales*

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## I. INTRODUCTION

The main charges to the workshop were to examine the interpretation of ovarian corpora, to review the reproductive components of quantitative models currently used in assessment and management, and to explore how research in the field and laboratory on the one hand and quantitative modelling on the other, can be better integrated. The agenda (Appendix A) was structured to alternate group discussions and laboratory sessions. Discussion leaders and rapporteurs prepared draft reports that formed the basis for this report. The organization

and content of the report do not correspond entirely to the workshop agenda, but rather reflect the course of the discussions. Participants in the workshop are indicated in the list of conference participants at the beginning of this volume.

The following participants acted as discussion leaders and/or rapporteurs during the workshop sessions: Barlow, Benirschke, Braham, Brownell, DeMaster, Donovan, Goodman, Hester, Kirkwood, Lockyer, Marsh, Mead, Mizroch, Odell, Perrin, Reilly and Wells. Marsh and Benirschke prepared the meeting draft and subsequent revisions of Appendix B.

## II. QUESTIONS OF MORPHOLOGY AND PHYSIOLOGY

### (A) Interpreting ovarian scars

Implicit in the use of ovulation rate as a vital parameter in modelling reproduction of cetaceans (see Section B) is the assumption that corpora albicantia (CA) persist through life and thus reflect the actual number of ovulation events. Some workers have also assumed that corpora of simple ovulation can be distinguished from those of pregnancy, yielding an accurate history of calf-bearing.

#### (1) *Do corpora albicantia persist indefinitely?*

The consensus opinion is that CAs do persist indefinitely in the ovaries of at least some cetaceans, e.g. sei whales and fin whales (Gambell, 1968; Laws, 1961). It is likely, however, that not every ovulation results in a corpus luteum (CL). This can be investigated only by steroid monitoring coupled with ovarian histology. The implication of this possibility is that we cannot necessarily assume that ovulation rate is measurable by counting corpora.

For the short-finned pilot whale, *Globicephala macrorhynchus*, no major gaps in the size distribution of CAs indicative of CA disappearance were noted and they are thought to persist indefinitely (Marsh and Kasuya, this volume). The smallest were about 3 mm in diameter. Ohsumi reported that the same is true for the sperm whale, *Physeter macrocephalus*, although final size is greater (about 8 mm in diameter, Gambell, 1972). CAs may also persist indefinitely in *Stenella* spp. (Perrin and Reilly, this volume); however, it was noted that some apparently 'old' females have shrunken ovaries with relatively few CAs. Two explanations were suggested: as a result of ovarian shrinkage many CAs were still present but no longer detectable by gross observation; or some types of CAs may disappear while others persist. The group recommends that the shrunken ovaries be re-examined, using histological techniques, to determine if very small CAs have been missed.

Regarding rate of CA regression, data from *Globicephala* spp., *Stenella* spp., *Delphinus delphis* and other species indicate that CLs regress very quickly initially (first few days or weeks), then slowly thereafter. Regression in the sei whale is rapid immediately after calving, from about 84 mm to about 36 mm in diameter in the first month, then slowing during the balance of the lactation period. Minimal size is reached after perhaps years or decades (Gambell, 1968).

A distinction has been made in some studies between corpora atretica and CAs. In *G. macrorhynchus*, for example, the size distribution of corpora atretica is very different to that of CAs. Corpora atretica shrink to a smaller size (< 1 mm) and may ultimately disappear (Marsh and Kasuya, this volume). Kasuya, Miyazaki and Dawbin (1974) were able to distinguish these two types of corpora for *Stenella* spp. in the western Pacific, but this is not true for the eastern Pacific populations of the same species (Perrin, Coe and Zweifel, 1976). Consequently, corpora counts and size distributions for these two areas for similar species may not be strictly comparable.

Marsh noted much variation in the number of corpora atretica in mature *G. macrorhynchus*, ranging from 0 to

34 per pair of ovaries (usually less than ten). Some of the whales with very high numbers of corpora atretica were found to have low CA counts for their age, but not all with high corpus atreticum counts had low CA counts.

#### (2) *Are corpora albicantia of simple ovulation distinguishable from those of pregnancy?*

The group concluded that a difference cannot be discerned with currently used methods. Marsh, Ohsumi and Benirschke reported no discernable difference for odontocetes, either macroscopically or histologically. It has been reported by Laws (1961) that no difference exists for fin whales. However, Zimushko (1970) reported that he could distinguish the two types of CAs in gray whales. Other Soviet researchers report similar findings (Ivashin, this volume). Ivashin mentioned his (1958) study in which this was also done for humpback whales, based on the size of the CA, under the assumption that a CL of pregnancy regresses more slowly than a CL of ovulation only. He also reported finding morphological differences between CLs of pregnancy and of ovulation. It was pointed out, however, that lactation can affect the rate of regression, and it was agreed that size of the CA alone, (even when adjusted for age) cannot be considered an indicator of the original nature of the event giving rise to it. Marsh noted that in *G. macrorhynchus* large CAs do not appear to regress further during pregnancy and suggested that in this species the rate of regression of a CA may be affected by hormonal status. In contrast, Larsen reported that he found significant regression of corpora during pregnancy in minke whales.

The group discussed possible new techniques to distinguish between CLs of pregnancy and ovulation. Erickson noted that the compound relaxin appears in a CL of pregnancy but not in a CL of ovulation, and it is only necessary to freeze specimens very soon after death to test tissues for presence of this substance. The substance disappears rapidly during regression of the CL. However, it is necessary to fix ovaries properly and immediately following death in order to examine structure at this level, and this may be impractical under field conditions. Miyazaki suggested that since organochlorines (PCBs and DDT) are flushed from a female during lactation (Tanabe, Tanaka and Tatsukawa, 1981), perhaps differential presence of these residues may be used to distinguish between CLs of the two types; work on this is in progress in Japan. Ohsumi noted that it should be possible to determine whether a female with one CA has been pregnant by histological examination of the mammary glands. This may offer a method of identifying reference CAs of the two types so that they can be compared histologically.

### (B) Variation in ovulation rate

#### (1) *Variation among species*

It is clear that there is great variability among species. Evidence for varying ovulation rates exists in the literature for both mysticetes and odontocetes. For example, in Southern Hemisphere fin whales, the ovulation rate is one corpus per 1.4 years (Lockyer, 1972; Gambell, 1973) whereas in minke whales the rate is approximately one corpus per year (Masaki, 1979). For the sperm whale, Gambell (1973) has calculated a mean

ovulation rate of 1 corpus per 2.33 years. For the gray whale, a rate of one ovulation per 1.93 years has been calculated (Reilly, this volume).<sup>1</sup>

## (2) *Variation within species*<sup>2</sup>

Mizroch (1981) has found evidence of age-specific ovulation in southern fin whales, the rate decreasing in old animals. Evidence by Best (1967; 1980) and Gambell (1972) for sperm whales and Marsh and Kasuya (this volume) for pilot whales suggests a fall-off in rate with older age. Sergeant (1962) reported that in *G. melaena* there is evidence of multiple ovulations per pregnancy in young females. Similar findings have been reported for *Lagenorhynchus obliquidens* (Harrison, Brownell and Boice, 1972).

There are indications that frequency of ovulation as recorded in CAs (disregarding the question as to whether every ovulation results in a CA) decreases in older individuals in some populations, while *per-capita* pregnancy rate does not. This was reported by Mizroch for Southern Hemisphere fin whales (although other factors, such as the difficulty of accurate age determination, may be involved) and by Kasuya for western Pacific striped dolphins, *Stenella coeruleoalba*. The implication is that decline in frequency of CAs with age does not necessarily indicate a decline in pregnancy rate.

Gambell (1968; 1972) has used regression rates of corpus size to estimate age-independent ovulation rates from sei and sperm whales in catches. Lockyer, Gambell and Brown (1977) also used this technique to determine ovulation rates for fin whales taken in the Icelandic catch. However, Collet and Harrison (1981) found that in *Delphinus delphis* the rate of regression of a corpus is not constant but seems to follow a complex pattern. Perrin reported data from *Stenella longirostris* in the eastern Pacific for two stocks, one heavily exploited and the other lightly exploited (Perrin and Henderson, this volume). His data on size frequency of CAs indicate that young females in the more-exploited stock have a lower number of ovulations per unit of age.

Recent studies of reproductive physiology have determined that captive dolphins may have highly variable ovulation rates. Kirby and Ridgway (this volume) reported multiple ovulations per year for *Tursiops* and *Delphinus*, and Wells (this volume) reported similar findings for *Stenella*. Kirby also found that a female that is anoestrous one year may cycle the next. Based on ovarian morphology, Collet and Harrison (1981) observed multiple successive ovulations in *D. delphis* and possible variation in ovulation rate related to age and social hierarchy.

Benirschke noted that similar variation in ovulation rates occurs in other mammals. Some human females

<sup>1</sup> Editors' note. Other published ovulation rates (years per corpus) include: Bryde's whales – Best (1977), 0.4 (S. African inshore), 2.4 (offshore); sei whales – Lockyer and Martin (1983) 1.7 (N. Atlantic), Gambell (1968) 1.4 (S. Hemisphere); fin whales – Lockyer and Brown (1979) 1.6 (N. Atlantic); minke whales – Kato (1982) 1.1–1.2 (S. Hemisphere); humpback whales – Chittleborough (1965) 0.9 (S. Hemisphere); sperm whales – Best (1974) 1.7–3.0 (review of various estimates).

<sup>2</sup> Editors' note. Best (1977) reported an interesting variation in ovulation rates for Bryde's whales found in Southern African waters: the average number of ovulations per reproductive cycle was found to be 3.75 for whales of the 'inshore' form but only 1.00 for whales of the 'offshore' form.

ovulate only once per year. There is also evidence in the literature of 'sterile ovulations', or Graafian follicles without eggs in humans. It can be assumed that these become corpora atretica. Mules also exhibit sterile ovulations in which a CL-like body forms and the follicle becomes atretic.

## (3) *Accessory corpora lutea*

Accessory CLs, defined as occurring when there is more than one CL per foetus in a pair of ovaries, are found in some species. After a brief discussion on the differentiation between the main CL and the accessory corpora, a consensus was reached that in most cases one cannot differentiate between the two, and further that one cannot distinguish between a CA formed from the regression of an accessory CL and one formed from the regression of a primary or single CL. This led to the question of the interpretation of ovulation rates in species that are known to have accessory corpora. It was agreed that for species in which accessory corpora are likely to occur and the rate of occurrence is known, the estimated ovulation rate should be adjusted, as, for example had been done for *Delphinapterus leucas* by Sergeant (1973).

The group agreed that nothing is known of the origin or function of accessory CLs. They seem to be most common in the odontocete genera *Delphinapterus* and *Monodon*, where they have been reported as occurring in about 12% of pregnant females (Brodie, 1972; K. Hay, pers. comm.). Members of the group reported them as being very rare in all *Balaenoptera* species, *Megaptera*, *Eschrichtius*, *G. macrorhynchus*, *Delphinus delphis*, *Stenella longirostris*, *S. attenuata* and *S. coeruleoalba*. Mitchell reported an occurrence of 0.45% in fin whales taken in the former hunt in the maritime provinces of Canada. Laws (1961) reported a rate of 3.5% and Gambell (1968) a rate of 2.0% in fin and sei whales respectively in the Southern Ocean.

## (C) Biases in estimating the reproductive interval

It was noted that calf mortality may shorten the average reproductive interval of a female if that female is capable of becoming pregnant shortly after a calf's death. Several factors were identified that might influence the time between calf loss and re-impregnation: (i) the age of the calf at death; (ii) the degree and timing of reproductive seasonality; (iii) Kirby & Ridgway (this volume) presented evidence that *Tursiops* females in captivity tend to ovulate seasonally and need not be synchronous within a group. This may also influence the length of time between calf death and the next ovulation.

Calf death would, in effect, shorten the average lactation time in a population. Depending on how the reproductive interval is estimated, calf death can introduce a bias. For instance, 'method 2' of Perrin *et al.* (1976), which is based on the maximum length of calves assumed to accompany lactating females, estimates reproductive interval from something that is closer to the maximum lactation time rather than the average. Calf death would thus increase the bias that is inherent in this method. However, 'method 1' in the same paper, which is based only on proportion of adult females lactating, would not be biased in its estimate of reproductive interval by calf death. It should be remembered when

using this method that the calving intervals calculated are averages that include some cycles for which fetal or neonatal death may have decreased the time to re-impregnation.

#### (D) Definition of 'sexual maturity'

The group discussed the question of whether the usual definition of the attainment of sexual maturity in females as being the first ovulation is adequate for modelling purposes. Pubescent females may ovulate more than once before conceiving. It was concluded that three criteria of maturity are useful: first ovulation, first conception and first lactation. The first can be ascertained from examination of ovaries. With regard to ascertaining conception, Benirschke noted that the gross aspect of the uterus in terms of development of stretch marks along the uterine body, marked increase in diameter of the uterine horns and the increase in vascular supply to the uterus, are all indications that the female has borne a large foetus. In addition, the myometrium may show changes in its histology in terms of thickening and vascularity which persist after a pregnancy. These all indicate that the female has born a foetus of substantial size but will occur regardless of whether the foetus is aborted or borne until term. Benirschke also reported that there are irreversible changes in the mammary gland that reflect lactation. These indicate whether a female has borne her calf until at least full term but not whether she has successfully maintained it until weaning.

Histological examination of the endometrium from both cornua may be helpful in identifying whether or not pregnancy existed at the time of capture in situations which are known to have a high risk of causing foetus loss, either through mode of operation of a fishery resulting in spontaneous abortion and/or during work-up of the carcass.<sup>3</sup>

It was noted that in newly-mature fin and sei whales, the apparent pregnancy rate is similar to that for older ages (Laws, 1961; Gambell, 1968) and hence in these and other baleen whales, age at first ovulation is perhaps still the best definition of age at attainment of sexual maturity.

#### (E) Male seasonality

The group discussed the question of seasonal aspermatogenesis in cetaceans. Several examples were noted of reduced activity evidenced by decrease in testis weight, but histological evidence for aspermatogenesis was cited for only 3 odontocetes: *Delphinus delphis* (Collet and St. Girons, this volume), *Phocoenoides dalli* (by Kasuya) and *Monodon monoceros* (K. Hay, pers. comm.), and two mysticetes: fin whales (Laws, 1961) and humpback whales (Chittleborough, 1955). Gambell (1968) did not find histological evidence of seasonality in *B. borealis*. Collet reported that while she found aspermatogenesis in most adult males in the eastern north Atlantic population of *D. delphis*, during the apparent breeding season (February to November), at least some individuals were spermatogenic throughout that period. This suggests that in this area, while there is an overall pattern of seasonality in breeding, male seasonality may be individual rather than populational. Some of the

participants were of the opinion that the activity of a single male should not make any difference as long as there are enough sexually active males to service all of the sexually active females, but some other participants thought that the seemingly complex social structure in odontocetes could make the status of individual males more important, e.g. as in the polygynous mating system of sperm whales.

Kasuya noted that in *G. macrorhynchus* in Japan, the pubertal animals produce small amounts of sperm in the breeding season but no sperm in the nonbreeding season.

Perrin described seasonal change in testes weight in two populations of *Stenella longirostris* in the eastern tropical Pacific with different histories of exploitation by the tuna purse-seine fishery (Perrin and Henderson, this volume). Males that have combined testis-epididymis weight of more than 700 g are fully 'potent', that is, have copious sperm in the epididymes. In the less exploited population (northern whitebelly spinners) a large proportion (about 50%) of adult males attain such testis weights seasonally (in February and in July–August), with maximum weights of more than 2 kg. In the more exploited population (eastern spinners), testis weights increase seasonally, but only a very small number of adult males (less than 5%) reach testis weights of 700 g or more, and maximum recorded testis/epididymis weight is less than one kg. This is correlated with lower pregnancy rates in young, but not old, females in this population. It is possible that some aspect of the exploitation has resulted in reproductive difficulties in the more heavily exploited population. The group agreed that this phenomenon should have high priority for further investigation, as it runs counter to the conventional wisdom that lower density (due to exploitation) leads to higher reproductive rates.

It was agreed that from the point of view of assessing male sexual maturity, in addition to recording testis weights, both the routine examination of the epididymis for sperm and the histological examination of smears of the testis tissue from the periphery and centre are essential to differentiate between immature, pubertal, active and resting mature animals. This is especially important because of the fact that an inactive older male can have testes larger than those of a younger but active male (as found for *D. delphis* by Collet and St. Girons, this volume).

Indications of seasonal testicular activity for dolphins are also available from studies of reproductive physiology. Wells (this volume) found an apparent annual cycle in testosterone production in male *Stenella longirostris*, and Kirby and Ridgway (this volume) reported seasonal variation in testosterone concentrations for *Tursiops*.

#### (F) Pathology and Anomalies

##### (1) Reproductive senescence

Senescent ovaries apparently exist in some odontocete cetaceans, but they have not been found in mysticetes. Marsh reported that in *G. macrorhynchus* from Japan, such ovaries are characterized macroscopically by a lack of follicles, CLs and young or partially regressed CAs. Histological samples indicate a lack of primordial and Graafian follicles, with much of the tissue being fibrotic and sclerotic. While there is no evidence of follicular

<sup>3</sup> Editors' note. E.g. see Martin (1982).

activity, numerous, generally easily counted CAs may be evident both macroscopically and microscopically. In the 50-year-old pilot whale presented in the laboratory session as an example, there were 13 CAs present. Sergeant (1962) reported up to 14 corpora in ovaries of apparently senescent *G. melaena* females.

Female *G. macrorhynchus* exhibit a high incidence of reproductive senescence. Marsh and Kasuya (this volume) found that although females live up to about 63 years, the oldest pregnant female was 34.5 years, the oldest with a CL of ovulation was 37.5 years, and the oldest with a young CA was 38.5 years. Sixty-one (26%) of the 235 mature females sampled were older than 35 years, and ten of these, including the 50-year-old example given above, were lactating. The old lactating females did not show any greater ovarian activity than other old females.

Perrin reported that reproductive senescence in *Stenella* spp. is probably indicated by the presence of 'withered' ovaries (Perrin *et al.*, 1976; Perrin, Holts and Miller, 1977). This condition first appears when there are ten or more corpora present in the ovaries. The frequency of 'withered' ovaries in *Stenella* appears to be very low, on the order of 0.1%, but this figure should be considered approximate as it is not known if these females may be more vulnerable to capture. A comparison of the *Globicephala* spp. with the *Stenella* spp. suggests that the frequency of reproductive senescence may be quite variable from species to species within the odontocetes.

Changes in ovulation rates (discussed above) may be indications of reproductive senescence, but the available evidence is inconclusive.

Reproductive senescence has not been reported for baleen whales. Withered ovaries have not been found, nor have any whales lacking follicular activity been seen in several hundred ovaries examined by Lockyer and colleagues. Female whales over 70 years old have been examined and still exhibit folliculate activity; as many as 50 corpora have been found in some ovaries (although no accessory CLs have been reported).

In summary, reproductive senescence apparently exists in some cetaceans, although it has not yet been identified for baleen whales, and may be of a highly variable frequency from species to species in the odontocetes. The question remains of why it should exist at all; the answer probably cannot be obtained except through sociobiological research.<sup>4</sup>

### (2) Cystic follicles and ovarian cysts

Cystic follicles can apparently only be distinguished from mature follicles on the basis of histology. During a given ovarian cycle, follicle stimulating hormone (FSH) induces many follicles to develop, and the granulosa cells begin to multiply. When an egg is released from one follicle and pregnancy occurs, the others become atretic i.e. cystic with some thecal luteinisation. During atresia, the granulosa cells are the first to die. The loss of or change in the granulosa cells provides the distinction between cystic follicles and mature follicles, but the distinction cannot be made grossly. The group recommends that identification of such bodies be made through

<sup>4</sup> Editors' note. There will be some discussion of this in *Rep. int. Whal. Commn* (special issue 8): Behaviour of Whales in Relation to Management, which will be published in late 1984 or early 1985.

histological examination. Information on occurrence and histology of cystic follicles and other 'ovarian cysts' in baleen whales is contained in Laws (1961) and Gambell (1968).

### (3) Parasites

In dolphins, parasites are frequently found in the lungs or in the hilus of the reproductive tract but generally are not on the surfaces where they can interfere with reproduction. Tapeworm cysts (*Monorygma* sp.) have been seen in the ovarian hilus of *Stenella* spp., forming flimsy adhesions to the ovarian surface. Usually there is fibrosis around the cysts, and histologically some granuloma formation; the granuloma are an indication of the animal's mobilization against the foreign organism. It is believed that these parasites do not interfere with the reproductive function of the ovary.

Parasites have been found to lower reproductive success in at least two cases, however. Geraci, Dailey and St. Aubin (1978) found that parasites in the mammary glands can interfere with successful calf-rearing in *Lagenorhynchus acutus* (through necrosis of mammary tissue), and Walker reported a similar situation in *Phocoenoides dalli*. The rate of infection and its consequences as reported for *L. acutus* suggest that parasitism can significantly affect reproduction in a population.

### (4) Abortion

Abortions occur in cetaceans, but determining if an abortion has occurred when there is no foetus in the vagina is difficult. In the absence of an obvious foetus, neither macroscopic nor histologic examination can confirm abortion, but certain criteria can be used to provide the impetus to look more closely for a possible aborted foetus. The presence of a recent CA, asymmetry of the uterine horns and histologic differences between the horns suggest abortions. Differences in the uteri include a thickened endometrium with evidence of chronic inflammation and remnants of secretions and placental tissue in the larger horn. Abortions of pre-implantation embryos will show only minimal changes in the uterus, and will therefore be even more difficult to detect.

Ichihara (1962) reported on 13 incidences of prenatal death of the foetus in fin whales taken in the Antarctic. The great majority of these incidences occurred in older mothers with 10 or more corpora. Ichihara estimated a minimal prenatal death rate of 0.14% for animals actually observed. Prenatal death in early pregnancy had resulted in rapid foetal disintegration and reabsorption whilst that in late pregnancy resulted in mummification and retention for long periods; lack of a CL and partial decomposition of the foetus had commenced. Prenatal death was observed most frequently for multizygotic foetuses yet one dead and one live foetus were discovered simultaneously in one uterus. A few of the foetuses were deformed.

### (5) Multiplets

Multiplets have been found *in utero* in cetaceans, but there is no evidence of mature delivery of these young. About 1% of fin whale foetuses are twins (Laws, 1961; Gambell, 1968) and Mizroch reported that this proportion

had not changed from 1931–1974. About 25 of 95,000 (0.003%) pregnant fin whales reported to the International Bureau of Whaling Statistics had triplets in their uteri. Jonsgård (1953) reported a fin whale with 6 foetuses, of varying sizes. All of these multiple foetuses have been smaller than term. Kimura (1957) reported multiplet frequencies of 0.57% for humpback whales to 2.28% for sei whales. Kato (1982) reported 0.56% twins and 0.03% triplets for Southern Hemisphere minke whales. The largest fin whale twin was reported to be about 20 ft long, but most were 12 ft or less in length. Two sets of sei whale twins, including one conjoined pair, were about 6 ft long. Multiple calves accompanying their presumed mothers have not been seen in long-term field observations of *Tursiops* or *Stenella* populations by Scott or Wells, nor have they been reported for baleen whales except for a drawing of a humpback whale with two calves published by Scammon (1874).

Benirschke noted that the frequency of *in utero* twins for fin whales is similar to that reported for humans. Humans have an average twinning frequency of 1–2%, but this is highly variable between races. For example, some African tribes have a frequency of 5%, while in Japan the rate may be 0.5 to 0.7%.

The rate of twinning may increase with age in cetaceans, e.g. 0.1% (at 1–5 corpora) to 6.25% (at 30–35 corpora) in Southern Hemisphere fin whales, (Kimura, 1957).

Both monozygotic and dizygotic twins have been reported for the Cetacea. The presence of conjoined or incompletely-split foetuses indicates the existence of monozygotic or identical twins. The presence of two foetuses with a single CL was reported for fin whales by Ohsumi (Kimura, 1957) and for sei whales by Gambell (1968), but the presence of a single CL does not necessarily indicate identical twins (e.g. Gambell found a foetus of each sex in a sei whale with one CL). Collet has found a single Graafian follicle with two eggs in *Delphinus*. This is relatively common in cats, humans and other mammals. Dizygotic twins have been identified by the presence of two CLs or because the foetuses were of different sexes.

An observation of twinning in a bottlenose dolphin in captivity suggested that the CL in dolphins is under local rather than systemic control. Gray and Conklin (1974) reported that a female bottlenose dolphin died one week after aborting one twin. Upon examination it was found that the CL for the aborted foetus had regressed, while that for the foetus *in utero* was still active. This is one of the few available observations on the regression rates for CLs.

In summary, it is believed that the mature delivery of twins is unlikely, as it is as yet unrecorded, and that typically either the calves are aborted or the female dies.

#### (6) Vaginal calculi

Vaginal calculi have been reported for a variety of cetacean genera, including *Stenella*, *Delphinus*, and *Lagenorhynchus*. In one *S. attenuata*, 13 vaginal calculi of calcium phosphate were reported, but their origin is unknown (Sawyer and Walker, 1977). Collet reported that she found calculi in 3 of approximately 30 stranded specimens in France. Sawyer and Walker summarized other calculi data. In some cases the calculi may be

calcified semen or vaginal mucus, but in at least three cases calculi have been shown to contain bones from embryos (Benirschke, Henderson and Sweeney, this volume). The incompletely expelled foetus was located in the false cervix between the vagina and cervix in each case. The fate of this kind of calculus is unknown. It may be resorbed eventually, or it may remain in the false cervix for a long time. It is not known if the false cervix opens except during copulation. Walker reported a large calculus in a *Delphinus* with a large foetus. It is believed that the unusual structure of the dolphin reproductive system, especially the false cervix, contributes most significantly to the presence of these calculi, which in at least some cases may interfere with reproduction.

#### (7) Other pathology

Benirschke noted that cetaceans are remarkable in their lack of pathology in the reproductive system. The incidence of pathology is much less than that seen for humans or other terrestrial mammals. In addition to the granulomas from worms described above, two other pathologies were noted in the material available to the workshop:

(1) A granulosa cell tumour previously undescribed for cetaceans that was found by Marsh in a 34.5-year old *G. macrorhynchus*. The tumour did not have the infoldings of cavity remnants found in a typical corpus luteum, and showed a great proliferation of granulosa cells. This type of tumour is found in humans and can be induced in rats.

(2) Uncharacteristic calcifications were found in the ovaries of two *G. macrorhynchus* aged 44.5 years and 62.5 years. These abnormal calcifications may have resulted from old bleeding.

In addition, Collet reported finding 3 cases of hydramnios in 5 stranded females of *Delphinus delphis* and another in a stranded pygmy sperm whale, *Kogia breviceps*, and felt that this may have been the cause of death.

Differences in the incidence of pathology exist between genera, but it is unclear if the total occurrence of pathology within a population can be used as an index of the status of the population. Kasuya reported less pathology in *Stenella* spp. than in *G. macrorhynchus*, but there were apparently no differences between *S. attenuata* and *S. coeruleoalba*. It was suggested that the difference between genera may at least in part be explained by the difference in life spans. In humans and other terrestrial mammals, cancers, fractures and congenital abnormalities are seen more frequently than in animals with shorter life spans.

Pathologies in cetacean reproductive systems are apparently so unusual that any specimens are noteworthy and should be examined in detail. Part of the reason for the low rate of occurrence may be related to examiner acuity and experience. Greater attention to pathologies should be paid in the future.

### III. MODELLING REPRODUCTION

#### (A) Terminology and assumptions

The group considered a draft glossary of terms used in modelling reproduction. After considerable discussion, it was concluded that there really is no accepted 'standard'

terminology; many terms, for example, have been used differently in IWC assessment and management of whales than in terrestrial game management. Given this lack of consensus, the group decided that it would be impractical to try to develop a comprehensive glossary during the workshop. The problem of terminology remains, and the workshop recommends strongly that terms which might be interpreted in more than one way are fully defined whenever used. Some particular points brought out in the discussion are summarised below.

(1) *Density dependence*

It was agreed that 'density dependence' should be thought of as a general term relating to *some* specific resource, which is not necessarily area. The limiting factor could be, for example, abundance of food or of predators.

(2) *Pregnancy rate*

Frequently models assume pregnancy is synonymous with birth. Although this is not true, it is usually unimportant in practice, as the assumed juvenile mortality rate incorporates pre-natal mortality.

(3) *Age at first parturition*

The value of the mean age at first birth, used as a parameter in most models, is often estimated as the mean age at maturity plus the gestation period. This is appropriate, however, only if the first ovulation results in a birth. If it does not, the age of first birth should be increased.

(4) *Specifying intervals*

With the discrete-time models used for real populations, it is necessary in light of both the discrete intervals of our sampling and the tendency for seasonality in population dynamics, to specify when, with respect to the interval(s), the censuses which describe the population trajectory (or the vital rates which define the *per capita* dynamics) are to refer. Commonly, the census refers to the beginning of the interval, age class  $x$  refers to the sum of individuals aged  $x-1$  to  $x$  at that time, survival rates refer to proportion surviving from one census to the next, and fecundities refer to the number of offspring censused (alive) at time  $t+1$  per mature female in the appropriate age class censused at time  $t$ . Other sets of definitions are possible, but it is important to note that it is not necessarily innocuous to mix them.

(5) *Specifying assumptions underlying terminology*

It is unfortunately only very rarely that the elementary parameters for a population dynamics model can be estimated directly from feasible experiments or field programmes; what can be measured are certain population parameters, such as relative frequencies of individuals in different age classes or reproductive states. Various assumptions are then made (usually concerning age distributions and mortality rates in between censuses) depending on the particular instance, to enable one to compute the desired parameters from the available measures. Since the opportunities both for errors and inappropriate data manipulations are fairly extensive at this stage, all models should thoroughly describe how the dynamical parameters they employ were calculated from

observed biological quantities, so that this process may be scrutinized. This is important because although the underlying mathematical theory of the computations may be standard, the improvisation carried out in each particular model may require some unravelling, and the reasonableness of the assumptions must be evaluated case by case.

(B) **Current models**

The participants in the workshop expressed a desire to examine a sample of the models currently being used in cetacean population assessment and management. Three approaches to modelling cetacean populations were reviewed, with emphasis placed on the role of reproductive rates as inputs to these models. The models presented were (1) the current [1981] sperm-whale management model used by the IWC (presented by Kirkwood), (2) the NMFS model for managing dolphins involved in the tuna fishery (presented by Smith), and (3) the IWC management model for North Pacific baleen whales (presented by Horwood).

(1) *The sperm whale model*

The IWC model for sperm whale dynamics (Allen, 1973) belongs to a large class of population models known collectively as age-structured models. With such models, a strict accounting is kept of the numbers of individuals estimated to be within each age class; in this case, age classes are given in one-year intervals. In addition, in the sperm whale model the numbers of males and females are both significant to population growth rates and are examined separately. At the core of this model is the simple updating relationship; the number of individuals in a given age class in a year is equal to the number of individuals in the previous age class one year earlier minus the catch from the previous age class during that year, all multiplied by the survival rate of that age class. The number of individuals entering the first age class is given by the number of mature females in the previous year times the birth rate of mature females.

The assumptions of this approach have to do with the functional form given to the age-specific survivorship and birth-rate parameters. Females are classified as either juveniles (0–2 years), sexually immature (3–9 years), or sexually mature (10+ years). Males are classified as either juveniles (0–2 years), sexually immature (3 to ~20 years), sexually mature (~20 to 24), or socially mature (25+ years). The first assumption used is that survival rates for all non-juvenile males and females are constant with age and through time. These rates are estimated from age samples from the catches. The second assumption is that the juvenile mortality rate is the same for males and females and is constant through time. This rate is estimated from a balance equation by assuming that, at unexploited equilibrium, the number of adult females dying in any year will equal the number of females being recruited into the adult population. Because pregnancy rates are used rather than birth rates, the estimates of juvenile mortality by this method will be biased; this will not, however, affect the results of the model.

All aspects of density dependence are incorporated into the assumptions about the functional form of the

pregnancy rate.<sup>5</sup> Pregnancy rates are assumed to be equal for all mature females. These rates are assumed to be related to the ratio of the number of mature females in the population to the number of mature females in the unexploited population by a non-linear function. The maximum pregnancy rate is taken to be 0.25 and the minimum is taken as 0.20 (corresponding respectively to 4- and 5-year calving cycles). The degree of non-linearity was chosen so as to obtain a single-sex maximum sustainable yield level (MSYL) of 60% of equilibrium density. The pregnancy rates are also dependent on the number of socially mature males in the population. Once the number of socially mature males falls below some threshold, pregnancy rates are assumed to be linearly related to the abundance of such males. The number of males can thus strongly influence pregnancy rates if they fall below this threshold (IWC, 1981a, pp. 100–1).

It was emphasized that actual evidence for density-dependence in the pregnancy rate of sperm whales is insufficient to empirically determine relationships such as those assumed here. For most stocks, the estimates of population sizes are not sensitive to the form of the pregnancy model. However, estimates of replacement yields and MSY levels are very sensitive to the pregnancy model.

### (2) *The ETP dolphin model*

The second example of a management model is that used by the United States National Marine Fisheries Service (NMFS) to determine the status of the dolphins which are involved in the tuna purse-seine fishery in the Eastern Tropical Pacific (ETP). Reproductive rates enter into two rather distinct models, which are both inputs to the management decision process. The first model involves the estimation of the ratio of current abundance to historical (assumed equilibrium) abundance of the populations. The second model involves the estimation of the MSYL of these populations. As currently mandated by US law, the classification of populations of marine mammals as 'depleted' is defined by population levels falling below MSYL (maximum net productivity level, or MNPL in NMFS' terms), hence both elements are required for management decisions.

The ratio of current to historical abundance is estimated by back calculating the abundance of dolphins in 1959 (the beginning of incidental dolphin mortality) from the abundance of dolphins estimated in the last aerial survey (1979). The back calculation can be thought of as a simple accounting exercise. The number of dolphins in a given year is calculated from the number in the next year minus the net recruitment into the population plus the mortality due to fishing in that year. Although reproductive rates do enter into this calculation as an element of the net reproductive rate, the model is quite insensitive to the actual functional form of this net reproduction relationship. It is relatively insensitive to the value chosen for the maximum net reproductive rate over the range of values (0–4%) considered in a recent stock assessment exercise (Smith, 1979). An example can be

given for the offshore spotted dolphin: if the MSYL is assumed to be 0.65, the ratio of current to historic abundance would only change from 0.45 to 0.52 if the net reproductive rate were doubled from 0.02 to 0.04.

The net reproductive rate was assumed to be density dependent, and the specific functional form of this density dependence is of prime importance in determining the second element of the management decision processes, the estimation of MSYL for the species involved. The net reproduction function used in the above model is given by

$$\rho(N) = \rho_0 \left( 1 - \left( \frac{N}{N_{1959}} \right)^\zeta \right) \quad (1)$$

The parameter  $\rho_0$  in this equation is what can be referred to as a phenomenological parameter. Simply stated, this means that this parameter is a composite of many processes which for convenience have been lumped into a single term. As is usually the case, these processes were lumped because they could not be measured separately. Roughly,  $\rho_0$  can be thought of as the difference between the gross annual birth rate and the gross annual death rate in a population that is growing at its maximum rate. The parameter  $\zeta$  affects the shape of the density dependence. Values of this parameter can be chosen so as to obtain MSYLs from any desired fraction of the equilibrium population levels (Smith, 1979). The assumption here that is of concern to the workshop is that reproductive rates and/or survival rates are density dependent. Currently there is no solid evidence that either of these life history parameters of ETP dolphin are density dependent.

### (3) *The North Pacific baleen whale model*

The third management model presented was that used for the North Pacific large whale populations and for the Southern Ocean species before the interspecific relationships were recognized. Unlike the sperm and to a lesser extent the current BALEEN (Allen and Kirkwood, 1979) models, but similar to the above dolphin model, this model does not involve detailing age structure. The number of whales in the component of the population recruited to the fishery is given by those surviving from the previous year plus the incoming recruitment (Breiwick, 1978).

The natural survival rates are assumed to be constant for all population densities. Recruitment rates are assumed to be density dependent and the functional form of this is modelled in a similar way to the net reproductive rate in the dolphin model.

$$N_{t+1} = N_t(1 - M) + \left( r_0 \left( 1 - \left[ \frac{N_t}{N_0} \right]^s \right) + M \right) N_t$$

Where  $N_t$  is the recruited population size at time  $t$ ,  $M$  is the proportional mortality and  $(r_0 + M)$  is the maximum gross recruitment rate. Often  $M$  is estimated from the age composition of a catch taken in the early years of the fishery and  $r_0$  and  $s$  are given by assuming that MSY is 4% of the population size at 50–60% of the initial population size. If exploitation has existed for a shorter time than the age of recruitment then exploitation will have no effect on current levels of recruitment (similar to that described for sperm whales). In this case a modified DeLury estimation technique can be used (Chapman, 1974; Tillman and Grenfell, 1980).

<sup>5</sup> Editors' note. There has been considerable discussion in recent years over the appropriateness of this aspect of the model, e.g. see IWC, 1980, pp. 67–9, 111–12; IWC, 1982a, p. 73; IWC, 1983, pp. 687–8.

### (C) Density dependence

As evident from the examples discussed above, reproductive rates in cetaceans are often assumed to be density dependent in management models. In none of these examples do sufficient data exist to actually estimate the functional response of birth rates to changes in population density. In some cases, there is no direct evidence at all for density dependence in reproductive rates. A question was therefore directed to the participants in the workshop: 'What direct evidence is there for density-dependent responses in reproductive parameters for Cetacea?'

#### (1) *Pregnancy rate or calving interval*

The evidence for density dependence in reproductive rates of Southern Hemisphere fin whales was examined in two papers presented in the Symposium (Beddington and Grenfell, this volume; Mizroch and York, this volume). Although these reports were not in agreement, both included important points for consideration which should be kept in mind when reviewing the evidence for density dependence that follows. First, apparent pregnancy rates may be correlated with other factors such as the area, season and methods of sampling; hence, care should be taken to properly stratify samples. Second, by considering only the mean pregnancy rates, significant patterns in the residuals can be missed. Third, analyses of density dependence should not be limited to correlations between vital parameters and absolute abundance: the response of prey species may also be important, as well as competition and other factors. Finally, since pregnancy rates can be dependent on the age of females, care should be taken to ensure that changes in length frequencies do not confound attempts to examine density dependence.

Evidence for density dependence in eastern Pacific dolphins was discussed in two symposium papers (Hester, this volume; Smith, this volume). Hester showed an extremely rapid decrease in apparent pregnancy rates of spotted dolphins which occurred during a period of decreasing incidental mortality. Possible implications of this are that the population was increasing very rapidly during this time, or that sampling bias changed during this time, or both. There are, however, no data on changes in population size during this period. Smith (this volume) showed evidence of a higher gross annual reproductive rate in those populations of spinner dolphin that had been subject to greater reductions in population size as a consequence of tuna net mortality. Possible problems with these results are, again, sampling bias and the differences in the habitat of the three populations. Another problem is the number of fitted parameters involved in the analysis.

Positive evidence of density dependence in pregnancy rates was cited at the workshop for two other odontocetes. Best (1980) presented data for sperm whales. Kasuya (this volume) showed that the apparent pregnancy rate of striped dolphins changed through time in an exploited stock, however, the area fished expanded during this time period.

Two cases were pointed out for which evidence for density dependence might have been expected. Sergeant

reported the case of long-finned pilot whales in the western North Atlantic, where approximately 50% of a local stock was removed and no change was seen in apparent pregnancy rates. The time period of this study was, however, very short. Reilly mentioned that although the California gray whale stock is apparently growing, insufficient data exist for determining any consequential change in pregnancy rates.

Mitchell cited one case of apparent inverse density dependence in pregnancy rates, in Atlantic fin whales (Mitchell, 1974). Apparent pregnancy rates were lower in one stock (heavily fished over a long period, from Dildo and Williamsport, Newfoundland) than in another, less-heavily exploited stock (fished from Blandford).

#### (2) *Age at attainment of sexual maturity in females*

Perhaps the strongest evidence for density dependence in reproductive rates is a decrease in the age at sexual maturity of females as population size decreases. It was noted that in several cases (Lockyer, this volume), although the average age at sexual maturity did decrease with population density, the average length at sexual maturity did not change, implying changes in growth rates.

The only evidence cited for odontocetes of a reduction in the age of sexual maturity was for striped dolphins. Kasuya (this volume) documented that the age at which 50% were mature in an exploited population of this species decreased from 9.7 to 7.4 years during the period 1955–1970. Sexual maturity was inferred from ovarian activity.

Two sources of data were used to show a reduction in the mean age at sexual maturity in Southern Hemisphere fin and sei whales (Lockyer, 1972; 1974; 1977a; 1979). First, age at sexual maturity was inferred from ovarian activity and number of earplug laminae. Second, the onset of ovarian activity was found to be correlated with a reduction in the thickness of the annual layers in the earplugs of these whales (Lockyer, 1972; 1974). The first method was used to calculate the age at sexual maturity for both recent harvests and those in the 1950s. Earplugs were not, however, collected during the earlier history phase of fin and sei whale exploitation. The second method used therefore was to back-calculate the age at sexual maturity of females that had matured many years prior to the time when earplugs were first collected. Three possible problems were identified with this approach. The average age of sexual maturity for the most recent years will tend to be biased downward because those females that would mature late have not yet come of age. Second, early-maturing animals may be under-represented in the earlier cohorts if their mortality rates are higher. This would also lead to a downward bias. Third, an early age of sexual maturity would not result in increased birth rates if younger-maturing animals had a lower survival rate. The order of decline in age at first maturity is from about 10 years to about 6–7 years in fin whales and from about 11 years to about 8 years in sei whales.

There is one case where the age at sexual maturity has shown resource dependence. Although the Southern Hemisphere minke whale has only recently been exploited, its food supply might be expected to have increased as a result of the depletion of the great whales.

Indeed the age at sexual maturity has apparently decreased in this species (Lockyer, this volume).<sup>1</sup>

### (3) *Percentage simultaneously lactating and pregnant*

The length of the calving interval in cetaceans could be reduced if they were capable of ovulating and becoming pregnant while still lactating. A change in the proportion of pregnant and simultaneously lactating females may therefore indicate a density-dependent response. At least since the establishment of the IWC in 1946, protection has been granted to animals accompanied by calves, which effectively means that for all large whale species, lactating females are protected – hence detecting any change would be difficult. Mitchell (1974) showed that for fin whales in a previously heavily exploited population, 6% were both pregnant and lactating, as opposed to 0–2% in a stock only recently fished. No other evidence was cited for density dependence in this parameter. Kasuya noted that the pregnant and lactating category was limited to those spotted dolphins less than 20 years of age and striped dolphins of less than 35 years in populations off Japan. Perrin stated that this category was uncommon in dolphins of the ETP. No evidence for density dependence was cited for any of these dolphin species.

### (4) *Mean age in the population*

If the rate of population growth is density-dependent, the equilibrium age structure of a population will typically vary with density. For example, if calf survival is the only density-dependent factor, then as a population increases, the mean age in that population will also increase. If only adult survival were density-dependent, the mean age would decrease. For cetaceans, no evidence was cited for a change in age structure associated with a change in density. This kind of change would be difficult to detect in exploited species since most harvests show age specificity.

It was pointed out that in the case of small odontocetes, difficulty in ageing old animals has sharply limited the use of age-structure data in modelling population dynamics.

### (5) *Population growth in depleted populations*

These are essentially two approaches to determining density-dependent response of populations. The above discussions have dealt only with the deductive approach: what effect does density have on the life-history attributes of a population? An alternative approach would be to ignore the details and look for the gross effect of density dependence: a change in the growth rate of a population. At equilibrium, net growth rates are zero. If growth rates increase in an exploited population, this is evidence for density dependence. The choice of approaches will depend on the types of information that can be gathered and the precision of each.

Evidence for positive growth rates in depleted stocks was cited for two species of baleen whale: gray whales from shore counts (Reilly, this volume) and right whales from shore and aerial counts (Mermoz, 1980; Best, 1970; 1981; Best and Roscoe, 1974).

<sup>6</sup> Editors' note. A recent workshop (IWC, 1984b) discussed the available evidence for a decline in age at sexual maturity in the Southern Hemisphere minke whale but was unable to conclude whether or not such a decline had taken place. The discussion was also relevant to other species.

### (6) *Additional comments*

(a) *The problem of 'noise'*. Any population which persists must, as a mathematical certainty, exhibit some density dependence in its population dynamics. This mathematically necessary property does not establish what time lags the density dependence operates on, which components of the life history display the density dependence, or the functional form of the density dependence. The biological problem lies in discovering the mechanism by which the density-dependence occurs, and the associated statistical difficulty lies in demonstrating this from a limited and noisy data base. It will often be the case that density dependence cannot be 'demonstrated' nor can statistically defensible values be estimated for the parameters of the governing dynamics of the population, even though it is certain, on other grounds, that the dynamics are indeed density dependent. For similar reasons, it may only be possible to justify parameterization of a linear model for density dependence, but this is more in the way of a conventional linear approximation than an assertion that the response really is linear.

(b) *The dangers of extrapolation*. The estimation of parameters for a density dependent model of population growth is an empirical exercise in curve fitting. Thus some data will be available concerning population growth rates at a set of densities and parameterization of the model will consist in fitting some function to the observed growth-density relationship. Once the parameters of the function have been fitted, it becomes possible to compute a predicted population growth rate at any density, but the security of these predictions will, of course, deteriorate as the densities to which they refer depart from those densities bracketed by the data which were used in the actual curve fitting. For example, it is possible to compute the theoretical density at which the fitted growth curve yields a zero value (and call this the 'carrying capacity'), or to compute the percentage growth rate associated with a zero density (and call this the 'maximum reproductive rate'), but these values should not be taken seriously if the data were remote from these particular external densities. The temptation to be seduced by extrapolations is greater when the parameters of the equation used are conventionally given names such as 'k' or 'intrinsic rate of increase' which seem to denote some biological reality that in fact does not exist.

## IV. DATA AND SPECIMEN NEEDS FOR STOCK ASSESSMENT AND MANAGEMENT

### (A) *Information needs*

#### (1) *General comments*

The ultimate use of sampling data is in the fitting of bio-mathematical models to aid us in understanding what is happening to the particular stock. Simple models usually do not use all the types of data that are or should be collected, and more complex models are needed to incorporate behavioural and physiological data and information on life history in terms of ecological interactions.

In stock assessment models it is important to estimate

all the demographic characteristics of the population under study, but in most instances knowledge of many of these is limited. Often the effect of the characteristics is multiplicative e.g. pre-natal mortality and juvenile mortality; thus if only one is known; the outcome, as the product of the two, is also unknown. In many instances therefore, the accurate estimation of a particular parameter may not help in the short term, at least in terms of stock assessment. However when additional problems are resolved, our knowledge of the population demography will be greatly enhanced. Therefore, it is essential to maintain long term basic research, for only this will ultimately provide the knowledge to develop correct population models.

In conclusion, it is important to collect as much biological data as possible, even if the information provided may not be 'necessary' direct input for the population model currently being used; such data may, for example, provide a check on the internal consistency of these models as well as serve to develop a realistic model of a species' demography in the long run.

## (2) *Some specific needs*

In addition to the obvious need for data on age-specific pregnancy and maturity already discussed earlier in this report, other, less obvious needs can be identified.

(a) *Age composition of the catch.* Cohort-analysis techniques are available which can give good estimates of past population size (although not for very recent years) and an estimate of recruitment rates independent of information on pregnancy and juvenile mortality rates. For these techniques it is important to have accurate information on the age structure in the catch over a number of years. Various authors (e.g. Cooke and Beddington, 1982; Cooke and de la Mare, 1983; Shirakihara, Tanaka and Nakano, 1983) have recently described population estimation techniques for sperm whales which utilize the age and length distribution in the catch.<sup>7</sup> The exploitation history of most sperm whale stocks has been such that the estimates of population sizes from the start of exploitation to the present are little affected by recent possible changes in reproductive performance. Consequently, independent comparisons of observed and predicted pregnancy rates may be possible.<sup>8</sup>

(b) *Sex composition of the catch.* In certain fisheries the sex ratio in the catch varies significantly from 1:1. In some of the minke whale fisheries, for example off Norway, there is a preponderance of females in the catch in certain areas and at certain times (Christensen, 1975; 1979). In other fisheries, notably for sperm whales, where the males are considerably larger than the females, a preponderance of males is caught. The effect of these removals on reproduction may depend on the degree of reduction of mature whales (see description of the sperm whale model above). Further information on the social behaviour of individual species is essential if the effect of the distortion of the sex ratio is to be fully understood.

(c) *Calf counts.* In several sighting surveys, the proportion of calves to adults has been much lower than might be

expected from current population models (IWC, 1981 b). It is important that further work is undertaken to determine if these proportions are truly representative of the population or if they are the result of survey problems (e.g. segregation of cow/calf pairs, or differential sightability of adults and calves).<sup>9</sup> Payne (1984) reported that for right whales in Argentina, three separate breeding populations use the Peninsula Valdes area in separate years. This needs to be taken into account in right whale surveys in other areas.

## (B) *Data Sources and Sampling Problems*

Discussions on data sources and sampling problems in the estimation of cetacean reproductive parameters focused on the relationship between what is actually measured in field samples and the corresponding population values needed for stock assessment and management. Several distinct sampling methods were identified, each possessing its own set of sampling problems.

### (1) *Samples from commercial catches*

(a) *Large whales.* By far the greatest source of information on cetacean reproductive parameters lies in catches taken from stocks that are exploited in a directed or incidental fishery.

Since 1946 the following data have been routinely collected from each whale caught in accordance with The International Convention for the Regulation of Whaling: species, length, sex, position and date of capture, presence or absence of foetus, length and sex of foetus if possible, and whether lactating. More recently the requirements have been expanded to include the collection, wherever possible, of material for ageing (either earplugs or teeth), of ovaries and of testes weight or at least a sample of testis tissue, although much of this was already collected under national programmes. In addition, data on school size and on sightings of all species (including those protected) are included in the effort forms which each catcher boat must complete.

While very large samples have been taken from commercial catches, there are a number of problems in converting sample estimates of reproductive parameters to the population estimates. Most of them relate to the degree in which the samples are representative of the whole population. For large whales, IWC regulations prohibit the taking of animals accompanied by calves, with the result that the 'lactating' segment of the mature female population is largely missing from samples. Consequently, apparent sample pregnancy rates overestimate true pregnancy rates. Allowance for the under-representation of lactating females has been addressed by Horwood, Donovan and Gambell (1980) and Martin (1982).

Even if no specific segment of the population is absent from catch samples, several reasons can be identified for the possible failure of catches to be representative even of the segment of the population in the area from which samples were taken. By their nature, most fishing methods are selective. In the large cetacean fisheries, it was noted that deliberate selection of large animals could lead to bias in the samples.

A problem common to all catch samples is that due to

<sup>9</sup> Editors' note. This problem is discussed in IWC, 1984a.

<sup>7</sup> Editors' note. For a discussion of these see IWC, 1983.

<sup>8</sup> Editors' note. Some attempts to do this have been made e.g. see IWC, 1981a, pp. 79-80; IWC, 1983, p. 691.

changes in whaling/fishing grounds with time, samples are taken from different segments of the population at different times. Such problems have been noted for Antarctic fin whales by Mizroch and York (this volume). Time series of apparent pregnancy rates for North Pacific sperm whales have been partially confounded by changes in whaling grounds over time (e.g. see IWC, 1981b, p. 689).

It is apparent from the above discussion that while very large samples are available from commercial catches, there are a number of difficulties in using these data in stock assessment. Clearly, nothing can be done about the historical data. In discussing possible means for minimizing the bias in future samples from catches, several members suggested that it may be possible to increase the representativeness of the catch samples by requiring allowable catches to be taken over a wide area. Changes in methods of handling carcasses may reduce the incidence of lost foetuses. It was recognized that such suggestions may have a significant impact on profitability of the industry. Lockyer reported that new methods were being investigated in Iceland for determining whether captured mature females were pregnant in cases where the foetus had been lost. The methods involve histological study of the endometrium and assay of hormone levels in blood and urine (see Sigurjónsson and Kjeld, 1982).

(b) *Directed small cetacean fisheries*: Mitchell (1975) and subsequent reports of the IWC Sub-Committee on Small Cetaceans (IWC, 1976–1982) reviewed the known small cetacean fisheries of the world. The following additional information on data collection in certain fisheries was available to the workshop.

(i) *Japan*. Ohsumi reported that in certain prefectures a licence from the local government is required for small cetacean hunting, and catch statistics are systematically collected. In other prefectures, no licence is required, but statistics are collected. National research programs have been initiated on the populations of dolphins and other small cetaceans taken at Iki Island and in other directed fisheries. Kasuya and Marsh (this volume) have reported on the drive fishery for short-finned pilot whales and Kasuya (this volume) has reported on the exploitation of striped and spotted dolphins in Japanese coastal waters. Problems of representativeness exist here also. Miyazaki reported that in the striped dolphin fishery there were differences in apparent pregnancy rates between samples drawn from the harpoon fishery and the 'driving' fishery.

In fisheries for small cetaceans that segregate by age and sex (even when there may be no specific bias in catch samples), samples taken from individual schools show greater variability between than within schools. For example, Miyazaki and Nishiwaki (1978) found that apparent pregnancy rates in schools of striped dolphins varied from 0 to 94.4%. In such circumstances it is necessary to take samples from as many schools as possible.

(ii) *Canada*. Sergeant reported that there are no data collection requirements for the white whale and narwhal fisheries other than species and number caught, but some data on sinking-loss rate have been collected by (government and non-government) scientists.

(iii) *Greenland*. Larsen reported that no data beyond

species and numbers caught are collected from the small cetaceans taken in Greenland.

(c) *Incidental takes*. Incidental takes of cetaceans have been reviewed extensively in recent IWC Reports (IWC, 1976–82). Additional information made available at the workshop follows.

(i) *ETP tunafishery*. Hammond reported that although there are no obligatory requirements under IATTC (Inter-American Tropical Tuna Commission) regulations, the following data are routinely collected from incidentally killed dolphins by IATTC and NMFS scientific observers (on board US vessels): species, sex, length, reproductive tract of females, testis sample (including epididymis), sex and length of foetus (small foetuses are brought back in formalin), teeth. IATTC observers on non-US vessels, however, do not currently collect specimen material. Although the percentage varies considerably by year, this programme covers about 25% of the estimated total kill on observed cruises. It is noted that younger animals and lactating females are more frequently killed in 'sets' on tuna and dolphin schools that result in lower total mortality than in those that result in high mortality.

(ii) *Other incidental catches*.

*People's Republic of China* – Chen reported that although it is against Chinese law to catch river dolphins, they are sometimes killed accidentally during fishing operations. Chen reported about 10 specimens of *Lipotes vexillifer* and more than 20 of *Neophocaena phocaenoides* have been examined and the reproductive organs analysed by the Institute of Hydrobiology of the Academia Sinica (Chen, Liu and Lin, this volume).

*Brazil* – *Inia geoffrensis* and *Sotalia fluviatilis* are caught incidentally in fisheries in the Central Amazon, and where possible reproductive tracts (Best and da Silva, this volume) stomach contents, parasites, etc. are collected. Tucuxis (*Sotalia*) are occasionally taken near the coast and used for fish bait, and the increasing use of drifting gillnets may result in an increase in the incidental kill in the Amazon. Franciscanas, *Pontoporia blainvillei*, are also captured in the coastal waters of Rio Grande do Sul in fishing nets; over 200 have been collected and are under study.

*Japan* – Ohsumi reported that Dall's porpoise, *Phocoenoides dalli*, are taken incidentally in the Japanese gillnet fishery in American waters of the North Pacific. As part of the research programme, scientists on board certain vessels collect reproductive organs, stomach contents, whole animals and other specimens. There appears to be bias towards pregnant females (over 90% in the samples) and an over-representation of younger males.

*Denmark* – Harbour porpoises, *Phocoena phocoena*, caught incidentally in fisheries in Danish waters are sampled for studies of reproduction, parasite infection, etc. by the Institute for Physiology of the University of Odense.

(2) *Direct counts from surveys*

An alternative method to sampling from commercial catches for estimating the proportion of calves in the population is the use of direct counting techniques through aerial or ship-based surveys or coastal censuses. Where it is possible to cover most, if not all, of the range

of a stock, or if the entire stock migrates past a single point, survey techniques may provide much more representative data than those available from catch samples. Cliff-top or aerial surveys aimed at least in part at obtaining calf counts have been carried out for right, humpback, gray and bowhead whales. Several participants commented that for humpback and bowhead whales, much lower calf/adult ratios had been observed in these surveys than might have been expected. Much higher ratios had been observed for southern right whales off South Africa (Best, 1981; IWC, 1981b). Other participants, citing Payne's (1984) suggestion that there may be 3 separate groups of calf-bearing females off Peninsula Valdes, queried whether the estimates obtained by Best for the waters of southern Africa may be too high (Best, 1970; 1981; Best and Roscoe, 1974).

It was recognized that it is often difficult to obtain full counts of calves from shore-based observations. For example, for Alaskan bowheads Braham reported that the gross recruitment rates estimated from ice camp surveys (1–3%) were generally lower than estimated from aerial surveys (2–5%) (Marquette, Braham, Nerini and Miller, 1982; Cabbage and Rugh, 1982).<sup>10</sup> In this context, much interest was expressed in the application of aerial photogrammetric techniques described by Perryman, Scott and Hammond (this volume) for obtaining calf percentages and length distribution. They have developed a technique for measuring small cetaceans from vertical aerial photographs. Preliminary analyses of some of the data have revealed that modal length distributions can be seen which may correspond to 6-months age groups up to an age of 1½–2 years (i.e. during the linear phase of the growth curve) and may therefore enable estimates of first-year mortality to be obtained. Such techniques may be particularly useful for coastal species.

It was noted that use of aerial survey techniques has been restricted largely to coastal cetacean species, because of the high cost of farther-ranging surveys, such as that carried out in the eastern tropical Pacific (Smith, 1979). It was pointed out that in view of the diving synchrony of sperm whales, aerial photographic surveys may be particularly valuable under appropriate circumstances.

### (3) Strandings

The group agreed that stranded animals are a special and probably unrepresentative segment of a population, particularly single stranded animals. The causes for strandings are still unknown. A common observation in mass strandings is an apparent over-representation of very young and much older animals, as well as unbalanced sex ratios, although it was reported by Sergeant that stranded groups of *Globicephala* spp. and *Pseudorca* appear to resemble schools driven ashore in fisheries in age and sex composition. It was agreed that in most cases it is difficult to use estimates of reproductive parameters obtained from stranded animals for stock assessments. A possible exception noted is mass strandings of whole schools of predominantly sperm whale cows and calves. However, when a species is not taken in any directed or incidental fishery, stranded animals represent the sole source of samples from which

reproductive data can be obtained. Many participants commented on the difficulty in obtaining biological samples from mass strandings in isolated areas, and noted that it took many years for adequate sample sizes to be accumulated. In view of this, it is important that standard procedures be adopted in collecting biological data from mass strandings of cetaceans. 'Strandings networks' such as have been established in the US, the UK, Canada, France and Australia have proved extremely valuable in this regard. It was urged that tooth or earplug samples for ageing be taken from stranded animals.

### (4) Individual-animal studies

The final category of samples that may provide information on cetacean reproductive parameters is that of studies on individual animals. These fall into two types: captive-animal studies and long-term studies of population of identifiable individuals in the wild.

Captive-animal studies have included monitoring of births for individual females, measurement of reproductive hormone levels and observations of social behaviour coupled with measurements of reproductive-hormone concentrations in dolphin colonies dedicated to such research. The information from records of captive births is of value in determining reproductive seasonality or, in some cases, age of first reproduction, but complete records of the female's tankmates are necessary to obtain data on other parameters. Concentrations of reproductive hormones in either serum or plasma have been measured for a number of delphinid species in attempts to determine reproductive condition. The most extensive measurements have been made for *Tursiops truncatus* (Harrison and Ridgway, 1971; Judd and Ridgway, 1977; Kirby and Ridgway, this volume; Richkind, 1977; Sawyer-Steffan and Kirby, 1980; Sawyer-Steffan, Kirby and Gilmartin, 1983) *Stenella longirostris* (Wells, this volume) and *Delphinus delphis* (Kirby and Ridgway, this volume). Kirby reported that hormone information is also available from studies of single live specimens of *Globicephala macrorhynchus* and *Orcinus orca* and from occasional measurements from a few specimens of *Lagenorhynchus obliquidens* and *Delphinapterus leucas*. Measurements of concentrations of progesterone and oestrogens in female delphinids have generally shown that multiple ovulations within a given season are possible, as are seasons without ovulations, and spontaneous ovulations occur in at least some delphinids. Hormonal monitoring is also yielding information on gestation length for several of these species. Seasonal changes in testosterone production in male delphinids have also been recorded.

Detailed behavioural observations in conjunction with regular blood sampling have been made for three species of delphinids in captive colonies. Kirby has closely observed 1 male–2 female *Tursiops* combinations while monitoring steroid concentrations. Kirby and Ridgway observed captive female *Delphinus delphis* over a period of two years while regularly measuring progesterone and oestrogen. Wells observed a captive colony of *Stenella longirostris* and noted changes in association and interaction patterns of individuals correlated with changes in reproductive hormone concentrations.

Captive animals whose entire reproductive histories are known may eventually also contribute greatly in

<sup>10</sup> Editors' note. The most recent discussion of this problem is included in IWC, 1984a.

interpretation of the reproductive history via examination of ovaries after death.

In recent years, declining catch limits set by the IWC for large cetaceans and increasing national controls over small cetacean fisheries have resulted in samples from commercial catches becoming increasingly difficult to obtain. Thus greater emphasis must be placed on gathering data on population reproductive rates and parameters from free-ranging animals. Longterm studies of populations in which individuals have been reliably identified on a repeated basis have been carried out for coastal populations of both baleen and toothed whales. Observations of recognizable individuals over several years can provide information on calving cycles, recruitment and loss from the population, and the relative position of individuals in the social/breeding structure of the population. Payne has identified over 500 right whales, *Eubalaena australis*, off Patagonia over the last ten years and has constructed reproductive histories for his identifiable females. Glockner-Ferrari (this volume) and others have been able to identify several hundred humpback whales from colour patterns, 'facial' grooves, and scars, and have been able to follow a number of identifiable females through several breeding seasons on their wintering grounds. Bigg, Balcomb, and others have been monitoring populations of killer whales, *Orcinus orca*, in the northeast Pacific over the last ten years. They have been able to identify nearly every individual in the populations, and have determined the sex of most of the population members (IWC, 1982). Wells reported that Norris and Dohl began identifying individuals from a population of *Stenella longirostris* off Kona, Hawaii over ten years ago. Norris, B. Würsig, M. Würsig, Wells, and others have continued the observations of this population since 1979, and at present can identify nearly 200 individuals, including females with calves. Irvine, Wells, and Scott have been working with a marked population of *Tursiops truncatus* off the west coast of Florida since 1970 (Irvine, Wells, Scott and Kaufmann, 1981). They tagged approximately half of the resident population, thereby obtaining information on the approximate age and sex of those identifiable individuals, and identified much of the rest of the population from natural marks, allowing the construction of reproductive histories for identifiable females over the last eleven years in some cases. As techniques for individual recognition from natural markings become better developed and more widely applied, much of the requisite information for assessment of populations that were previously inaccessible should become available. However, it must be recognized that the application of such techniques to oceanic populations may be extremely difficult if not impossible. In addition, capture/tagging/sampling/release programmes such as those of Irvine *et al.* (1981) can (a) provide much information on the age/sex structure of a population (particularly for a sexually non-dimorphic species), (b) produce physiological and reproductive profiles for recognizable individuals on a long term basis, (c) identify population differences, and (d) potentially identify the relative contribution of particular males to calf production within populations through analysis of genetic characteristics as has been attempted by Duffield, Odell, Asper, Searles, Evans, Finley and Fraker (this volume).

## V. LITERATURE CITED

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- Best, R. C. and da Silva, V. M. F. Preliminary analysis of reproductive parameters of the bottlenose dolphin, *Inia geoffrensis*, and the tucuxi, *Sotalia fluviatilis*, in the Amazon River system. pp. 361-9.
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## VI. APPENDICES

### Appendix A

#### AGENDA

1. Opening business.
  - (a) Introduction
  - (b) Adoption of agenda
  - (c) Adoption of schedule
  - (d) Confirmation of appointments
    - (i) Discussion leaders
    - (ii) Rapporteurs
    - (iii) Laboratory-demonstration coordinators
  - (e) Review of conference documents
2. Terminology of reproductive morphology and physiology.
  - (a) Group discussion
  - (b) Laboratory demonstrations
3. Interpreting ovarian scars.
  - (a) Group discussion
  - (b) Laboratory demonstrations
4. Current models of reproduction.
  - (a) Terminology and concepts – group discussion
  - (b) Testing hypotheses inherent in current models and management
5. Sampling problems – group discussion.
6. Comparative morphology of reproductive system.
  - (a) Laboratory demonstrations
  - (b) Group discussion
7. Data and specimen needs for stock assessment and management – group discussion.
8. Pathology of the reproductive system.
  - (a) Laboratory demonstrations
  - (b) Group discussion
9. Collection, storage and preparation of reproductive materials – group discussion.
10. Discussion of additional topics.
11. Write and review report of the workshop.

### Appendix B\*

#### TERMINOLOGY OF FEMALE REPRODUCTIVE MORPHOLOGY AND PHYSIOLOGY

##### (1) Morphology of the cetacean ovary

The external appearance of the ovaries of various cetaceans have been described and/or figured. Harrison (1969) and Harrison, Brownell and Boice (1972) summarize the relevant literature. Subsequent papers include those of Brodie (1972), Harrison (1972), Harrison and Weir (1977), Harrison and McBrearty (1973–74, 1977), Harrison, Bryden, McBrearty and Brownell (1981), Collet and Harrison (1981) and Marsh and Kasuya (this volume).

The ovary, like several other visceral organs, is basically composed of a cortex and medulla. The larger cortex contains most of the active cell types and tissues, the most important of which are the follicles with their oocytes, the corpora lutea, corpora albicantia and corpora atretica (each of which is considered separately below), the interstitial cells supported by stromal connective tissue, nerves, and lymph and blood vessels. Surrounding the cortex is a dense connective-tissue capsule or tunica albuginea, which is itself positioned under the covering 'germinal' epithelium.

The medulla consists mainly of dense connective tissue and larger blood vessels, although interstitial cells, hilar cells and structures of the rete ovarii are also found. Fisher and Harrison (1970), Harrison (1949; 1972), Harrison *et al.* (1972), Harrison and McBrearty (1973–74) have briefly described the rete ovarii of various odontocetes.

##### (2) Follicular development (Fig. 1)

'The follicle consists of the oocyte and its envelope which is composed of cells and an outer membrane. During follicular development the morphology changes as the

oocyte and the surrounding cells differentiate' (Peters and McNalty, 1980).

The primordial follicle consists of a small oocyte, a single layer of granulosa cells and a basement membrane. Its appearance and size change little with advancing age. The primordial follicles represent the pool from which all follicles emerge.

The preantral (secondary) follicle is characterized by an oocyte that is in the growth phase with one or more layers of granulosa cells surrounding it. The wall of the follicle differentiates into two layers, the theca interna and theca externa. The transition from a preantral to an antral (tertiary, vesicular, Graafian) follicle is gradual and continuous. As the granulosa cells multiply, there is concomitant increase in the production and accumulation of fluid leading to the development of a follicular cavity or antrum.

As ovulation approaches, the (primary) oocyte resumes meiosis. After a reduction division, one set of homologous chromosomes remains in the cell, which is now called a secondary oocyte. A marked expansion of the whole follicle occurs shortly before ovulation and it bulges from the ovarian surface. In order to allow the secondary oocyte to exit, a localized part of the wall of the ovary and that of the follicle has to disintegrate. At ovulation, the secondary oocyte is released from the follicle and enters the oviduct. In cetaceans, ovulation is usually recognizable by the presence of a stigma, a scar on the surface of the ovary resulting from damage to the tunica albuginea and 'germinal' epithelium at ovulation.

##### (3) Follicular atresia and the development of corpora atretica

Coupled with the normal follicular development cycle is the concurrent normal phenomenon of follicular atresia,

\* Cited references are included in the Literature Cited section of the main body of the report above.

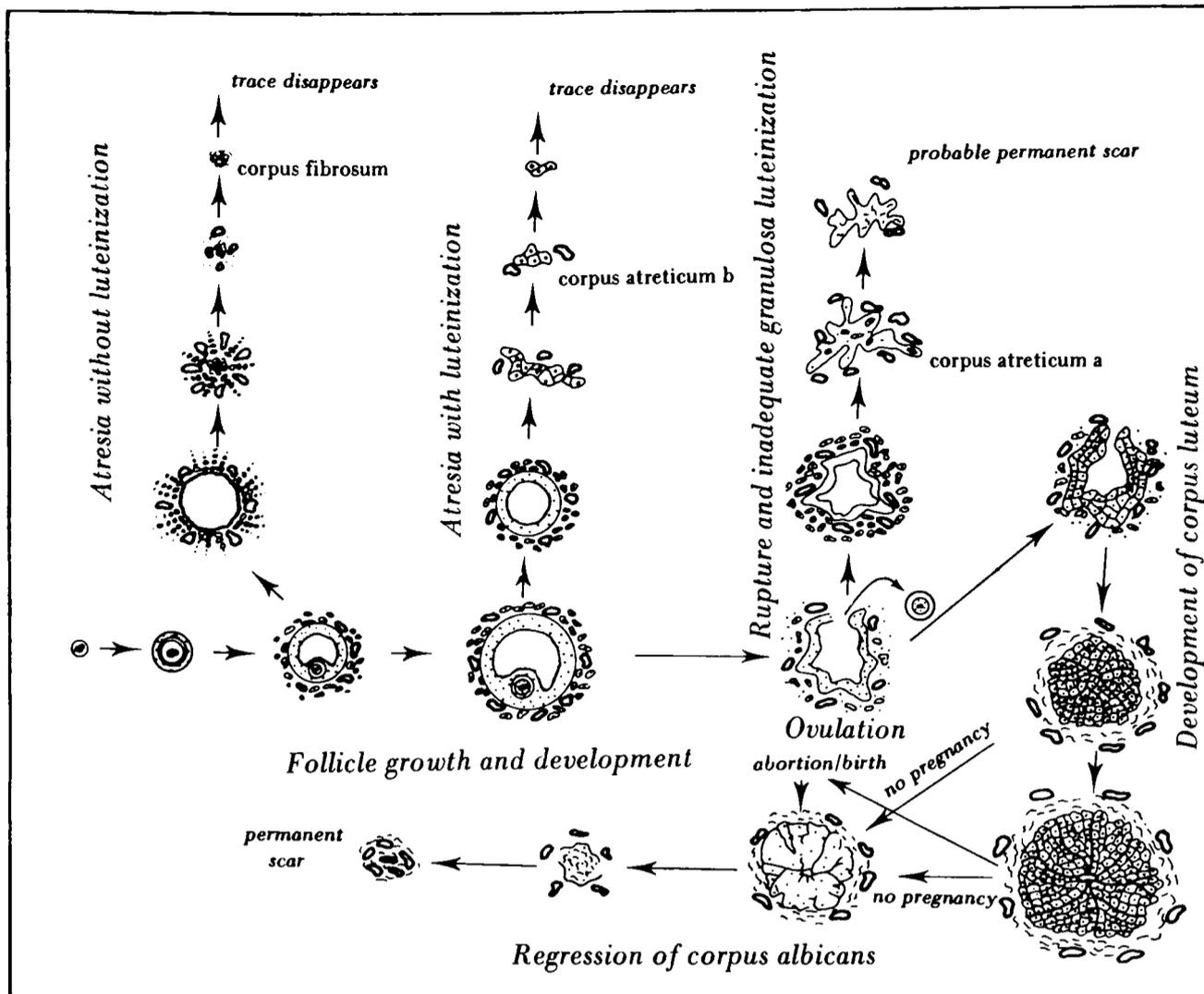


Fig. 1. A schematic representation in the form of a flowchart of the follicular changes occurring in a cycling cetacean ovary. It is also possible for a follicle to form an 'accessory' corpus luteum without releasing the egg. Some large antral follicles may also persist as cystic follicles. In this case macroscopically-detectable luteal tissue does not develop.

which is not necessarily simply a degenerative process. This metamorphosis of the follicle wall into a different kind of probably functional tissue occurs without ovulation as a normal and essential event in the ovarian cycle (Weir and Rowlands, 1977). Atresia gives rise to secondary interstitial tissue (usually considered difficult to find in cetaceans (Harrison and Weir, 1977), an exception being *Pontoporia blainvillei* (Harrison *et al.*, 1981)), or to accessory corpora lutea, both of which may be hormonally active (Weir and Rowlands, 1977). Relatively few Graafian follicles ovulate, many more become atretic.

Follicles may become atretic at any stage of their development (Byskov, 1979). Little is known about the atresia of small follicles, as this may not modify the macroscopic or microscopic structure of the ovary. However, the atresia of medium and large follicles is conspicuous and presents a variety of appearances depending on the stage of the follicle at the time it begins. In medium-sized follicles, atresia usually occurs without luteinization, i.e. without accumulation of lipids in the granulosa or theca cells. Small corpora fibrosa (Marsh and Kasuya, this volume) are derived from the basement membrane of atretic medium-sized follicles. These fibrous bodies are probably slowly resorbed; otherwise they would accumulate in far greater numbers than are seen in the ovaries.

Atresia of Graafian follicles of various sizes often progresses via different stages of luteinization. Lipid accumulation usually starts in the granulosa cells close to the basement membrane and in the cells of the theca

interna. As atresia continues, the granulosa cell numbers become reduced by lysis and phagocytosis with concomitant collapse of the follicle (Byskov, 1979). During the atretic differentiation few thecal cells become necrotic. Rather they hypertrophy and accumulate lipid droplets, undergoing a type of 'fatty' degeneration. The resulting lipid is usually pale yellow at first and readily soluble in fat solvents but gradually oxidizes, becoming darker and more insoluble. The resulting structures persist for some time but usually not indefinitely (Marsh and Kasuya, this volume).

Lutealized (luteinized) follicles have been described in the ovaries of several cetaceans. Different terms have been used by various authors to describe different stages in the development and regression of these bodies as follows: corpora lutea atretica (Best, 1967); atretic follicles (Zimushko, 1970); unruptured lutealizing follicles (Harrison and McBrearty, 1973-74); luteinized follicles (Sergeant, 1962; 1973); atretic lutealized follicles (Harrison and Ridgway, 1971; Harrison, 1972; Harrison *et al.*, 1972); atretic corpora (Zimushko, 1970); yellow bodies (Laurie, 1937), corpora atretica (Laws, 1961; Kasuya, Miyazaki and Dawbin, 1974; Collet and Harrison, 1981; corpora atretica *b* (Best, 1967; Marsh and Kasuya, this volume), or corpora albicantia type 5 (Perrin, Coe and Zweifel, 1976). Most authors have not included them in counts of corpora albicantia; an exception being Perrin *et al.* (1976). We suggest that in future they should be called corpora atretica *b*. (Corpora atretica *a* are discussed below).

Another form of atresia occurs when a follicle behaves

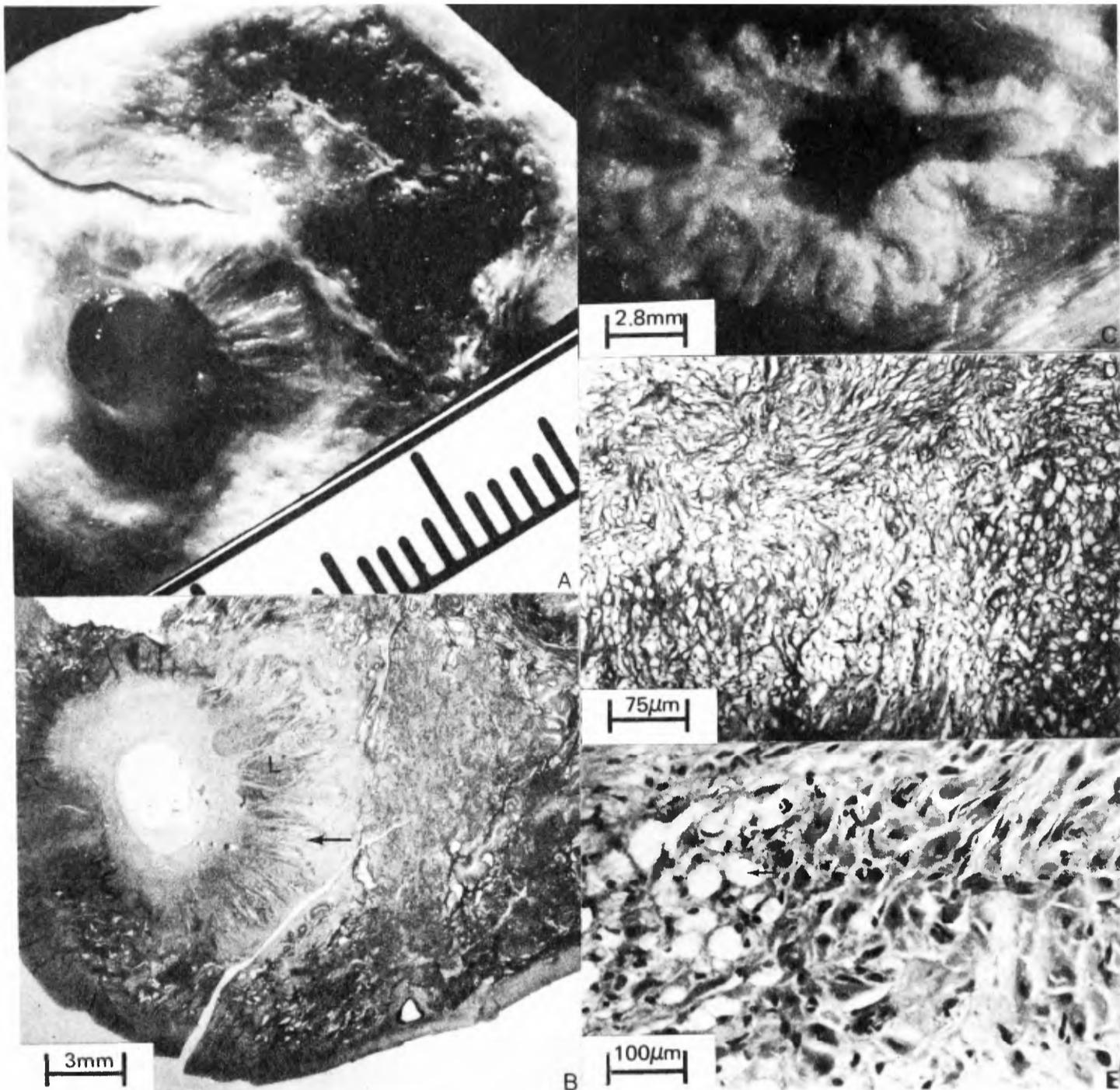


Fig. 2. Structures observed in the ovaries from minke whales, *Balaenoptera bonaerensis*, brought to the workshop by C. Lockyer. The scale is in mm.

- A. Macro-photograph of a young corpus atreticum *a* (lower left) and a corpus albicans (upper right). The young corpus atreticum *a* had a fibrin-filled centre and a prominent stigma on the ovary surface.
- B. Histological section of the structures in A. The granulosa layer of the corpus atreticum *a* (left side) has been replaced by fibrous tissue. The theca layer has luteinized. Some of the theca luteal cells (L) are still active; others (arrowed) are undergoing fatty degeneration. The corpus albicans is on the right. Stained with van Gieson's stain (Curtis, 1905) and celestin blue haemalum.
- C. Macro-photo of an older corpus atreticum *a*.
- D. Histology of part of the corpus atreticum *a* in C. Some theca cells, all of which have undergone fatty degeneration, are still present (examples arrowed) but there has been extensive fibrous replacement. Stained with van Gieson and celestin blue.
- E. Higher-power photograph of the theca layer in B showing the theca lutein cells before (L) and during (arrowed) fatty degeneration. Stained with van Gieson and celestin blue.

as it would have done had ovulation occurred, but the egg is not released, thus forming an accessory corpus luteum (see multiple corpora, below).

Laws (1961) described 'yellow', 'buff-cellular' and 'yellow and white' corpora aberrantia in fin whale ovaries, which he included in counts of corpora albicantia. Gambell (1968; 1972) also recorded corpora aberrantia in sei and sperm whales respectively and included them in corpora counts. Similar structures were also observed in sperm whale ovaries by Chuzhakina (1963). Best (1967) described similar bodies, also in the sperm whale, which he called corpora atretica *a*, excluding them from his counts of corpora albicantia. Marsh and Kasuya (this volume), observed these

structures in *Globicephala macrorhynchus* ovaries, followed Best's terminology and did not include them in corpora counts.

These structures can be derived from ruptured follicles in which corpus luteum development has not proceeded normally (Best, 1967). As these bodies seem to result from mainly thecal luteinization (like the smaller corpora atretica *b* described above), Best (1967) suggested that these structures should be called corpora atretica *a*.

The term 'corpora aberrantia' should be avoided, as it has a different and precise meaning in the general ovarian literature (see Harrison and Weir, 1977).

Fig. 2A shows the general morphology of a young corpus atreticum *a*. The granulosa layer has been

replaced by fibrous tissue. Extensive thecal luteinization has occurred on one side of this body. Some of the thecal lutein cells still appear active, others are undergoing fatty degeneration (Figs 2B, E). A fibrin clot fills the centre. Even though a conspicuous stigma was visible on its surface, this corpus atreticum *a* is macroscopically and histologically quite different from a normal corpus albicans (Figs 2A, B).

Figs 2C, D shows an older corpus atreticum *a* which also appeared to have developed from a ruptured follicle. In this case, a central fibrous clot probably did not develop. The number of lipid-rich luteal cells has been greatly reduced and the fibrous replacement is much more extensive. This structure (Figs 2C, D) is also macroscopically and histologically quite distinct from a corpus albicans. However, it is possible that an old corpus atreticum *a* in which fibrous replacement has been extensive could not be distinguished from a regressing corpus albicans (Laws, 1961; Best, 1967).

Miller and Campbell (1978) discussed cystic corpora lutea in cattle. Such cysts are considered non-pathological and perhaps normal if less than 10 mm in diameter. Like corpora atretica *a* these cysts are formed after ovulation and result from rapid infiltration by fibroblasts through the granulosa layer of the ruptured follicle. Factors which may predispose to this condition include explosive rupture of the follicle, premature closure of the ovulation point and an over-ripe follicle with the membrane propria degenerating at the time of ovulation. Cetacean corpora atretica *a* may have a similar etiology.

As outlined above, the inclusion or exclusion of corpora atretica *a* in counts of normal corpora albicantia is variable with author and results in differences in the interpretation of the ovulation rate and the record of possible past pregnancies. It is proposed that, whenever possible, workers distinguish between the different types of corpora (which may be difficult without histological evidence) bearing in mind that ovulation which is not followed by normal corpus luteum development almost certainly does not give rise to pregnancy.

#### (4) Corpus luteum

The corpus luteum is the endocrine gland which normally develops from the cellular components of the ovarian follicle after ovulation (Harrison and Weir, 1977). When a foetus is found in the uterus, the corpus luteum is generally referred to as a corpus luteum of pregnancy or a corpus gravidatum. A corpus luteum which persists for a short time without a subsequent pregnancy is termed a corpus luteum of ovulation or a corpus luteum of the cycle.

On morphological grounds cetacean corpora lutea have been classified as everted, cavitate, meandrine, vesicular and non-vesicular (see Laws, 1961). Despite the earlier claims (e.g. Robins, 1954) and the fact that in at least several species most presumed corpora lutea of ovulation are smaller than those accompanying a definite pregnancy (Mackintosh and Wheeler, 1929; van Lennep, 1950; Robins, 1954; Laws, 1961; Sergeant, 1962; Best, 1967; Marsh and Kasuya, this volume), it seems unlikely that the corpus luteum of early pregnancy can be distinguished with certainty from one from a non-pregnant animal (Benirschke, Johnson and Benirschke, 1980).

Several workers including Harrison (1949), van Lennep (1950), Best (1967), Hirose, Kasuya, Kazihara and Nishiwaki (1970), Mossman and Duke (1973), Harrison *et al.* (1981) and Marsh and Kasuya (this volume), have observed two distinct types of gland cells in the corpora lutea of various cetaceans. These have sometimes been referred to as theca and granulosa lutein cells but, as Harrison (1949) pointed out, this classification cannot be verified without following the development of corpora lutea through several stages.

The corpus luteum persists throughout pregnancy in all cetaceans studied. There is also histological evidence that the activity of the corpus luteum changes during pregnancy, in at least some species (e.g. blue and fin whales (Mackintosh and Wheeler, 1929); sperm whales (Chuzhakina, 1963); *Phocena phocena* (Fisher and Harrison, 1970); *Stenella graffmani* [= *S. attenuata*] (Harrison *et al.*, 1972); *Globicephala macrorhynchus* (Marsh and Kasuya, this volume).

#### (5) Multiple corpora lutea

Pregnant cetaceans have been described with more than one active corpus luteum but only one foetus. This phenomenon is very rare in most species (Chittleborough, 1954; Laws, 1961; Sergeant, 1962; Ohsumi, 1965; Best, 1967; Gambell, 1968, 1972; Perrin *et al.*, 1976; Harrison *et al.*, 1981; Marsh and Kasuya, this volume), exceptions being the white whale (Brodie, 1972; Sergeant, 1973) and the narwhal (K. Hay, pers. comm., 1981). The relative functions of members of a set of multiple corpora lutea have not been studied. If they differ in size, all but the largest are called accessory corpora lutea. Strictly speaking, the term accessory corpus luteum should not be so limited. In the general mammalian literature, it is applied to any unruptured follicle which forms a corpus luteum irrespective of whether the female is pregnant, (Harrison and Weir, 1977). (See also Laws, 1961; Best, 1967; Marsh and Kasuya, this volume.)

#### (6) Corpus albicans

Regressing and regressed corpora lutea are now almost always referred to as corpora albicantia whether they are pigmented or not. Even though regression is essentially a continuous process, various cetologists have divided corpora albicantia into several categories to analyse the course of regression (e.g. Laws, 1958, 1961; Sergeant, 1962; Best, 1967; Gambell, 1968, 1972; Perrin *et al.*, 1976; Harrison *et al.*, 1981; Larsen, this volume; Marsh and Kasuya, this volume).

Several workers have separated the corpora albicantia observed in various cetaceans into two types (usually on histological grounds) and have suggested that one type might have developed from corpora lutea of ovulation, the other from corpora lutea of pregnancy (e.g. Peters, 1939; Sleptsov, 1940; van Lennep, 1950; Robins, 1954; Zemskiy, 1956; Ivashin, 1958; Hirose *et al.*, 1970; Fisher and Harrison, 1970; Zimushko, 1970; Harrison and Brownell, 1971; Harrison, Boice and Brownell, 1969; Harrison *et al.*, 1972; Collet and Harrison, 1981). The essential distinguishing feature of the two types is usually the amount of amorphous, relatively acellular, hyaline material present. The validity of this distinction has never been confirmed. Most workers who have studied the corpora albicantia from a large series of conspecifics (e.g.

Laws, 1961; Sergeant, 1962; Best, 1967; Gambell, 1968, 1972; Kasuya, 1972; Kasuya *et al.*, 1974; Perrin *et al.*, 1976; Harrison *et al.*, 1981; Marsh and Kasuya, this volume), have not managed to separate corpora albicantia of pregnancy from those of ovulation.

#### (7) Terms used to describe female reproductive status

(a) *Immature*: The female has no corpora lutea or corpora albicantia on her ovaries.

(b) *Pregnant*: The female has a live embryo/foetus in her uterus.

(c) *Lactating*: The female has active mammary glands producing milk. Some simultaneously pregnant and lactating females have been observed in most cetaceans for which a large series has been studied. These animals should be considered as pregnant in estimating the average length of the reproductive cycle.

(d) *Resting*: The (mature) female is neither pregnant nor lactating. As pointed out by Perrin *et al.*, 1977, this is a catch-all phrase which includes females truly resting, i.e. not ovulating because of being between cycles, those which have just ovulated but did not get pregnant, some with extremely small embryos missed in dissections, those which have recently aborted, and those which have prematurely terminated lactation due to the death of the suckling calf.

(e) *Post-reproductive/senescent*: The female either

cannot conceive or cannot sustain a pregnancy successfully because of age-related changes to her reproductive system. Marsh and Kasuya (this volume) present evidence for a post-reproductive or senescent phase in the ovaries of *Globicephala macrorhynchus* in which there appears to be no evidence of ovulation after age 40, when females have a life expectancy of 13 years. However, post-reproductive *G. macrorhynchus* are not infrequently lactating. Sergeant (1962) also observed a small percentage of such females in *G. melaena* as did Perrin *et al.* (1976) in *Stenella attenuata* and Perrin *et al.* (1977) in *S. longirostris*. As discussed by Marsh and Kasuya (this volume), it is difficult to be certain that an individual female is post-reproductive.

(f) *Post-partum and post-lactation oestrus*: Problems arise in the precise definition of such terms. The shortest times a female can recycle after parturition, cessation of lactation or indeed after unsuccessful oestrus and ovulation are not known for most cetaceans and are likely to be highly variable with individuals both in and between species. The incidence of such events is likely to be more significant in some species than others. It is proposed therefore that these terms be avoided unless specific evidence of timing can be referred to, such as in closely-observed captive animals, or animals where past reproductive history is clear from examination of the entire reproductive tract.

### Appendix C

#### SPECIMEN COLLECTION, PRESERVATION, STORAGE AND PREPARATION

The collection and subsequent examination of cetacean reproductive material is an essential part of the documentation of the species' life history parameters which, in turn, are an essential component of population models. Collection of reproductive material must be accompanied by the collection of earplugs, bullae or teeth for age estimation. The nature and extent of specimen collection will vary greatly with the conditions under which the work is done (e.g. single specimens, mass strandings, drive fisheries, factory ships or incidental kills in other fisheries), personnel available, facilities, etc. The following section is intended to serve as a guide and not as a final determination as to how the work should be done. Each investigator must select the protocol most appropriate for the specific needs of the research project. In addition, new and better techniques will become available from time to time.

##### (1) Collection

The size of the animal and its components will have a great effect on the material collected.

(a) *Females*. For small odontocetes, wherever possible, the entire reproductive tract should be collected and should include the complete vagina (this is obviously impractical for large whales). This technique preserves tissue orientation and lessens the chance of mis-labelling ovaries and the loss of small embryos and vaginal mucous plugs. The flat width of each uterine horn should be taken at the mid-point of each horn. If the animal is obviously pregnant the foetus can be removed and the horn subsequently measured. The ovaries and foetus may be weighed fresh, and it is important that this be noted for

subsequent analyses. A detailed comparison of fresh versus preserved weights has not been made. A section of each uterine horn (and vagina) should be taken if the entire tract is not collected.

The mammary glands should be examined and a tissue sample taken. Length, width and thickness of the glands can be measured, but this is often impractical. If thickness is measured, it should be at the thickest part of the gland or a fixed distance from a topographical landmark. The colour of the freshly cut gland should be noted, using a consistent scale (e.g. pink, pink-brown, brown). A milk sample should be collected when possible for nutritional, pollutant and parasitic examination. Ideally, the milk should be taken directly from the teat to avoid contamination. Alternatively it can be taken from the incised reservoir. The colour of the uncontaminated milk should be noted.

Vaginal smears may be taken from fresh animals. Results may vary with the location within the vagina from which the smear is taken. Collections should be from a consistent location or the specific location noted.<sup>11</sup>

(b) *Males*. The testes should be weighed and measured (length, width, and thickness when laying flat). In some smaller cetaceans, the testes can be taken intact, while in most cases only samples can be taken. It is important to note whether the testes were measured or weighed fresh or preserved, and with or without the epididymis. If only one testis is taken, it should be so noted and taken consistently from the left or right side.

<sup>11</sup> Editors' note. In captive bottlenose dolphins, contents of vaginal smears were not correlated with ovulation, but copulation could be confirmed by presence of sperm (V. L. Kirby, pers. comm.).

Samples of the testes should be taken at mid-length and include the core from small whales and both core and peripheral samples from large whales, to account for differential maturation. Epididymis samples can be taken at mid-length, but more sperm are likely to be encountered in the cauda (posterior) epididymis. The testes of most species have not been sampled to determine if there are areas of differential maturation. In any event, sampling sites should be noted and consistent. Smears can be taken from both the cut surfaces of the testes and the epididymis.

The activity of a testis can be determined most accurately through histology, but in general there also appears to be a good correlation between sperm production and the weight of the testis. Histologically, an active or recrudescing testis is characterized by the presence of meiosis and mitosis. This can be easily determined through a 'touch preparation,' in which a few tubules are teased out and touched to a slide. The specimen is then fixed in ether alcohol, stained with haematoxylin and eosin and examined for very dark cells indicative of meiosis. When a testis is actively producing sperm, the cellular associations characteristic of spermiogenesis (spermatogonia through spermatozoa) can be observed in histological sections and sperm can be seen in smears or teased preparations.

In some terrestrial mammals (e.g. lemurs) testis size can change dramatically with season, but some spermatozoa may be present even when the testes are considered inactive; sperm can remain in the tubules for a long time after initial production, but generally they are not of the same quality as more recently produced sperm.

## (2) *Preservation*

(a) *Fixatives.* The most widely used fixative is 10% neutral buffered formalin (NBF) or 10% sea-water formalin. Bouin's solution is the traditional fixative for embryological material and may be used for other specimens. Problems arise, however, in the identification of gross structures because of yellow staining by the fixative. A further problem with Bouin's solution is its relatively low power of penetration of tissues. Material fixed in formalin can be refixed in Bouin's (or other fixative) at a later time. Electron microscope (EM) material usually requires fixation in glutaraldehyde, but this is not usually practical when large numbers of animals are being processed. Specimens should be fixed within minutes of death for the best EM results.

Tissue samples should be on the order of one cubic centimetre, to permit rapid permeation of the specimen. Tissue-to-fixative volumes should be on the order of 1:10. Smaller volumes can be used if the fixative can be changed one or more times and the samples agitated. Tissue samples can be individually placed in perforated plastic tissue containers and remain there through most histological processing. Perforated plastic bags can be used to store all samples from one individual. Samples from several animals can be placed in a large container of fixative.

Gross specimens (e.g. large whale ovaries and whole testes) should be slit once longitudinally to ensure fixative penetration. Uterine horns can be injected with 10% NBF.

Containers holding several specimens should be

agitated to ensure the samples are not packed together and thus retarding fixation.

Alternative preservation methods include freezing and packing in dry-salt, although these will usually not yield adequate histological preparations.

Milk samples should be preserved by freezing. Formalin can be used if nutritional analyses are not done.

Smears can be adequately preserved by air drying. Specific spray fixatives are available.

(b) *Storage.* Formalin-preserved material can be stored indefinitely in tightly sealed containers kept in the dark, although storage for years may affect the quality of histological preparations due to hardening of the tissue. Some routine curation is necessary to prevent samples from being damaged from fluid loss. Addition of 59% (by vol.) glycerine can temporarily prevent specimen damage if fluid is lost.

Smears can be stored in slide boxes, without further attention until stained.

Five-percent (5%) formalin is adequate for the storage of thoroughly fixed material. Likewise, the tissue-to-fluid volume ratio can be reduced to about 1:5. Recent concern has been expressed, however, over the health and safety aspects of the use of formalin, which may be banned from usage in certain laboratories. Consensus was that once fixed in 10% NB formalin, specimens may be transferred to other less noxious preservatives for personnel safety. Alcohol was considered a possible alternative for some tissues, although tissue shrinkage might be a problem.

The use of heat-sealed plastic bags appears to be a superior method for long-term storage. A bag is constructed by heat-sealing one end of a piece of 'Lay flat' plastic tubing; the specimen, preservative and label are inserted, and the bag sealed. A second label can be sealed dry in an adjacent compartment. It is important that nonpermeable (polyester) plastic tubing be used.

Frozen samples can, of course, be stored in the frozen state. Containers should be tightly sealed to prevent oxidation ('freezer burn') and drying.

Samples for EM work must be removed from the fixative after about 24 hours and then stored in a buffer solution until further processing.

## (3) *Preparation*

Samples for histological examination are usually embedded in paraffin and stained with hematoxylin and eosin (H & E) after sectioning. Other stains (trichromes) are a matter of individual preference. H & E is the choice of pathologists, as it allows for structure identification in poorly preserved or autolyzed samples. Smears can be stained appropriately and a cover-slip mounting medium applied.

Prior to cutting an intact specimen (especially ovaries), it should be photographed in more than one plane. The resulting working prints may then be used to document the location(s) of any part sliced and subsequently removed for histological examination. Further photographs of cut surfaces, particularly of ovaries, prior to the dehydration and embedding process are also useful; it is often the case that an impression gained macroscopically is different from the final histological picture. Photos should include a scale and relevant identification numbers.

Ovaries have been sliced (in order to count corpora) at varying thicknesses. Certainly thinner slices are necessary for small cetacean ovaries than for large cetaceans, where 2–5-mm is adequate, given the relative sizes of the structures. Sections should be left attached along one side of the ovary where possible, to preserve sequence and orientation. If sections are cut too thin, they will not lay

flat during embedding if a complete histological section is subsequently required.

It is important to save ovaries and any other material that may require re-examination and/or reinterpretation. It is impossible to corroborate an interpretation if the material has been discarded.

**Session I**  
**Review of Cetacean Reproduction**



# Review of Baleen Whale (Mysticeti) Reproduction and Implications for Management

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## ABSTRACT

There are three living families of baleen whales: Balaenidae, Eschrichtiidae and Balaenopteridae. Of these, the first has three species, the second one species, and the third six species. There is one recognized sub-species in the Balaenopteridae. Most of these species have similar patterns of reproduction.

The mating pattern is usually monogamous. There appears to be less social schooling of the type common to many Odontoceti. The formation of loose aggregations occurs during migration and seasonally. Geographical segregation of sexes, sexual classes and age classes sometimes occurs, for example in *Balaenoptera acutorostrata*, and this can seriously bias the sex ratio and age distribution of catches. In small and greatly reduced stocks such catches can seriously alter the population structure.

The female reproductive cycle is generally two years, with a gestation period of about one year. Lactation lasts about half a year. Normally just one calf is conceived and born in warm temperate or sub-tropical waters. Most baleen whales undertake extensive migrations for feeding, an exception being *Balaena mysticetus*, and the reproductive cycle appears to be geared to this annual cycle of migration and feeding.

Baleen whales feed mainly by filtering small swarming planktonic Crustacea, the production of which is greatest in cold high latitude waters. Baleen whales thus need to leave the home breeding grounds for the high latitude seas each spring in order to feed and store energy in the form of fat as reserves for the months of poor feeding. Even *Eschrichtius robustus*, a bottom-feeder, undertakes such migrations. Weaning in most species is believed to occur during or after the summer feeding season. The success of factors such as fertility, pregnancy, lactation, developmental growth and sexual maturity, and net recruitment are all dependent on the efficient storage of energy for body maintenance, foetal growth and milk production. The apparent inter-correlation between history of exploitation, pregnancy rates and individual growth rate and the attainment of sexual maturity is discussed in relation to possible changes in food supply for certain stocks.

Information which would aid management is still needed on survival from conception to birth, survival of calves in the first year of life, and the relation of this to the age of the cow and general feeding conditions.

## INTRODUCTION

There are three living families in the order Mysticeti (baleen whales): the Balaenidae, Balaenopteridae and Eschrichtiidae. These comprise genera and species as listed in Table 1.

The bowhead is circumpolar but exclusively Arctic in distribution, whilst the pygmy right is only found in the Southern Hemisphere north of the Antarctic Convergence and in water cooler than 20 °C. The right, blue, fin, sei, humpback and minke whales are all either known or believed to be highly migratory, with worldwide distributions. Northern and southern stocks do not intermingle although each is found between the tropics or sub-tropics and the polar seas. The Bryde's whale is

found in both hemispheres, but only in the warm waters from the tropics to temperate zones. The gray whale is found only in the Northern Hemisphere, and is restricted to the Pacific Ocean. The main population is in the eastern Pacific, the western Pacific stock being small and once thought to be extinct. Today, the gray whale is usually known as the California gray whale migrating between Baja California in Mexico and the Bering Sea.

The mysticetes display slight consistent sexual dimorphism, the female generally being about 5% greater at maximum body length.

The majority of mysticetes have a life-cycle of migration, breeding and feeding; they are believed to undertake migrations involving generalised N-S movements, rather than movements between longitudes,

Table 1  
Families of Mysticeti

Family	Genus	Species (and sub-species)	Common name
Balaenidae	<i>Eubalaena</i>	<i>E. glacialis</i> (Müller, 1776)	right
	<i>Balaena</i>	<i>B. mysticetus</i> (Linnaeus, 1758)	bowhead
	<i>Caperea</i>	<i>C. marginata</i> (Gray, 1846)	pygmy right
Balaenopteridae	<i>Balaenoptera</i>	<i>B. musculus</i> (Linnaeus, 1758)	blue
	"	<i>B. musculus breviceuda</i> (Ichihara, 1963)	pygmy blue
	"	<i>B. physalus</i> (Linnaeus, 1758)	fin
	"	<i>B. borealis</i> (Lesson, 1828)	sei
	"	<i>B. edeni</i> (Anderson, 1878)	Bryde
	"	<i>B. acutorostrata</i> (Lacépède, 1804)	minke
Eschrichtiidae	<i>Megaptera</i>	<i>M. novaeangliae</i> (Borowski, 1781)	humpback
	<i>Eschrichtius</i>	<i>E. robustus</i> (Lilljeborg, 1861)	gray

(Lockyer and Brown, 1981). Payne and Webb (1971) observed however, that some animals are found in both high and low latitudes throughout the year.

Migration in bowhead and Bryde's whales may involve only local seasonal movements, whilst migration in humpbacks and gray whales for example, constitutes movements over thousands of miles between polar and sub-tropical or temperate waters. Apparently no one environment is ideal year long, and whilst the breeding ground in low latitude warm waters is regarded as the home ground during the autumn-winter months, migration to the more productive higher latitude colder waters in spring-summer is essential so that the whales can feed, fatten and store fat energy in order to survive the rest of the year when feeding conditions are poor.

This seasonal annual migration usually involves all ages and sexual classes of the population, although there is a known sequence of migration for some species, for example, humpback (Dawbin, 1966) and gray whales (Rice and Wolman, 1971). The baleen whale breeding cycle appears to be linked intimately with this annual migratory scheme, as we shall discuss in greater detail later, with gestation lasting about one year. Normally only one calf is born in warm waters, which may favour survival of the relatively poorly insulated neonate by reducing maintenance costs. Lactation occurs here, with weaning usually taking place either during or after the summer migration, so that the calf can learn to feed itself in the productive colder waters. The timing of these events means that optimally the cow can bear one calf annually, whilst simultaneously lactating and pregnant. This is usual in minke whales and has been observed in humpback whales (Glockner-Ferrari and Ferrari, 1984), but normally a calf is produced every two or three years.

The reproductive interval may be even longer than this – three years in right whales (Payne, 1984).

## SOCIO-SEXUAL BEHAVIOUR

### General behaviour

Baleen whales are generally observed in loose aggregations rather than large cohesive schools, with the basic units being a cow and calf, pairs and 'families' of adult and sub-adult animals. Usually animals occur singly or in groups of 2–6 whales although larger groups of more than 20 have been observed both on and outside the feeding grounds (Gunther, 1949; Nemoto, 1964; Tomilin, 1957; Gambell, 1968; Budylenko, 1977; Lockyer, 1977a; Best, 1982).

Bonding between individuals in baleen whales does not appear very notable, although mother-calf bonds are probably strongest during the suckling period: see Tomilin (1957) for gray whales and Thomas and Taber (1984) for right whales. Matthews (1937) reported a simultaneously pregnant and lactating humpback cow accompanied by a calf, indicating that subsequent pregnancy does not necessarily interfere with the existing mother-calf relationship. It is likely however, that the older calf will be shunned or at least distanced after parturition.

Tomilin (1957) reported (from whaling incidents) on a close bonding between humpback pairs during the

breeding season, in that the female may remain near the wounded mate until he is killed. Close bonding in pairs or small groups in fin and blue whales has not generally been observed, and in fact the opposite has been reported in fin whales (Tomilin, 1957) with the unharmed member(s) deserting the wounded whale.

Various behaviours have been observed in gray whale groups in the Chukotka waters. Zimushko and Ivashin (1980) reported that females often remained near another wounded female, but that a cow would usually depart immediately if a male was wounded. Exceptions to this pattern have been observed, but generally males remained longer with wounded congeners, especially females, and Bogoslovskaya, Votrogov and Semenova (1982) confirmed this.

In conclusion it would seem that there is generally restricted epimeletic behaviour between baleen individuals, and both the short-term cow-calf bond, and the absent or loose bond between other individuals, will not greatly affect ease of capture in whaling: the former animals are protected (IWC, 1950), and the latter behave as essentially lone individuals when stressed. It seems likely that removal of a group member, other than a cow or calf will not be greatly disruptive.

### Reproductive behaviour

Baleen whales are generally believed to tend towards a monogamous mating system, but do not form permanent pair bonds. Unlike some Odontoceti such as sperm whales, they do not exhibit hierarchical schooling and mating systems characterized by the harem structure.

Donnelly (1967; 1969) has described right whale mating between members of pairs in sheltered coves off South Africa. Courtship can occur continuously throughout the day and night and is frequently accompanied by leaping, vertical head-up postures, spy-hopping, tail-bobbing and rolling belly to belly. Such breaching and spy-hopping behaviours have been described for other baleen whales but not necessarily in the mating context. Right whale matings have also been reported by Payne (1984) around Peninsula Valdes, Argentina in sheltered bays, although conception may not occur at these times.

Donnelly (1967; 1969) described evasive behaviour by a right whale female which rolled to present her back to a courting male or even turned upside down.

Rice (1983) and Rice and Wolman (1971) reported that gray whales carried out courtship including apparent mating, indicated by the erect penis in the male, during northward migration and also in the Arctic feeding region (Bering Sea). These are times inappropriate to the seasonal conceptions and births. Tomilin (1957) reported that mating takes place throughout the year in humpback whales despite strongly seasonal conceptions.

The majority of gray whale matings are observed around the calving grounds near Baja California in January (Gilmore, 1960). Walker (1971) reported, with photographs, on the presence of more than one male during gray whale mating. The role of the accessory male (or males) is uncertain. Both males may attempt copulation. Rice (1983) also reported promiscuous mating in the gray whale. Group mating has also been reported in bowhead whales (Everitt and Krogman, 1979) when as many as six whales were involved. Whitehead

Table 2  
SIZES OF CORPORA LUTEA OF OVULATION AND PREGNANCY

Species	Corpus luteum size in mm $\pm$ S.E.				Reference
	Ovulation	Pregnancy			
		Early	Mid	Late	
Blue	108.6 $\pm$ 1.0	137.5			Mackintosh and Wheeler (1929) Laws (1961)
Fin	82.8 $\pm$ 8.2	114.4 $\pm$ 5.4			Mackintosh and Wheeler (1929) Laws (1961)
Sei	54.7 $\pm$ 2.7	76.2 $\pm$ 1.8	79.9 $\pm$ 2.1	83.8 $\pm$ 1.0	Gambell (1968)
Humpback	(60-80)	105.7		123	Matthews (1937) Chittleborough (1954)
Minke	40.0 $\pm$ 1.5	66.4 $\pm$ 1.0 (fresh) and 65.5 $\pm$ 1.2 (formalin fixed)			Best (1982), Lockyer (in Best, 1982).
Gray Bryde's	56.0 $\pm$ 16.0'	82.0 $\pm$ 11.0*	84	87.0 $\pm$ 12.0*	Rice and Wolman (1971)
Inshore form			77.8		Best (1977)
Offshore form			72.1		

\*  $\pm$  S.D.

(1981) has described behaviour in humpback whales off the West Indies which may be a prelude to mating. The female in oestrus (whether accompanying a calf or not) initially attracts a principal male escort and then subsequently up to an additional five secondary male escorts. These males jostle for position close to the cow, trying to oust each other using tactics such as tail-lobbing, lunging and bubble-stream blowing. The principal escort rarely remains so for more than a day or even a few hours before he is replaced.

Another aspect of courtship, the interpretation of which is still speculative, is complex vocalization. Payne and McVay (1971) and Winn and Winn (1978) reported on seasonal 'singing' of humpback whales on the breeding grounds as a means of communication between individuals. At least in the Northern Hemisphere,<sup>1</sup> such complex 'singing' has not been heard outside these breeding areas, and thus implies a link with locating a mate. Winn and Winn (1978) provided evidence that the singing whales are in fact solitary males. Whitehead (1981) observed that male escorts usually sang before joining a cow and then ceased, but resumed singing after leaving her. This may imply that singing advertises sexual availability. The cow was never heard to sing.

Little is known about courtship and mating postures in the other pelagic baleen whales, for which the precise breeding and calving grounds are uncertain.

As in the gray and humpback whales, copulation in other baleen whales may occur incidentally outside the usually recognized breeding season, and may also be attempted by juveniles and between males (Rice, 1983).

## ANATOMY OF THE REPRODUCTIVE SYSTEM

### Female

It is not intended to give a detailed description of the morphology and histology of the mysticete ovary and reproductive tract here, as it does not relate directly to management. Much of this information can be found in the report of this meeting (Perrin and Donovan, 1984), particularly in relation to follicular development, corpus structure, function and anomaly (e.g. corpora aberrantia, c. atretica, follicular cysts, etc.). Excellent descriptions for these can be found in Laws (1961) for fin whales, and in Slijper (1966) and Harrison (1969).

The two ovaries in Mysticeti are morphologically similar, being rather oval, elongate and convoluted (see Fig. 3). The large Graafian follicles and corpora protrude from the surface, and the corpora lutea attain very large sizes, often dwarfing in both volume and weight the ovary to which they are attached. Average sizes of corpora lutea for different species are shown in Table 2. The corpus luteum increases rapidly in size after ovulation and conception have occurred, and then continues to increase until late pregnancy when it may start to shrink slightly pre-partum, although Laws (1961) found no evidence for this in fin whales. Shortly after birth, the corpus luteum shrinks dramatically, although it is unknown whether the time scale of this is in days or weeks. The regressing corpus continues to shrink as a corpus albicans throughout successive reproductive cycles, until a critical minimum size is attained, beyond which no further regression or degeneration histologically appears to occur. We may assume that these corpora albicantia are permanent features in the mysticete ovary. Best (1982) observed that despite small size of old corpora in minke whale ovaries, he found no evidence to support resorption or alter the assumption on permanency. However, some old corpora might be missed without histological examination. If this is possible it may explain

<sup>1</sup> Dawbin (1983) has recently recorded humpback whales singing during both the northward and southward migrations off Australia, adding further complications to the interpretation of the functions of singing.

the apparent decline in ovulation rate with age, reported by some authors (Masaki, 1978; Mizroch, 1981a; see later section on reproductive parameters in the female), whilst pregnancy rate with age remained constant. Laws (1961) classified the regression of fin whale corpora albicantia into three categories based on morphological and histological studies, and this classification has generally been applied to other cetacean species.

The persistence of corpora albicantia has enabled the total number of ovulations to be estimated for the mature female, although it is doubtful whether or not the corpus due to ovulation alone or pregnancy can be distinguished morphologically or histologically (see Perrin and Donovan, 1984).

In mysticetes (unlike several odontocete species, where the left ovary usually predominates and is more active at least initially), both ovaries are fully functional and able to ovulate from first sexual maturity. Ohsumi (1964a) found left and right ovaries equally active in blue, fin, Bryde's, sei, minke, humpback and right whales. Rice and Wolman (1971) found a suggestion (barely statistically significant at 0.05 probability) that the left ovary might be dominant in gray whales. In some species there is also a tendency for ovulations to occur mainly from the anterior pole of the ovary (Rice and Wolman, 1971), but most old mysticetes with many corpora evidence ovulations occurring all over the ovary.

### Male

A brief description will again be given for the male; readers are referred to Slijper (1966) and Harrison (1969) for fuller details of the reproductive tract.

The testes are smooth elongate sausage-like organs which remain permanently within the abdominal cavity. The testes appear to develop synchronously and are of similar size, weight and shape. The penis can be retracted into a groove flush with the ventral body surface, but falls out limply after death. As in all other cetaceans, the penis is erected by muscle fibres and not by vasodilation.

### Secondary sexual characteristics

In all baleen whales the distance between the genital groove and anus is 2–3 times longer in males than females.

At sea, it is difficult to determine the sex of a whale because the ventral sexual characters are hidden from view. Only during mating, calving and specific behavioural displays such as breaching, can the sex of an individual be identified.

Sometimes secondary sexual characteristics may be apparent. Jurasz, McSweeney and Jurasz (1980) reported that in humpback whales, females generally had smooth dorsal outlines posterior to the dorsal fin, whilst males had scalloped outlines. Such outlines could easily be seen during arching of the back prior to diving, and as such could be used to sex whales at sea. Another secondary sexual characteristic is snout protuberances in sexually mature male fin whales from the North Pacific (Nemoto, 1962). This characteristic, however, is probably very difficult to observe at sea unless one is very close to the animal. It cannot differentiate the sexes in immature whales, unlike the dorsal outline in humpbacks that is apparent even in calves.

Winn, Bischoff and Taruski (1973) have devised a technique for live skin sampling from humpback whales at sea. The animals can then be sexed cytologically.

The ability to sex individuals at sea would be useful in those fishery operations where sexual segregation leads to imbalanced sex ratios in the catches. However, this is most commonly found in minke whale fisheries and there is as yet no method for sexing this species at sea.

### REPRODUCTIVE CYCLE

The life cycle revolves around seasonal migration and feeding. Appendix Table 1 gives data on gestation times, seasonal conceptions, births and suckling period. Knowledge of the timing and duration of the reproductive cycle is useful information in fishery biology for predicting birth rate, population growth and recruitment

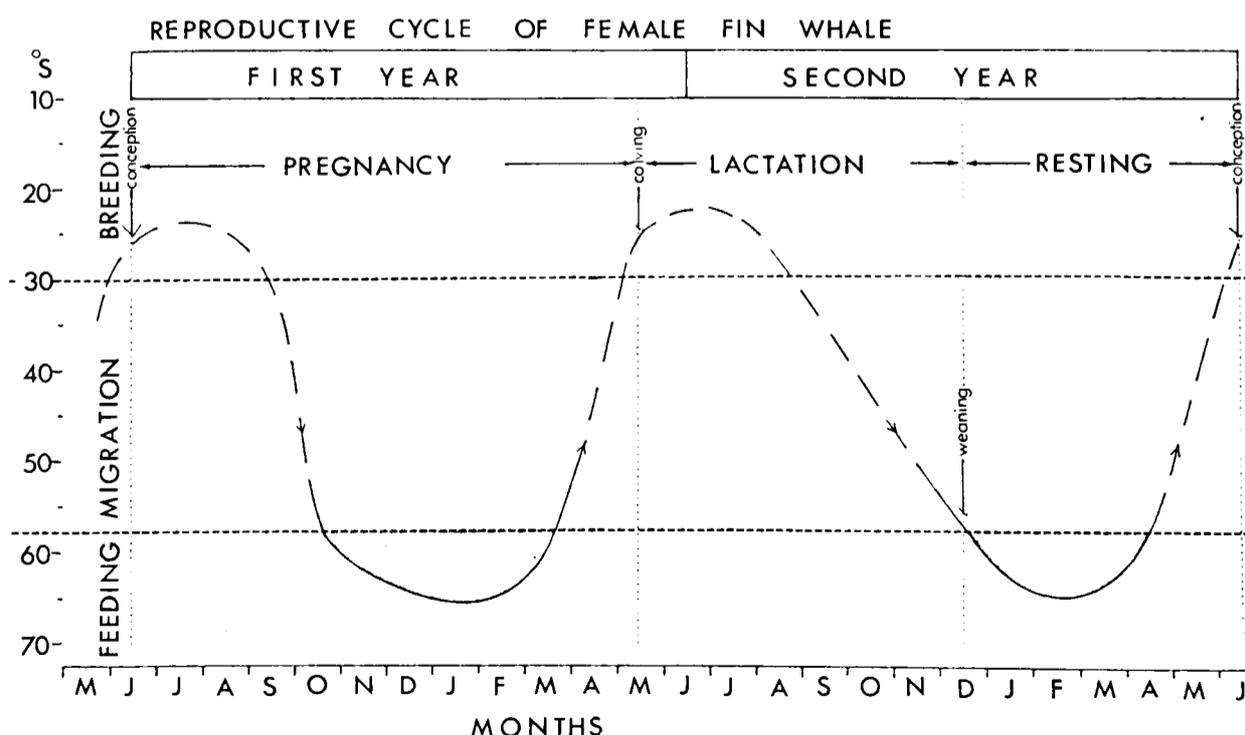


Fig. 1. Schematic reproductive cycle for the Southern Hemisphere female fin whale (after Lockyer and Brown, 1981).

and hence production. The cycle has a minimum duration governed by gestation time, which in all Mysticeti is about one year. In fact, a two-year cycle is usual and a three years or longer reproductive interval is possible depending on circumstances.

Fig. 1 shows a generalized breeding cycle for an adult female fin whale in the Southern Hemisphere in relation to migration and feeding. This general pattern is probably true for other large baleen whales, allowing for individual variations in timing, geographic range and location, as indicated in Appendix Table 1.

The timing of migration varies slightly for the different sexual classes. This has been directly observed in humpback whales (Matthews, 1937; Dawbin, 1966) and gray whales (Rice and Wolman, 1971). Data on seasonal abundance from the catches indicate that it is probably also the case in blue, fin and sei whales (Lockyer and Brown, 1981; Mackintosh and Wheeler, 1929; Matthews, 1937).

In nearly all species, newly pregnant females are the first to migrate to and arrive on the summer feeding grounds and the last to leave, an exception being the pregnant gray whale (Rice and Wolman, 1971) which leaves the feeding grounds first. In blue, fin (Lockyer, 1981a) and humpback (Dawbin, 1966) whales, they may spend up to 50% longer time feeding than the rest of the population; the significance of this will be discussed later. Lactating females with calves are usually the last to arrive, possibly because the calves slow up the migration rate. These cows are often amongst the first to leave after their calves are weaned. Adult males and resting (anoestrous and non-lactating) females usually precede juveniles of both sexes by two to four weeks. However, migration is a succession of non-discontinuous waves so that there is considerable overlap in the time of arrival of migrating groups on the feeding grounds (Lockyer and Brown, 1981).

Some species demonstrate both segregation by sex and reproductive condition. Juvenile blue, fin and sei whales tend not to penetrate such high latitudes as adults (Lockyer, 1981a; Lockyer and Brown, 1981) as evidenced by the smaller sizes of whales caught in lower latitudes (BIWS).

Minke whales also show marked sexual segregation in both hemispheres. The sexes are unevenly represented in catches from certain areas and months (Ohsumi and Masaki, 1975; Lockyer, 1979a; Christensen, 1979). Lactating females are virtually absent from higher latitudes of the Antarctic (Best, 1982).

### Reproductive parameters in the female

Most information on cetacean reproduction comes from animals killed in whaling. Pregnancy rate is usually defined as the proportion of females in the catch which have a foetus i.e. it is an apparent pregnancy rate. However, because International Whaling Commission regulations forbid the taking of animals with calves, simultaneously lactating and pregnant females are effectively not represented in the catch. Also, this measure over-estimates the true pregnancy rate. Unless otherwise stated the apparent pregnancy rate has been quoted here.

The baleen whales ovulate seasonally, and when

conception succeeds ovulation, the pregnancy rate and ovulation rate are similar.

There are arguments that the mysticetes are probably monoestrous spontaneous ovulators, and not induced (Laws, 1961; Harvey, 1963), although Rice and Wolman (1971) and Chittleborough (1965) might dispute this, particularly the latter who obtained evidence of polyoestry (several oestrus cycles) in humpback whales if conception failed to occur. Rice and Wolman considered polyoestry to be an advantage in a species producing only one calf every two years, where no permanent pairing occurred and individuals were widely dispersed. Whitehead's (1981) observations on the mating system of the humpback whale (discussed in the section on reproductive behaviour) would be compatible with polyoestrus. The very high ovulation rate for the inshore form of Bryde's whale off South Africa (Best, 1977), which is resident year-round, could be explained by polyoestrus.

The minimum reproductive interval is fixed by the gestation period, assuming that pregnancy goes to term. This is about one year in all mysticetes. Because conceptions are usually seasonal, the reproductive interval is usually a multiple of a 12-month period. However, some aseasonal conceptions can alter this, and will be discussed in context for different species.

### Gray whales

Rice and Wolman (1971) reported a pregnancy rate of 0.46 for California gray whales and calculated and observed an ovulation rate of 0.52, consistent with a two-year reproductive cycle.

Swartz and Jones (1983) gave some information on calf production from cow/calf observations. Despite the sheltered nature of the California lagoons, there is evidence of high neonate mortality in the gray whale. Swartz reported a mortality rate of 5.3% in the lagoons and a total of about 31% including the northward migration. Possible causes are stillbirths, accidental stranding, predation or even harassment by motorboat traffic. Accounting for all these mortality factors, Reilly (1984) calculated a maximum net reproductive rate of 6.7% per annum but averaging 3.7% over the last 13 years. For comparison, the proportion of calves passing Pt Piedras Blancas, California in 1980 and 1981 were 4.5% and 5.0% respectively (IWC, 1983). These are all considerably less than the gross theoretical maximum of 13% (Rice and Wolman, 1971), even allowing for 31% neonate mortality (Schwartz, 1983), which has been considered extremely high (IWC, 1983), and may be a function of calf count underestimates.

### Bowhead whales

Little is known on reproduction in the bowhead whale. Ray, Wartzok and Taylor (1984) reported that aerial surveys in the Bering, Chukchi and Beaufort Seas revealed that 8% of the population were 3.5–5 m in body length, thus implying these were calves. Recently, Nerini, Braham, Marquette and Rugh (1982) reported a pregnancy rate of 0.31 for the bowhead based on a very small sample size, and observed calf production to be between 2.0% and 3.2% of the total population, depending on whether observations were ice-based or aerial. They deduced a three-year reproductive cycle. The

apparently low calf counts may be due to the lesser sightability of calves relative to adults, and hence estimates of calf production may be biased downwards. A full discussion of current knowledge on calf production in the bowhead whale is given in IWC (1984).

#### *Right whales*

Seasonal observations over several years on right whales off Peninsula Valdes (Payne, 1984) indicated an average three-year reproductive cycle. Best (1981) reported that 15–28% of the total population of right whales off South Africa were calves. Payne apparently observed a similar proportion off Peninsula Valdes (Nerini *et al.*, 1982). The right whale has been totally protected from exploitation for several decades, so that much basic reproductive information is lacking.

#### *Humpback whales*

Pregnancy rates for humpback whales have been reported as 0.43 for coastal eastern North Pacific (Rice, 1963) and 0.40 for western North Pacific (Nishiwaki, 1959). For the Australian fishery, Chittleborough (1965) calculated 0.37. In the northwest Atlantic Mitchell (1974) reported 0.54 from a very small sample.

Herman and Antinaja (1977) reported that an anticipated annual calf production for Hawaiian waters, assuming an average pregnancy rate of 0.43 would be 10.8% of the entire population. Throughout several aerial surveys on the nursery grounds they observed 9.1–9.6% of the population were calves, a value which they regarded as perhaps biased upwards because of the location.

#### *Minke whales*

Current evidence indicates annual reproduction in the minke whale, although the actual reproductive interval is probably about 14 months (IWC, 1979). Masaki (1979) assumed that a 12½-month reproductive cycle was feasible even if unlikely, because many lactating females have been found to be ovulating (IWC, 1979), and hence in theory could conceive. Such a situation would favour the maintenance of seasonal breeding, unlike a 14-month cycle which might ultimately make breeding aseasonal or necessitate missing some years (Lockyer, 1981b). This latter appears unlikely, however, as observed pregnancy rates are consistently high. However, segregation is so marked for this species that observations on a representative sample are difficult and realistic pregnancy rates hard to obtain. Published values are as follows: 0.89 for the Antarctic (Masaki, 1979); 0.96 (including lactating cows) for Norway (Jonsgård, 1951); 0.88 for West Greenland (Larsen, 1984); 0.96 for Newfoundland (Mitchell and Kozicki, 1975); 0.90–0.97 for the Barents Sea (Christensen, 1974); 0.66 in the Huanghai Sea (Wang, 1982). Masaki (1979) also reported an average ovulation rate (measured as number of corpora formed annually) of 0.96 for Antarctic minke whales. In the northwest Atlantic, Mitchell and Kozicki (1975) reported an ovulation rate of 0.60 which is rather lower than the pregnancy rate. Best (1982) found ovulation rates of about 0.81 for minke whales caught off Durban, although females older than 20 years had a lower rate. Best estimated a true pregnancy rate of about 0.78 which is in good agreement with the ovulation rate.

Other balaenopterid whales usually have a two-year reproductive cycle. Information for these is summarized below.

#### *Bryde's whales*

Best (1977) reported average observed pregnancy rates of 0.227 and 0.222 for two allopatric populations (inshore and offshore forms) of Bryde's whales off South Africa. These values agree with the calculated ovulation rate of 0.42 for the offshore (pelagic) form, but a discrepancy exists for the inshore (coastal) form where an ovulation rate of 2.35 suggests a 19-month cycle comprising pregnancy and lactation but with no resting (anoestrous) period. Although estimates were confounded by sampling problems and possible differences between inshore and offshore populations, Best nevertheless estimated a two-year reproductive cycle for this species. Ohsumi (1977) reported a pregnancy rate of 0.42 for the pelagic North Pacific Bryde's whale and an ovulation rate of 0.46, suggesting a two-year cycle. Ohsumi (1980) calculated a pregnancy rate of 0.43 for South Pacific Bryde's whales.

#### *Sei whales*

Pregnancy rates for the North Pacific sei whale average 0.60–0.65 (Masaki, 1976), but a gradation exists across the North Pacific from west to east, with higher rates being found for coastal Japan than eastern pelagic. Masaki also found mean ovulation rates of about 0.60 for females under 25 years and be much less in older females, implying differences in age-specific fecundity, which could directly affect pregnancy rate with age. Rice (1977) calculated a value of 0.70 for eastern North Pacific sei whales and suggested that the rate may exceed this in females under 25 years, and be much less in older females. Rice estimated a true pregnancy rate of 0.36, suggesting a three-year cycle for most females. In general, however, there do not appear to be variations in age-specific pregnancy rates in baleen whales, although Rice and Wolman (1971) and Laws (1961) have reported for species other than sei that primiparous females often conceive later than multiparous ones, so that, dependent on time of sampling, a variable age-specific fecundity might appear to exist. Mizroch (1981a) reported no variations in age-specific pregnancy rates in Antarctic fin whales aged up to 85 years but found a decline in ovulation rate with age.

For sei whales in the North Atlantic, Mitchell and Kozicki (1974) calculated an ovulation rate of 0.26, although the method of calculation causes the estimate to not be directly comparable with others (zero corpora age classes were included in a regression of corpus number on age). Lockyer and Martin (1983) recently calculated a pregnancy rate of 0.40–0.44 for Icelandic sei whales, and an ovulation rate of 0.59. They found no age-specific variation in ovulation rate for females up to age 45 years.

Gambell (1973) and Lockyer (1974) reported ovulation rates of 0.61 and 0.68 respectively for the Southern Hemisphere sei whale. Current pregnancy rates approach 0.70 (IWC, 1978). Masaki (1978) reported monthly variations in pregnancy rate in the catch decreasing from 0.65 in December to 0.50 in March, and also variations between latitudinal sectors and Areas (as defined in Mackintosh, 1965).

Masaki observed pregnancy rates of 0.49 in Area I (lowest) and 0.65 in Area V (highest). Ovulation rates varied between 0.42 and 0.57 for different Areas and seasons. In all cases, these values were for females of age less than 30 years.

#### *Blue and pygmy blue whales*

Little recent information exists on pregnancy rates for blue whales anywhere. However, Mizroch (1981b) gave data for Southern Hemisphere blue whales up to 1963. The data are very sparse but post-war values average 0.51 for Norwegian catches and 0.46 for United Kingdom catches in Area IV in latitudes 60°–69° S.

Ichihara (1966a) reported pregnancy rates of 0.27–0.36 in pygmy blue whales. He concluded that this species had two breeding seasons: a main one during winter and a smaller complementary one in summer.

#### *Fin whales*

Pregnancy rates in Antarctic fin whales have been variously reported, but most recent (although not current) estimates are about 0.54 (Gambell, 1973). Mizroch (1981a, b) reported a value of about 0.50, a value similar to that of blue whales. Ovulation rates for Antarctic fin whales were calculated at about 0.71, equivalent to the estimate of Laws (1961), here corrected for altered assumptions in age determination, and 0.67 (Lockyer, 1972) and 0.68 (Gambell, 1973). As stated earlier, Mizroch (1981a) reported a decline in ovulation rate with age, which was not reflected by age-specific pregnancy rates. The reasons for this anomaly may be complex and imply possible errors in aging or ovarian assessment techniques, or other unknown factors in assessing pregnancy.

In the North Atlantic, pregnancy rates for fin whales are 0.36–0.42 off Newfoundland and Nova Scotia (Mitchell, 1974), and 0.49 off Iceland (Martin, 1982) where average ovulation rates of 0.62–0.64 (Lockyer and Brown, 1979; Lockyer, Gambell and Brown, 1977) have been calculated.

#### *Changes in pregnancy rates*

Laws (1961), Mackintosh (1942) and later Gambell (1973) reported apparent increases in the pregnancy rate with time for blue, fin and sei whales of the Southern Hemisphere; as early as 1930 for blue and fin whales. Laws (1961) and Gambell (1973) hypothesized that the reason for these increases might be reduced intra- and interspecific competition for food, correlated with the exploitation histories of these stocks (Fig. 2). If so, the more food *per capita* available for growth, reproduction and maintenance implies an average reduction in the reproductive interval for these stocks. In effect, for seasonal breeders this could mean a reduction in the reproductive interval, with a greater proportion of annual and biannual calvings for species with two or three-year cycles, and/or increased incidence of aseasonal conceptions. Unfortunately, direct information on survival *in utero* and survival rates of neonates is lacking (and likely to remain so) so that an increased pregnancy rate *per se* does not necessarily indicate increased reproductive rate.

Clark (1982; 1983) has examined Antarctic fin whale cohort data in order to detect trends in recruitment rate which might reasonably be anticipated as a result of

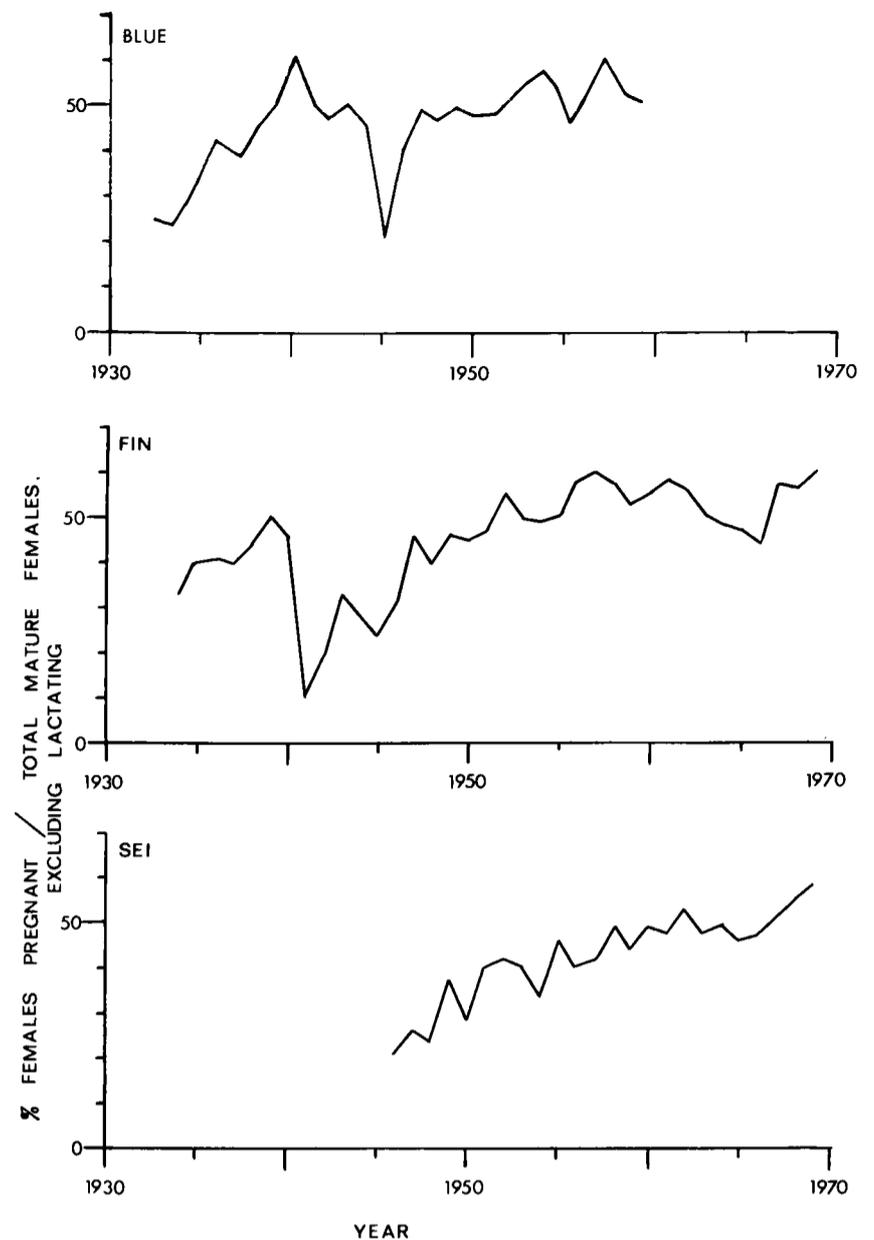


Fig. 2. Observed apparent pregnancy rates with time for Antarctic blue, fin and sei whales (after Gambell, 1973).

increased pregnancy rate, and also changes in other reproductive parameters, namely age at first ovulation, but has so far found nothing conclusive. In fact, he actually found lower recruitment rates than expected, and has also brought to light some discrepancies in data between nations.

Results on changes in pregnancy rates are mostly confused by the fact that most workers have pooled all Antarctic data, not allowing for Area and sector of origin, the season and dates of data collection, age, length of females and national origin of data, all of which could introduce bias into an examination of annual trends. Masaki (1978) has already indicated that these are important. Mizroch and York (1982) have recently reanalysed the fin whale data by allowing for all these factors, and have not found any consistent trends either by nationality or Area. They concluded that the actual data, once corrected for biases, did not indicate any trend in pregnancy rates. The considerable variability in the data, however, could probably mask any trends. The situation rests here at present, but as Mizroch and York pointed out, if there is no actual trend of increase in pregnancy rate, the incorporation of a density-dependent pregnancy rate in population models could adversely affect a harvested population by overestimating the sustainable yield and hence an appropriate catch limit. At the present time, Southern Hemisphere blue, fin and sei whales are protected, but the Mizroch and York analysis

Table 3

Incidences of post-partum and post-lactation ovulations (after Gambell, 1968; 1973; Laws, 1961)

Species	Locality	Proportion of population in post-partum oestrus	% population* conceiving	Proportion of population in post-lactation oestrus	% population* conceiving
Fin	Antarctic	0.179	17.9	0.390	8.2
Sei	Antarctic	0.111	11.1	0.125	1.3

\* Non-pregnant mature females.

has highlighted the need for caution in handling data for other populations and species.

If we return to the strictly biological basis for increased pregnancy rates, we need to examine yearly data on seasonal percentages of post-partum and post-lactation ovulations for several species and determine if these have changed with time. Here again, there may be problems in bias due to the quality of material and data collection (Gambell, 1973).

#### Post-partum and post-lactation ovulation

The mysticetes, as we have already observed, are generally seasonal breeders, the reproductive cycle being intimately linked with the feeding migration to ensure optimum conditions for survival of the single calf. Assuming gestation must remain a constant period of time, increased reproductive rate must depend partly on increased proportions of seasonal conceptions post-partum and also on increased proportions of aseasonal conceptions arising from post-lactation ovulation (see earlier section on changes in pregnancy rates).

Information on incidences of post-partum and post-lactation ovulations are given for fin and sei whales in Table 3.

Increases in either or both of these need not necessarily result in net increased reproductive rate, as the fate of such ovulations/conceptions is unknown and aseasonal births may not favour the calf's survival. Also, if increased *per capita* food is the key factor in increased fecundity, the pregnancy may ultimately be unsuccessful or the neonate die if lactation fails due to insufficient food supply to the mother. This aspect will be discussed in greater detail later. Overall, it would appear that in species where a seasonal male reproductive cycle exists, aseasonal oestrus in the female (usually post-lactation oestrus) is unlikely ever to result in pregnancy and is essentially unimportant to stock assessment.

#### Male Reproductive Cycle

##### *Gray whales*

Rice and Wolman (1971) reported that in the California gray whale, the testes and seminiferous tubules were larger during the southward breeding migration than on the return. They concluded that this indicated a marked seasonal cycle with peak spermatogenic activity in late autumn or early winter correlating closely with the main female oestrus.

##### *Right and bowhead whales*

Whilst no histological evidence is available, southern right whales are known to mate in the winter (Donnelly, 1967; 1969). Bowhead whales appear to mate between March and May (Nerini *et al.*, 1982).

##### *Humpback whales*

The humpback whale in the Southern Hemisphere has been shown to have a seasonal sexual cycle from examination of spermatogenesis and seasonal increase in testis weight (Chittleborough, 1965; Nishiwaki, 1959; Omura, 1953; Symons and Weston, 1958). In winter, the spermatozoa are plentiful in the seminiferous tubules and vasa deferentia.

##### *Minke whales*

Mitchell and Kozicki (1975) reported that sexually mature males taken in the Newfoundland fishery lacked sperm. After taking into consideration the pattern of foetal growth they concluded that the main breeding season preceded the fishing season (May–July) by a few months. Best (1982) found that the average testis weight for different sizes of animals was about 40% heavier during winter for minke whales taken off Durban compared with those taken in the Antarctic during summer, implying a seasonal testicular activity. However, Best stated that this assumption needed future histological confirmation.

##### *Bryde's whales*

Best (1977) could make no statement on the probability of a seasonal reproductive cycle in male Bryde's whales because of small sample size and limited five-month seasonal coverage. However, the scatter of foetal lengths at any time suggested that mating in the South African offshore population is not restricted by season.

##### *Sei whales*

No evidence of a male sexual cycle has been found for the Southern Hemisphere sei whale (Gambell, 1968). Here the female oestrus must be the governing factor in seasonal breeding.

##### *Blue and fin whales*

Mackintosh and Wheeler (1929) reported some seasonal testicular activity in blue and fin whales. Laws (1961) found testicular activity in Southern Hemisphere fin whales during the winter breeding season, which was quite protracted from April to August, peaking in



Fig. 3. Fin whale foetus with one of the ovaries displaying an active corpus luteum.

May/June close to the usual time of conception for this species (see Appendix Table 1).

In summary, the males of most mysticete species display a seasonal reproductive cycle which closely correlates with a main winter oestrus in the female. A protracted breeding season for both sexes would have the advantage of ensuring conception, should pregnancy fail or terminate.

## PREGNANCY, BIRTH AND LACTATION

### Pregnancy

Pregnancy is maintained by a single corpus luteum. Laws (1961) and Gambell (1968) reported incidences of accessory corpora lutea in about 3.7% of fin and 2.0% of sei whales and multiple ovulations in 2.6% of sei whales and 2.2% of fin whales. Rice and Wolman (1971) only found one incidence of multiple (they describe it as simultaneous) ovulation in gray whales, in which two recently ruptured follicles were of the same size.

During pregnancy, the uterine myometrium thickens considerably (personal observation) and the endometrium undergoes histological changes, the surface becoming deeply furrowed, frond-like, secretory and engorged with blood (Matthews, 1948; Rice and Wolman, 1971). Some of these changes can be seen macroscopically, even in early pregnancy, along with gross enlargement of the cornua (both pregnant and non-pregnant sides). Martin (1982) used these criteria together with presence of an active corpus luteum to determine pregnancy in Icelandic fin whales. These animals, when caught, are slit ventrally

at sea to cool the meat, and any foetuses present are almost invariably lost.

Mackintosh and Wheeler, (1929), Laws (1961), Gambell (1968) and Rice and Wolman (1971) all reported cyclical changes in the size and structure of the corpus luteum throughout the reproductive cycle, and in the presence and size of follicles. The follicles are largest in recently ovulated females and shrink throughout pregnancy, being smallest in late pregnancy. Laws (1961) and Rice and Wolman (1971) also found evidence of cyclic follicular activity in pre-pubertal females, during the breeding season. Follicles during anoestrus are actually larger than during late pregnancy for species where data exist, implying suppression of follicular development by progesterone.

Kimura (1957) summarised data for blue, fin, sei and humpback whales. Multiplets (mostly twins), occurred most often in sei whales – 2.3%, compared with values of about 0.8% in blue, 0.9% in fin and 0.6% in humpback whales. More than two foetuses have been reported for fin, blue and sei whales, but they are exceedingly rare – all being less than 0.1%. Sextuplets have been recorded in fin whales, (Kimura, 1957) and Laws (1961) recorded quintuplets developing from a multiple ovulation of 13 corpora lutea. Gambell (1968) estimated that the previously reported multiplet incidence in sei whales was too high, and after considering only biologists' foetal records, obtained 1.3%, still higher than for the other three species. Ohsumi (1977) reported a multiplet incidence in North Pacific Bryde's whales of 0.8%.

These records are probably only of academic interest, in that it is unlikely that multiplets would go to term and even less likely that they would both or all survive as calves, because of the insufficient milk supply caused by a massive energy drain on the cow.

In general, it can be assumed that pregnancy in Mysticeti results from ovulation and conception during a winter breeding season. There is usually only one foetus, which can lie in either the left or right horn of the uterus, although instances of multiple conceptions have been recorded. The gestation period is about one year (see Appendix Table 1).

### Birth

Observations on cetacean birth in the wild are few, although Mills and Mills (1979) and Balcomb (1974) described birth in the gray whale. Best (1981) gave information on the birth of a right whale off South Africa. At birth the usual presentation in cetaceans is caudal, so that the head is last to emerge. Quite by chance the gray whale births witnessed were cephalic presentations. The placenta and membranes part easily from the uterine wall, and there is no evidence available of placental scars in Mysticeti. Thus, examination of the uterus itself gives no clue as to the number of past pregnancies, although stretch marks in the uterine wall may be present, indicating that at least one pregnancy has occurred.

Most information on location of calving is available for the right, humpback and gray whales, as these all seek sheltered coastal areas, often shallow lagoons in the case of the gray whale. Water temperature appears important

Table 4  
Composition of baleen whale milk

Species	Calorific value Kcal/g	% Wet weight				Reference	
		Fat	Protein	Ash	Lactose*		
Blue		34-37	14-22		41-51	Clowes (1929)	
		50.07	49.93			Kirpichnikov (1949) in Tomilin (1957)	
		38.1	12.8		47.2	Sivertsen (1941)	
	3.99	42.3	10.9		42.9	Gregory <i>et al.</i> (1955) Tomilin (1946)	
Fin		30.2	15.61		54.19	Clowes (1929)	
	3.8	32.4	12.8		54.2	Ohta <i>et al.</i> (1953)	
		31-33	11.95-13.3	1.43-2.16	0.2-1.79	53-55	Ohta <i>et al.</i> (1955)
		48-52	10		40	Institute of Oceanographic Sciences, unpublished	
		30.6	13.1		54.1	Sivertsen (1941)	
	3.52	28.6	11.4	1.6	2.6	57.9	Lauer and Baker (1969)
		51.0	13.0		4.5		White (1953)
	28.3	11.4			57.9	McConnell (pers. comm.) Tomilin (1946)	
3.66							
Sei		22.2	12.0		1.8	Takata (1921)	
		26.2	12.6			59.1	McConnell (pers. comm.)
Humpback		38.5				46.7	Pedersen (1952)
	3.86	33.0	12.5		1.1	51.6	Chittleborough (1958) Tomilin (1946)
4.30							
Minke		24.4	13.6	1.6			Best (1982)
		range (4.8-61.7)	range (5.3-17.1)	range (0.7-2.3)			
Gray		53.04	6.38		40.58	Zenkovich (1938)	
	5.32					Tomilin (1946)	

to the right whale, 16°–18.5 °C being favoured (Donnelly, 1967; 1969).

### Lactation

Mysticeti have paired mammary glands, the nipples of which are concealed in long grooves running along the body either side of the vulva (Mackintosh and Wheeler, 1929). The thickness (depth) of the gland varies with the sexual status of the female. The immature gland in blue and fin whales is thin (e.g. 2.5 cm thick) and increases in depth with sexual maturity. The glands of the anoestrous (resting), ovulating and pregnant cow are similar in depth (e.g. 4–10 cm) except in primiparous females. The lactating gland is usually at least double this thickness – maybe up to 30 cm. The actual depths vary slightly with species, and Rice and Wolman (1971), Laws (1961), Gambell (1968), Best (1977), Mackintosh and Wheeler (1929), and Best (1982) gave gland measurements for gray, fin, sei, Bryde's, blue and fin, and minke whales respectively.

The depth of the gland and colour are important criteria in assessing the sexual status of the female. In nulliparous females, or at least in females which have never suckled, colour is pinkish to pinkish white, whilst in anoestrous, parous females, the colour is yellowish brown. This colour change, visible macroscopically, is caused by developmental changes in the secretory lobules and alveoli.

Laws (1961) reviewed evidence that the mammary tissue does not thicken and the lobules and alveoli do not develop until almost term in Mysticeti. In Bryde's whales

correlation has also been observed between the stage of lactation, measured by mammary gland depth, and the diameter of the largest corpus albicans (Best, 1977). Best (1982) has estimated that by late lactation the corpus luteum has shrunk to 40–41% of its size during pregnancy in sei and Bryde's and 52.5% in minke whales.

Macroscopically it is difficult to assess the stage of lactation. Laws (1961), van Lennep and van Utrecht (1953) and Chittleborough (1958) have noted that at the end of lactation, milk may be present in the ducts (or at least a whitish or turbid yellowish, thin liquid) but histological study is essential to establish whether or not the alveoli are actively secretory. In a fishery where lactating cows are effectively protected and heavy penalties are levied on infractions of this ruling, it is thus necessary for a full histological investigation of potentially lactating mammarys to be undertaken in order to assess whether or not a cow was truly lactating. It is interesting to note that the rules of the International Whaling Commission in fact protect *animals accompanied by calves* and that a strict interpretation of the rules would not necessarily result in the imposing of a penalty if an animal was found to be lactating.

Milk compositions and calorific values for different species are tabulated in Table 4. The most notable feature of baleenopterid milk is its high fat content, comparable to that in Pinnipedia (Lavigne, Barchard, Innes and Øritsland, 1982). This feature is probably significant in the rapid growth of the neonate during suckling when the calf may increase body weight by five to eight times (Lockyer, 1981a; 1981b).

Whale milk composition has been found to be highly

variable. Best (1982) reported a significantly lower fat level ( $21.5\% \pm 2.5\%$ ) and higher ash content ( $1.8\% \pm 0.1\%$ ) in milk from simultaneously lactating and ovulating minke females, compared with only lactating ( $33.4\% \pm 4.6\%$  in fat and  $1.4\% \pm 0.2\%$  ash). Ovulation in minke whales generally occurs late in lactation, so that it may be reasonable to assume that the fat content of milk falls in late lactation.

## FOETAL GROWTH

### Sex ratio

Normally the foetal sex ratio is about one to one. Rice and Wolman (1971) found an equal ratio of the sexes *in utero* for the gray whale.

In bowhead whales, Nerini *et al.* (1982) reported a slight foetal predominance of males, which was not statistically significant.

Chittleborough (1965) reported on actual predominance of males at birth for humpback whales. Kato and Shimadzu (1983) reported a slight, but significant predominance of females foetuses in Antarctic minke whales, although Larsen and Kapel (1983) found no significant difference for Greenland minke whales. Wang (1982) reported a slight predominance of female foetuses in minke whales from the Huanghai Sea. Although no direct observations of sex ratio at birth are available in minke whales, Kato and Shimadzu (1983) calculated that at birth, the sex ratio would be equal. Best (1982) reported seven males and seven females amongst 15 stranded (mainly alive) minke whale calves, some with unhealed umbilici.

Kato and Shimadzu (1983) reviewed literature on foetal sex ratio for blue, fin, sei and Bryde's whales, and reported a slight predominance of males *in utero*.

### Growth pattern

Foetal growth in cetaceans has been reviewed by Mizue and Jimbo (1950), Laws (1959) and Mikhalev (1980). There are specific accounts for gray whales (Rice and Wolman, 1971; Rice, 1983), bowhead whales (Nerini *et al.*, 1982), humpback whales (Chittleborough, 1958; Ivashin, 1965), minke whales (Sergeant, 1963; Jonsgård, 1951; Omura and Sakiura, 1956; Ivashin, 1976; Ivashin and Mikhalev, 1978; Best, 1982; Ohsumi, Masaki and Kawamura, 1970; Wang, 1982), Bryde's whales (Best, 1977; Ohsumi, 1980), sei whales (Laws, 1959; Gambell, 1968; Masaki, 1976; Lockyer, 1977b; 1981a; Lockyer and Martin, 1983), blue whales (Symons, 1955; Laws, 1959; Lockyer, 1981a), fin whales (Ommaney, 1932; Laws, 1959; Ohsumi, Nishiwaki and Hibiya, 1958; Jonsgård, 1966; Mikhalev, 1970; Lockyer, 1981a).

In the majority of mysticetes there is an accelerated growth phase in the latter part of gestation (Laws, 1959). Gestation times and size at birth are given in Appendix Table 1.

Various authors have attempted to describe foetal growth by formulae, notably Laws (1959) who modified a formula of Huggett and Widdas (1951), Mikhalev (1980) and Rice (1983). All these formulae were evolved for describing linear growth with time, and not growth in weight with time as was the formula of Huggett and Widdas (1951) and later Frazer and Huggett (1974). The main argument concerns the pattern of the second

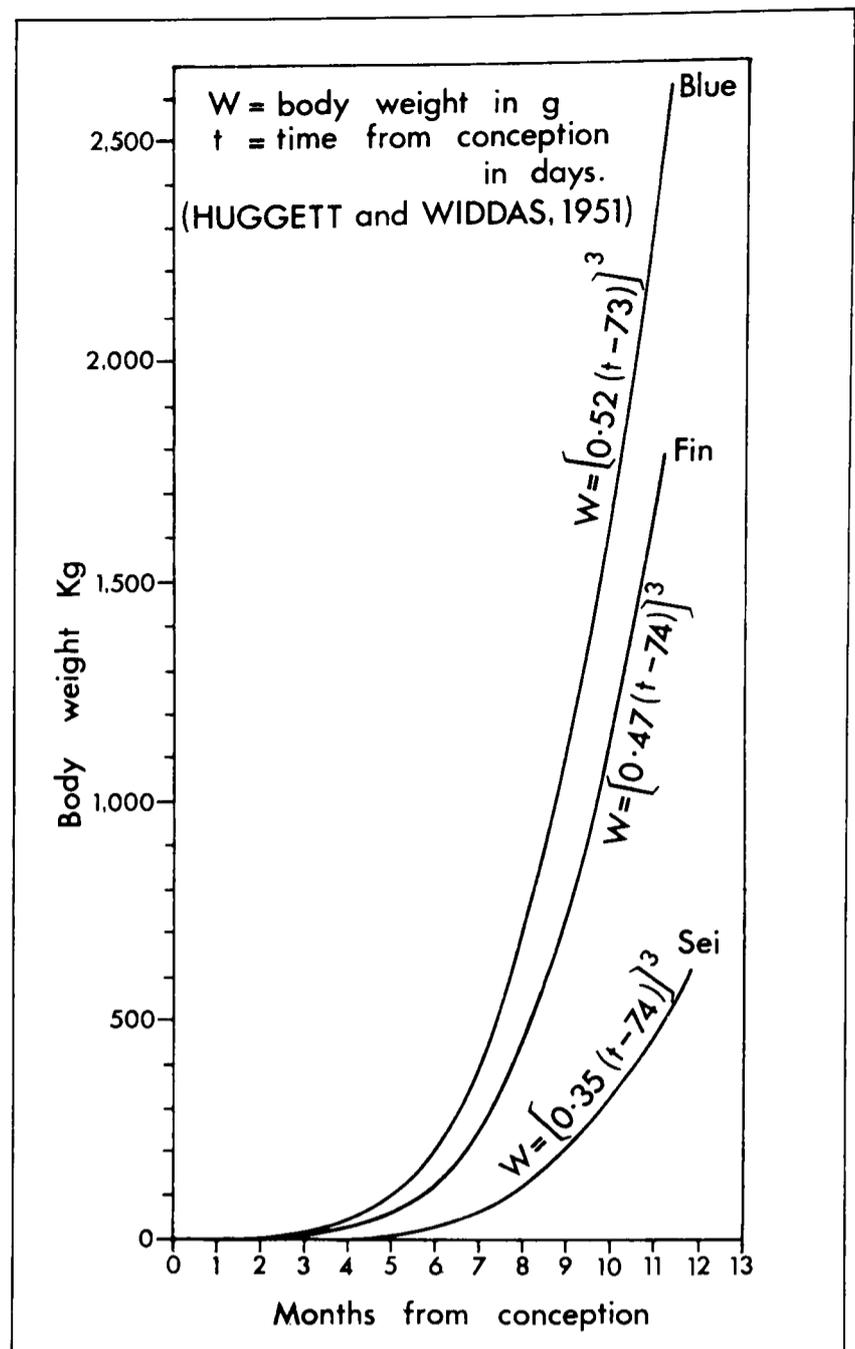


Fig. 4. Foetal growth in weight with time from conception for blue, fin and sei whales described by formulae calculated according to the theory of Huggett and Widdas (1951).

accelerated growth stage in Mysticetes. Rice (1983) proposed that the accelerated growth phase for gray whales falls off prior to birth, whilst Laws (1959) considered that growth continues to accelerate at this time in baleen whales.

The Huggett and Widdas formula, relating gestation time and foetal body weight for the period of accelerated growth, was

$$W^{\frac{1}{3}} = a(t - t_0),$$

where  $W$  = body weight in g,  $a$  = growth velocity constant,  $t_0$  = time constant in days since conception prior to the linear growth phase,  $t$  = time in days since conception.

Assuming the validity of its application, in cases where the accelerated phase is rectilinear and not exponential as proposed by Laws (1959), it is a useful tool for estimating total gestation times and extrapolating back to conception date. Mysticeti are assumed to implant normally *in utero* after conception and do not display delayed implantation common in some marine mammals (seals). Huggett and Widdas found similarities between many mammals and were able to predict growth constants for large Balaenopteridae. They predicted values of  $t_0$  of about  $0.2 \times$  gestation period (100–400 days) which are about 67–72 days for most baleen whales. Values of  $a$  predicted by Frazer and Huggett (1973; 1974) were 0.58 for blue,

0.46 for fin and 0.36 for sei whales, the highest growth rates for all mammal foetuses.

In Fig. 4, curves of mean body weight with time from conception are given for blue, fin and sei whales. These curves are the results of comparing length at age and weight at length curves, based on Lockyer (1981a). It will be seen in fact, that the theoretical predictions of the above authors are close to the values of  $t_0$  and  $a$  given in Fig. 4 for these three species.

The second phase of foetal growth generally coincides with migration onto the feeding grounds, when food energy is readily available for conversion into growth. As we have already seen, most baleen whales have a gestation period of just under one year. This has been thought to be favourable to species with an annual behavioural cycle with a fairly rigid breeding season. Rice (1983) has argued that for species with a normal two-year reproductive cycle, a gestation period exceeding a year is no real problem. His main argument was that accelerated growth of the foetus would place too large an energy drain on the mother, and therefore a more protracted gestation with slower growth would be energetically less demanding. The present author does not agree with this. It has been shown that lactation is more energetically demanding than pregnancy (Lockyer, 1981a; 1978; 1981b; – and discussed more fully below). In addition should parturition occur immediately before the main breeding season, there is a potential for greater production if environmental conditions are suitable and the cow experiences a post-partum oestrus and conceives. This feature may ultimately be a measure of species survival ability and must be reflected in ovulation and pregnancy rates, (see earlier section on reproductive parameters in the female).

### ENERGETICS OF FEMALE REPRODUCTION

Baleen whales feed by filtering and consuming swarming planktonic organisms (Nemoto, 1959; 1970). The Balaenidae take mainly copepods, whereas the Balaenopteridae consume mostly euphausiids; shoaling fish and other organisms are also taken if plentiful. Gray whales feed chiefly from the bottom, sucking up (Ray and Schevill, 1974) and sifting mud for crustacea (Rice and Wolman, 1971). Feeding is a highly seasonal activity peaking during summer. Little feeding takes place during winter. Lockyer (1981a) calculated that for blue and fin whales, daily intake during winter may be only about a tenth of that in summer. The usual main feeding period is about four to six months, with pregnant females staying longest on the feeding grounds. Lockyer (1981a) calculated that, on the basis of four months of intensive feeding and eight months of reduced feeding, daily intake averaged over the whole year amounted to only 1.2–1.6% of body weight. The daily intake during the feeding season however, probably reaches 4% of body weight (Sergeant, 1969) and may exceed this under favourable conditions during pregnancy (Lockyer, 1978; 1981a).

To survive long periods of poor feeding conditions, whales fatten during the summer. The most obvious sign of this is the increase in blubber thickness which, relative to body size, is thickest in pregnant females and thinnest in lactating cows (Lockyer, 1981a; Rice and Wolman, 1971).

Lockyer (1981a) estimated that for all sexual classes,

fattening occurred in muscle and viscera with weight increases of up to 71% in blubber, 64% in muscle and 82% in viscera observed during the feeding season. Increases in total body weight were made up of 13% due to blubber, 17% due to muscle and 7% to viscera. Bone could hold up to 80% oil, but actual weight increases would not be detectable, as oil which is less dense would replace water. Lockyer (1981a) observed that blubber of pregnant blue and fin whales was about 25% thicker than that of resting (anoestrous) females, corresponding to an overall body weight increase of at least 60–65% compared with 50% for the resting population during summer feeding. This extra 10–15% fat could be accumulated by remaining longer on the feeding grounds; up to 6½ months has been observed for humpback whales (Dawbin, 1966) and is suggested for other species by the timing of arrivals and departures from the feeding grounds.

Most of this extra energy is channelled catabolically into milk production in winter and spring (Lockyer, 1978). The initial energy costs of pregnancy are minimal, and costs only become important in the last half or third of gestation. In fin whales, lactation costs can be double those of total gestation and foetal development (Lockyer, 1981b) and are in excess of gestation costs for blue, sei and minke (Lockyer, 1978; 1981a; 1981b).

On a daily basis, lactation is even more expensive energetically than pregnancy. There is a possibility of variation in age-specific reproductive performance. Evidence from pregnancy rates by age is that success in conception is similar for all ages (see earlier). However, success in lactation is vital to net production; should lactation fail, the calf will die from starvation. Alternatively the mother may become so depleted in energy reserves because of the costs of milk production, that the two-year reproductive cycle is extended to three years in order for the cow to recover. These situations are more likely to affect young, recently mature females which are themselves actively growing. The net reproductive costs of the growing foetus and milk production are probably similar in all age-classes, but during a two-year cycle these form about 19% of total energy costs (growth and maintenance) in physically mature female fin whales and 26% in recently mature ones (based on data from Lockyer, 1981a; 1981b).

One can only speculate on the effects of variable food supply on the reproductive interval for baleen species, particularly as individual growth rates and age at attainment of sexual maturity may vary with circumstances (see the section on average age at first sexual maturity). However, theoretical predictions are often not borne out under test observation, and few data are available for the period between parturition and anoestrus.

### CRITERIA FOR DETERMINATION OF SEXUAL MATURITY

The sexually mature female is relatively easy to identify, as the generally accepted criterion is evidence of at least one ovulation (either a corpus luteum or corpus albicans). Of course all pregnant and lactating females are sexually mature. The criteria used for determining male maturity are less clear.

It is important in population modelling to know

Table 5  
Criteria for assessing sexual maturity in male baleen whales – mean values in recently mature animals

Species	Locality	Testis			Reference
		Mean weight (g) ± usual range	Mean seminiferous tubule diameter ( $\mu$ m) ± usual range	Penis length (cm) ± usual range	
Blue	Antarctic; S. Africa	ca 5,000		ca 150	Ohno and Fujino (1952); Mackintosh and Wheeler (1929)
Fin	Antarctic; S. Africa	≥ 2,500	115 ± 5	ca 150	Mackintosh and Wheeler (1929) Laws (1961) Ohsumi (1964b) Ichihara (1966b) Ohsumi <i>et al.</i> (1958)
	N. Pacific	≥ 2,000 or ≥ 2,600		ca 130	
Sei	N. and W. Norway	≥ 3,000			Haug (1981)
	Antarctic; South Africa	≥ 1,500	100 ± 5	ca 100	Gambell (1968)
	N. Pacific	≥ 1,300	100 ± 10	ca 100 ± 30	Masaki (1976)
	Iceland	≥ 1,100	135		Lockyer and Martin (1983)
	E. Canada	≥ 1,000	130		Mitchell and Kozicki (1974)
Humpback	Australia	≥ 2,000 (puberty)		ca 107	Chittleborough (1955)
	Antarctic	ca 2,500			Matthews (1937)
Bryde	Japan	≥ 2,000			Nishiwaki (1959)
	S. Africa	≥ 1,500	ca 113 ± 35		Best (1977)
	Japan	≥ 650 ≥ 750			Nishiwaki <i>et al.</i> (1954) Omura (1962)
	S. Pacific	≥ 1,150			Ohsumi (1980)
Minke	S. Africa	500–625			Best (1982)
	Brazil	≥ 400 ≥ 600			Williamson (1975) da Rocha (1980)
	Antarctic	≥ 400 or ≥ 350			Ohsumi and Masaki (1975) Ohsumi <i>et al.</i> (1970)
	N. Pacific	200–300			Omura and Sakiura (1956)
	N. Atlantic	≥ 112.5			Jonggård (1951; 1962); Sergeant (1963)
Gray	California	ca 3,500 ± 700	100 ± 5	110 ± 5	Rice and Wolman (1971)

certain biological facts associated with sexual maturity, for example size and age at first maturity, age at first parturition and fecundity at first maturity. It is difficult to assess the reproductive performance of the baleen whale male at first sexual maturity, as unlike the female, no data are available. Body length and sex are often the only biological data available for certain catches, so that the estimation of the proportions of mature and immature whales in the fishery hinges on an accurate assessment of mean body length at first sexual maturity. Significant shifts and trends in these proportions often indicate possible changes in population dynamics.

For females the only valid evidence of sexual maturity is a normal corpus luteum or corpus albicans (which could have been associated with pregnancy). Corpora atretica, corpora aberrantia (Laws, 1961), and other bodies, including cystic follicles, do not qualify. In some juvenile fin females, several 'yellow' bodies (Laws, 1961) may be present, and the present author has also observed this in Antarctic minke whales. These are thought to result from atretic follicles.

Male sexual maturity is usually assessed from the histological evidence of spermatozoa in the testis and epididymis, spermatogenesis throughout the testis, open seminiferous tubules exceeding a critical diameter (species dependent) in the testis, testis weight in excess of a critical value, and penis length. In practice, seasonal reproductive cycles can confound most of these factors.

Laws (1961) and Rice and Wolman (1971) reported seasonal increases in testis weight and tubule diameter correlated with breeding activity for fin and gray whales respectively. Testis weight is the most widely used criterion, and histological study is desirable for confirming maturity in pubertal males. Detailed criteria and classification based on histological studies of the Leydig and Sertoli cells, for assessment of sexual maturity, have been undertaken by Chittleborough (1955), Gambell (1968) and Masaki (1976).

Sampling of whale testis tissues usually occurs a long time after death of the animal, so that histological study of spermatogenesis is difficult, and tubule measurements may be unreliable.

Table 5 gives data on mean testis weight and mean seminiferous tubule sizes associated with first sexual maturity in males of different species and stocks. Appendix Table 1 gives data on mean body lengths at first sexual maturity for both males and females, values which clearly depend directly on an accurate diagnosis of sexual maturity from a study of the gonads.

#### AVERAGE AGE AT FIRST SEXUAL MATURITY

##### Estimation of average age at attainment of sexual maturity

The mean age at sexual maturation can be derived directly from an analysis of the proportion of mature

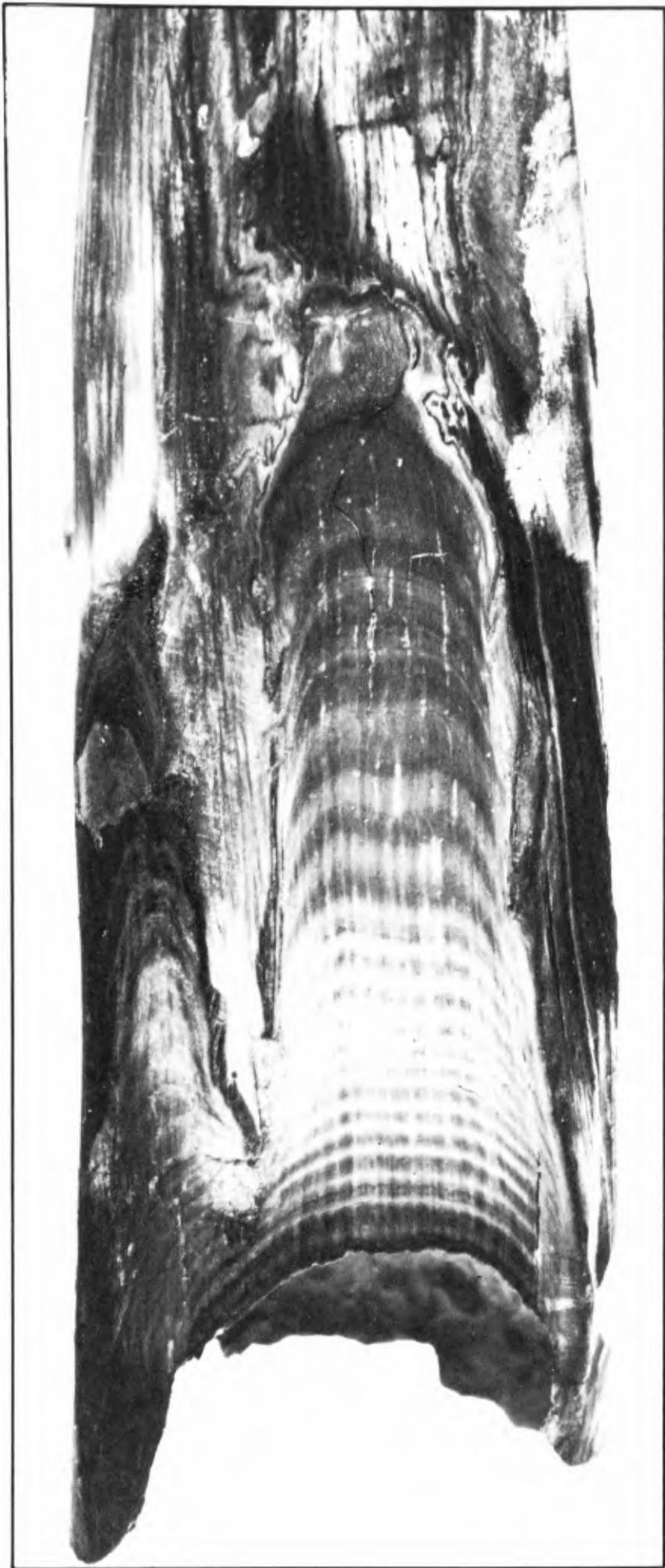


Fig. 5. Earplug from a fin whale cut to display annual growth layers (paired light and dark laminae), from which total age and age at sexual maturity may be estimated.

animals at each age in the catch. Usually the age at which 50% of the animals are sexually mature is taken as the average age at first sexual maturity. In the past, a 75% level was sometimes adopted by authors, and literature on this subject needs to be examined carefully in order to assess what criteria have been adopted. DeMaster (1978; 1984) presented a technique for estimating average age at first sexual maturity and the

associated confidence intervals. However, size selectivity in the catch can lead to over-representation of fast-growing precocious individuals and bias the mean age downwards.

Indirect methods of estimation of mean age at sexual maturation ( $t_m$ ) include estimating  $t_m$  from mean length at age curves when mean body length at first sexual maturity is known, calculating the age at first ovulation from regression of age on corpus number, and analysis of the ear plug transition phase by year class (Lockyer, 1972) (see Fig. 5) or year of maturation. (Best, 1982; Kato, 1983).

Reliable age estimates for baleen whales were unavailable prior to 1955, when Nishiwaki (1957a), Purves (1955), Purves and Mountford (1959), Laws and Purves (1956) and Ichihara (1959) all reported a new method of ageing mysticetes from the laminae in the earplugs. Initially, doubt existed over the formation rate of these laminae, until Roe's (1967) discovery that one pale and one dark lamina together form an annual growth layer in fin whales. This has since been applied to other species: sei (Lockyer, 1974; 1977a; 1979b, Masaki, 1976; 1978; Lockyer and Martin, 1983); Bryde's (Best, 1977; Ohsumi, 1980); minke (Ohsumi *et al.*, 1970; Ohsumi and Masaki, 1975, Masaki, 1979; Kato, 1983; Best, 1982); pygmy blue (Ichihara, 1966a) and gray (Rice and Wolman, 1971), often with indirect supporting evidence. However, no studies similar to Roe's have since been undertaken, and no useful data exist for known-age animals, so that some residual doubt about true age persists for some species. Indeed, from limited evidence, on time between marking and capture of an individual humpback whale, Chittleborough (1960) believed 2 growth layers formed annually in the earplug. Prior to the use of earplugs for ageing, baleen plates were used with limited success (Ruud, 1945; Ruud, Jongsård and Ottestad, 1950), mainly because the plates wear at the tip, and are only useful for the juveniles. Earplugs, however, in contrast, hold a total record of the age of the whale, and have also been found useful for predicting  $t_m$  (Lockyer, 1972).

Appendix Table 1 gives data on  $t_m$  for different species and stocks based on growth layer counts in the earplug. Problems exist for all methods of determining  $t_m$  owing to biases being introduced either through the technique itself or through using fishery data from catches. Age distributions of catches may not truly represent the population because of regulations on minimum body size and gunner selection for larger animals. Identifying such biases and allowing for them is important. Comparing results from as many different approaches as possible is probably the most reliable way of obtaining best estimates of  $t_m$  and associated confidence intervals.

#### Changes in mean age at first sexual maturity

Changes in  $t_m$  with time have been reported for fin (Lockyer, 1972; 1977c; 1979b; 1981c), sei (Masaki, 1976; 1978; Lockyer, 1974; 1979b; Lockyer and Martin, 1983) and minke (Masaki, 1979; Kato, 1983; Best, 1982), from ear plug transition phase studies.

In all instances  $t_m$  has declined with time. However, not all these trends have been significant; examples of this have been reported by Lockyer (1979b) for Antarctic

Area V fin whales and Antarctic Areas IV and V for female sei whales.

Whilst linear regression analyses have frequently been used to describe trends, if any, and test their significance, the decline in  $t_m$  is probably exponential, whether or not the real cause is biased data, artifactual or biological.

In the analyses of Lockyer (1979b, 1981c), Lockyer and Martin (1983) and Kato (1983), either individual cohorts or small groups of cohorts have been analysed separately for mean and confidence limits. The present author believes this to be a better approach than linear regression analysis which may be heavily weighted by the ends of the period of analysis (i.e. the earliest and the most recent year classes). The most recent year classes are well known to be biased, with the older maturing whales not being recognized as they are not mature at the time of capture – the truncation effect. Free and Beddington (1980) attempted to compensate for this bias. It is thus important that if regression analysis is to be used, only data unbiased by the truncation effect should be analysed.

The pattern, extent and timing of the trend in  $t_m$  has often differed between stocks and also sometimes between the sexes (Lockyer, 1979b; 1981c; Lockyer and Martin, 1983). Kato (1983) recently attempted to compare direct estimates of  $t_m$  for yearly catches with corresponding values of  $t_m$  anticipated from transition phase data in Antarctic minke whales. He found correlation in Areas III and IV combined and parallel trends for Area IV alone. He had problems with small sample sizes and with making the estimates from the two methods comparable. Recently doubts have been expressed as to the genuineness of observed declines in  $t_m$  as determined from ear plug transition phase. Cooke and de la Mare (1983) expressed the view that the observed declines in  $t_m$  by cohort could be an artifact of the variability in age readings. However, they assumed that variability of estimates of  $t_m$  and total age from any one plug were interdependent, whereas dependency may only be partial. Cooke and de la Mare had to assume very high variabilities in order to generate declines in  $t_m$  which paralleled or coincided with those observed. Their main hypothesis thus merits further investigation but requires actual data on variability of age readings to become at all meaningful.

Examination of age data for females using corpora number and ovulation rate to arrive at age after sexual

maturity and then combining this with  $t_m$  determined from earplug transition phase may give some indication as to variability of total age. Even though individual ovulation rates probably vary, ovulation rates can be assessed independently of age from an examination of corpora regression. True variability of age cannot be determined because there are no known-aged animals.

Let us compare values of  $t_m$  for Southern Hemisphere fin whales, over time. In Table 6 below are shown estimates of  $t_m$  from catch data, using the 50% proportion mature-at-age criterion for seasons 1955–59 and 1960–64 (A).

Mean values of  $t_m$  derived from ear plug transition phase studies for cohorts of years 1940–44, 1945–49 and 1950–54 with attached 95% confidence intervals are also shown (B). It is seen that there are declines in both (A) and (B) which are similar and parallel, despite the differences in the two methods of analysis of  $t_m$ .

### Effects of exploitation on biological parameters

Lockyer (1972; 1974; 1978; 1979b), Gambell (1973), Laws (1977a; 1977b) and Kawamura (1978) have discussed apparent changes in biological parameters such as  $t_m$  and pregnancy rate and explored the possibilities of reduction in inter- and intraspecific competition as a result of intensive exploitation of whale stocks in the Antarctic. Certainly, Lockyer found that trends to decline in  $t_m$  appeared to be correlated with the history and pattern of exploitation. For the present then, it will be assumed that trends in  $t_m$  for baleen whales are genuine, even if exaggerated through bias.

Changes in  $t_m$  for Southern Hemisphere fin and sei whale stocks (Lockyer, 1979b) may be the result of reduced intraspecific competition for food amongst the surviving whales of these species. However, Kawamura (1978) and Lockyer (1972) also considered that the massive depletion of blue, humpback and right whale stocks prior to exploitation of fin, sei and minke whales could be important in reducing interspecific competition. Nemoto (1959) indicated the considerable overlap in food preference, feeding area, and timing of feeding for all the Antarctic baleen whales. Laws (1977a; 1977b) in particular has explored this situation, and attempted to identify the main components of the food web in the Antarctic, and the impact of each on the system.

Lockyer (1972; 1978) found that despite a declining trend in  $t_m$ , the mean body length at first sexual maturity,  $L_m$ , had remained constant for fin and sei whales, at approximately 90% maximum length. The observed mean body lengths at sexual and physical maturities have been found to vary slightly according to the area of origin; they differ between hemispheres (see Appendix Table 1), and Ichihara (1966b) and Laws (1962) reported differences between Antarctic Areas. This change in  $t_m$  could thus be explained only by a faster pre-pubertal growth rate. There has always been a wide range in values of  $t_m$  and thus variable growth rate of individuals within populations. A range in  $t_m$  of up to 13 years has been observed in fin and sei whales (Lockyer, 1972; 1974) and even more in minke whales (Masaki, 1979).

Lockyer (1978; 1981b) attempted to calculate whether or not a growth rate increase resulting from a decline in  $t_m$  from 10–6 years in fin, 11.4–7 years in sei and 14–6

Table 6

Comparison of values of  $t_m$  from 50% maturity in catch data (A) and  $t_m$  from ear plug transition phase (B). (Data used by Lockyer 1972; 1977c; 1979b for Antarctic Area II fin whales.)

Catch seasons	A $t_m$		Cohorts	B $t_m \pm 95\% \text{ C.L.}$	
	♂	♀		♂	♀
1955–59	8.1	7.2	1940–44	8.69 ± 0.51	8.61 ± 0.44
			1945–49	6.56 ± 0.74	7.15 ± 0.53
1960–64	6.2	6.6	1950–54*	5.87 ± 0.61	6.19 ± 0.53

\* Some downward bias here, due to truncation effect.

years in minke whales was energetically feasible. She found that an extra 5% food annually could cover the energetic costs of a decline in  $t_m$  of one year in fin whales. For a decline of four years, an extra 20–25% food would be required. In minke whales, the equivalent food increase was 27% for a decline in  $t_m$  of eight years. The gathering of this extra food would presumably not be a problem if it was available. We have already seen that primiparous females have a similar extra requirement.

Laws (1977a; 1977b) and Mackintosh (1973) have calculated that the overall reduction of the baleen whale stocks from *ca* 43 million tonnes in the 1900s to *ca* 6.6 million tonnes today has liberated a 'surplus' of *ca* 153 million tonnes of krill (*Euphausia superba*), the principal food of baleen whales.

Over a total summer Antarctic feeding area of *ca* 16.7 million km<sup>2</sup>, the current whale density has declined from 2.6 g/m<sup>2</sup> to 0.4 g/m<sup>2</sup>.

Whilst we cannot identify for certain genuine trends in biological parameters, it is inconceivable that such a massive disruption of the food web in the Antarctic could have had no effect.

Many factors other than age at sexual maturity and pregnancy rate may be density-dependent. Age at first parturition, ovulation rate, calf, juvenile and adult survival rates are all vulnerable to environmental stress, although data on such factors are lacking. The general stability and sex and age composition of the population closely influence the gross parameter values. Here we will consider just one parameter,  $t_m$ , in detail.

The concept of density-dependence in age at sexual maturation is not new. Laws and Parker (1968) reported that in adjacent elephant populations where one was severely malnourished due to over-grazing of the habitat, onset of sexual maturity could be delayed for up to eight years through hardship. Tanner (1973) reported a decline in menarche in humans from 17 to 13 years over a *ca* 100 year period. Dann and Roberts (1973) similarly reported such a decline. The reasons for this decline are unclear but may be correlated both with nutritional and social factors. Unlike Cetacea, a change, albeit small, in body size was also noted in humans.

These comparisons are useful with Cetacea, because life spans are similar. Mean age at first sexual maturity has also declined in crabeater seals (Laws, 1977a), the interesting point here being that this species is a competitor for food in the Antarctic with the Mysticeti.

#### Consideration of specific examples of changes in $t_m$

Let us consider the possibility of a true decline in  $t_m$  in three species frequenting the Antarctic. More specifically, we will examine the pattern of decline by area in relation to history and intensity of exploitation. Declines in  $t_m$  have been observed in both sexes, but it is perhaps more useful for management purposes to consider only the female.

Fig. 6 shows mean  $t_m$  by year class groups in female fin whales from Areas II (0°–60° W) and VI (120° W–170° W) and sei and minke whales from Areas III (0°–70° E) and VI. Declining trends are observed in all Areas: 10.4–6.1 years (Area II) and 12–9.2 years (Area VI) for fin whales, 11.3–7 years (Area III) and 11.5–8.8 years (Area VI) for sei whales (all four trends have already been shown significant by Lockyer, 1979b), and 14.7–5.1 years (Area III) and 14.2–6 years (Area VI) for minke whales. Table 7 shows the percentage declines in  $t_m$ . The decline in  $t_m$  is greatest in Areas II and III.

Table 7

Relative decline in mean age at sexual maturity by Antarctic Area, in females only, expressed as recent  $t_m$ /original  $t_m$  per cent

Area	Fin	Sei	Minke
II	58		
III		62	35
VI	77	77	42

The major exploitation of all three species occurred after blue and humpback whales were depleted (Lockyer, 1976). The order of interest by the whaling industry was fin, then sei and finally minke whales, each species becoming important in the catch as catches of the

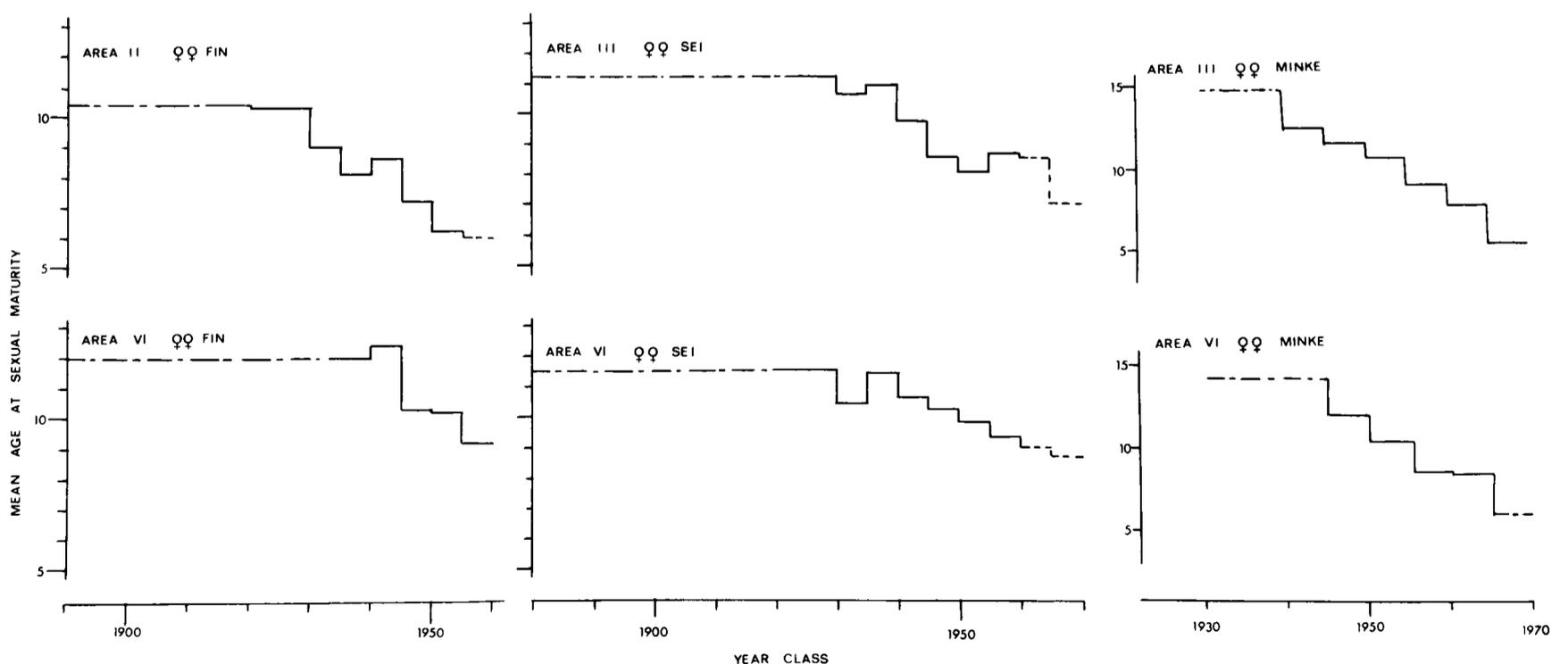


Fig. 6. Trends in mean age at sexual maturation for female Antarctic fin, sei and minke whales. (Means are shown for 5-year blocks minimum.)

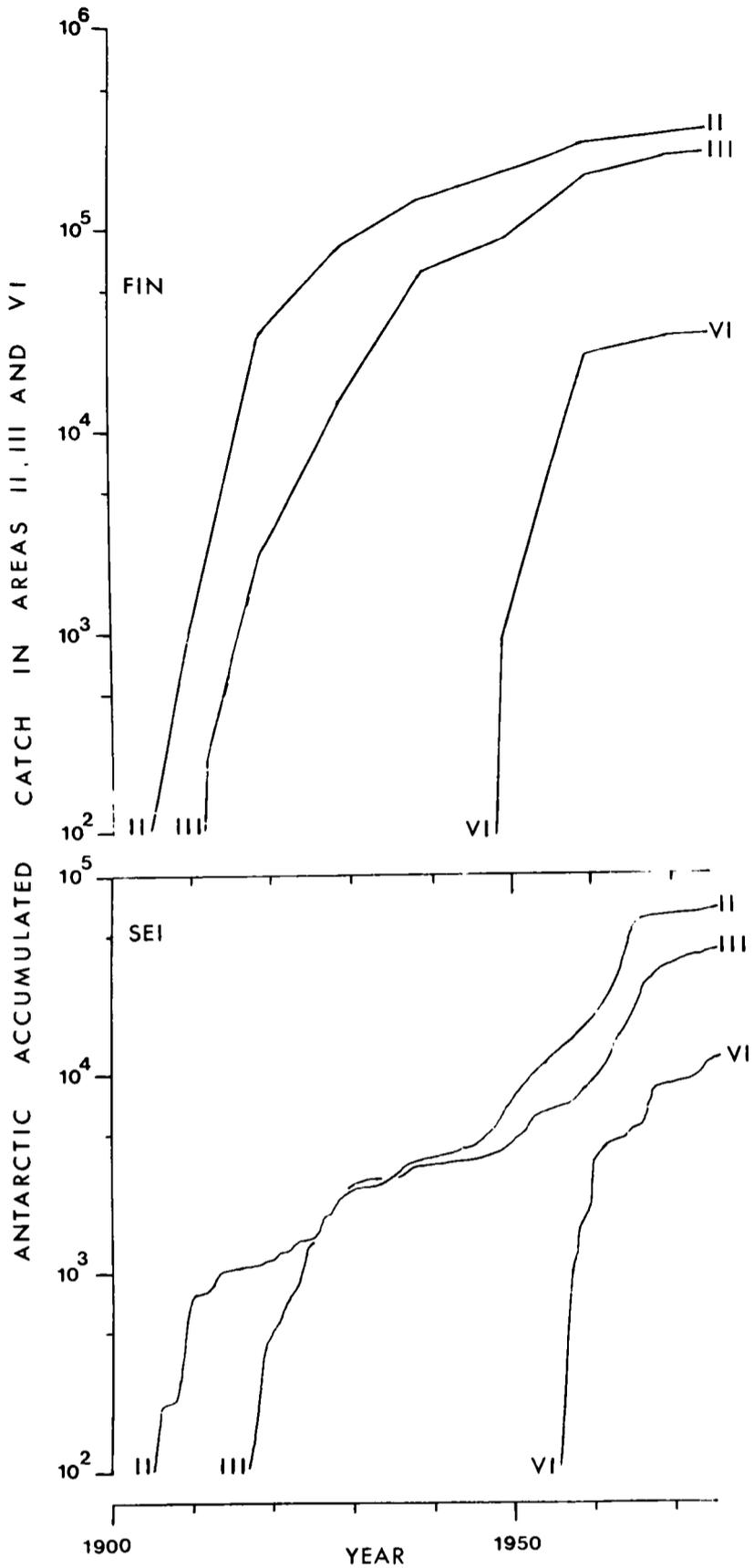


Fig. 7. History and level of exploitation of fin and sei whales in different Antarctic Areas.

previous species started to wane due to depletion. Minke whales were of no commercial importance at all until the 1970s, when they rapidly became the prime target after fin and sei whales were protected. Fig. 7 shows the pattern of exploitation for fin and sei whales. Areas II and III have the longest histories of exploitation and Area VI has the shortest and most recent. Exploitation began in Area VI 40 years after it began in Areas II and III.

Examining the relative depletions of these four stocks in Table 8, it is clear that Areas II and III are the most heavily reduced and have less than a quarter of the original standing stock. The initial stocks in Areas II and III are four to five times larger than that in Area VI, when species are combined.

Lockyer (1979b) has argued that prolonged heavy depletion may be correlated with the extent of decline in  $t_m$  observed. For the Areas and two species considered here, the argument seems to be upheld. It seems likely that in the Antarctic, there have been real declines in age at sexual maturity in some species brought about by faster growth rate, but the actual extent of the decline is uncertain and may be impossible to quantify exactly.

For example, the minke whale has been shown in Table 7 to have an extraordinary decline in  $t_m$ . It is well known that this is partly due to truncation biases (Kato, 1983; Cooke and de la Mare, 1983). Even so, such a decline must reflect depletion of other competitors. It should also be borne in mind that the minke whale has an annual reproductive cycle, making it as a species, far more productive. It may thus be inappropriate to compare minke whale parameter changes directly with those of fin and sei.

Lastly, we may note that in population modelling it is the age at first parturition rather than age at sexual maturity, which is the important parameter, and this cannot be estimated reliably simply by adding on the gestation period to the age at maturity (DeMaster, 1981), because ovulation cannot be equated with conception, and even less with live birth. Bearing this in mind, the true implications of a decline in age at sexual maturity are uncertain.

### ABNORMALITIES OF REPRODUCTION

Like all animals, aberrations occur both in the reproductive organs and during the development of the foetus in Cetacea. Nearly all of this information comes as a side product of whaling.

Table 8

Proportional reduction in total stock biomass through exploitation (after Lockyer, 1979b)

Area	Initial biomass of population (tonnes $\times 10^{-3}$ )			% Current biomass of population Initial* biomass of population		
	Fin	Sei	Fin + Sei	$\frac{\text{Fin}}{\text{Fin}}$	$\frac{\text{Sei}}{\text{Sei}}$	$\frac{\text{Fin + Sei}}{\text{Fin + Sei}}$
II	5,952	997	6,949	14	42	18
III	7,296	623	7,919	23	25	23
VI	1,152	378	1,530	46	76	54

\* Initial = pre-1920 level.

Multiple ovulations and resulting conceptions of multiples have been discussed earlier. These fetuses probably rarely, if ever, go to term. Ichihara (1962) has reviewed such incidences in relation to death *in utero* and the subsequent tissue degeneration, necrosis and calcification or resorption. Ichihara also found active corpora lutea present in the ovaries of pregnant females carrying multiples, some of which were dead. The remaining live fetuses were normal and healthy. He also recorded a corpus luteum in the ovary of the pregnant horn of the uterus which bore a dead and decomposing fetus. In some cases where dead and live fetuses were found together, it appeared that the dead fetus was the unexpelled product of an earlier pregnancy. Ichihara estimated a minimum *in utero* death rate of 0.14% for Antarctic fin whales. He noted however, that nothing is known of the abortion rate, particularly in early pregnancy. Ichihara believed that the observed death rate *in utero* was higher in some localities notably between 10° E and 40° E.

Ivashin (1977) and Ivashin and Zinchenko (1982) recently reported that nearly three times as many foetal malformations and multiples occurred in minke whales from Area IV than in those from the other five Antarctic Areas. The authors speculated that there might be some teratogenic factor in Area IV, especially as nearly all the observed abnormalities were confined to Pridz Bay.

Deformities of the foetus have been described for nearly all Mysticeti (Ivashin, 1960). Ohsumi (1959) and Nishiwaki (1957b) reported on monsters of fin whales, and Ivashin and Zinchenko (1982) reported on such in minke whales. Deformities include abnormalities of the central nervous system, skeleton (particularly the skull), and external development of viscera (hernias of several kinds). Other less usual deformities reported have been siamese twins in minke (Ivashin and Zinchenko, 1982), sei (Kawamura, 1969) and humpback whales (Zemsky and Budylenko, 1970). Further abnormal development of fetuses has been reported for minke whales by Ivashin and Zinchenko (1982) in the form of extrauterine pregnancy. They reported three specific instances to those reported earlier by Ivashin (1977). In all cases, the fetuses were located within the abdominal cavity and were usually deformed, necrotized and calcified, sometimes inosculated with viscera. One aged female had several fetuses of different sizes within the abdominal cavity. Yet another female had a live normal fetus within the uterus as well. The largest intra-abdominal fetus reported was 290 cm in length, about the normal size at birth (see Appendix Table 1).

Another rare occurrence is of intersex or hermaphrodite whales. Bannister (1963) reported such an instance in the fin whale. This animal had both testes and uterus, the external genitalia being mainly female with abnormalities. Bannister was unable to give a true definition of the sexual status of the animal, but did not discount the possibility that it was the equivalent of the bovine freemartin. The actual incidence of such examples is uncertain because, as Bannister pointed out, in whaling operations the sex of the whale is often recorded only on the evidence of the external appearance.

It is unlikely that the abnormalities described here are

of more than academic interest. However, environmental pollution may have teratogenic effects, and their frequency should be carefully monitored since they do affect reproductive output (Viale, 1978).

### GENERAL SUMMARY AND CONCLUSION

Baleen whales are generally very seasonal in their habits, both in feeding and breeding, often engaging in extensive migrations in between these two major activities which centre around summer and winter respectively. The reproductive interval varies from a minimum of one to three or more years; the minimum time limiting factor being the gestation period, which is about one year and normally results in the birth of one calf. The sex ratio of fetuses is approximately one to one. Lactation, which usually suppresses ovulation, lasts from four to ten months depending on the species.

The onset of sexual maturity is identified by examining the gonads. Evidence of ovulation, with or without pregnancy, is an indication of maturity in females, whilst histological examination of the testis for spermatogenesis and presence of sperm is often the only positive identifier of sexual maturity in males, although other criteria are frequently used for practical reasons.

Parameters such as ovulation and pregnancy rates and age at sexual maturation, all appear to vary according to species, stock and environmental circumstances, and certainly affect dependent factors such as age at first parturition, birth rate, recruitment and survival. That whale populations respond to environmental changes, is suggested by indirect evidence of density-dependence of some reproductive parameters.

In connection with the above factors, information currently lacking which would aid management is data on survival *in utero* and calf survival between neonatal and first year stages. The relationship of these factors to the age of the cow and general feeding conditions is also important. Net reproductive energy costs are likely to be similar for all ages of mature females within species, but the gross costs could vary according to individual and environmental conditions. Variations in these gross costs could be one of the root causes of apparent changes in reproductive parameters. The most energetically costly aspect of reproduction is estimated to be lactation, during which the cow subsists mainly on stored fat. The effect of this could be either that recovery of the cow to optimum breeding condition results in a variable period of anoestrus dependent on local food supply, or that should the cow fail to recoup her energy losses, yet ovulate and conceive, the subsequent pregnancy may abort or result in a high neonate mortality in the population.

Abnormalities of the reproductive system and cycle are considered here, but in the absence of information on causative agents, it cannot be said whether these are likely to be of biological or teratogenic origin. At the present there are insufficient data to suggest that pollution may significantly threaten whale populations. However, a system of monitoring any such data would be useful for future management.

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Appendix Table 1  
Data on reproductive cycle and parameters, and growth data

Species	Location	Peak month(s) of conception	Gestation period (months)	Peak months of birth, and length of neonate (m)	Suckling period (months)	Length at weaning (m)	Mean lengths and ages at sexual maturity		Maximum recorded length in physically mature females (m)	References	
							♂	♀			Age $t_m$ years
Blue	Antarctic; S. Africa	June/July	11	May; 7.0	7	12.8	22.6	24.0	5	31.0	Mackintosh and Wheeler (1929) Ruud <i>et al.</i> (1950); Lockyer (1976); Brinkman (1948)
Pygmy Blue	Antarctic	Two seasons: Main: Feb.-April and Compl.:	< 12?	Main: Mar/Apr.? Compl.: Nov.-Jan.? ca. 6.3	?	?	ca 18.9	19.2	ca 5-6	24.1	Ichihara (1966a)
Fin	Antarctic (all Areas); S. Africa	June/July	11	May; 6.4	7	11.5	19.0	20.0	10 → 6 or 7	26.0	Mackintosh and Wheeler (1929); Lockyer (1972; 1976; 1977c; 1979b)
	N. Atlantic	December?	11?	November?	?6	?	16.8-17.6	17.7-19.1	11 → 8	22.5	Jonsgard (1966); Lockyer (1981c) Lockyer, Gambell and Brown (1977); Martin (1982); Haug (1981); Lockyer and Brown (1979) Fujino (1954); Ohsumi <i>et al.</i> (1958)
Sei	N. Pacific	December	11-12	Nov./Dec.; 6.4	?	?	17.6-17.7	18.3-18.6	8-12	22.6	
	Antarctic (all Areas); S. Africa	July	11-11½	June; 4.5	6	8.0	13.6	14.0	11 → 8	18.3	Matthews (1938); Lockyer (1974; 1977b; 1979b) Gambell (1968)
	N. Atlantic	Nov.-Feb.	> 10½	Nov./Dec.; ?	?6	?	12.9	13.3	8	14.9	Lockyer and Martin (1983); Mitchell and Kozicki (1974) Masaki (1976)
	N. Pacific	Oct.-Nov.	> 10½ (W. Pac.) 12-13 (E. Pac.)	Nov./Dec.; ? (W. Pac.) Nov.; 4.4 (E. Pac.)	7 (W. Pac.) 9 (E. Pac.)	? (W. Pac.) 9.0 (E. Pac.)	12.8 12.9	13.3 13.4	10 → 6 (W. Pac.) 10 (E. Pac.)	15.0+	Rice (1977)
Minke	Antarctic; S. Africa Brazil	Aug.-Sept.	10	May/June; 2.8	4	4.5	7.2	8.0	14 → 6 or 7	10.7	Ohsumi and Masaki (1975); Williamson (1975); Ivashin and Mikhailov (1978); Best (1982)
	N. Atlantic	February	10	Dec.; 2.6	< 6	ca 4.5-5.5	6.9	7.3-7.45	7.3	9.2	Mitchell and Kozicki (1975); Sergeant (1963); Jonsgard (1951) Larsen and Kapel (1983)
	N. Pacific Huanghai Sea	Feb./March July-Sept.	10 10-11	Dec./Jan.; 2.8 May-July; 2.5-2.7	?6 ?	?4.6	6.9	7.3 6.6-7.0		8.6	Omura and Sakiura (1956) Wang Pielie (1982)

Table 1 (continued)

Species	Location	Peak month(s) of conception	Gestation period (months)	Peak months of birth, and length of neonate (m)	Suckling period (months)	Length at weaning (m)	Mean lengths and ages at sexual maturity		Maximum recorded length in physically mature females (m)	References	
							Length (m)				Age $t_m$ (years)
							♂	♀			
Humpback	Antarctic; Australia	July/Aug.	11½	July/Aug.; 4.3	10½-11	8.8	11.5	12.0	4 or 5 (× 2)	Chittleborough (1965); Matthews (1937) Nishiwaki (1959)	
	N. Pacific (W.)	February	10-11	January; 4.1	10-11 or 12	ca 8.0	11.6	12.0	11(-2)?	Nishiwaki (1959)	
	N. Pacific (E.)		ca 12							Rice (1963)	
Bowhead	Arctic	May	ca 12-13	Apr./May; 4.5	5-6	6.1	11.6	12.2-14.0	4	Durham (1979); Marquette (1978); Johnson <i>et al.</i> (1981); Nerini <i>et al.</i> (1982)	
Pygmy Right	Southern Hemisphere	?Probably extended	ca 12	Probably extended ?; ca 1.6-2.2	?5-6	ca 3.2-3.6	?	?	?	Ross <i>et al.</i> (1975)	
Right	Southern Hemisphere (S. Africa, S. America) Northern Hemisphere	Aug/Oct.	10	May/July; 5.5 Aug; 6.1 ?4.4-4.8	?	?	13.0-16.0		?	Donnelly (1969); Whitehead and Payne (1981) Best (1981) Klumov (1962); Slijper (1962); Kraus and Prescott (1983)	
Gray	N.E. Pacific	December	13¼	Jan.-Feb.; 4.6	7	8.5	11.1	11.7	8	Rice and Wolman (1971); Zenkovich (1937); Rice (1983);	
Bryde	S. Africa (Inshore) (Offshore)	Year round March	12 12	Year round; 3.96 Feb./Mar.; 3.96	?6 ?6	ca 7.1 ca 7.1	12.0 (13.0	12.5 Few ?12.0) data	ca 10 8-11	Best (1977) Best (1977)	
	N. Pacific (coastal Japan) (pelagic) S. Pacific (2 stocks)	Mainly Dec. but protracted	?12	?Nov. but protracted; 3.95	?	ca 7.1	11.9	12.0	9	Omura (1962; 1966); Nishiwaki <i>et al.</i> (1954)	
		Protracted Protracted	?	Protracted > 3.95 Protracted; < 4.15	?	?	11.9 11.6-12.4	12.0 12.2-12.8	10 and 8 10	Ohsumi (1977) Ohsumi (1980)	

Notes: Age at sexual maturity ( $t_m$ ) based on one ear plug growth layer (one dark and one light lamina) per annum; data for humpback whales originally based on two growth layers per annum - see original references for data.

Data indicated '?', or *ca.* are either unknown or of limited reliability, either through sparsity of data, or because they are based on extrapolations from other species, e.g. Pygmy blue whale.

# Patterns of Reproduction in Sperm Whales, *Physeter macrocephalus*

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## ABSTRACT

From ovarian activity the peak period of breeding in the sperm whale seems to occur between October and December in the Southern Hemisphere and between April and June in the Northern Hemisphere. While large males (over 13.7 m in length) may be the prime breeding animals, the density of spermatozoa in seminal fluid suggests that males may be physiologically fertile at an average length of 12.5 m. Gestation (estimated from the difference between peaks of mating and calving) may last 15 to 16 months, though a comparison of neonatal and adult brain weights indicates a longer period (18.9 months). Equal numbers of male and female calves are born at an average length (from an examination of 15 neonates) of  $4.00 \pm 0.13$  m: sexual dimorphism in size at birth cannot be demonstrated. Sperm whale milk is composed on average of  $35.5 \pm 1.3\%$  total solids,  $24.4 \pm 1.2\%$  fat,  $9.1 \pm 0.3\%$  protein and  $0.7 \pm 0.04\%$  ash. Diving ability of newborn animals seems to be relatively poor. Neonates demonstrate a strong 'following response' that wanes rapidly with age. An interdependence of school members is suggested from behavioural observations. Calves grow to about 6.1 m in length at one year of age and weigh 2,689 kg, or an increase of 1,673 kg since birth. Tests for lactose in stomach contents were positive in males up to 13 years of age and in females up to  $7\frac{1}{2}$  years. Solid food is taken for the first time before the age of one year. Juvenile sperm whales tend to eat smaller and younger squid than adults. Heart weight relative to body weight may be about twice that of adults, suggesting a higher metabolic and thus feeding rate. Criteria for accurate measurement of reproductive (= pregnancy) rates are discussed. Mean calving interval for Donkergat (west coast of South Africa) is estimated as 5.2 years and 6.0–6.5 years for Durban (east coast of South Africa). A decrease in the calving interval from 6 to 5.2 years at Durban was observed between 1962–65 + 1967 and 1973–75. The mean duration of lactation may increase with the age of the female. Some of the older juveniles found with lactose in their stomach may represent offspring of older females in an extended period of lactation. The benefits of possible communal suckling by sperm whale calves are discussed.

## INTRODUCTION

The sperm whale is the largest odontocete and the most sexually dimorphic in size of all cetaceans. Because of its valuable oil it has formed the target of two largely separate episodes of whaling, the first from about 1715 to 1925, when it was hunted with hand harpoons from open boats, and the second from about 1910 to the present day, when it has been subjected to modern whaling. It has been estimated that about 691,520 sperm whales were taken between 1800 and 1909 (IWC, 1969), and the total recorded catch from 1910 to 1973 was 604,100 animals. Despite this large take our knowledge of several aspects of sperm whale biology is still incomplete. This has been demonstrated recently by discussions concerning the rôle of the schoolmaster, the effects of male depletion on the female reproductive rate, and the nature of the response of female sperm whales to exploitation (IWC, 1979; 1980).

In this paper a broad definition of reproduction is adopted, from events surrounding conception to weaning of the calf, and particular attention is paid to the period of dependence of the young.

This study has been based mainly on observations of the sperm whale catch made at the South African land stations at Durban (29° S, 31° E) and Donkergat (33° S, 18° E). Of particular value were 27 calves or juveniles examined at Durban in 1971 and 1973 and 12 calves stranded on the South African coastline.

## MATERIAL AND METHODS

Special scientific permits under Article VIII of the International Convention for the Regulation of Whaling, 1946, were issued by the South African Department of Industries to the senior author in February 1971, July 1971, January 1972 and March 1973 for the taking of up to 15, 15, 10 and 15 sperm whale calves respectively. Due to unexpected commitments the 1972 permit was not utilized. Nine animals were collected in February/March 1971, two in September 1971 and 10 animals in March/April 1973. In addition, some data were collected from six animals less than 9.8 m in length taken incidental to the commercial harvest in March/April 1973. Details of the animals concerned are given in Table 1. It should be noted here that all whales landed at Durban were measured in feet and inches, but these have been converted to their metric equivalents for this paper.

For most of March 1971, August and September 1971 and March and April 1973 the senior author was at sea on a catcher boat of the Union Whaling Company Ltd, Durban, supervising the selection and capture of sperm whale calves under these permits. Each animal selected was killed using a cold grenade (i.e. a harpoon loaded with a grenade but no detonator) and compressed air inserted in the neck region with a spear. In this way damage to the carcass and vomiting of stomach contents were kept to a minimum. After death each animal was individually numbered with cuts on the tail and either lifted on deck (if small enough) or towed alongside with the normal catch. The tail flukes were usually left intact on request.

Upon delivery to the factory the animals were cut up and samples collected under the supervision of a

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Table 1  
Juvenile sperm whales examined at Durban (those marked C collected under special permit)

Whale number	Date killed	Time killed	Position <sup>1</sup>	Length (m)	Sex
C 1	11.2.71	1030	165° 50 nm	3.545	F
C 2	9.3.71	1310	165° 76 nm	6.83	M
C 3	9.3.71	1400	165° 76 nm	6.045	F
C 4	16.3.71	1330	107° 65 nm	6.705	M
C 5	16.3.71	1545	107° 65 nm	6.35	M
C 6	18.3.71	0830	80° 75 nm	3.96	F
C 7	18.3.71	1100	80° 75 nm	3.86	F
C 8	28.3.71	1445	105° 70 nm	6.145	F
C 9	28.3.71	1545	110° 68 nm	6.06	F
C 10	21.9.71	0845	100° 60 nm	8.38	M
C 11	28.9.71	1630	135° 90 nm	8.355	M
C 12	3.3.73	1500	68° 110 nm	4.60	F
C 13	6.3.73	1330	90° 140 nm	4.22	M
C 14	8.3.73	1650	90° 60 nm	3.94	M
C 15	8.3.73	1800	90° 60 nm	8.46	M
U 73/70	8.3.73	1650	90° 60 nm	9.105	M
C 16	9.3.73	1520	65° 102 nm	8.575	F
C 17	13.3.73	1420	85° 120 nm	7.135	F
U 73/241	26.3.73	1205	170° 60 nm	9.45	M
U 73/259	26.3.73	1252	80° 163 nm	8.84	M
C 18	6.4.73	1610	85° 40 nm	8.27	F
C 19	7.4.73	1210	120° 90 nm	8.38	F
C 20	12.4.73	1400	105° 102 nm	8.33	F
U 73/528 <sup>2</sup>	13.4.73	1330	145° 45-50 nm	8.435	M
U 73/537 <sup>2</sup>	13.4.73	1320	138° 50 nm	8.18	F
U 73/575	17.4.73	1037	105° 72 nm	9.625	M
C 21	27.4.73	1200	68° 85 nm	5.64	F

<sup>1</sup> Bearing and distance in nautical miles from Cooper Light, Durban.

<sup>2</sup> Gunners fined for killing undersized whales.

technician (M. A. Meyer) or the senior author and a technician. Animals less than 7.3 m in length were weighed whole on a spring balance (with the exception of the smallest calf which was cut up and weighed in pieces aboard the catcher boat). One animal was weighed whole and in pieces. It was unfortunately not possible to weigh animals longer than 7.3 m. A series of 15 body measurements besides total length were taken following the procedure suggested by Norris (1961). The condition of the umbilicus was examined and the animal inspected for external parasites (most animals were also examined for parasites shortly after death either on the deck of the catcher boat or, in the larger animals, whilst alongside the boat). A count of erupted and unerupted mandibular teeth was made, and at least six teeth collected, boiled lightly to remove the gum and stored in an alcohol/glycerine solution. The animal was then flensed and cut up normally except that care was taken not to damage the stomach. After opening the first and second stomachs a sample of about 40 cc was taken from the liquid contents of each and the entire solid contents usually collected. The liquid samples were then deep frozen for subsequent analysis for lactose. Blubber and stomach parasites were recorded. The hearts of 11 animals were weighed whole after blood clots had been removed.

The gonads were measured, weighed and collected.

Thin sagittal sections of mandibular teeth were prepared and examined for age under transmitted light as described in a previous publication (Best, 1970).

Frozen samples of the stomach liquids were later examined at the Department of Physiology, University of

Natal. One gram of whale gastric juice was mixed with 1 ml of H<sub>2</sub>O, 2 ml methanol (CH<sub>3</sub>OH) and 4 ml of chloroform (CHCl<sub>3</sub>) in a stoppered tube and shaken mechanically for five minutes. The phases were allowed to settle out, when the aqueous upper layer was withdrawn, placed in a clean tube and evaporated to dryness under reduced pressure. The residue was reconstituted with six drops of 10% isopropanol in H<sub>2</sub>O. A 20 × 20 cm glass plate was prepared for thin layer chromatography by spreading a slurry of silica gel H (40 grams) and 80 ml of 0.03 M Boric acid to a thickness of 25 μm. The plates were activated at 110 °C for 30 minutes. Five μl of the isopropanol extract of gastric juice were then applied to the plates and developed twice in the solvent ethyl acetate: isopropanol: H<sub>2</sub>O::25: 25: 12.5. The developed plate was blown dry with a dryer and sprayed with a solution of 0.5 g of naphthalene-1-3-diol, 95 ml of absolute ethanol and 5 ml of conc. H<sub>2</sub>SO<sub>4</sub> and heated at 110 °C for 10 minutes. The spots depicting sugars faded on standing and had to be ringed. Standards of lactose, glucose and galactose were run with each plate.

The collections of cephalopod beaks were examined and identified at the Institute of Oceanographic Sciences, UK, where each stomach's sample was sorted, measured and the number of beaks of each taxonomic group determined.

Data are also available from 12 sperm whale calves stranded (or entangled in nets) along the South African coastline.

## CONCEPTION

### (a) Breeding season

Published estimates of the peak season of conceptions in sperm whales differ by about six months between Northern and Southern Hemispheres. In the Northern Hemisphere there is reasonable agreement between authors that most pairing activity takes place between March and May (Fig. 1). In the Southern Hemisphere, however, agreement is not as good, and while the extent of the season is roughly from August to January, some authors place the peak in September and others in December. Nearly all these analyses, however, are based on the distribution of foetal lengths and some assumptions regarding the duration of the initial slow phase of foetal development. Very little corroboratory evidence from a study of the reproductive organs is available because (by chance) the whaling season frequently did not coincide with the peak of the pairing season.

In Fig. 2 the proportion of resting (i.e. non-pregnant and non-lactating) females that showed ovarian activity each month has been plotted separately for sperm whales from the west and east coasts of South Africa (Best, 1968; Gambell, 1972) and from the coast of Japan (Ohsumi, 1965). Ovarian activity has been defined as the presence of a Graafian follicle 3 cm or more in diameter or (in the case of the South African data only) the presence also of an active corpus luteum with no associated foetus. Also illustrated in Fig. 2 are the monthly percentages of mature females in the southeast Pacific that had recently ovulated (corpus luteum present but no foetus). These data are particularly valuable as they cover every month of the year, but are not directly comparable with the other data sets or strictly accurate because no correction has

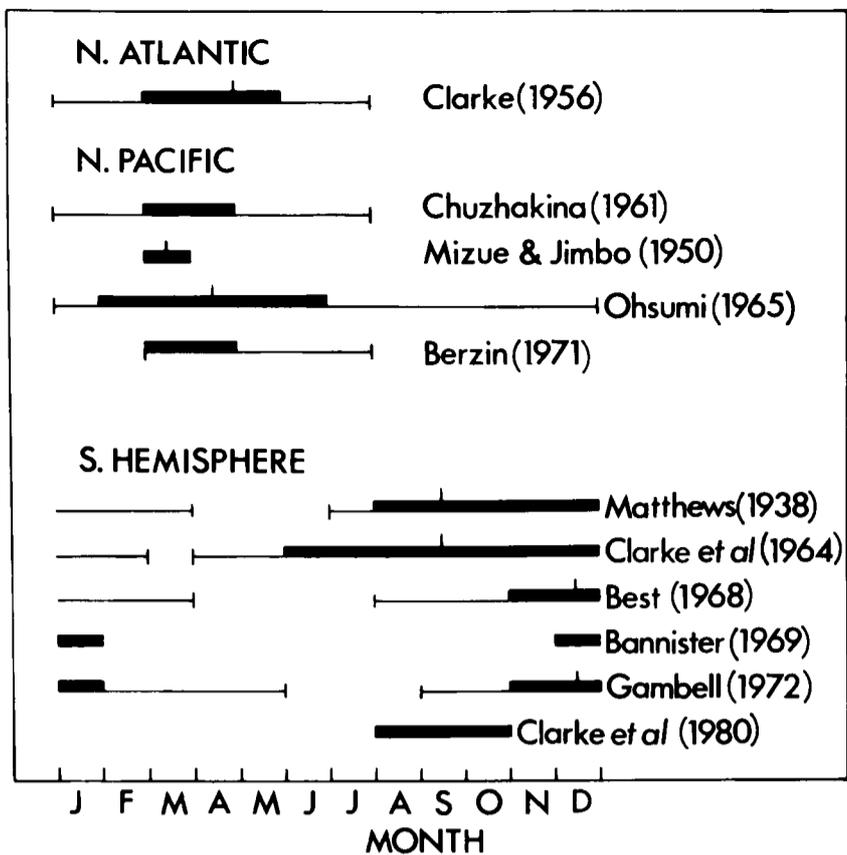


Fig. 1. Published estimates of the breeding season of sperm whales (thin line = range, solid line = peak, vertical line = mean date).

been made for the proportions of lactating and pregnant females in the sample (Clarke, Aguayo and Paliza, 1980). The Japanese data as plotted have been shifted six months to accommodate probable differences in the timing between hemispheres. In the periods for which data are available, ovarian activity seems to be lowest in June in the Southern Hemisphere and in November in the Northern Hemisphere, while it is at its highest in September/October in the Southern Hemisphere and June/July in the Northern Hemisphere. Unfortunately seasonal coverage of the data is incomplete for any region except the southeast Pacific. Even if the comparable data for all regions are combined (assuming that there is six months' difference between hemispheres), the actual peak

in ovarian activity still seems to lie outside the temporal range of most of the data, i.e. between October and December (S) or April and June (N). It is impossible to give a more precise estimate of the breeding season with the ovarian data or analyses available at this time. This estimate however is more direct (and potentially more accurate) than those based on foetal size distributions, as mentioned above. When more details are available of the data from the southeast Pacific it should be possible to give a more precise estimate of the timing of the breeding season, at least for that region.

Regional differences in the pairing season do occur: Best (1968) and Gambell (1972) demonstrated that sperm whales on the west coast of South Africa conceived on average 21–25 days earlier than those on the east coast. The disparity between the estimates of the pairing season by these two authors and Matthews (1938) for essentially the same area, however, was attributed to either unreliable foetal measurements in the earlier data or to a temporal change in the timing of the breeding cycle (Gambell, 1972). Clarke, Aguayo and Paliza (1980) reanalysed their earlier results to show that the peak of the pairing season in southeast Pacific sperm whales was between August and October, when 70% of conceptions took place. Consequently the possibility of a seasonal difference in the pairing season between South African and some South American stocks of sperm whales still exists.

Both Ohsumi (1965) and Gambell (1972) demonstrated that newly mature sperm whales conceived later on average than older females (by about 27 and 43 days respectively), a trend that was also noticed in pubertal fin whales by Laws (1961), who attributed it to delayed ovulation.

The possibility of ovulations in sperm whales being induced has been discussed by Tormosov (1975). Because of the relatively slow maturation rate of Graafian follicles and the apparently high ovulation rate relative to rate of conception, Tormosov concluded that ovulation is more likely to be spontaneous. For other species of Cetacea the

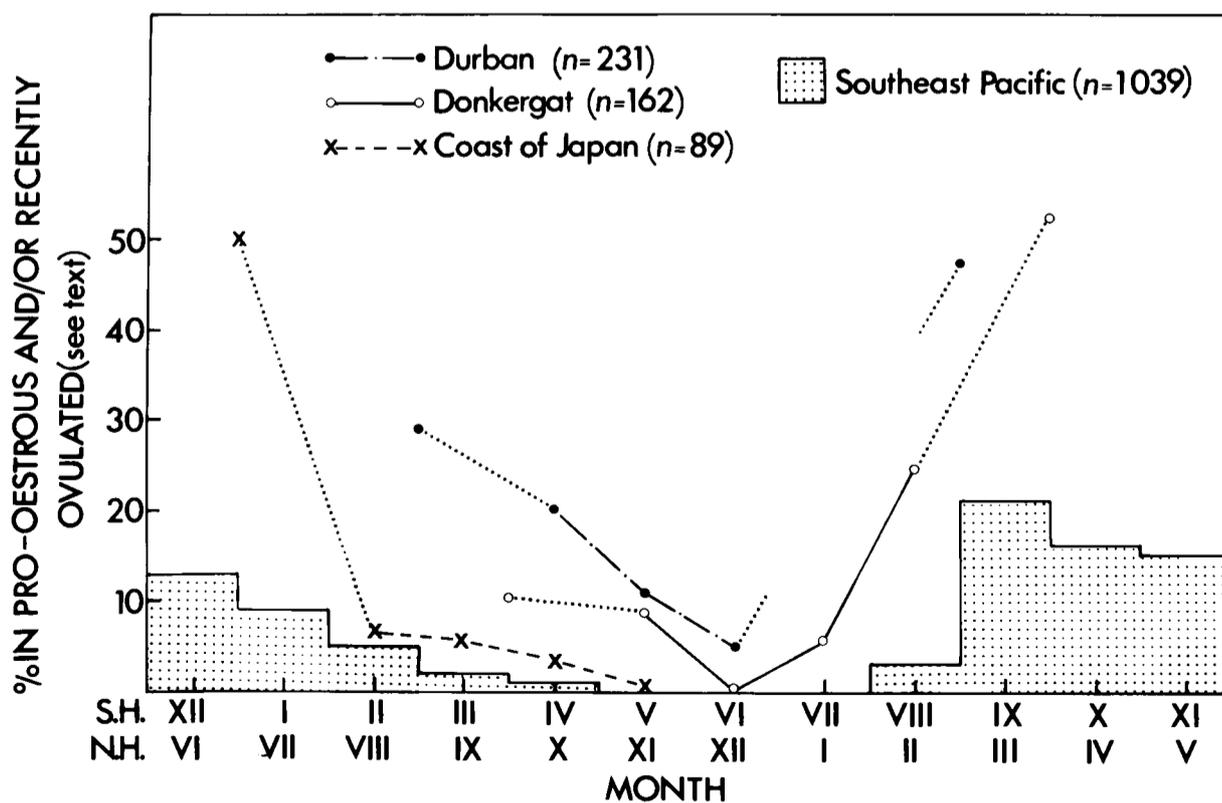


Fig. 2. Monthly trends in ovarian activity in sperm whales.

evidence is not conclusive either way, and both opinions have been expressed for various species (Harrison, Boice and Brownell, 1969; Benirschke, Johnson and Benirschke, 1980). It is even possible that a combination of induced and spontaneous ovulations may occur, e.g. ovulations outside the main breeding season being spontaneous ('silent heat') and those inside the breeding season being induced. As stated by Benirschke *et al.* (1980), a resolution of the problem can only come from long-term endocrine studies of isolated females, something that is clearly impractical for sperm whales at the present level of technology.

Best and Butterworth (1980) found some evidence for synchrony of oestrus within schools of female sperm whales. They concluded that (in the absence of conclusive evidence of induced ovulation) this phenomenon may have a nutritional basis. However, for several species of mammals it has been found that the presence of adult males can induce synchronous oestrus (the 'Whitten' effect – see Sadleir, 1969), and it is possible that the arrival of the schoolmaster(s) during the breeding season may have some synchronizing effect on oestrus in the females in that school. Such an effect would be advantageous in that it might (a) increase the efficiency of fertilization, (b) minimize the period that the adult male must remain with the school (when it is believed that he may be at a nutritional disadvantage – Best, 1979), and (c) reduce interference in the social organization of the female school, especially with mother–infant bonds.

#### (b) Breeding behaviour

Behavioural events occurring around conception are still largely unknown. Tormosov and Sazhinov (1974) described observations from a helicopter of mating behaviour between a large male sperm whale (14–15 m long) and an assumed female (10 m long) in December in the southwest Atlantic. Further aerial observations off Durban that involved 'big' or 'medium' sperm whales apparently mating with 'small' sperm whales have been listed by Gambell (1968), but these observations were made by the aircraft crew and it is not certain that mating was actually taking place. An additional similar observation is now available from the Durban spotter aircraft records.

On 24 August 1971 the aircraft found 83 sperm at 0916 hours in a position 87° and 98 to 105 n. miles from Durban. Notes made at the time read '4 family Flocks seen, with 1 Big and several cows+calves. Whilst boats were chasing about 35–40 small sperm clustered together, in a "Productive" or "Reproductive" session – surrounded by dolphins (many hundred) who attacked the odd shark observed. They stayed in this position for over 2 hours – 3 calves seen amongst them – 2 about 18–20 feet 1 about 14 feet or smaller – excrement in water. No Big sperm seen at this time, but later after they started swimming NW a big sperm was seen with this group of about 40 whales'.

During a whale-marking cruise on 24 January 1974, one of us (PBB) observed what might have been copulation in a school of about 15 sperm whales at 33° 58' S 62° 43' E. The school was composed of cows 9.1 to 10.7 m long (later confirmed by mark recoveries from animals) and one bull 14 m long. The bull was believed

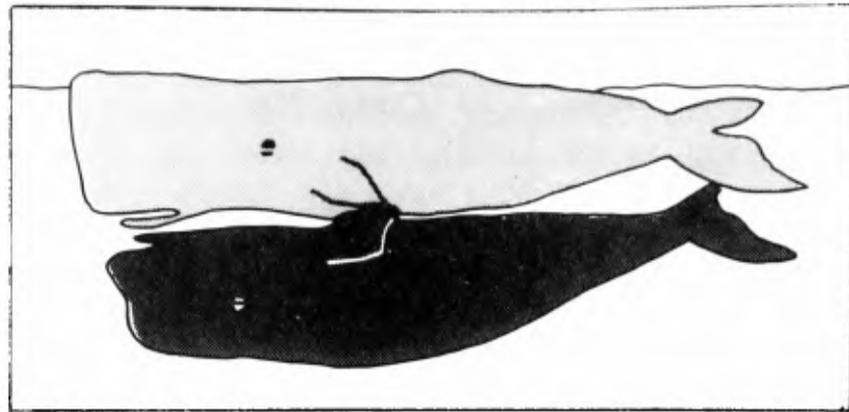


Fig. 3. Apparent mating behaviour observed in sperm whales.

to be mating with cows on our arrival: he was seen underneath a group of small whales with one tip of his tail flukes visible. Later on a group of about five whales was seen in the 'Marguerite flower' pattern described by Nishiwaki (1962), with their heads pointing in towards the centre. The bull was marked soon after our arrival, and he then split off from the rest of the group.

During apparent copulation the partners have been described in the vertical (Bennett, 1840) or horizontal positions (Ruspoli, 1955; Tormosov and Sazhinov, 1974). One of us (PBB) has also seen a sperm whale pair resting belly to belly, one on top of the other, for at least half a minute (Fig. 3). The animals concerned were seen at 33° 54' S 16° 56' E on 24 February 1963, and were from a school of 20–25 whales including one calf and one animal less than 9.1 m. The remainder were all estimated to be 10.1 to 10.7 m long. The sexes of the participants were unknown.

#### (c) Identity of breeding males

Although a subject of controversy, it is probably the large sperm whales over 13.7 m (45 feet) in length that are the prime breeding bulls (Best, 1979). Male sperm whales can produce spermatozoa when as small as 10 m in length (Best, 1969), but their potential fertility may be substantially lower than that of the larger males. Independent studies have been made of the density of spermatozoa in the seminal fluid of sperm whales by Best (1974) and Blokhin (1981), shown in Fig. 4 for four different size-groups, 10–11.5 m (33–38 ft), 12–13.5 m (39–45 ft), 14–15.8 m (46–52 ft) and 16–18 m (53–59 ft). Although actual density values differed by a factor of about 20 (possibly due to differences in sampling technique), both studies demonstrated a marked rise in the density of spermatozoa with body size, particularly in males over 14 m (46 feet) in length. The minimum density required for normal fertility in sperm whales is unknown, but it is clear that although even the smallest males (10–11.5 m in length) were producing spermatozoa, the potential fertility of the largest males was very much greater.

Because of their greater size, male sperm whales generally have been more heavily exploited than females, resulting in a change in the adult sex-ratio and in the age structure of the male population. The implications for management of these changes have been discussed previously (Best, 1979). Unknown factors are (a) the threshold age for breeding bulls, below which adequate fertilization rates cannot be maintained, and (b) the ratio of breeding bulls to adult females required to maintain

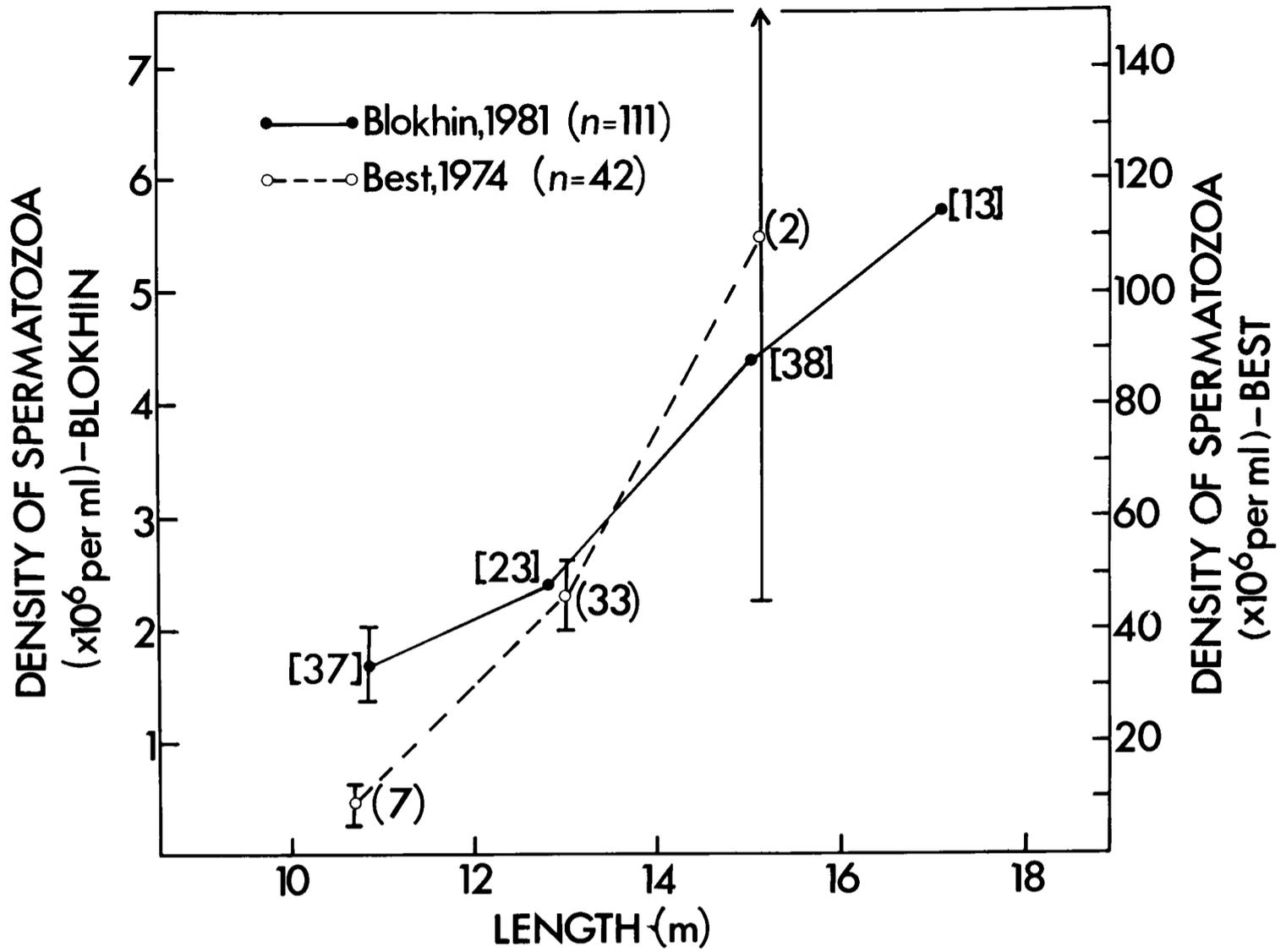


Fig. 4. Mean density of spermatozoa in seminal fluid of sperm whales.

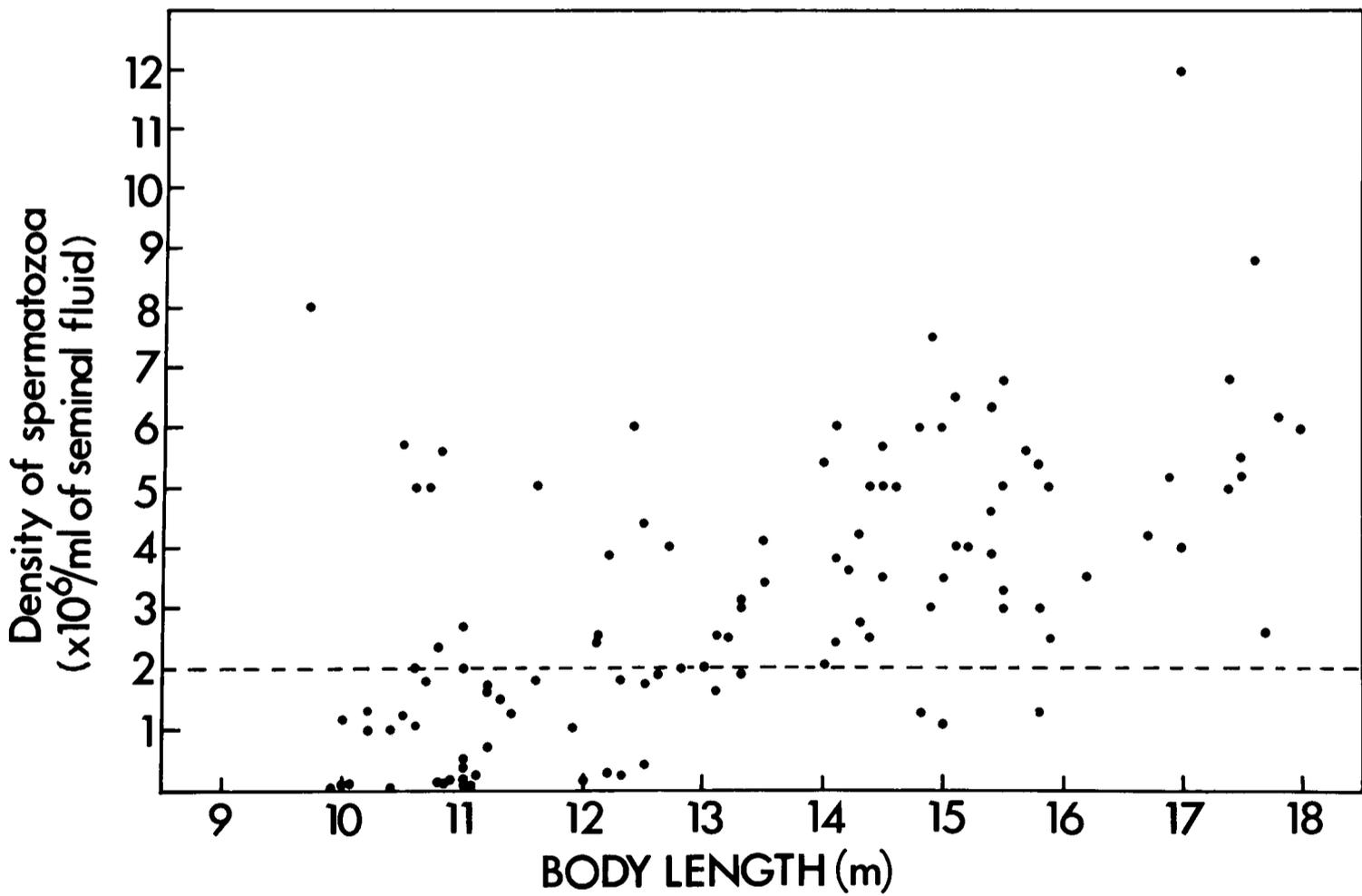


Fig. 5. Individual densities of spermatozoa in seminal fluid of sperm whales.

adequate fertilization. Comparisons with other sexually dimorphic, polygynous marine mammals (the northern fur seal *Callorhinus ursinus* and the southern elephant seal *Mirounga leonina*) suggested that the mean age of breeding bulls could decline by about half, or to about 1.9 times the age at puberty, and that an 80% reduction in the idle: active bull ratio is possible. However comparisons between these pinnipeds (highly aggregated and relatively sedentary during the breeding season) and sperm whales (dispersed in small, highly mobile schools) may not be valid. Possibly the only way to resolve these problems would be by experimental management of one or more sperm whale stocks, but for this to be productive accurate means of monitoring stock levels as well as reproductive rates would be required: the former have so far proved elusive.

The existing sperm whale model used by the IWC (summarised in Perrin and Donovan, 1984) assumes that all males below 25 years of age (equivalent to about 45 ft or 13.7 m) are effectively infertile, playing no part in breeding even when the abundance of larger males is reduced. Given the densities of spermatozoa found in the seminal fluid of some of these animals this assumption seems unreasonable. In an attempt to obtain a more realistic estimate of the threshold age for breeding bulls, individual spermatozoa densities were kindly provided by Dr Blokhin, and these are plotted in Fig. 5. The assumption has been made here that virtually all males above 13.7 m in length are physiologically fertile. Fig. 5 shows that virtually all males (94%) above this length have more than  $2 \times 10^6$  spermatozoa per ml of seminal fluid, which can be therefore taken as the level of minimum physiological fertility. Using this criterion, the proportion of 'fertile' animals at each body length has been calculated, and the smoothed data are shown in Fig. 6. Fifty percent fertility is reached at 12.5 m, or about 41 feet. This is equivalent to an age of 20 years (Ohsumi, 1977), and is coincidental with the spurt of accelerated growth in the male (Best, 1970), the formation of schools of 'medium-sized' bachelors, and their penetration into higher latitudes during their summer migration (Best, 1979). It therefore seems to represent a biological 'milestone' for the species.

If it is accepted that younger and smaller males (i.e. medium-sized bachelors) can play an effective reproductive rôle, it follows that a different ratio between the sexes may be necessary for reproductive rates to be maintained. The ratio in the current sperm whale model (1 male 25 years or more in age to every 10 mature females, with a reserve of 0.3 males) is based essentially on the premise that 2 large males rendezvous with each mixed ('harem') school, containing on average 15 mature females. The implicit assumption is that the basic breeding units are not individuals but schools, and it has been pointed out that the mean number of large males found with mixed schools is very similar to the mean size of schools of large bachelors (Best, 1979). If this underlying biological model is adopted, the number of medium-sized (12.2–13.7 m) males that would be required per school of mature females would be equivalent to the mean school size of medium-sized bachelors, or about 5 animals (IWC, 1981a). The effective minimum sex-ratio for males of this size and age would therefore be 5 males per 15 mature females, or an overall ratio of 1:3 (cf. 1:7.5 for large

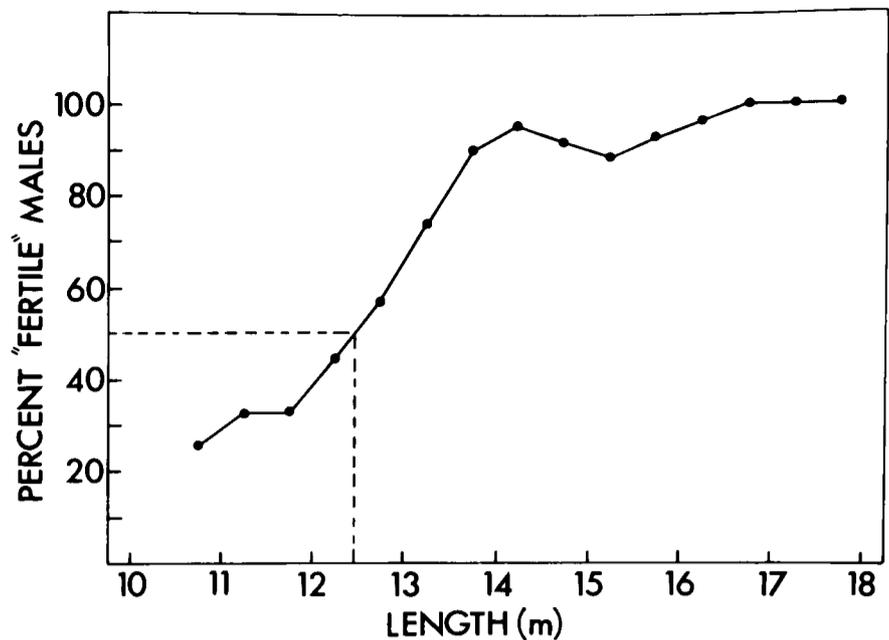


Fig. 6. Percentage of male sperm whales with  $2 \times 10^6$  or more spermatozoa/ml in their seminal fluid (data from Fig. 5 smoothed).

bachelors). Provision in the sperm whale model for the involvement of medium-sized bachelors in reproduction following depletion of larger males (with due allowance for the increased number of such animals needed relative to mature females) might provide a better quantitative fit between observed pregnancy rates and those predicted from the assessments.

#### (d) Relationship between breeding male and female school

Based on the recovery of marks and the incidence of cyamids of different species, it has been proposed that the association between the breeding bull(s) and a school of female sperm whales is only transitory (Best, 1979). The exact duration of this association is unknown but may be significantly less than the duration of one breeding season (Best and Butterworth, 1980). The evidence from cyamid infestation, in fact, would suggest that the association may be extremely brief, possibly only a matter of days, although this evidence was collected at the beginning of the breeding season.

The similarity between the social organization of African elephants and that of sperm whales has already been noted (Best, 1979). Except at very low population densities, an elephant bull has a higher probability of associating with an oestrous female if he adopts a searching strategy rather than living permanently with a cow group (Barnes, 1982). Similar considerations (short supply of receptive females due to extended calving interval, restricted breeding season, and gregariousness of females) suggest that male sperm whales might also maximize their mating opportunities if they moved between female groups within one breeding season, particularly if a Whitten effect should occur amongst the females in these groups.

## PREGNANCY

### (a) Foetal sex ratio and incidence of multiplets

Sperm whales normally carry a single foetus. The incidence of twin foetuses has been recorded as 0.47% (Gambell, 1972,  $n = 844$ ), 0.45% (Ohsumi, 1965,  $n = 2,664$ ) and 0.55% (Matsuura, 1940,  $n = 364$ ). At

Table 2  
Published foetal sex ratios for sperm whales

Area	Sample size	% male	Source
N. Atlantic	42	40.5	Clarke, 1956
N. Pacific	535	46.2	Mizue and Jimbo, 1950
"	1,068	48.1	Ohsumi, 1965
S. Africa, west coast	115	48.7	Best, 1968
" east coast	220	59.2	Gambell, 1972
Africa	491	45.6	Ohsumi, 1965
Chile	1,118	56.2	Ohsumi, 1965
Peru			
W. Australia	55	50.0	Bannister, 1969

Table 3  
Foetal sex ratios for sperm whales at Durban, 1973–75 (official records)

Foetal length group (m)	Males	Females	Unknown	Total
0–0.50	67	49	1	117
0.51–1.00	95	78	1	174
1.01–2.00	53	66		119
2.01–3.00	8	7		15
3.01–4.00	21	31		52
4.01+	19	11		30
Total	263	242	2	507

Durban from 1973 to 1975 the incidence of twin foetuses in 503 pregnancies was 0.40%. There appears to be only one record of more than two foetuses in a sperm whale, three embryos 1.47–2.70 m long in a female captured off British Columbia in 1962 (IWS, 1964). Some at least of these multiplets are carried to near term: Berzin (1971) records two sets of twins 3.48 m/3.34 m and 3.47/2.66 m long. There appear to be no authentic records of twin sperm whale calves seen at sea, but their recognition may be obscured by the close schooling behaviour of female sperm whales.

Foetuses can lie in either breech or head presentation, at least up to a length of 2.5 m (Best, 1968).

Foetal sex ratios rarely differ from parity (Table 2). Only the data for Durban collected by Gambell (1972) show a significant imbalance between the sexes (in favour of males). A larger sample from Durban (collected from 1973 to 1975) has an overall proportion of 52.1% males (Table 3), and this ratio between the sexes is not significantly different from parity (chi-square = 0.87,  $P > 0.3$ ). Presumably, therefore, equal numbers of male and female calves are born.

#### (b) Calving season and length of gestation

Gestation in the sperm whale has been variously estimated as lasting from 10–11 to 17 months (Table 4). Most modern interpretations, however, are that it occupies 14–15 months, and certainly exceeds a year. These estimates have been based essentially on calculating conception ages from seasonal trends in foetal lengths. The main source of uncertainty in these estimates is the duration of the initial period of non-linear embryonic growth ( $t_0$ ). This has usually been calculated by taking various arbitrary estimates of  $t_0$  given by Huggett and Widdas (1951) for gestation periods of different lengths, and converting them for foetal length rather than weight data (Laws, 1959). Rice and Wolman (1971) have criticised the manner in which this conversion has been made, pointing out that the conclusions (an inverse relationship between  $t_0$  and the length of gestation) were in contradiction with Huggett and Widdas' data (which showed that  $t_0$  increased as gestation time lengthened but formed a decreasing fraction of total gestation time). Their conclusion therefore is that most calculations of  $t_0$  (and ultimately of total gestation period) are too low.

An alternative approach to using foetal length data to determine the duration of pregnancy is to assess independently the timing of the breeding and calving seasons. The calving season for large whales has normally been derived from the foetal growth curve and a length at birth. Although this is a less tenuous procedure than that involved in estimating the breeding season, its

Table 4  
Estimates of duration of pregnancy in sperm whales (using only biologists' data where available)

Source	Rate of foetal growth	Size at birth	Duration of pregnancy	
			$t_0$ (days)	Total (months)
<i>North Pacific</i>				
Mizue and Jimbo (1950)	(0.86 ± 0.02) <sup>1</sup>	4.27–4.57 m	—	17
Chuzhakina (1961)	(0.90 ± 0.01) <sup>1</sup>	—	—	16–17
Tomilin (1957)	—	3.5–5 m	—	10–11
Ohsumi (1965)	—	4.05 m	—	16.4
<i>North Atlantic</i>				
Clarke (1956)	(0.92 ± 0.02) <sup>1</sup>	3.92 m	—	16
<i>Southern Hemisphere</i>				
Matthews (1938)	(0.96 ± 0.22) <sup>1</sup>	'4 m or a little more'	—	16
Clarke <i>et al.</i> (1964)	0.83	4.02 m	36	17
Best (1968)	1.00 ± 0.06	4.04 m	40	14.6
Gambell (1972)	0.99 ± 0.01	4.05 m	40	14.8
Bannister (1969)	—	—	—	15.8

<sup>1</sup> As reanalysed by Gambell (1972).

Table 5

Weight and umbilical condition of sperm whale calves collected under special permit or stranded on South African coast

Whale no./Date stranded	Length (m)	Sex	Weight (kg)	Condition of umbilicus	Where stranded
C 1	3.545	F	634 <sup>1</sup>	partly healed	—
C 2	6.83	M	3,556	healed	—
C 3	6.045	F	2,083	healed	—
C 4	6.705	M	3,505	healed	—
C 5	6.35	M	2,718	healed	—
C 6	3.96	F	813	healed	—
C 7	3.86	F	635	unhealed	—
C 8	6.145	F	2,718	healed	—
C 9	6.06	F	2,794	healed	—
C 12	4.60	F	1,450	unhealed	—
C 13	4.22	M	1,050	unhealed – open, raw	—
C 14	3.94	M	1,000	healed	—
C 17	7.135	F	4,550	healed	—
C 21	5.64	F	2,400	healed	—
14.9.77	3.72	F	—	unhealed – stalk present	Kidds Beach, East London
18.2.78	3.52	M	506	healing	Umdoni Beach, Natal
23.2.78	3.67	F	630	healing	Vetchies Beach, Durban
7.3.78	3.82	M	748	healed	Rufane's River, E. Cape
21.3.78	4.06	—	—	—	Fish Point, East London
27.3.78	4.75	M	—	healed	Gibson Bay, E. Cape
30.3.78	ca. 4.50	F?	—	—	Smelly Creek, Port Elizabeth
13.3.80	4.08	M	—	healed	Kromme River mouth, E. Cape
20.3.80	3.45	F	550	unhealed – stalk present	Illovo Beach, Natal
7.1.81	3.52	F	615	unhealed	Jeffreys Bay, E. Cape
11.4.81	4.02	F	726 <sup>2</sup>	unhealed	Silverstroom Beach, W. Cape
16.2.82	4.07	M	—	unhealed	3 km west Oyster Bay, E. Cape

<sup>1</sup> Cut up in pieces to be weighed, others weighed whole.<sup>2</sup> Approximate, estimate made of meat and blubber removed.

Table 6

Monthly distribution of newborn sperm whales and observations of births (Northern Hemisphere records in brackets)

Month	Strandings	Captures	Observations	Total
Aug.		(3)		(3)
Sept.	1			1
Oct.				
Nov.				
Dec.				
Jan.	1			1
Feb.	3	1	1	5
March	1	3	1	5
April	2			2
Total	8	7	2	17

accuracy depends on the validity of the parameters used. There are now 15 records of newborn sperm whales available, all of which had raw or unhealed umbilical regions. Besides the published records of Clarke (1956) and Best (1968), there are records of 11 such calves from South Africa, either stranded or collected under special permit (Table 5). In addition, there are two definite observations of sperm whale births (Pervushin, 1966; Gambell, Lockyer and Ross, 1973). These have all been plotted by month of occurrence in Table 6. If the three

Northern Hemisphere records are shifted six months, 76.5% of these records occurred in February and March. It is assumed that these correspond to the peak months of calving in the Southern Hemisphere.

If the peak of breeding occurs from October to December in the Southern Hemisphere, and the peak of calving in February and March, it follows that the length of gestation is 15 to 16 months. This is about one month longer than the more recent calculations based on foetal length analysis, but if  $t_0$  has been underestimated (as claimed by Rice and Wolman) then this would be consistent with the present result.

Sacher and Staffeldt (1974) have correlated mammalian gestation periods with three independent variables, neonatal brain weight, litter size and neonatal brain weight expressed as a proportion of adult brain weight (= brain size advancement). Only three small cetacean species (*Tursiops truncatus*, *Stenella graffmani*, *Phocoena phocoena*) were included, because data on the neonatal brain weights of the great whales did not exist.

Brain weights are now available for the sperm whale calves stranded at Umdoni Beach, Kromme River mouth and Oyster Bay: these weighed 2,865, 3,150 and 3,286 g respectively. As the Umdoni Beach animal was much smaller than the others (and well below the average size at birth, see below), a more accurate measure of brain size

at birth is probably the mean of the Kromme River mouth and Oyster Bay animals, or  $3,218 \pm 68$  (s.e.) g.

The brain weight of 20 male sperm whales over 14 m in length averaged  $7.82 \pm 0.20$  (s.e.) kg, and of 2 females 10.4 and 10.9 m long  $6.00 \pm 0.50$  kg (Berzin, 1971). Brain size advancement is thus 0.412 (using adult male data only). From Sacher and Staffeldt's (1974) multiple regression equation

$$\log Y = 0.274 \log E_n - 0.173 \log N + 0.144 \log A_e + 1.853$$

where  $Y$  = gestation period (days);  $E_n$  = neonatal brain weight (g);  $N$  = litter size (= 1.0) and  $A_e$  = brain size advancement, the theoretical gestation period can be calculated as 574 days, or 18.9 months.

This estimate refers essentially to the reduced gestation time ( $t-t_0$  in the terminology of Huggett and Widdas, 1951). Previous estimates of  $t-t_0$  for the sperm whale have varied from 440 to 552 (mean  $489 \pm 11$ ,  $n = 9$ ) days, or (from biologists' records only) from 440 to 500 (mean  $468 \pm 14$ ,  $n = 4$ ) days (Gambell, 1966). The predicted period is therefore some 17 to 25% greater than observed: Sacher and Staffeldt found a standard error of  $\pm 26\%$  for individual estimates. This discrepancy would be greater if adult female brain weights were used in the brain size advancement factor.

## BIRTH

### (a) Behaviour at parturition

Behavioural events surrounding the birth of sperm whale calves have been described by Gambell (1968), Gambell *et al.* (1973) and Pervushin (1966). These occasions are characterized by bunching of the adults, unusual postures of one or more animals (often head-up in a vertical position) and support of or close association with the parturient female or its calf by other adults in the group. Two further descriptions of possible calving are available from observers on the Durban spotter aircraft.

On 20 April 1972 30 sperm whales were found  $93^\circ 95$  miles from Durban. 'When catcher arrived skipper reported one whale had just calved (est. 8 ft long) the pod of whales surrounded by porpoises then sharks. Whales stayed in same position all day'. On 6 April 1971 45 sperm whales were found  $150^\circ 80$  miles from Durban. 'All at first in a tight bunch with all the calves in the middle. Whales thrashing their tails and now and again bursting into a frenzy of activity. Outside the circle were many killer whales and dozens of sharks. The killer whales were standing straight up in the water at times or just cruising round the sperm and trying to get inside circle. Probably a sperm giving birth.'

The latter description may portray a protective reaction to the presence of the killer whales rather than a social response to the calving female. Killer whales do occasionally prey on sperm whale calves: a 4.02 m female calf stranded alive at Silverstroom Beach near Cape Town in April 1981 bore clear evidence of a recent killer whale attack (Fig. 7). Nevertheless, the bunching reaction seen frequently during episodes of apparent calving may itself have evolved as a means of protecting the newly-born animal from predation, not only from killer whales but also from sharks. Gambell (1968) has given evidence of the attraction of sharks to calving sperm whales (see also

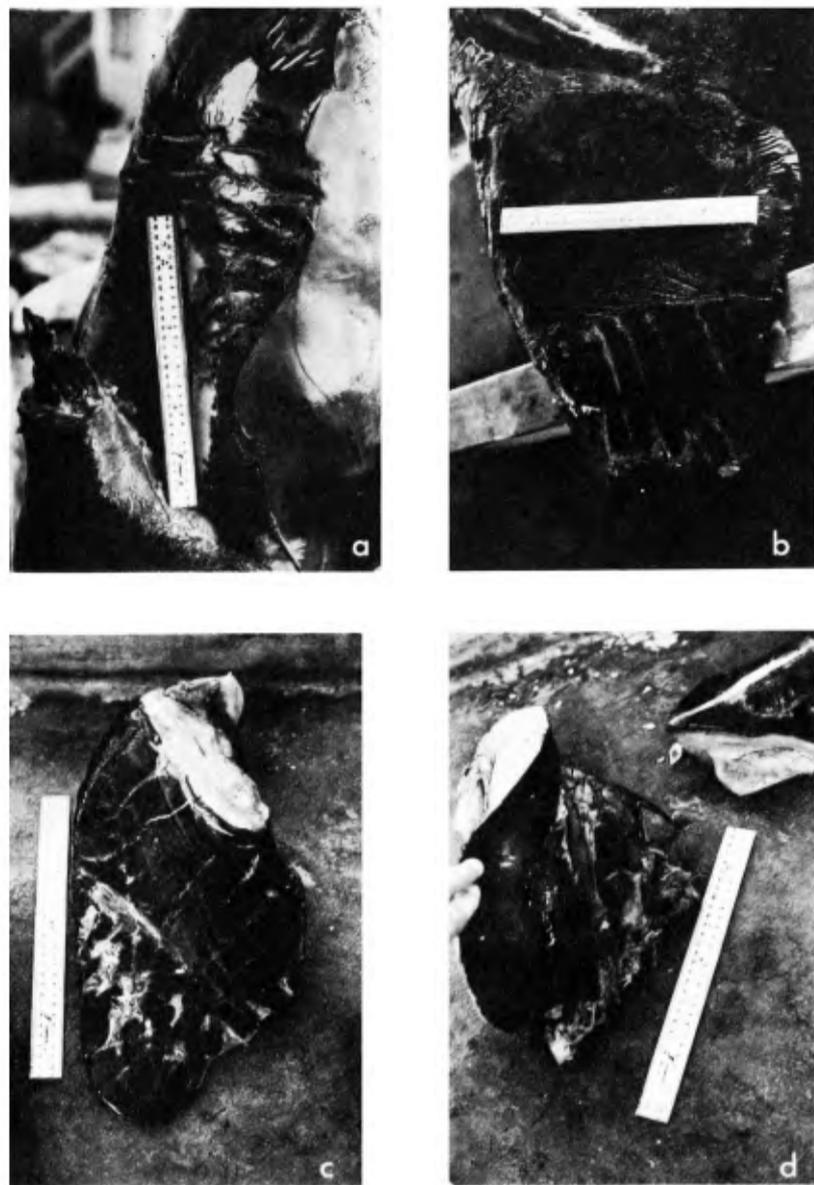


Fig. 7. Killer whale damage to sperm whale calf that stranded at Silverstroom Beach, Cape Town, April 1981. (a) Mouth showing truncated lower jaw. (b) Left tail fluke, tip missing. (c) Right flipper, tooth scars present. (d) Left flipper truncated.

the two records above), and one of us (PBB) has noted the presence of oceanic white-tipped sharks (*Carcharinus longimanus*) trailing sperm whale schools in the southwest Indian Ocean. Sharks also often accompany schools of bottlenosed dolphins in the Gulf of Mexico (Leatherwood, 1977). The sharks may be attracted principally as scavengers (one was seen feeding on foetal membranes from a sperm whale calf – Gambell *et al.*, 1973), but they obviously form a potential threat to the newly-born animal: a sperm whale calf stranded alive at Umdoni Beach (see Table 5) bore possible shark bites around the dorsal fin and caudal hump that appeared to be partly healed (Fig. 8a).

'Mouthing' of the neonatal sperm whale by its mother or another member of the school may occur. A calf 4.21 m long with a raw umbilicus and foetal creases still present (C 13) bore two wavy but roughly parallel linear scars on the underside of its left flipper (Fig. 8b). The spacing between these two lines varied from 2.9 to 7.3 cm, and (as there were no corresponding scars on the upper surface of the flipper) could conceivably have resulted from the mandibular teeth of an adult animal that had grasped the flipper in its mouth: Tomilin (1957) gave the interdental space in large female sperm whales as 4.3 to 5.3 cm. The calf 3.52 m long from Umdoni Beach with an unhealed umbilicus bore several parallel linear scars on its flanks, tail and caudal peduncle (Fig. 8c), similar to those seen on the heads of male sperm whales and attributed to

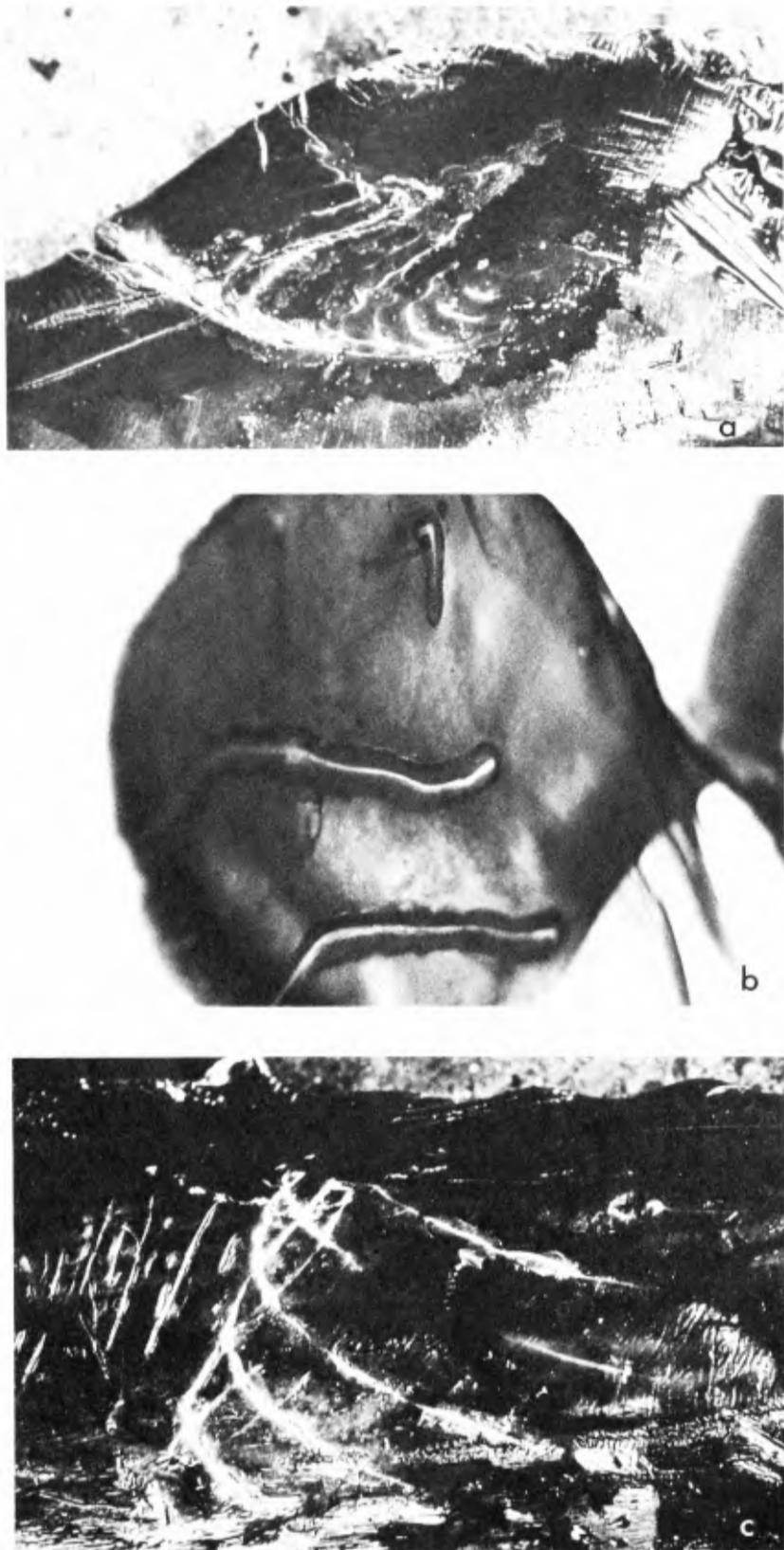


Fig. 8. Tooth scarring on sperm whale calves (see text). (a) Possible shark bite on caudal hump. (b) Parallel scars under left flipper. (c) Parallel scars on left flank.

intra-specific aggression (Best, 1979). The spacing of these 'tooth-rakes' on the left flank (5–6 cm), and the absence of corresponding scars on the right, suggests that the responsible agent was again an adult sperm whale. Connor and Norris (1982) speculated that similar tooth rakes on stillborn dolphin calves indicate that they have been pulled from the mother by a schoolmate. Alternatively such scars could represent play with or 'scolding' of an infant, such as that figured by Caldwell and Caldwell (1967) for the bottlenosed dolphin.

#### (b) Size of the calf at birth

Previous calculations of the length of the sperm whale at birth, based mainly on a comparison of the size distribution of small calves and the largest foetuses, have varied from 3.92 to 4.57 m (Table 7). The total number of calves used in these analyses, however, has been only 13, and these have ranged from 3.71 to 5.5 m in length. As indicated by Ohsumi (1965), some of the larger calves examined may not have been neonates, and in fact only four of the records include definite evidence (from the condition of the umbilicus) of recent birth.

In the present data (Table 5) there are a further 11 animals with unhealed or healing umbilical regions (Fig. 9a). Including the 3 neonates from the Azores (Clarke, 1956) and the one previous record from South Africa (Best, 1968), there are a total of 6 male and 9 female neonates, with mean lengths of  $3.93 \pm 0.10$  m and  $3.82 \pm 0.12$  m (S.E.) respectively. These are not significantly different ( $t = 0.71$ ,  $P > 0.4$ ), suggesting that both sexes are born at a similar size. Gambell (1972) found identical growth rates for male and female foetuses, whereas Clarke, Aguayo and Paliza (1964) calculated a slightly higher foetal growth rate for males (though this was not tested statistically) and estimated that males would be 0.12 m longer than females at birth. Berzin (1971) stated that there is definite sexual dimorphism in the newborn sperm whale.

Assuming no difference between the sexes, the mean size at birth from the 15 neonates is  $3.86 \pm 0.08$  m (S.E.). This sample may not be homogeneous, as seven of the calves were taken at sea and eight were stranded. Because the strandlings may actually represent a component of

Table 7

Published estimates of length of sperm whales at birth

Area	Length (m)	Sample size		Source
		Calves <sup>1</sup>	Late pregnancies <sup>2</sup>	
N. Atlantic (Azores)	3.92	5	16	Clarke (1956)
N. Pacific	4.27–4.57	3	156	Mizue and Jimbo (1950)
All areas	4.05	9	811	Ohsumi (1965)
S.E. Pacific	4.02	5	?	Clarke <i>et al.</i> (1964)
S. Hemisphere (S. Africa)	4.00 <sup>3</sup>	1	28	Matthews (1938)
„	4.25	5	36	Gambell (1966)
„	4.04	4	13	Best (1968)
„	4.05	3	47	Gambell (1972)

<sup>1</sup> Sample of calves not unique for each source.

<sup>2</sup> > 3 m long.

<sup>3</sup> 'or a little more'.



Fig. 9. Newborn sperm whale calves, showing (a) unhealed umbilicus (indicated with arrow) and foetal creases, and (b) large tongue.

natural mortality, they are unlikely to be a random sample of the population and may involve the smaller and weaker animals. The mean length of the captured animals was  $4.00 \pm 0.13$  m and of the stranded animals  $3.74 \pm 0.09$  m (S.E.). Although these means were not significantly different ( $t = 1.73, P > 0.10$ ), the discrepancy of 26 cm between the two groups suggests that stranded animals may not be truly representative of the population. The value of  $4.00 \pm 0.13$  m for the mean length of captured neonatal calves is therefore considered a more reasonable estimate for the size of the sperm whale calf at birth. As such it is in good agreement with most of the estimates previously given (Table 7).

Assuming the mean size at birth is 4 m, the possibility of sexual dimorphism in size at birth can be examined by comparing the sex ratio of animals above 4 m with that of animals less than 4 m in length: presumably if males are born at a greater length than females, the sex ratio above and below 4 m should be different. Two sets of data have been used, the first a large sample from the International Whaling Statistics, covering several different areas of the world and based essentially on company returns, and the second a smaller sample from South Africa using data collected by biologists or under their supervision (Table 8). In neither case was there a significant difference between the sex ratios above and below 4 m. Sexual dimorphism in size at birth is thus not demonstrated by these data.

One of the animals captured (C 1) was (at 3.54 m), the

Table 8

Foetal sex ratios for sperm whales above and below 4 m in length

Area and period	Males (%)	Females (%)	Chi-square (prob.)
All areas, 1937-61 <sup>1</sup>			
≤ 4 m	1,476 (50.7)	1,435 (49.3)	
> 4 m	58 (48.7)	61 (51.3)	0.18 (> 0.5)
South Africa, 1962-75 <sup>2</sup>			
≤ 4 m	417 (53.0)	370 (47.0)	
> 4 m	32 (60.4)	21 (39.6)	1.09 (> 0.25)
Total			
≤ 4 m	1,893 (51.2)	1,805 (48.8)	
> 4 m	90 (52.3)	82 (47.7)	0.08 (> 0.75)

<sup>1</sup> From IWS (1938-63).

<sup>2</sup> From Best (1968), Gambell (1972) and Table 3.

smallest free-living calf so far recorded for the species (Best, 1974). The calf of 2.46 m recorded by Robson and van Bree (1971) from a mass stranding at Gisborne, New Zealand, is so much smaller than any other recorded (being 39% below the mean size at birth) that it must be viewed with caution as a true live birth. In a later mass stranding in New Zealand, Stephenson (1975) recorded five instances of female sperm whales aborting fetuses ranging from 2.59 to 3.66 m, and a sixth possible instance of an aborted fetus measuring 2.28 m in length. One of these fetuses was aborted 10 hours after the death of the female (Frank Robson, in litt. 22.2.75). An aborted foetus about 3 m long is also recorded in a mass stranding of sperm whales at Huatabampito, Mexico (Balcomb, 1981). It is therefore possible that the Gisborne calf was also delivered prematurely under the stress of stranding, though the evidence on this point is inconclusive (F. Robson, in litt. 29.7.71 and 22.2.75).

## LACTATION

### (a) Suckling behaviour

Nursing in sperm whales has not been precisely described (Berzin, 1971). According to Bennett (1840), 'Intelligent whalers, who have occasionally seen the female Cachalot in the act of suckling her young, agree very closely in their descriptions of this process. They state, that the mother reposes upon her side, with the pectoral fin raised above the surface of the sea, while the calf, which is thus enabled to retain its spiracle in the air, receives the protruded nipple within the angle of the mouth - a part where it is reasonable to suppose that the tongue would also be found of some assistance.' The tongue of the newborn calf is more prominent than that of the adult sperm whale, extending in the dead animal as far as the middle of the mandibular tooth row (Fig. 9b). The dorsal surface of the tongue is bounded on its anterior and lateral sides by a distinct, somewhat crenellated fringe which may facilitate grasping of the female's teat.

According to G. Joyce (pers. comm. 14.10.81), a captive newborn sperm whale in the Seattle Aquarium was able to exert weak but definite suction to a hand placed in its mouth, and the preferred position for suckling was in the corner of the mouth near the angle of the gape.

In a 4.60 m female calf (C 12), 1,400 ml of milk was measured from the first and second stomachs combined, with an additional 400 ml estimated as spilt. As the stomach was not recorded as full, greater quantities can presumably be ingested at one time. Lockyer (1981) estimated the total stomach capacity of a newborn calf as 20 l, with the forestomach capable of containing up to 6–7 l.

### (b) Composition of milk

Milk samples were collected from 13 lactating sperm whales taken by accident at Durban in 1970. The samples were frozen and later analysed for total solids, fat, protein and ash (Table 9). Samples which appeared contaminated, or for which insufficient material was available for repeat analyses, were rejected. The values obtained were reasonably consistent, despite being taken post mortem, and the mean values (with their associated standard errors) were  $35.5 \pm 1.3\%$  total solids,  $24.4 \pm 1.2\%$  fat,  $9.1 \pm 0.3\%$  protein and  $0.7 \pm 0.04\%$  ash. Berzin (1971) tabulated the chemical composition of sperm whale milk as published by several authors. Excluding two greatly different records from a total list of ten references, the average composition was  $36.2 \pm 0.9\%$  fat,  $54.9 \pm 0.5\%$  water and  $7.4 \pm 0.6\%$  dry residue. The Durban values for fat content thus appear substantially lower than most of those previously published. If the calorific values for fat and protein of 9,450 kcal/kg and 5,650 kcal/kg respectively are adopted, the calorific value of sperm whale milk can be calculated as 2,820 kcal/kg: this is substantially less than that found for balaenopterid whales or the white whale, *Delphinapterus leucas*, (Lockyer, 1981).

Table 9  
Composition of sperm whale milk collected at Durban

Platform no. of female	Date killed	Length (m)	% Total solids	% Fat	% Protein	% Ash
579	21.4.70	10.36	29.5	19.9	7.7	—
656	28.4.70	10.06	37.6	25.0	10.5	0.7
737	12.5.70	10.67	33.2	20.8	10.5	0.8
739	12.5.70	10.36	40.4	26.9	11.5	0.9
870	25.5.70	10.06	28.9	17.5	9.1	0.8
871	25.5.70	10.06	38.3	27.6	9.3	0.7
1071	9.6.70	10.67	32.6	22.0	8.7	0.5
1072	9.6.70	10.06	33.0	22.4	8.5	0.6
1120	17.6.70	10.67	34.0	23.2	8.8	0.7
1121	17.6.70	10.06	38.0	28.0	8.3	0.5
1122	17.6.70	10.36	45.4	34.1	9.5	0.8
1132	17.6.70	10.06	33.0	25.3	7.1	0.5
1458	29.7.70	9.45	37.6	24.8	8.9	0.6

However, it is not clear how representative such samples are of the true composition of milk when taken from the gland post-mortem.

### (c) Mother-infant behaviour

The periods spent at sea to supervise the collection of special permit animals provided opportunities to make observations of behaviour relevant to mother–infant relationships. Unfortunately the circumstances under which the observations were made complicated interpretations as the schools were usually under stress from chasing and frequently had already had some members removed by other catcher boats prior to the start of observations.

Newborn calves could be easily identified as two of the research periods covered the months March and April, while the main calving season off Durban is between February and April (Gambell, 1972). These animals were strikingly small and usually swam close to and beside the flank of the mother (or a large whale assumed to be the mother). When the school or pod of whales to which they belonged dived as a result of being chased, newborn calves frequently stayed on the surface or dived for a short duration and then resurfaced. Thus on 18 March 1971 the catcher boat encountered a school of 11 whales including two newborn calves. When the flock submerged the two calves reappeared after one minute and swam together on the surface, one of them then being harpooned (C 6). Later the same day while chasing a submerged group of four whales from this school on Asdic, an adult and the second newborn calf remained on the surface swimming parallel to the submerged whales throughout their dive. They later joined the survivors of this group, but the calf remained on the surface when the group dived again and the ‘mother’ came up before the other whales to join it at the surface. This calf (C 7) was later collected after it had stood by at about 10 m distance from a harpooned animal that on examination proved to be a sexually immature female. The calf had an unhealed umbilicus and foetal creases were still visible in the posterior half of the body. On 22 March 1971 three unsuccessful attempts were made to harpoon a newborn calf on its own, but at no time did the animal dive, even when fired at. This calf had white tissue about 0.5 m in length streaming from the posterior edge of the blowhole, possibly the remains of foetal membranes. On 13 April 1973 a school of about 8 whales including 1 newborn calf was chased by the catcher vessel for about 90 minutes, during which time the group made four long dives. On the first and third of these the calf accompanied the rest of the group and was not seen on the surface despite excellent weather conditions. On the second and fourth dives, however, the calf remained swimming on the surface when the rest of the school dived. The diving ability of the newborn animal therefore appears to be relatively poor, and under these conditions most of the school may abandon it at the surface when diving (at least under conditions of stress). The observation of 13 April suggests however that the calf soon begins to learn or becomes physically able to make long dives.

There appears to be a strong behavioural drive for the newborn sperm whale to swim close to another whale, or even to another large object moving through the water. On 13 April 1973 a newborn calf stayed close to the catcher vessel after an adult had been harpooned and was being flagged, and such behaviour is often seen, even during whale-marking cruises when no animals are killed.

Small calves frequently approach and swim within 5 m of the side of a catcher for long periods if they have become temporarily separated from all other members of the school, and particularly if the catcher is under way at slow speed. This 'following response' may represent an attempt to adopt an assisted swimming position as observed in dolphin calves (Leatherwood, 1977), but it may also have survival value, for (as mentioned earlier) many mixed schools of sperm whales off Durban are followed by oceanic sharks (*Carcharias longimanus*). A young, unaccompanied calf might therefore be particularly vulnerable to shark predation, while schools of sperm whales containing calving females can exhibit strong defensive reactions to the presence of sharks (Gambell, 1968). It has also been postulated that female sperm whales might leave their newborn young with other members of the school while they dive to feed (Best, 1979), and the existence of a following response not specific to the mother would facilitate such behaviour. On three occasions, in fact, newborn sperm whale calves were observed to 'stand by' harpooned members of their school that could not have been their mothers – on 6 March 1973 and 13 April 1973 the whales concerned were non-lactating females, and (as mentioned above for C 7) on 18 March 1971 the animal was a sexually immature female.

There were only two definite instances of an older calf standing by while another animal was harpooned. On the first of these the catcher boat encountered a group of seven sperm whales including one small calf estimated at 5.5 m long on 27 April 1973. Two adults were killed from this group and the calf stood by the second animal briefly, leaving after less than a minute despite the fact that the whale was still alive and blowing. This adult was a lactating female. When the next whale (also a lactating female) was harpooned, however, the calf stood by it for three minutes until a second harpoon was fired. It swam close to the wounded whale all the time, actually lying on top of the caudal peduncle at one stage, and then moved up towards the head, continually touching the body. The calf was later harpooned and proved to be a 5.64 m female with traces of milk in the stomach (C 21), and the second whale which it stood by was (presumably) its mother. At the time this adult was harpooned, however, this calf was not swimming next to it but one whale away.

This observation may partly explain the contention commonly held by the Durban whale gunners that sperm whale calves can be adopted by other females in the same school if their mother is killed. It also suggests that identification of the actual mother of a small sperm whale calf (as required under the Schedule of the International Whaling Commission) may be very difficult.

On the second occasion (on 12 April 1973) the catcher boat chased two sperm whales, one considered to be an adult and the other a juvenile. These whales were swimming together though on occasion they were separated by as much as 12 m. After diving for 21 min 45 secs to a depth of 418 m (data obtained from an analysis of the Asdic recordings), three animals surfaced, though the third animal then separated from the original pair almost immediately. The larger of the pair was shot, proving to be an adult female with milk in the mammary glands. The smaller animal stood by for one to two minutes very close to the harpooned whale and right beneath the bows of

the ship, blowing frequently. It then slowly moved away from the ship but did not dive and lay just below the surface, occasionally blowing, being harpooned without submerging again. It was a female 8.33 m long (C 20), with traces of milk in the stomach and therefore presumably the calf of the larger animal. A similar incident occurred on 25 April 1973 when the larger of two whales running together was shot and found to be a lactating female: the smaller animal (estimated at 8.53 m in length) stood by the wounded female for about one minute but in this instance was not captured.

These observations suggest that the non-specific 'following-response' of the newborn calf wanes rapidly with age, presumably as the animal becomes physically more independent and is able to keep up with the diving herd. The 'mother-infant' bond, however, persists.

There were very few instances seen of adult females standing by wounded calves. In part this may be due to the fact that gunners almost invariably chose to kill the larger animals in a school first, so removing most of the adult females before it was possible to collect a calf. On the other hand there were two instances of newborn calves (C 1 and C 6) being killed before any other whales were taken from the school, and on neither of these occasions did any other animal in the school stand by. The only recorded instance of an adult standing by a presumed calf occurred on 13 March 1973 when the catcher boat shot the smallest of a group of four whales being chased. This proved to be a 7.135 m female (C 17), but with no trace of milk in the stomach. After this animal had been harpooned, a bigger whale from the group stood by it for at least five minutes before itself being harpooned. During this period the latter (a lactating female) lay close to or swam around the smaller animal, always within 10 m of it even though the calf was right beneath the bows of the catcher boat. At first it was even thought that the harpoon fired at the calf had struck the bigger animal as well, and that both were fast on the same line. This impression was heightened by the fact that the 'mother' was defecating intermittently and had her mouth wide open.

In general the behavioural observations suggested an interdependence of school members that might be expected in an animal with such a well-defined social organization. Such observations also proved invaluable in providing information on the possible suckling status of an individual whale that was supplementary to that obtained from stomach contents.

### GROWTH OF YOUNG CALF

The age of each of the 27 animals taken under special permit was estimated from the number of growth layer groups (GLGs) in the dentine (Table 10). Because of the rapid growth rate of animals at this stage of their development, ages were estimated sometimes to fractions of a year. The deposition of the first translucent lamina (by transmitted light) was taken as completing one year's growth, the deposition of the second translucent lamina as two year's growth, etc. This is not strictly correct, as most births take place off Durban from February to April while translucent laminae appear to be deposited from June to August, or only 4 months later. The actual ages of all the animals (apart from newborn

Table 10

Age, stomach contents and tooth eruption of juvenile sperm whales examined at Durban (arranged in order of increasing age)

Whale no.	Sex	Age (= GLGs)	Stomach contents				Percentage of mandibular teeth erupted
			Lactose <sup>1</sup>		Solid food <sup>2</sup>		
			1st stomach	2nd stomach	1st stomach	2nd stomach	
C 1	F	0	—	—	0	0	0
C 7	F	0	—	0	0	0	0
C 13	M	0	***	***	0	0	0
C 12	F	0	—	***	0	0	0
C 14	M	0.25	***	***	0	0	0
C 6	F	0.25	—	***	0	0	0
C 21	F	0.5	*	***	0	0	0
C 3	F	2	—	***	0	s	0
C 17	F	2.25	0	—	s	s	0
C 5	M	2.5	0	0	s	s	0
C 8	F	3	*	—	s	0	0
C 9	F	3.25	—	**	s	s	0
C 4	M	4	—	—	s	—	0
C 2	M	4.5	—	0	s	s	0
C 15	M	5	0	—	s	0	0
C 20	F	5.75	**	**	s	s	0
C 11	M	7	—	**	s	s	—
U 73/537	F	7.5	**	**	s	s	0
U 73/70	M	7.5	**	*	s	s	0
U 73/528	M	8	0	0	s	s	61.2
C 10	M	8.5	**	—	S, F	—	—
C 18	F	9	0	0	s	s	0
C 16	F	9	0	0	M, s	M, s	0
U 73/259	M	11	**	**	s	s	—
U 73/575	M	11.5	0	—	s	—	0
C 19	F	13	0	0	s	M, s	72.3
U 73/241	M	13	*	**	—	—	—

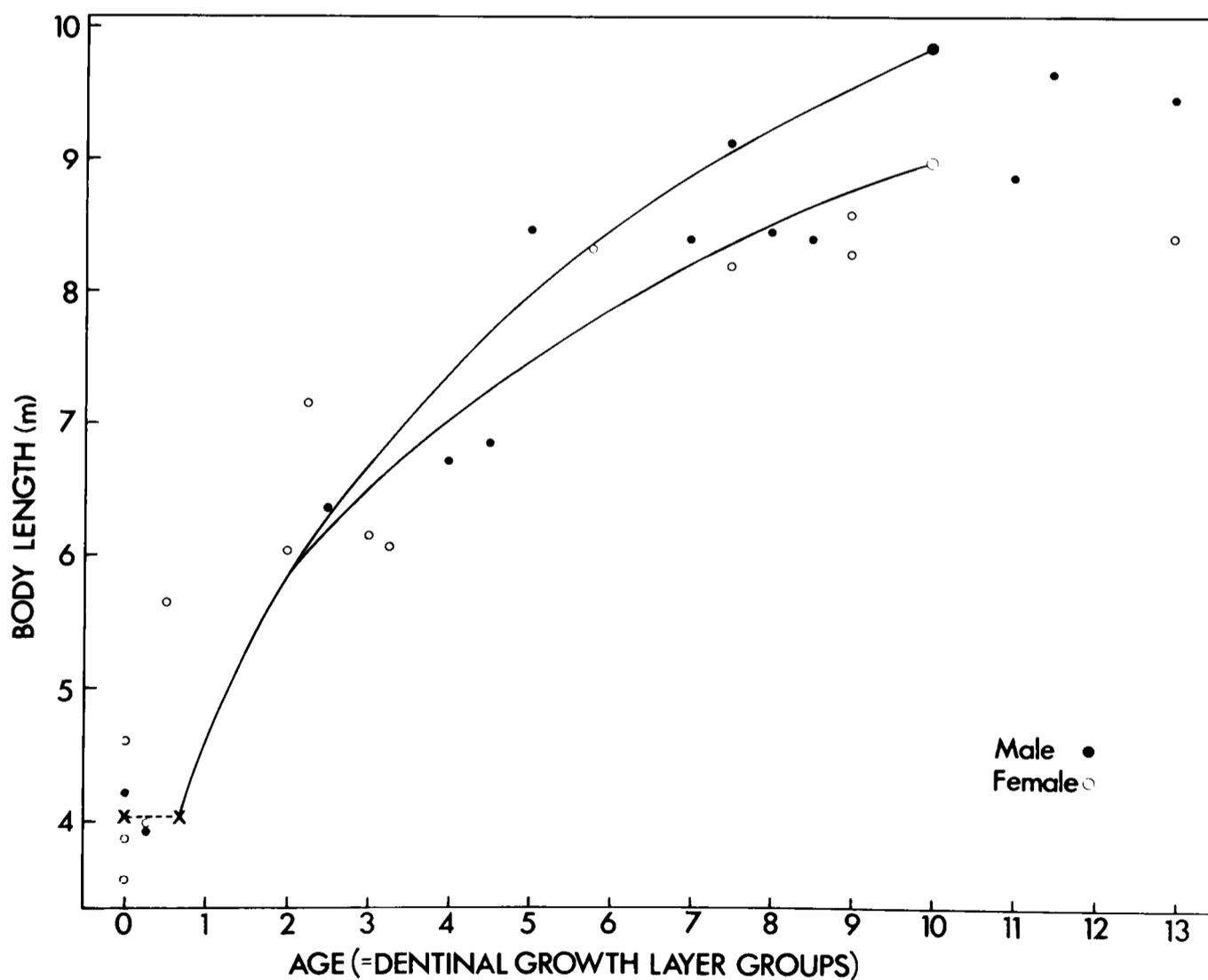
<sup>1</sup> 0 = absent; \* = trace; \*\* = moderate amount; \*\*\* = strongly positive; — = no observation.<sup>2</sup> 0 = absent; s = cephalopod remains (beaks, etc.); S = whole squid; F = whole fish; M = mysids; — = no observation.

Fig. 10. Growth curve of juvenile sperm whales.

calves) may therefore be about eight months less than those estimated from GLGs. This factor is probably only of real significance in age determination of the youngest animals of this series, for difficulties in counting growth layers accurately in older animals must obscure any comparatively minor correction of this nature. Nevertheless the point of origin for the growth curve given below has been adjusted to account for this.

A growth curve has been fitted by eye from a mean length at birth of 4 m for either sex to the mean lengths at age 10 of 8.97 m for females and 9.8 m for males (from a growth curve published earlier – Best, 1970). Data points fall close to the growth curve drawn up to age 10 but thereafter seem to fall below it (Fig. 10). A similar trend was noticed in an earlier attempt to fit a growth curve to some of the same data (Best, 1974) and attributed to size selection at capture. This explanation now seems very likely, as a deliberate attempt was made in 1973 to collect larger calves than in 1971, and this seems to have corrected most of the bias shown in the previous curve. It now appears possible that for males at least, some of the bias shown in Fig. 10 in length-at-age for older animals may be due to social factors. Collecting was confined to mixed schools, whereas males leave such schools to form bachelor groupings before puberty, and such groupings tend to be more homogeneous for size than for age (Best, 1979). Departure from the mixed school may therefore be more closely linked with developmental status than with age, so that after a certain stage larger-at-age animals are absent.

In an earlier report (Best, 1974), it was possible to distinguish three size (and presumably age) classes amongst juvenile sperm whales in autumn, i.e. during the calving season. These were newborn calves, animals from 5.79 to 6.40 m and animals over 6.705 m long. It was assumed that the second class corresponded to animals one year old. The four animals 5.79 to 6.40 m long in this collection had a mean 'age' of 2.69 GLGs, which, if 0.67 GLG is subtracted (to account for the timing of the formation of the first translucent lamina) gives a mean figure of 2.02 GLGs. It is therefore possible that 2 GLGs are deposited in the first year of life (as suggested for the spotted dolphin, *Stenella attenuata* – Perrin, Coe and Zweifel, 1976).

The length/weight relationship for the 19 calves weighed (Table 5) is

$$W = 0.0192 L^{2.733 \pm 0.103}$$

where  $W$  = weight in tonnes and  $L$  = length in metres. This includes the animal (C 1) that was cut up in pieces to be weighed, for which adjustment for fluid loss has been made from the calf that was weighed both whole and in pieces (C 12), and in which fluid loss amounted to 6.3%. It excludes the animal from Silverstream Beach for which the weight was partly estimated. All other animals were weighed whole.

This relationship is very similar to that calculated for 44 adult sperm whales (10 m or more in length) by Lockyer (1976):

$$W = 0.0196 L^{2.74 \pm 0.18}$$

The regression coefficient ( $2.733 \pm 0.103$ ) is however less than that for sperm whale foetal growth in the Durban area ( $2.932 \pm 0.055$ ) as calculated by Gambell

(1972). Estimates of the body weight at birth thus differ considerably, depending on whether the foetal or calf regression is used: for a birth length of 4.00 m these estimates are 1,016 and 849 kg respectively. Presumably there is considerable weight loss immediately post partum, and the more appropriate value may be that derived from the foetal data.

According to the length/weight relationship for calves, one-year-old sperm whales that averaged 6.1 m in length would weigh 2,689 kg. This represents an overall increase of 1,673 kg since birth, or a daily weight gain of 4.6 kg.

## WEANING

### (a) Incidence of suckling

Because it was suspected that lactation was a prolonged affair in this species, and that for a large part of this time the calf might be feeding on both solid food and milk, a test had to be designed to determine whether an animal had been feeding recently on milk. In the case of a young calf this might be fairly obvious from a physical examination of the stomach contents, but in an animal already feeding on solid food the presence of milk could easily be obscured by the remains of digested squid, etc.

Lactose or milk sugar seemed to be the most promising constituent of milk for which to test, as it is unique to milk. Although cetacean milk normally contains only a small amount of lactose (3.9% in the sperm whale, according to Yablokov, Bel'kovich and Borisov, 1972), and digestion takes place fairly rapidly in the stomach, sufficient quantities of lactose were found to give positive chromatographic readings, and in doubtful cases the presence of its breakdown products glucose and galactose usually provided confirmation. The colour reagent used in the tests could detect levels of lactose as low as 10 micrograms, and of glucose and galactose as low as 5 micrograms. This is equivalent to a concentration of lactose in the original stomach content sample of 0.12%, or a dilution factor from the original milk of about 30 times. As a control, a frozen ommastrephid squid caught off Durban was analysed identically and no lactose, glucose or galactose found.

Results were classed as either 'strongly positive', 'moderately positive', 'a trace', or 'negative'. All samples classified as 'a trace' were retested at least once and each time were found to be positive. In one instance a stomach sample taken from an adult female was initially classified as containing a trace, but on repeat this was found to consist of a positive glucose reading, and no trace of lactose or galactose was found. It was therefore classified as negative. The results of all chromatographic tests are given in Table 10.

Obviously a negative lactose test could as equally represent an animal whose most recent milk feed had already been fully digested as an animal that had not fed on milk. Nevertheless the high overall proportion of positive results (60%) and trends in their incidence with age showed that this technique could provide invaluable information on suckling behaviour.

The results were generally unexpected. Previous estimates of the duration of lactation had usually been around two years and the size of the calf at weaning had been taken as about 7.6 m (Best, 1974). In this series of

calves, however, positive lactose readings occurred up to age 7.5 in females and age 13 in males, and in females as large as 8.33 m and males as large as 9.45 m. It is difficult from these data to determine when suckling ceases, especially for males where the oldest animal examined gave a positive lactose result. There were three females older than 7.5 years that gave negative lactose results, whereas 80% of animals 7.5 years old or younger gave positive results, and for this sex it might be concluded that suckling continues up to about 7 or 8 years. However, the sample may not be representative because animals accompanying adult females were selected, and because juveniles may segregate from their parent school shortly after weaning, as has been proposed elsewhere, particularly for males (Best, 1979). Sampling in this manner from mixed schools might exclude most animals that had already been weaned and would therefore give the impression that suckling lasted longer than in the population as a whole.

The significance and interpretation of these lactose results will be discussed more fully below when other data have been considered.

### (b) Eruption of mandibular teeth

No animal with a positive lactose determination from its gastric juice had any erupted mandibular teeth (Table 10). Furthermore, the ingestion of solid food commenced long before any mandibular teeth erupted. The presence of functional teeth in the lower jaw therefore seems to have little significance in the interpretation of feeding behaviour – it has been frequently observed that adult sperm whales with twisted or shortened mandibles appear as capable of feeding as normal animals (Nakamura, 1968). Ohsumi (1963) showed that mandibular tooth eruption is correlated with sexual maturation, whereas Berzin (1971) believed this may only be true for males.

### (c) Incidence of solid food

Remains of solid food were only found in animals with two or more GLGs in the teeth (Table 10). Assuming two GLGs are laid down in the first year, the young sperm whale must begin to take solid food sometime before it is one year old. This stage is probably most closely linked with the development of diving ability.

Only one of the calves collected (C 10) had squid in the stomach that were intact enough for identification – these proved to be two specimens of *Histioteuthis miranda*. The stomachs of the remainder of the animals feeding on solid food contained cephalopods that were either digested remains or beaks or both.

A total of 59,598 cephalopod beaks was collected (Table 11) from which it was possible to identify 26,425 lower beaks to family (and even to species in many cases). It is clear from a comparison with the family composition of cephalopods eaten by adult male and female sperm whales off Durban (Table 12) that there are differences in the diet of different age and sex groups. In general, the composition of the food eaten by juveniles more closely resembles that taken by adult females than males, as might be expected from schooling and migratory behaviour (Best, 1979). However, the youngest calves show a greater dependency on histioteuthids (and less diversity in diet) than adult females, with older juveniles somewhat intermediate.

It also appears that juvenile sperm whales in general eat smaller cephalopods than adults. In some squid families, particularly *Cycloteuthidae* and *Histioteuthidae*, the proportion of juveniles taken (judged by the size and lack of pigmentation in the beak) is high in calves. In addition, in the series of calves examined those cephalopod species which are known to grow to a very large size (e.g. *Architeuthis*, *Mesonychoteuthis*) were represented only by beaks from very young individuals. The actual weights of the cephalopod consumed have

Table 11

Numbers of lower beaks of cephalopod families found in stomachs of juvenile sperm whales landed at Durban

Family of cephalopod	C 2	C 3	C 4	C 5	C 8	C 9	C 11	C 16	C 17	C 18	C 19	C 20	Mean percentage occurrence <sup>1</sup>
Histioteuthidae	1,006	48	244	7,436	1	2,344	236	1,304	805	805	599	4,381	68.5
Octopoteuthidae	1,656	9	15	265		72	12	432	130	258	34	410	13.1
Cranchiidae	24		1	369		102	18	66	17	53	4	339	2.6
Chiroteuthidae	20	11	6	176		67	26	88	50	55	52	492	5.1
Cycloteuthidae	9	1	1	230		105		35	6	34	13	81	1.4
Enoploteuthidae	59	3	5	139		46	30	60	11	31	10	69	2.5
Ommastrephidae	130		3	22	1	4		77	4	110	84	24	2.5
Onychoteuthidae	12	1	1	6		7	9	20	2	24	12	25	0.9
Pholidoteuthidae	8			1		2		37	3	41	5	12	0.5
Lepidoteuthidae	3		2	3		2	1	37	8	15	7	20	0.5
Architeuthidae	5			9		11		8	3	4	8	10	0.2
Vampyromorpha				28				2	4			3	0.1
Octopoda			1	23		1			3			1	0.1
Mastigoteuthidae			1	1				1				1	< 0.1
Others	8		4	102	1	118	24	12	6	7	5	282	1.9
Total	2,940	73	284	8,810	3	2,881	356	2,179	1,052	1,437	833	6,150	
Fragments with tips	1			420		105		1	6	4	2	353	
Total	2,941	73	284	9,230	3	2,986	356	2,180	1,058	1,441	835	6,503	
Upper beaks	1,299	41	215	9,943	4	4,061	280	2,819	932	1,706	832	9,576	

<sup>1</sup> Excluding C 8.

Table 12  
Mean percentage occurrence of cephalopod families by number in sperm whale stomachs off Durban

Family	Juveniles < 5 years	Juveniles 5-13 years	Adults <sup>1</sup>	
			Females	Males > 12.2 m
Histioteuthidae	71.4	65.1	47.1	29.3
Octopoteuthidae	15.3	10.4	22.5	9.2
Cranchiidae	1.8	3.6	3.5	11.4
Chiroteuthidae	4.5	5.9	8.9	3.1
Cycloteuthidae	1.5	1.4	1.3	0.5
Enoploteuthidae	2.0	3.1	5.7	6.2
Ommastrephidae	1.0	4.3	3.6	2.8
Onychoteuthidae	0.4	1.4	1.5	28.3
Pholidoteuthidae	0.1	1.1	0.6	0.2
Lepidoteuthidae	0.3	0.8	0.2	0.2
Architeuthidae	0.2	0.4	0.2	0.3
Vampyromorpha	0.1	< 0.1	0.3	0.1
Octopoda	0.2	< 0.1	0.1	2.8
Mastigoteuthidae	0.1	0.1	0.1	0.1
Others	1.1	2.2	4.4	5.5

<sup>1</sup> From Clarke (1980).

Table 13  
Weights of cephalopods eaten by juvenile and adult sperm whales off Durban<sup>1</sup>

Family	Juveniles		Adult females <sup>2</sup> Mean wt. of cephalopod (kg)	Males > 12.2 m <sup>2</sup> Mean wt. of cephalopod (kg)
	No. measured	Mean wt. of cephalopod (kg)		
Histioteuthidae	4,318	0.16	0.23	0.22
Octopoteuthidae	1,026	0.30	0.63	3.22
Cranchiidae	556	0.19	1.00	3.04
Chiroteuthidae	709	0.22	0.11	0.10
Enoploteuthidae	417	0.13	1.18	1.55
Ommastrephidae	435	2.24	2.26	1.83
Onychoteuthidae	99	0.78	1.50	5.21
Lepidoteuthidae	75	1.46	2.50	3.32
Architeuthidae	28	1.76	7.35	13.02
Octopoda	9	0.14	0.37	0.70
Total (all spp <sup>1</sup> )	7,672	0.23	0.52	2.55

<sup>1</sup> Excluding Cycloteuthidae, Pholidoteuthidae and Vampyromorpha.

<sup>2</sup> From Clarke (1980).

been calculated using the lower rostral length/body weight graphs in Clarke (1962), except for the three families *Cycloteuthidae*, *Psychroteuthidae* and *Pholidoteuthidae*, for which no such graphs were available. As these three families together constitute only 2.2% numerically of the diet, their contribution by weight to the diet is unlikely to be very significant. Where the total number of beaks of one species in one stomach exceeded 100, the lower rostral length of a sample of 100 was measured in order to calculate their weights (Table 13). Because many beaks were not measurable owing to damage in digestion, no complete picture of the weights of cephalopods consumed can be obtained. However, the mean weights of the cephalopods eaten as given in Table 13 provide an interesting comparison with adults, for whom almost identical limitations to the method probably apply. With the exception of the *Chiroteuthidae* and *Ommastrephidae*, the cephalopods of each family eaten by juveniles were smaller than those eaten by either

adult females or males, and on average females ate animals more than twice as large and males more than ten times as large as those eaten by juveniles.

In a fuller analysis that included allowance for seasonal changes in the availability of different cephalopod species, Clarke (1980) also demonstrated that large male sperm whales (> 12.2 m long) at Durban favoured larger cephalopod species than females, and that they generally ate larger specimens of a particular species than females. As the cephalopods were so small in relation to the size of even the smallest adult whales, Clarke concluded that the difference was far more likely to reflect the vertical distribution of the cephalopods rather than differences in selection by size of prey or the catching aptitude of the two groups of whales.

Roper and Young (1975) have reviewed the available evidence on the vertical distribution and migration of pelagic cephalopods. Although several cephalopod species exhibit ontogenetic descent (i.e. they occupy

progressively greater depths during successive stages in their life history), this distinction is usually between larvae and juvenile/adults: in most species Roper and Young (1975) examined, juveniles seemed to exhibit the same distributional patterns as adults. There are no data suggesting that members of the *Histioteuthidae* or *Octopoteuthidae* (the two most important prey species of juvenile sperm whales) undergo ontogenetic descent, though in the case of the *Histioteuthidae* in particular, information on vertical distribution is 'sketchy'. It is therefore possible that the differences in the size of the prey eaten between juvenile and adult sperm whales may reflect active selection on the part of the whale rather than feeding at different depths: however, information on the vertical distribution of those cephalopod species eaten by sperm whales is really insufficient to be sure on this point. Certainly juvenile sperm whales are capable of taking juvenile squids of some families that are much larger than the juveniles they eat of other families, indicating that there is no physical reason why they should not be able to consume much larger squid than they actually take. However, it is also possible that the catchability of juvenile cephalopods may be higher, so that they are easier prey for animals adjusting to a solid food diet.

Solid food other than cephalopods was rare in the calf stomachs. Mysids (*Gnathopausia ?ingens*) were found in two stomachs, in one of which (C 16) the animals were nearly complete. Fish remains were found in only one stomach: an almost complete specimen of *Trachipterus ?arcticus* (C 10).

#### (d) Feeding rate

Sergeant (1969) has demonstrated a relationship between heart weight expressed as a proportion of body weight and feeding rate in several cetacean species. Heart weight relative to body weight is in fact considered indicative of metabolic rate.

The weights of 11 hearts collected from the series of sperm whale juveniles are shown in Table 14. For six of these animals body weights are also available, and the weight of the heart expressed as a percentage of the body

Table 14

Heart weights of sperm whale juveniles landed at Durban

Whale number	Heart wt. (kg)	Body wt. (kg)	Heart % body wt.
C 1	4.09	676	0.61
C 12	8.18	1,450	0.56
C 13	6.82	1,050	0.65
C 14	6.14	1,000	0.61
C 15	34.43	—	—
C 16	30.00	—	—
C 17	22.73	4,550	0.50
C 18	42.05	—	—
C 19	43.52	—	—
C 20	32.61	—	—
C 21	16.82	2,400	0.70

weight in these animals ranges from 0.5 to 0.7% with a mean of  $0.61 \pm 0.03$  (S.E.)%. This is a somewhat higher proportion than that given for adult sperm whales by Sergeant (1969) – 0.24 to 0.61% with a mean of 0.33%. The real difference is probably greater than this, as all the data for adults were gathered from animals cut up in pieces to be weighed: their relative heart weights will therefore be exaggerated as their body weights were underestimated. A more appropriate comparison might be with juvenile heart weights expressed as a percentage of the body weight with a factor (derived from C 12) incorporated to scale down body weights as if they had been cut up into pieces to be weighed. Under these circumstances their mean relative heart weight might have been  $0.65 \pm 0.03\%$  of body weight, or about twice that of adults.

Sergeant (1969) has also found that heart weight (relative to body weight) is higher for young than for adult Cetacea of the same species, and this is associated with a high feeding rate and so a high metabolic rate. In the case of sperm whales this means that recently weaned juveniles may have a feeding rate almost twice that of adults. As these same animals eat smaller squid than adults it appears that the weaning period may constitute a critical stage nutritionally for the young animal. This

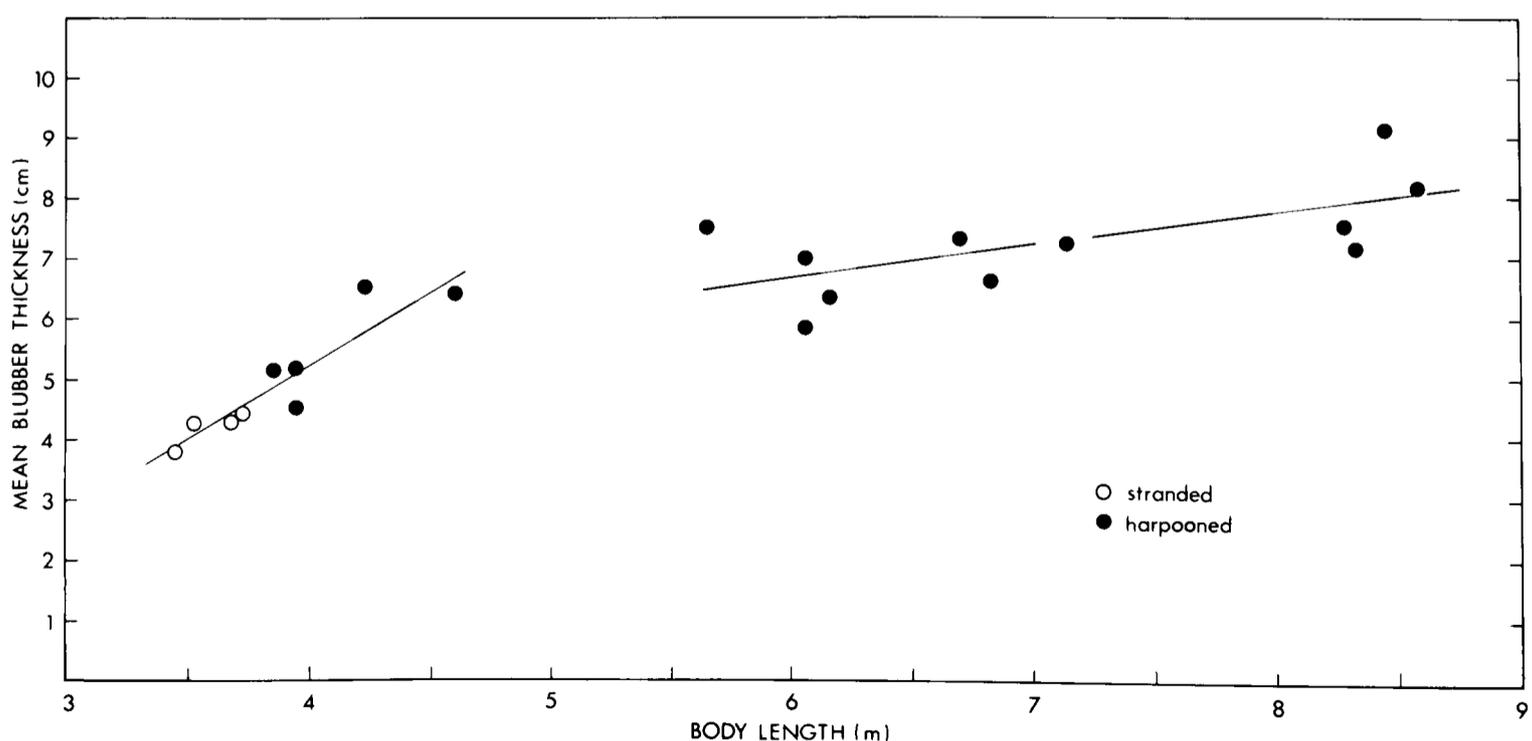


Fig. 11. Relationship between body length and blubber thickness in juvenile sperm whales.

may account for the prolonged period of combined suckling and solid food consumption in the species, as the milk with its high energy content may provide a useful feeding supplement.

#### (e) Blubber thickness

The thickness of the blubber layer was recorded at the midlength of the animal in three places, mid-dorsal, mid-lateral and mid-ventral. The average of all three measurements can be used as an index of fatness.

There appears to be an extremely rapid accumulation of blubber immediately after birth (Fig. 11). The rate of increase in mean blubber thickness at this stage is  $2.45 \pm 0.41$  cm/m body length. However, by the time the animal is one year old (and approximately 6.1 m long) the blubber is barely thicker than it was at a body length of 4.5 m, and the accumulation rate of blubber between a length of 6 and 8.5 m is only  $0.53 \pm 0.20$  cm/m. This compares with accumulation rates for dorsal and ventral blubber respectively of 2.03 and 1.28 cm/m for sexually mature males, and of 1.14 and 0.82 cm/m for mature females (Gambell, 1972). The apparently slow rate of blubber accumulation after the initial post natal fattening could be due to the animal's rapid growth in length. Unfortunately the data coverage is too poor over the range 4.5 to 6 m body length to determine whether an actual decrease in blubber thickness may also occur some time during the first year of life, possibly associated with the commencement of feeding on solid food.

### PARASITES AND COMMENSALS OF CALF

#### (a) External

Only two organisms were found associated with the body surface of the juvenile sperm whale (Table 15). Remoras (presumably *Remilegia australis*) were found or seen on four of the animals collected: they usually fell off the whale shortly after its death. Remoras have been previously reported from sperm whales by Berzin (1971 - 'shark suckers') and Krefft (1953 - as reported

by Follett and Dempster, 1960). These fish are frequently seen on sperm whale calves off Durban, but do not seem to occur on adults. In the series of juveniles collected here, for instance, remoras were only seen on animals up to 6.045 m in length and an age of two growth layers.

Seven remoras were collected from C 7, with standard lengths of 38, 40, 64, 70, 70, 93 and 99 mm. The viscera of the two largest were removed after fixation in formalin and the contents of the stomach examined. The bulk of the food in both individuals consisted of whale epidermis, but crustacean remains were also present in one animal. These included the copepod species *Candacia ethiopica* (4), *Clausocalanus lividus* (3), *Acrocalanus gracilis* (3), *Acrocalanus gibber* (3), *Undinula darwinii* (2), *Scolecithrix danae* (2), *Labidocera detruncata* (2), *Undinula vulgaris* (1), *Copilia* sp. (1), plus 3 unidentified calanid juveniles and the remains of four chaetognaths. Rice and Caldwell (1961) found remains of epidermal tissue in the stomachs of two whale suckers 399 and 222 mm long, the larger of which also contained unidentified crustacean remains (too large and thick to have been from the euphausiids on which the whale had been feeding).

Remoras therefore appear attracted to cetaceans not only as direct sources of food (whale epidermis) but also as a platform from which independent predation can occur. The apparent preference for attachment to small sperm whales may reflect a higher rate of skin sloughing in such animals associated with their higher metabolic rate. Alternatively, remoras may not be able to tolerate the pressure change associated with the deep diving of adult sperm whales.

Cyamids were seen on most animals killed. These were exclusively *Neocyamus physteris*, or the same species as normally occurs on adult females and young male sperm whales (Best, 1969). Infestation must occur very rapidly after birth, as all four of the calves with an unhealed umbilicus for which observations were available had cyamids present.

#### (b) Internal

Only two internal parasites were found in the series of juveniles examined (Table 15).

The presence of cestode cysts (*Phyllobothrium* sp.) in the blubber was looked for in the normal cuts made through the blubber during flensing, but a thorough investigation was not made of the whole blubber layer. A similar pattern of infestation to that found for *Stenella graffmani* by Dailey and Perrin (1973) appears to occur in the sperm whale. The parasite was completely absent in neonates, and was found only in five of the remaining 15 juveniles examined, four of which were animals with 5 or more growth layers in the teeth. How the cetacean host fits into the life cycle of this species is still obscure, but it presumably reaches the whale via the squid or fish consumed. Fundamental hosts for this parasite are presumed to be sharks.

Stomach nematodes (*Anisakis* sp.) were only found in animals that had solid food in the stomach, and were therefore completely absent from neonates (as Dailey and Perrin, 1973, found for the dolphin *Stenella graffmani*). Cetaceans are apparently infested via solid food with third stage larvae that later develop into adults in the stomach of the host (Dailey and Brownell, 1972).

Table 15

Parasites and commensals of juvenile sperm whales off Durban

Whale number	Remoras	Cyamids	Stomach nematodes	Cestode cysts in blubber
C 1	—	several	0	0
C 2	0	many	many	0
C 3	several	0	present	0
C 4	—	—	present	0
C 5	0	few	many	0
C 6	several	few	0	0
C 7	several	several	0	0
C 8	—	—	present	0
C 9	0	several	present	0
C 12	—	—	0	0
C 13	0	2	0	0
C 14	0	many	0	0
C 15	0	3 or 4	present	present
C 16	0	2	present	0
C 17	0	5	present	0
C 18	—	—	present	present
C 19	0	0	present	present
C 20	0	present	present	1
C 21	ca. 6	present	0	1

The close correlation between nematode infestation and the presence of solid food in this series of juveniles seems to indicate that it is unlikely that any of the animals in which no solid food was found had been regularly feeding on squid or fish previously.

## REPRODUCTIVE RATE

Sperm whale reproductive rates (usually expressed as the pregnancy rate or its reciprocal, the calving interval), have attracted considerable attention recently, especially in connection with attempts to monitor the degree of male depletion in a stock. The sperm whale model also assumes a density dependent response in pregnancy rate as the female population is reduced from its unexploited level. As this is the only density dependent response incorporated in the model, it is important that it should be substantiated by data where available.

### (a) Factors affecting measurement of pregnancy rate

Observed pregnancy rates can be affected by a number of important factors. Firstly, all the foetuses may not be discovered or recorded, so producing an underestimate: such a phenomenon is most likely to occur in 'official' records, or in operations where the data are not collected by trained scientists or technicians. This bias can be considerable, especially if small foetuses are concerned. At the Donkergat land station, the average pregnancy rate of sei whales (most of which were carrying foetuses less than 1 m long) was recorded as 0.076 from 1957 to 1961 and 0.695 from 1962 to 1967 (an increase of 900%!). A biologist was present on the station in 1962 and 1963 and subsequently trained personnel to look for the foetuses.

Secondly, legal protection afforded lactating females by the IWC may (if enforced) result in under-representation of this reproductive class in the catch. As a consequence the proportions of other reproductive classes (including pregnant animals) in the catch will be exaggerated. This effect is likely to be most marked when catching effort for female sperm whales is low. At Albany (Western Australia) for instance, the proportion of lactating sperm whales in a sample of 115 mature females examined by biologists in 1964 and 1965 was less (0.16) than that of pregnant animals (0.28). If it is accepted that lactation lasts significantly longer than pregnancy (see below), this sample must have been unrepresentative of the population, presumably because of selection against taking lactating females (IWC, 1981b). Similarly, the proportion of pregnant females in the catch examined by biologists at Coal Harbour, Canada, from 1951 to 1967 was high, averaging 0.3301, but there appeared to be a decline with time. This was associated with an increasing catch of females (particularly from 1964 onwards when they formed more than 40% of the annual sperm whale catch) and an increasing ratio of lactating to pregnant animals. Prior to 1964, this ratio was always less than 1.0, but steadily increased thereafter from 1.46 in 1964 to 2.03 in 1967 (Mitchell, 1980). Presumably selection against

lactating animals gradually weakened as interest in taking females increased. Selection of this nature can distort not only estimates of the true pregnancy rate, but also the extent of any change in observed pregnancy rate over time (Best and Harwood, 1981).

Due to the fact that gestation lasts more than a year, estimates of true pregnancy rate must also distinguish between foetuses conceived at the current and previous breeding seasons. This is usually done by stratifying the data to exclude the period of overlap between the two cohorts. Alternatively correction factors can be applied to either cohort to account for foetuses born or yet to be conceived, based on a model of the distribution of births and conceptions over time (e.g. Best, 1980). Where the period of sampling only covers the period of overlap between the two cohorts, the latter is really the only method that can be used. Where the carcasses of whales are slit open for cooling before delivery to the factory, foetuses can be lost and although the pregnancy can still be detected from the presence of a corpus luteum in the ovaries, the size of the foetus is obviously unknown. In these circumstances indirect methods of separating cohorts of foetuses must be used (Ohsumi, 1965).

Anatomical studies of sperm whale ovaries reveal clear indications of a drop in fertility with age, particularly after about 13 corpora have accumulated. Follicular atresia increases sharply, primordial follicles disappear, and there is evidence of ageing in the tunica albuginea, stroma and blood vessels (Best, 1967; Chuzhakina, 1961). It is not surprising therefore to find age-specific differences in the proportions of reproductive classes in the catch. Age-specific pregnancy rates have been demonstrated by Best (1968; 1980), Gambell (1972) and Ohsumi (1965), although only the latter used chronological (i.e. GLGs) rather than reproductive (i.e. corpora number) ages. Ohsumi's analysis showed that when analysed against reproductive age, pregnancy rates showed a rather larger decline than when analysed against chronological age (maximum pregnancy rates of 40–50% declining to *ca.* 20% or 30% respectively in the 10% oldest animals). Because carcasses were opened at sea, these percentages represented the incidence of corpora lutea rather than foetuses.

Data are now available for the incidence of different reproductive classes at each chronological age for 725 females landed at Durban from 1962 to 1965 and 1967 (Table 16). The pregnancy rate rose in newly mature females to a peak of *ca.* 25% at ages 10–14 and then declined, reaching 6.7% in the oldest age class, 40+ years (Fig. 12). The incidence of ovulating animals however, showed no obvious trend with age, so that the proportion of unsuccessful ovulations must increase with age. A similar conclusion was reached by Best (1967) and Gambell (1972).

To summarize, if the reproductive rate is to be measured accurately, the following criteria must be satisfied.

1. The data should be collected by or under the supervision of biologists or suitably trained technicians: if not, as a minimum, the data for pregnancy rate should be based on the examination of ovaries collected from the harvest.

Table 16  
Age-specific pregnancy and lactation rates, Durban, 1962-5 + 1967

Age (GLGs)	No. mature females examined	No. pregnant		No. lactating	No. resting	No. ovulating
		Early	Late			
5	2			1	1	
6	4			2	2	
7	3	1			2	
8	8	1		1	5	1
9	12	3		4	4	1
10	28 <sup>1</sup>	5	2	10	12	
11	29 <sup>2</sup>	6		13	11	1
12	39	9	1	13	14	2
13	28 <sup>3</sup>	7	2	9	8	3
14	31	7		10	14	
15	33	7		13	11	2
16	41 <sup>2, 4</sup>	6	2	17	18	2
17	45	8	1	19	15	2
18	30 <sup>2</sup>	9	2	13	6	2
19	39 <sup>3</sup>	4	1	18	15	2
20	47 <sup>1</sup>	5	2	22	17	2
21	31 <sup>1</sup>	5	2	12	12	1
22	32 <sup>1</sup>	3		16	13	1
23	34 <sup>2, 3</sup>	3		16	17	1
24	24	2		6	12	4
25	23	4	1	5	13	
26	30 <sup>3</sup>	5	1	11	11	3
27	23	1	2	7	12	1
28	13	1		3	8	1
29	12	2		3	7	
30	7			7		
31	7	2		2	2	1
32	3				3	
33	7	2		1	4	
34	4			2	2	
35	6	1	1	3	1	
36	4				4	
37	6	1		3	1	1
38	3			1	2	
39	7	2		3	1	1
40	2			1	1	
41	6	2			3	1
42	2			1	1	
43	3			1	2	
44	7			1	6	
45	2				2	
46	1			1		
48	3			2	1	
49	2				2	
54	1				1	
61	1				1	
Total	725	114	20	272	300	36

<sup>1</sup> Includes one pregnant and lactating (scored as both).

<sup>2</sup> Includes two pregnant and lactating (scored as both).

<sup>3</sup> Includes one ovulating and lactating (scored as both).

<sup>4</sup> Includes two ovulating and lactating (scored as both).

2. The assumption that the data is fully representative of the recruited population should be substantiated, or allowance made for any known bias.

3. Analysis of the data should include allowance for seasonal changes in the proportions of animals in early and late pregnancy.

4. Age-specificity in pregnancy rates should be recognized and allowed for in the analysis.

Many of the data sets used in previous analyses of the reproductive rate have either failed to satisfy criteria 1 and 2, or have not been tested at all.

**(b) Population pregnancy rates**

Three data sets will be examined here: 406 mature females from Donkergat between 1962 and 1965 (Best, 1968), 1,029 mature females (of which 725 were aged from GLGs) from Durban between 1962 and 1967 (Gambell, 1972), and 1,127 mature females from Durban between 1973 and 1975 (Best, 1980). The first two data sets were collected under the supervision of biologists whereas the third was basically a collection of ovaries made by inspectors. Only the first two data sets therefore fully

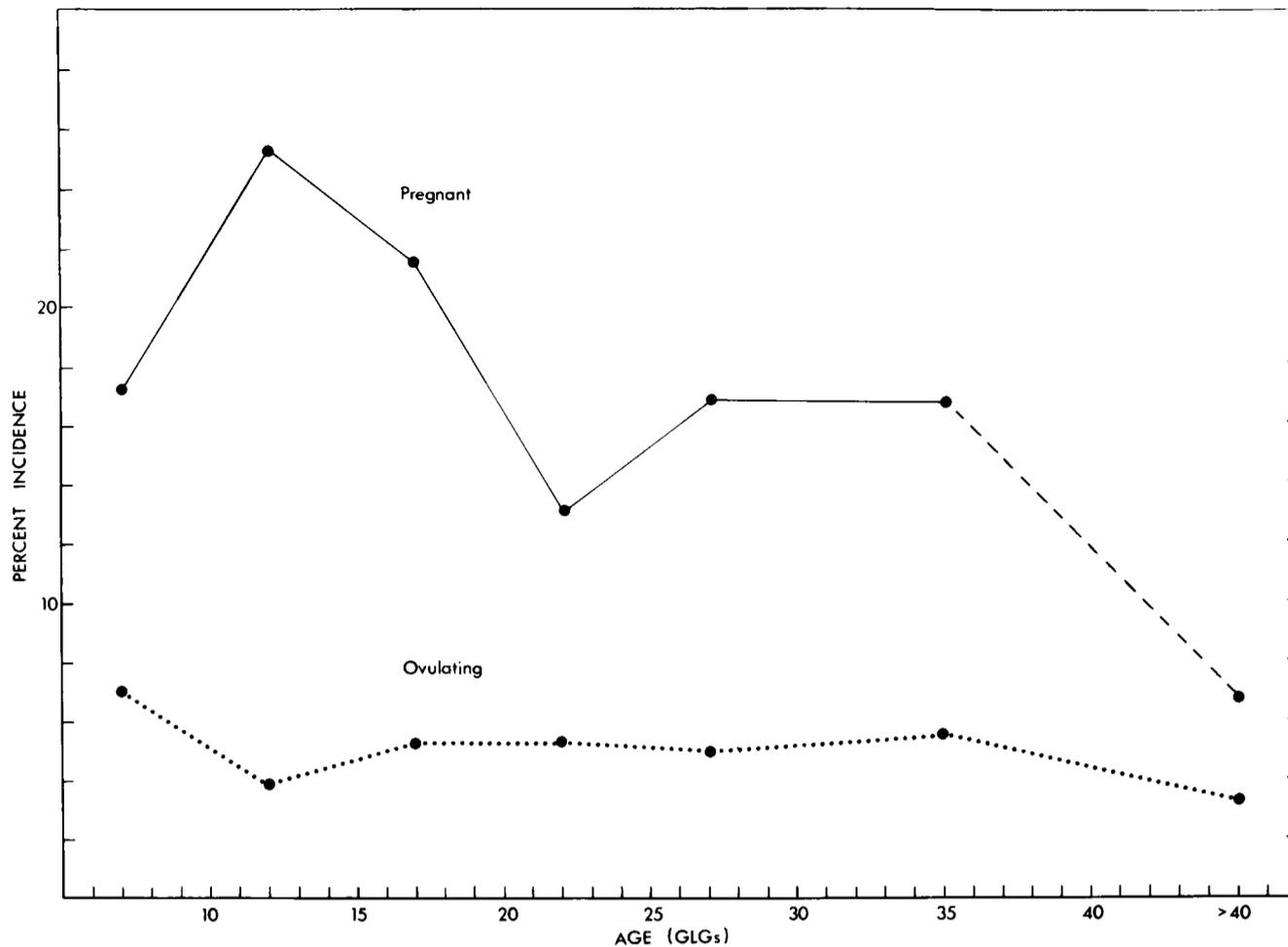


Fig. 12. Age-specific proportions of pregnant and ovulating animals amongst mature female sperm whales, Durban, 1962-5 + 1967.

satisfy the first criterion, although the third set can be used for determinations of pregnancy rate.

Meeting the second criterion is much more difficult. Both Best (1968) and Gambell (1972) have commented that complete selection against lactating sperm whales is difficult to apply due to the schooling behaviour of the animals. Nevertheless (as mentioned above), Gambell (1972) later assumed that there must have been some selection against animals in their first year of lactation.

An independent estimate of calf production in the Durban population is possible from observations made at sea before the start of the whaling season. During two whale-marking cruises off Durban in February 1971 and 1972, 370 sperm whales were seen, of which eight were newborn calves (easily recognizable from their small size and naïve swimming behaviour). The proportion of females in the area at this time of year has been obtained from CPUE values for Durban (Best, 1981), the proportion of these that were sexually mature from the composition of mixed schools (Best, 1979), and the proportion of calves born by mid-February from a calculated distribution of births (Best, 1980). Calf production ( $B$ ) is then

$$B = \frac{N_c}{N_a \cdot P_1 \cdot P_2 \cdot P_3}$$

where  $N_c$  = number of newborn calves seen;  $N_a$  = number of other sperm whales seen;  $P_1$  = proportion of females in the population;  $P_2$  = proportion of mature females in mixed school;  $P_3$  = proportion of calves born by mid-February.

Thus,

$$B = \frac{8}{362 \times 0.71 \times 0.75 \times 0.19} = 0.22$$

The degree of reliability of this estimate is unknown, but it is very sensitive to the value for  $P_3$ .

If an error of 15 days either way is accepted in the distribution of births (Best, 1980),  $B$  would range from 0.13 to 0.35, which covers the whole range of observed pregnancy rates (Best, 1974). Observations should really be carried out after April, when the majority of calves have been born. The pregnancy rates observed in the Durban catch in 1970 and 1971 (or essentially the same cohorts seen as calves in 1971 and 1972) are only available from official statistics. The closest biological samples were those taken in 1973 ( $n = 491$ ), which yield a pregnancy rate for animals in early pregnancy (corrected for seasonality - Best, 1980) of 23.2%. This is close to the value for  $B$  calculated above, and so provides some (though weak) support for the conclusion that the Durban catch was representative of the mature female population. No such confirmatory data are available for Donkergat.

Separation of early from late pregnant animals in the catch is possible in all of the data sets. The timing of the whaling seasons at both Durban and Donkergat (February or March to September or October) meant that conceptions were almost completed by the start of the season but that births were still actively taking place in the first two or three months. Consequently the data for animals in early pregnancy is more abundant and does not have to be adjusted to any great extent, whereas that for animals in late pregnancy needs major adjustments for the seasonality of births that could introduce serious errors. Furthermore there is the possibility that the data for animals in late pregnancy is biased due to the abortion of near-term foetuses after death, as suggested by the presence of females early in the Durban whaling season with a large corpus luteum in the ovaries but no

Table 17  
Age-specific pregnancy rates in sperm whales at Donkergat and Durban

Age	Durban, 1962-65 + 1967					
	Donkergat, 1962-65		Corpus counts		GLGs	
	<i>n</i>	Proportion early pregnant	<i>n</i>	Proportion early pregnant	<i>n</i>	Proportion early pregnant
Corpus counts (years)						
1-4 (< 19)	104	0.202	296	0.182	—	—
5-8 (19-28)	154	0.279	338	0.204	—	—
9-12 (29-37)	96	0.146	205	0.156	—	—
13-22 (> 37)	52	0.058	123	0.073	—	—
GLG's						
< 10	—	—	—	—	29	0.172
10-14	—	—	—	—	155	0.219
15-19	—	—	—	—	188	0.181
20-24	—	—	—	—	168	0.107
25-29	—	—	—	—	101	0.129
30-39	—	—	—	—	54	0.148
40+	—	—	—	—	30	0.067
Total and mean	406	0.200	962	0.170	725	0.157
Population equilibrium mean		0.192		0.167		0.154

foetus (Best, 1980). Thus it is considered more reliable in these instances to use the cohort of animals in early pregnancy as an index of the pregnancy rate. As 90.7% of conceptions have occurred off Durban by mid-February (Best, 1980), corrections to the data for seasonality are considered trivial and have been ignored.

The implications of the age-specific pregnancy rate in the Durban stock have been reviewed by Holt (1980) and Horwood (1980). Their calculations however have used all pregnant females in the catch, whereas a more accurate representation of the 'true' pregnancy rate would be to use early pregnant animals only. New calculations have therefore been made of the population pregnancy rates from the data sets for Durban (1962-65 + 1967) and Donkergat (1962-65), assuming that both stocks of mature females were in equilibrium with an unexploited age structure where  $M = 0.055$  (Table 17). For the corpus count data, age at first ovulation has been taken as 10 and the accumulation rate of corpora as 0.45 per year (Gambell, 1972), although this may rather underestimate the age of the oldest females, in which the ovulation rate is believed to decline (Ohsumi, 1965). The equilibrium pregnancy rates predicted are close to those observed in the catch, so the age distributions of the samples are not very different from those that would be expected in a steady-state unexploited stock where  $M = 0.055$ . With the proviso that these proportions of the different reproductive classes are representative of those in the mature female population, the mean calving interval can thus be calculated as

$$\frac{1}{0.192} = 5.2 \text{ years for Donkergat and } \frac{1}{0.167} \text{ or } \frac{1}{0.154} = 6.0$$

or 6.5 years for Durban.

The values for Donkergat support the contention that the normal pregnancy rate for an unexploited sperm whale stock is around 20%, with the average calving interval being five years (Best, 1974). Gambell (1972) claimed that the typical reproductive cycle lasted four years, and explained that the excess of resting females in the Durban catch arose because of the reduced numbers of pregnant and first-year lactation whales in the catch. However, although selection via legal constraint might be responsible for the reduction in lactating females, it is not clear why there should be a reduction in the numbers of pregnant animals. The Durban pregnancy rate calculated here is in fact one of the lowest recorded to date, and apparently results from a high failure rate at the main post-lactation oestrus (Best, 1974).

Clarke, Aguayo and Paliza (1980) have proposed a three-year reproductive cycle for the southeast Pacific. Their data from 1959-62 indicates a single-cohort pregnancy rate of 29.5% (including 2.1% pregnant and lactating), with lactating animals comprising 38.1% of the catch. The remaining pregnant animals comprised 4.3%, and recently ovulated animals 7.1%, so presumably resting animals constituted 23.1% of the catch. Because of the effectively unregulated nature of the whaling operation at that time, Clarke *et al.* (1980) believe their data to be fairly representative of the population, and they conclude that their three-year reproductive cycle includes only one year's lactation. It is difficult to reconcile this apparently anomalous result with conclusions reached elsewhere, but a fuller analysis of the age and reproductive material collected in Chile and Peru may help to clarify the situation.

In conclusion, it should be stressed that the values for mean calving intervals discussed above are time-specific,

and could be greatly influenced by short-term fluctuations in the pregnancy rate. They are in actuality 'instantaneous mean calving intervals' (Laws, Parker and Johnstone, 1975).

### (c) Response to exploitation of females

The two data sets on pregnancy rate for Durban have been compared and a significant increase found in the proportion of animals in the catch in early pregnancy between the two time periods (Best, 1980). This conclusion has been criticized by Beddington and Cooke (1981) on the grounds that the proportion of animals in late pregnancy actually declined between the two data sets, and that the null hypothesis of no decline in the proportion of animals in early pregnancy was illegitimate given the predictions from their assessment model.

Best (1980) gave reasons (reiterated above) why he considered the proportion of animals in early pregnancy in these data to be a more reliable index of the pregnancy rate than those in late pregnancy. However both data sets included a separate category of animals in which a large corpus luteum was found but no apparent foetus. As indicated by Best (1980), these animals were most abundant near the peak of the calving season, and so may have represented females that either gave birth shortly before being killed or aborted their foetuses after death. As such they would form part of the cohort of animals in late pregnancy, but were not included with them in the analysis. If they are now combined they form a higher proportion of the catch in 1973–75 than in

1962–65 + 1967 in every month but one (February), and the overall proportion of such animals in the catch (uncorrected for seasonality) is also higher in the later period (0.097 versus 0.071 for the months February to June when more births than conceptions are expected). The latter difference is significant at the 5% level in a two-tailed test (chi-square = 4.55). Hence, leaving aside the question of the validity of comparisons between animals in late pregnancy, the conclusion that there was a decline in the proportion of animals in late pregnancy between the two periods seems unjustified.

Beddington and Cooke's (1981) criticism of the null hypothesis of no decline in pregnancy rate assumes that the male depletion model used in predicting pregnancy rates is valid, whereas a comparison of observed pregnancy rates and those predicted by the model in the estimation of Divisions 3 (Durban) and 5 stock sizes did not indicate consistency in the predicted trends (IWC, 1983).

Hence the model predictions of a decline cannot be taken as necessarily invalidating the null hypothesis of no decline. Indeed Horwood (1980) has concluded that if there had not been an *improvement* in the male to female ratio over the period concerned then the extent of the increase in pregnancy rate observed would imply that the density dependent exponent would have to be very high, as most assessments of the Division 3 stock have placed the current mature female population at about 80–90% of its initial size (IWC, 1978; Kirkwood, 1981).

The extent of the observed increase in pregnancy rate at Durban (Fig. 13) is greatest in the oldest females (Holt,

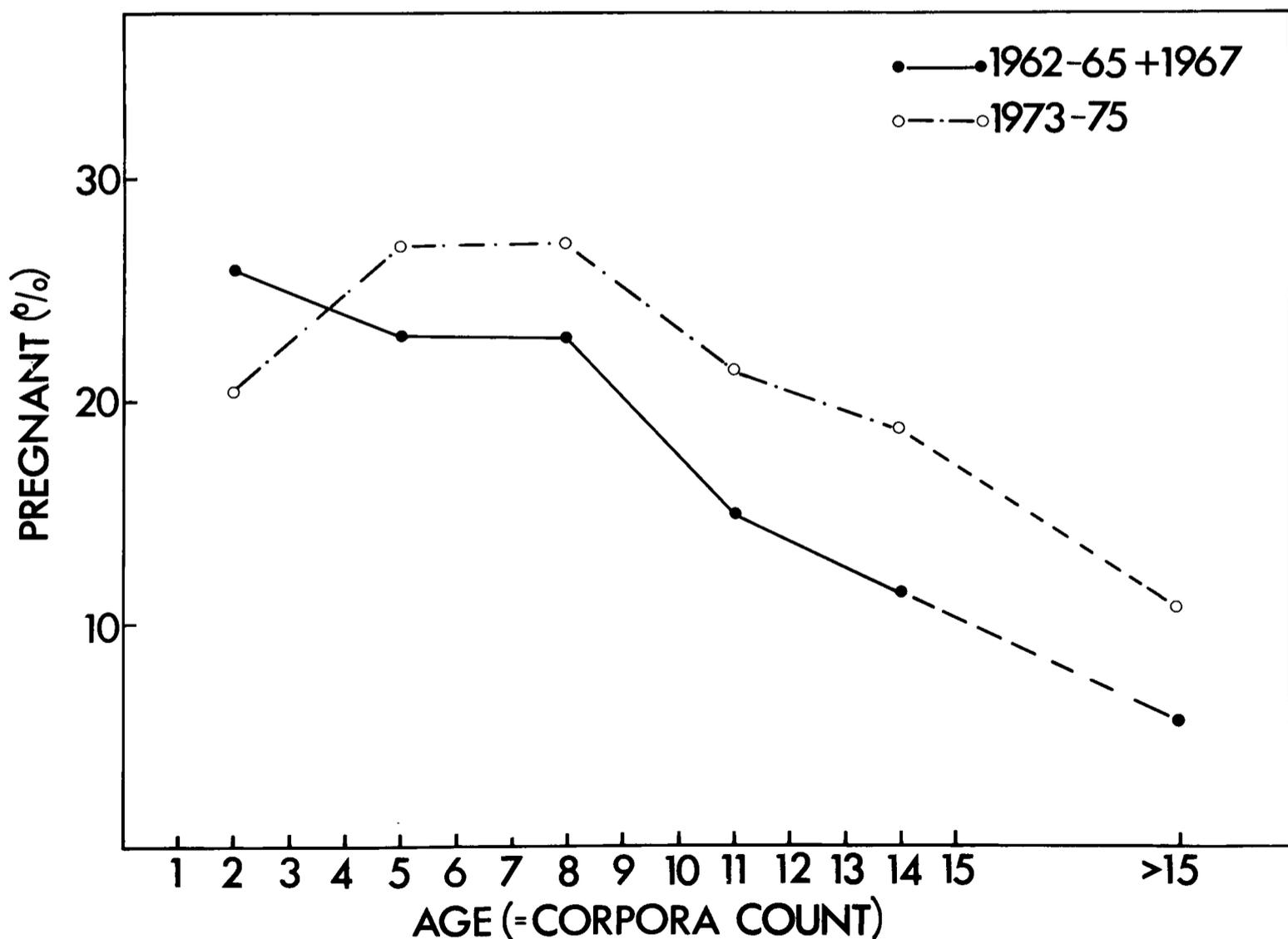


Fig. 13. Comparison of age-specific proportions of animals in early pregnancy amongst female sperm whales landed at Durban in 1962–65 + 1967 and 1973–75. Data are calculated as weighted means for animals with 1–3, 4–6, etc., corpora.

1980), suggesting that the high proportion of unsuccessful ovulations seen in such animals must have declined. The population pregnancy rate has been recalculated for the 1973–75 data assuming the age at recruitment was equal to (or less than) the age at sexual maturity, and that the total mortality rate ( $Z$ ) was 0.0643 which was the value found by Horwood (1980) to be necessary to stabilize the stock at its new level. Data from animals in early pregnancy only have been used. The population pregnancy rate so calculated is 19.3% or an increase of 15.5% since the earlier data set (cf. 14–16% as calculated by Horwood, 1980). The calving interval has thus declined from 6 to 5.2 years.

Unfortunately reliable data on the proportion of lactating animals in the catch between 1973 and 1975 is unavailable, so that possible associated changes in the proportion of lactating animals are unknown.

So far these two samples from Durban represent the only known example of an apparent increase in pregnancy rate in a sperm whale stock following exploitation. Their real significance can only be established when reliable assessments for the Durban stock are available. In the meantime the time-specific nature of the data should be appreciated, and the possibility of there being natural fluctuations in pregnancy rate recognized.

#### DURATION OF LACTATION

Estimates of the length of time for which sperm whales suckle have varied greatly (six months – Matsuura, 1936; Matthews, 1938: 10–11 months – Chuzhakina, 1961: 13 months – Clarke, 1956: 24–25 months – Best, 1968; Gambell, 1972 and Ohsumi, 1965). The earliest estimates are clearly unrealistic given the year-round abundance of lactating females. Many of the estimates have simply utilized the percentage of lactating females in the catch to obtain their results: this assumes that the catch is fully representative of the population – an assumption that is unjustified without some substantiation, particularly as female whales accompanied by calves have been legally protected in most operations. Other estimates have utilized the body length at weaning (6.7 m) proposed by Clarke (1956) and a growth curve to determine the age at which suckling ceases. However the results of the analysis of stomach fluids described in this paper suggest that a superficial examination of the contents of the stomach (as carried out by Clarke) may be misleading, and many of the larger suckling animals might have gone undetected (see also Sergeant, 1962). Best (1968) and Gambell (1972) have listed evidence from changes in the depth of the mammary gland, size of corpora albicantia and diameters of the uterine cornua that lactation definitely must exceed a year, and in their opinion lasts two years. However the latter conclusion rests mainly on detection of bimodality in either the depth of the mammary glands (Best) or the diameters of the largest corpora albicantia (Gambell). Closer inspection of the data reveals that the bimodality of mammary gland depths is not well established, as can be seen from a larger sample (Gambell, 1972). The bimodality in size of the largest corpora albicantia is more convincing, but the adoption of the criteria used to separate the two ‘year classes’ means that there were in the catch 2.5 times as many females in their second year of lactation as there were in

their first. Gambell (1972) attributed this difference to a greater degree of selection by the whale gunners against animals in their first year of lactation (as these were presumably easier to identify from the small size of their calves). If this explanation is accepted (and selection against ‘second-year’ animals is taken to be zero) the proportion of lactating animals in the catch can be adjusted for selection by doubling the number of second-year lactation animals. However such a correction has serious implications for the estimates of the proportions of other reproductive classes in the population. Alternative explanations might be that (a) the criteria used to separate the year-classes are incorrect, or (b) the so-called ‘second-year’ group of lactating females could include more than one year-class i.e. lactation lasts longer than two years.

The data from calf stomach contents given in this paper are insufficient to provide an independent estimate of the age at weaning, and may in any case be biased (as explained above). However, the presence of milk traces in the stomachs of juveniles up to 13 years old is in apparent contradiction to recent estimates of the duration of lactation.

An alternative approach for estimating the duration of lactation is to investigate the ages of the youngest calves within a mixed school corresponding to the number of lactating females present (as has been done for dolphins by Kasuya, 1972; Kasuya, Miyazaki and Dawbin, 1974; Perrin, Coe and Zweifel, 1976; and Perrin, Holts and Miller, 1977). Data on the composition of mixed schools of sperm whales are available from groups either taken under special permit by Japanese whalers (Ohsumi, 1971; Masaki, Wada and Ohsumi, 1972) or stranded (Stephenson, 1975). In the case of the schools captured under special permit, only those in which 75% or more of the animals estimated to have been present were examined, have been included in the present analysis (Table 18).

In general, the number of lactating females found substantially exceeded the number of calves estimated to have been present at the time of sighting: in total this ratio for the Japanese data was 41:15 (chi-square = 12.07,  $P < 0.001$ ). If, instead of using the estimated number of calves, the number of animals of presumed suckling age ( $\leq 3$  GLGs) killed is combined with the number of calves believed to have escaped, the ratio for the Japanese data becomes 41:14 (chi-square = 13.25,  $P < 0.001$ ). Both Ohsumi (1971) and Masaki *et al.* (1972) commented on this disparity, which Ohsumi attributed to the undercounting of calves. If all the animals that escaped are assumed to have been calves, the ratio of lactating females to calves becomes 41:29, which is not significantly different from parity (chi-square = 2.06,  $P > 0.10$ ), although the underlying assumption seems highly unlikely. In the stranded school examined by Stephenson, four lactating females were found yet the smallest whale examined was a 7.93 m female: no ages are available for these animals.

These data suggest that the number of lactating females in a sperm whale school may exceed the number of animals of presumed suckling age (or size) present. If this is so, either lactation lasts longer or is more variable in duration than has so far been assumed, or calves are suckling from more than one female (including some that have no dependent calves of their own), or both.

Table 18  
Comparison of numbers of lactating females and calves in sperm whale schools

	Ohsumi (1971)		Masaki <i>et al.</i> (1972)			Total	Stephenson (1975)
	A	C	V	IX	X		
School identification							
Estimated school size	26	48	21	33 <sup>1</sup>	20	148	?
Number examined	20	39	18	33	15	125	72
% examined	76.9	81.3	85.7	100	75.0	84.5	?
Number of lactating females found	7	14	3	10	7	41	4
Number of calves estimated to have been present	5	2	3	5	0	15	?
Number of animals with $\leq 3$ GLGs examined	0	4	⏟ $\leq 2$			$\leq 6$	—
Number of calves that escaped	5	0	3	0	0	8	?

<sup>1</sup> Originally estimated as 30, but 33 animals killed.

Table 19

Variation in calving interval and length of lactation with age for sperm whales off Durban, 1962–65 + 1967

Age (GLGs)	Number examined	Percent		Length of lactation (years)	Calving interval (years)
		Pregnant (early)	Lactating		
5–9	29	17.2	27.6	1.60	5.8
10–14	155	21.9	35.5	1.62	4.6
15–19	188	18.1	42.6	2.35	5.5
20–24	168	10.7	42.3	3.95	9.3
25–29	101	12.9	28.7	2.22	7.8
30–39	54	14.8	40.7	2.75	6.8
40–61	30	6.7	23.3	3.48	14.9

Age-related changes apparently occur not only in the pregnancy rate but also in the length of lactation. Gambell (1972) drew attention to the fact that the proportion of lactating females at each corpus number falls only slightly in older females, so that the ratio of pregnant to lactating females declines from about parity in the youngest animals to 1 pregnant for every 4 or 5 lactating females in animals with 15 or more corpora. This tendency is not so pronounced when analysed against chronological rather than reproductive age, where lactation may increase in duration from 1.6–2.4 years in females less than 20 years old to 2.2–4.0 years in females older than 20 years (Table 19), or roughly a 67% increase.

Among cetaceans, similar trends with age have been seen in spinner dolphins, *Stenella longirostris* (Perrin *et al.*, 1977), and spotted dolphins *S. attenuata* (Kasuya *et al.*, 1974), and attributed to older females having fewer calves and nursing them longer (Perrin *et al.*, 1977). The energetic benefits of this are well illustrated by Lockyer (1981), who calculated that a newly mature (and thus still growing) sperm whale would have to increase its food intake by 63% to meet the costs of lactation, whereas an adult female would only need a 32% increase.

Individual variation in the length of nursing has also been proposed for the smaller delphinids. The size or age composition of the cumulative number of calves corresponding to the number of lactating females in a particular school showed that in *S. attenuata* from Japan,

lactation could last up to 4 or 5 years, although many females might finish lactation within a shorter period (Kasuya *et al.*, 1974). In captive bottlenose dolphins (*Tursiops aduncus*), suckling has been inferred in a calf up to three years and two months of age (Saayman and Tayler, 1977), even though the 'usual pattern' for captive animals is the first pick-up of fish at an age of six months and a progressive weaning thereafter until 18 months when nursing appears insignificant (Prescott, 1977). Different populations of *S. attenuata* in the North Pacific also appeared to have greatly different estimates for the mean duration of lactation (29.3 months versus 11.2 months), indicating that there is some general plasticity in this parameter (Perrin *et al.*, 1976). Prolonged suckling in these species is probably nutritionally a largely non-functional aspect of general prolonged parental care: it has been suggested that this period may permit the odontocete calf to learn communication and navigation skills essential for future survival (Brodie, 1969). Thus a shorter lactation period does not necessarily mean earlier effective weaning, but may reflect a truncated parental care period (Perrin *et al.*, 1976).

Communal suckling has not been recorded in Cetacea, but its detection would be difficult unless several lactating females were held together in captivity, or prolonged observations were made of known individuals in the field. Such behaviour has been observed in other wild mammal populations, however, including banded mongoose *Mungos mungo* (Neal, 1970), African lion *Panthera leo* (Schaller, 1972), and African elephant *Elephas maximus* (Laws, 1969). As discussed by Schaller, such communal suckling has the advantage to the offspring that if the mother should have inadequate milk, dry up early or die, its young can still obtain milk from other lactating females in the group. Disadvantages of such behaviour include the deprivation of milk for newborn young as a result of the attentions of older offspring. Alternatively, if a female should lose her young, her milk can contribute to the survival of other offspring in the group.

At an adult natural mortality rate of 0.055, female sperm whales have a life expectancy of 1/M or 18.2 years on reaching sexual maturity. Over this age range (10–28 years) the mean calving interval for the population at equilibrium with an unexploited age structure can be calculated as 5.8 years. This means that on average a

Table 20

Reproductive details of 'mothers' of sperm whale juveniles collected at Durban by special permit, 1971 and 1973

Calf no.	'Mother'					
	Length (m)	Mammary gland depth (cm)	Milk present	Diameter largest corpus albicans (cm)	Corpus count	Remarks
C 4	11.28	14	Yes	—	—	—
C 7	7.62	2	No	0	0	Immature
C 13	10.67	7	No	1.9	9	—
C 17	10.06	7.5	Yes	—	—	—
C 20	10.36	8.5	Yes	2.1	4	Corpus luteum 320 g 8.3 cm diameter
C 21	10.36	14.5	Yes	4.85	4	—

female might produce  $\frac{18.2}{5.8} + 1$  or 4.1 calves in its lifetime, half of which would be female. This low fecundity means that the survival of the calf is of paramount importance to the reproductive investment of the adult female. Prolonged parental care is one way of ensuring better calf survival; communal suckling may well be another, particularly if it allows some of the nutritional expense of lactation to be transferred from the reproductively more active to the less active individuals. Within an essentially matricentric group in which several of the members may be closely related and in association with each other for considerable periods of time, as in the elephant (Laws, Parker and Johnstone, 1975), and possibly the sperm whale (Best, 1979), such a system would seem to be a reasonable strategy to adopt. At this stage, however, it is not supported by any direct observations in the case of the sperm whale.

To summarize, it is unlikely that lactation on average lasts much longer than has been calculated here (Table 19). This would imply very significant segregation of or selection against lactating females in the catch, for which there is no evidence. Lactation apparently lasts longer in older animals than younger, but this increase may only be of the order of two thirds. From analogy with delphinids, there may also be considerable individual variation in the duration of lactation. Some of the older calves found with lactose in their stomach may therefore represent offspring of older females that are in an extended period of lactation.

Six of the 'mothers' of the concession calves were also killed (Table 20): these were the animals accompanying the calves at the time of death, of which two were not lactating. Of the remainder, only one had a calf older than one year (C 20), and this female had only 4 ovarian corpora. There is insufficient evidence therefore, to test whether the older suckling animals were the offspring of older females.

Even if the older suckling animals found are still nursing from their own mothers, it seems unlikely that a female could be kept in lactation for up to 13 years through intermittent suckling by its own calf alone. It is possible that younger offspring from other females may suckle from such animals, thus spreading the nutritional expense of lactation more efficiently within the school.

There is indeed evidence from the sample of 'mothers' that a female that has lost a newborn calf may accept

another juvenile. The mother of C 20 possessed a large corpus luteum but no foetus (Table 20). It is very unlikely that this female had recently ovulated, for it was taken in April, a month in which only 0.9% of conceptions are supposed to occur off Durban (Best, 1980), and the corpus luteum was bigger than all but one of 42 corpora lutea of ovulation measured by Gambell (1972), but close to the mean value for females in late pregnancy ( $7.48 \pm 0.16$  cm). The most likely explanation is that it had recently aborted a near-term foetus or lost its newly-born calf — unfortunately uterine material or measurements are not available on this point. The thickness of the mammary gland is less than would be expected from an animal with a newly born calf, but some regression may have already taken place. The diameter of the largest corpus albicans (2.1 cm) is similar to that found in late lactating or post-lactation resting females (Gambell, 1972), so the previous pregnancy must have finished at least a year previously. There seems a strong possibility that C 20 was in fact the previous calf of this female. Its age was estimated as 5.75 GLGs or (if two GLGs are formed in the first year) about  $4\frac{3}{4}$  years old, compared to an average calving interval of 5 years, while its behaviour when the 'mother' was harpooned seems to indicate a strong bond between them. Consequently some at least of the large juveniles found with milk traces in their stomach may represent past offspring that have resumed nursing when a subsequent calf born to their mother died before being weaned. Such nursing may alleviate the physiological or psychological stress of the female, and renew familial ties between the female and its offspring in the school. It is not known how long such suckling behaviour might continue after the loss of the calf, or whether other juveniles that were not the offspring of the female concerned might participate, but this example does indicate that nursing may serve more than a purely nutritional function in sperm whales.

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# Review of Reproduction in the White Whale, *Delphinapterus leucas*, Narwhal, *Monodon monoceros*, and Irrawaddy Dolphin, *Orcaella brevirostris*, with Comments on Stock Assessment

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## ABSTRACT

Estimates of vital reproductive parameters for white whales, *Delphinapterus leucas*, have been made over the past 20 years as a result of data collected from a long, but intermittent history of exploitation. Based on two dentinal growth layers per year, reported in the literature, they may live to 25–30 years. Females become sexually mature at 5 years of age and males at 8 years; they begin active breeding 1–3 years later. Evidence is presented which suggests that estimating age using current ageing methods may result in error in ages at which certain life history events occur. From an observed pregnancy rate of 0.41, and assuming an average gestation period of 14.5 months and a crude birth rate of 0.33–0.38, a gross annual reproductive rate of 0.09–0.12 is estimated. Observed rates are 0.09–0.14. Most vital reproductive rates are unknown for narwhals, *Monodon monoceros*. Almost no life history information is available on the Irrawaddy dolphin, *Orcaella brevirostris*.

Reevaluation and new estimates of stock abundance and vital rate parameters are needed for white whales because under present harvest levels 44% of the defined harvested stocks are being exploited at or above replacement yield.

White whales (*Delphinapterus leucas*) and narwhals (*Monodon monoceros*) are both hunted by natives of Canada and Greenland, and white whales by US and Soviet Natives. Only crude estimates of abundance and life history parameters are available for most stocks. A clear need therefore exists for better biological information so that rationally-based management decisions can be made and appropriate regulatory measures implemented.

My objective in this paper is to review reproduction in white whales and narwhals and relate this to abundance and harvest removals for the various identified stocks or populations so as to gain some insight into productivity.

At the request of the editors of this volume, the Irrawaddy dolphin, *Orcaella brevirostris*, is included in this review because of its anatomical affinities with *Delphinapterus* (Kasuya, 1973).

## METHODS

I depended heavily on research conducted in Canadian waters, as it provided estimates of many life history schedules not available from other studies. In some cases I reevaluated the available data from the literature and made additional calculations to refine previous estimates of certain life-history schedules, or to estimate previously undocumented parameters.

Additional data reported here were collected during aerial surveys of white whales during their spring migration along the northwest coast of Alaska in the Bering, Chukchi and Beaufort Seas, April–May, 1976–1978 (Braham, Krogman and Carroll, 1984) and in May 1981 (NMFS unpubl.). These data were collected to estimate abundance and the proportion of mature versus immature animals according to the presence of grey and white-colored individuals and young-of-the-year calves. White whales become sexually mature about at the time their skin color changes from grey to white. However, age and skin color at sexual maturity vary. Designation of

skin color can be difficult from an aircraft, and comparisons with data from ice-based studies near Point Barrow have indicated that one or both methods are biased (Braham *et al.*, 1984). Resolution of this problem is not discussed here.

Frequently, we encounter in the literature conflicting terms or definitions associated with life-history parameters. For example, Sergeant (1973) and IWC (1981, p. 144) referred to birth rate as the proportion of calves to total animals in the population, whereas Sterns (1976) and Davis, Finley and Richardson (1980) defined birth rate as calf production per mature adult (= sexually mature) female per annum. A glossary of terms is included here (Appendix).

## PATTERNS OF REPRODUCTION

### White Whales

Details of the life history of several stocks of white whales summering in Canadian waters are well documented (Table 1). This is a result of the important works of Brodie (1971), Sergeant (1973), and Sergeant and Brodie (1975), signifying that use of data describing the patterns of reproduction may lead to acceptable first-order population assessments. Except for the as yet unresolved conflict of whether one or two tooth growth layer groups (GLGs; terminology of Perrin and Myrick, 1980) are laid down annually (discussed below),<sup>1</sup> many annual life-cycle events for white whales are known.

With few exceptions (e.g. Cook Inlet, St Lawrence Estuary), white whales migrate from the southern pack-ice and ice-front area to coastal bays and estuaries from late winter to summer, when conception and calving occur (Sergeant and Brodie, 1975; Davis and Finley, 1979; Braham *et al.*, 1984). Finley and Renaud (1980) reported

<sup>1</sup> The following discussion presumes that 2 GLGs/year occurs in white whales, and approximately one GLG/year for narwhals. These are the currently accepted growth layer results (IWC, 1982, p. 114).

Table 1  
Estimates of reproductive parameters for white whales and narwhals

	White whales		Narwhals	
	Estimate(s)	Source(s) & Footnotes	Estimate(s)	Source(s) & Footnotes
Gestation (months)	14.5	a, b, c	14–15	d, e, f, g
Lactation (months)	20–24	a, b	20	g
Parturition	Late July– early August	a, b, d	July–August	d, e, f, h
	April– September	c, i		
Conception	April–May	a, j	mid-April	e, f
Generation time (years)	ca. 6	j	ca. 10	j
Age at sexual maturity (years)	4–7	a, b, c, k	5–8	g, j, l
	8–9		11–13	
First pregnancy (years)	6–7	a, b, k	10–12	j, l
Last pregnancy (years)	21	b, k		
Max. life span (years)	25–30	a, b, k	50	h
Female reproductive span (years)	14–15	j, k		

a Brodie (1971)

c Seaman and Burns (1981)

e Best and Fisher (1974)

g Ohsumi (pers. comm.)

i Braham *et al.* (1984)

k Based on 2 GLGs/year.

l Based on 3 GLGs/year until age 3 in males or 4.5 GLG/year until age 2 in females and one GLG/year thereafter (Hay, 1980).

b Sergeant (1973)

d Finley (1976)

f Mansfield, Smith and Beck (1975)

h Hay (1980)

j Author's estimate using the above literature.

that some (up to 500 in 1979) white whales overwinter in northern Canadian waters above 73° N. Time of conception is deduced from gestation to occur in early spring. The season of parturition has been estimated from the presence of neonates to be March to September, with peak calving in late July to early August (Table 1).

Gestation varies according to latitude, being shortest at higher latitudes (Vladykov, 1944; Sergeant, pers. comm.). Sex segregation was witnessed by Brodie (1971) in July and August, but no mating was observed. From a large sample of pregnant and postpartum females landed by subsistence hunters in Cumberland Sound and Hudson Bay, Brodie (1971) and Sergeant (1973), respectively, estimated from fetal and neonatal lengths that gestation lasts 14–15 months (14.5 months best estimate). Lactation was estimated at 20–24 months by Brodie (1971) and Sergeant (1973) and in Alaska at about 23 months (range 18–32 months based on a partial sample analysis of Seaman and Burns' (1981) data).

A long season of parturition (perhaps April–September, with a peak in July and August) and a short period of conception (April–May), suggests that a reproductive cycle of 3 years, reported by Brodie (1971), Sergeant (1973) and others, may vary from 2 to 4 years. An April–May conception date fits a late July–August birth date with a 14.5-month gestation but not earlier or later birth dates. Some variation in time of parturition is expected, however, as fetal growth is neither linear nor likely equal among animals, and gestation may vary.

Additional reproductive information may eventually help us to understand the timing and frequency of pregnancies. For example, although accessory corpora lutea were found in 11–15% of pregnant females in studies by Brodie (1971, 1972) and Sergeant (1973) there

was no evidence of postpartum estrus. This further supports the hypothesis of a > 2-year reproductive cycle. Also, older females frequently had fewer corpora lutea than younger animals, suggesting to Brodie (1971) that some females 'control' the coupling of ovulation and pregnancy. Fertilization and/or implantation may also vary greatly, and simultaneous multiple ovulations are perhaps common too. No postpartum mating behavior was observed in white whales (Brodie, 1972); however T. G. Smith (pers. comm. to Sergeant) observed possible mating by white whales in summer.

From study of several hundred animals landed during the 1960s, Brodie (1971) and Sergeant (1973) reported that white whales live to 25–30 years (assuming 2 GLGs/year; see discussion of ageing later); that age at sexual maturity for males is 8–9 years and females 4–7 years; and that age at first pregnancy is 6–7 years (Table 1). They also concluded that females stop active breeding at about 21 years of age, and that a female can produce 10 offspring in her lifetime. The maximum breeding lifespan of females, then, can be calculated from the difference between first (at 6 years) and last (at 21 years) pregnancy. This results in a 14–15 year active breeding period. However, if production of 10 calves per adult female per lifetime is possible, then a female's reproductive cycle would have to be less than 2 years. The evidence suggests an approximately 3-year cycle (Brodie, 1971; Sergeant, 1973). Assuming a 3-year reproductive cycle and a 14–15 year breeding period, one female typically could not produce more than six calves in her lifetime. This assumes that pregnancy rates reflect the number of calves produced, and that current methods of ageing are accurate.

## Narwhals

Narwhals are a high-arctic species, frequenting deep waters and fjords in summer. Spatially, white whales and narwhals are mutually exclusive (Finley, 1976; Sergeant, 1979). Much less quantitative information on reproduction is available for narwhals than for white whales (Table 1). Sex segregation is apparent, except during the mid-April mating period (Mansfield, Smith and Beck, 1975; Best and Fisher, 1974), and parturition occurs in July and August (Mansfield *et al.*, 1975; Finley, 1976; Hay, 1980) after a northward migration from wintering areas of the pack-ice and ice front in Baffin Bay and Hudson and Davis Straits.

Although the period of lactation has not been determined, Ohsumi (pers. comm.) estimated that it is 20–24 months. From samples of mature females in the Inuit hunt during the mid-1970s, Best and Fisher (1974), Finley (1976) and Hay (1980) estimated gestation to last 14–15 months. Maximum lifespan was estimated by Hay (1980) to be up to 50 years based on the 1-GLG/year method. Narwhals appear to reach sexual maturity at 5–8 years for females and 11–13 years for males (Table 1). These values are greater than for white whales, using the ageing methods of Brodie and Sergeant (1973). From age and pregnancy data reported by Finley (1976), Hay (1980) and others, age at first reproduction for narwhals appears to be 10–12 years (Table 1). By analogy, and assuming the reproductive biology of white whales and narwhals is similar as suggested by Sergeant (1981) and others (e.g. Andrews, Dill, Marsui and Fisher, 1973; Jarrell and Arneson, 1981), then narwhals would have a lifetime reproductive potential that is more than twice that of white whales. This is not likely, and it is probable that one of the approaches to ageing is wrong by a factor of two. There is a need to reevaluate present ageing methods (IWC, 1980, p. 119).

## Irrawaddy dolphin

Virtually nothing is known about the life history parameters of *Orcaella*. Body length in mature animals is 2.1–2.3 m (males are apparently slightly larger than females); a 2.1 m female was collected with a full-term fetus 85.7 cm long, but season of collection was not given (see Norman and Fraser, 1949). Details of the biology and ecology of the species in the Mekong region of Viet Nam are presented by Lloze (1973), as cited by Pilleri and Gahr (1974), but the paper was not available for this review.

## GROWTH AND AGE DETERMINATION

### Growth

Length at birth for white whales is 150–160 cm at 78 kg of weight (Brodie, 1971); narwhals measure 150–170 cm (Turner, 1875; Hay, 1980). Brodie (1971) reported maximum adult length for white whales was 427 cm for males and 362 cm for females. Fraker, Sergeant and Hoek (1978) reported maximum length for males at 580 cm. The largest female measured from the Mackenzie Delta region was 490 cm long. (P. Fraker pers. comm.). Differences in maximum length may reflect differences between stocks; Brodie (1971) studied animals from Cumberland Sound and the work of Fraker *et al.* (1978)

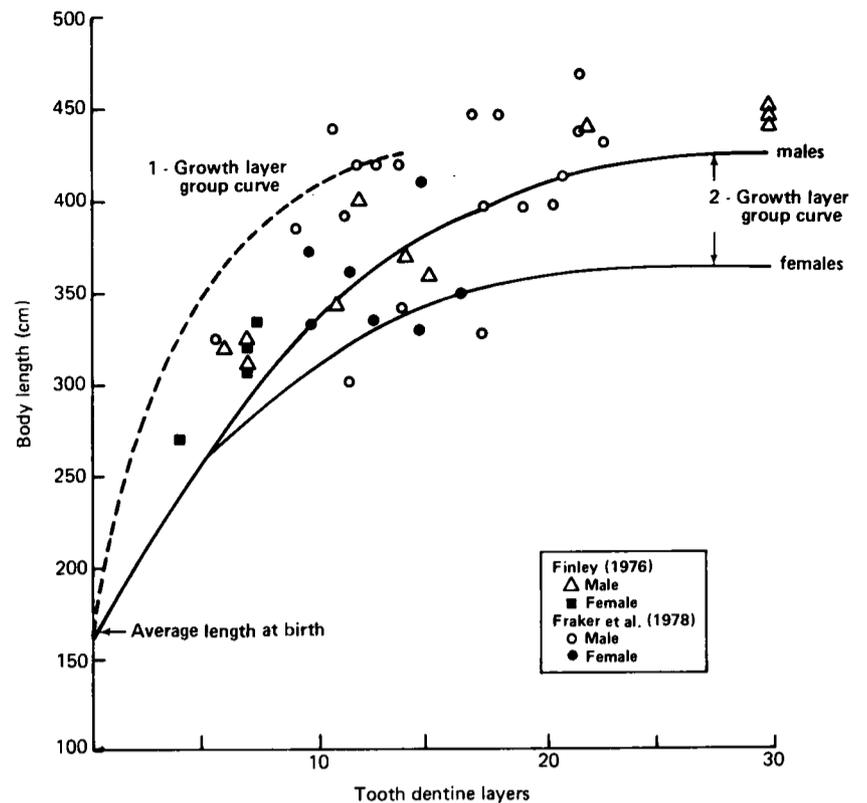


Fig. 1. Growth curves comparing body length and tooth layering in white whales. The solid line is the tooth-layer curve proposed by Brodie (1971, 1982) for 2 GLGs per year, based on data from the Cumberland Sound, Canada population. The dashed line is for one growth layer (1 GLG) per year, proposed by Brodie (1982). Plotted data are growth layers versus body length for white whales landed at Cresswell Bay, Canada (triangles and squares) reported by Finley (1976), and in the Mackenzie Bay region, Canada (circles) from Fraker, Sergeant and Hoek (1978).

was in the Mackenzie Delta area. Maximum length of narwhals is 470 cm in males and 400 cm in females (Mansfield *et al.*, 1975).

Length at sexual maturity is about 85% of that at physical maturity (at 5–7 years) in white whales, and on the average 390 cm in male narwhals and 340 cm in females. Fifty percent of adult body length in white whales is reached at 3 and 5 years of age in females and males, respectively (IWC, 1981, p. 144).

Yearling white whales average 216 cm (at a weight of 188 kg) in Cumberland Sound, with no teeth erupted; body length increases 16% and weight 42% during the first year (Brodie, 1971). Whitening of the skin begins at about 6 years (2 GLGs) and is complete by age 13 (Brodie, 1971; Sergeant, 1973; Ognetev, 1981). This overlaps age at sexual maturity (Table 1).

### Age determination

Provisionally, the sub-committee on small cetaceans of the IWC Scientific Committee (IWC, 1982, p. 114) has accepted the criterion of two-growth-layers-per-annum for ageing white whales, based on data reported by Brodie (1971) from approximately 90 male and female white whales taken in a harvest in Cumberland Sound, Canada, during the 1960s. Brodie (1982) reported on age versus body-length data from a captive white whale captured in Alaska as a juvenile (in 1967) which died at the Vancouver, B.C., Aquarium in 1980. Using the tooth-layer versus body-length growth curves reported by Brodie (1971, 1982) for 1 GLG and 2 GLGs per year, I plotted data from Finley (1976) for 15 animals, and Fraker *et al.* (1978) for 25 animals aged by the GLG method (Fig. 1).

Most of the data reported in Fig. 1 appear to fall between curve fits for the 1 GLG and 2 GLG hypotheses, although there is enough scatter to make an interpretation difficult. There are three possible interpretations of why these data do not seem to fit the expected curves, especially the 2 GLG line as reported by Brodie (1971, 1982). First, as Fraker *et al.* (1978) pointed out, tooth wear varies between individuals as well as among teeth within the same individual, and this can account for an underestimate of age (in some whales) by perhaps as much as 32%. Second, the 2 GLG curve in Fig. 1 is from data on eastern Arctic white whales, which have a mean adult length less than in the Mackenzie Delta stock. Variability in the data make this distinction difficult to evaluate considering that Finley's (1976) data are from the eastern (Canadian) Arctic as were Brodie's (1971). Lastly, data in Fig. 1 may reflect a true picture of the problem; i.e., current methods of ageing white whales may not truly reflect the relationship between body length and tooth layering. Careful evaluation and greater study of age determination in white whales is needed, and thus, as stated by Fraker *et al.* (1978, p. 45) 'Unless there is standardization in the selection of teeth for age determination, or refinement in the ageing techniques, the use of teeth for... age structure and growth studies is limited.'

A technique for ageing narwhals has been developed by Hay (1980). Hay found that up to 3 GLGs are laid down each year for the first few years; typically this period is three years, but it varies 1–2 years. After this early period, at least in females, apparently only one GLG is laid down each year.

## VITAL RATES

### Pregnancy rate ( $p$ )

The proportion of pregnant to all mature female white whales taken in a net fishery in Hudson Bay, Canada, 1962–64, was 0.41 (Table 11 in Sergeant, 1973). Seaman and Burns (1981) observed a pregnancy rate of 0.44 for white whales caught in Escholtz Bay, Alaska (Table 2).

The only estimate of  $p$  for narwhals comes from Finley

and Miller (1982) for females in Lancaster Sound. Using their data, I computed a rate of 0.39. Estimates of pregnancy rates for monodontids are similar to those for *Stenella coeruleoalba*, 0.422, but are greater than in *S. attenuata*, 0.254 (Kasuya, 1976).

### Crude birth rate ( $b_0$ )

The average annual rate at which a mature female will produce a viable calf, as applied here, is the crude birth rate. In white whales  $b_0$  has been reported to be 0.33–0.38 (Brodie, 1971; Sergeant, 1973). This means that, on average, mature females produce one calf every 32–37 months. Sergeant (1973) found that about 75% of the adult females produced a calf every 3 years, and 25% every 2–3 years, hence the range 0.33–0.38 (Table 2).

### Sex ratio and proportion of mature females ( $P$ )

Sergeant (1973), in reviewing previous studies, reported data on the sex ratio of white whales landed in various fisheries over the past half century which result in ratios of 1.00:0.34 to 1.00:1.73, males:females. However, the between-year variation was not statistically significant ( $n = 15$  sampled hunts), and the overall mean was 49.8% females. Although the data indicate that the two sexes may frequently be segregated when sampled and that selection for one sex (e.g. males) occurs in a hunt, I assume in the absence of convincing data and for discussion herein that the population sex ratio is 1.00:1.00. A sex ratio of unity suggests equal mortality rates. However, as mammals age, there is often higher natural mortality in males than females (Ralls, Brownell and Ballou, 1980). Kasuya (1976) found that adult mortality in *Stenella* was 4–7% lower in females than males.

From data collected in 1962–64 by Sergeant (1973), the proportion of females in the catch that were sexually mature and presumably breeding was 0.56–0.62 (Table 2). Assuming that some first-year ovulating females cannot become pregnant, this rate could be as low as 0.50, for example.

Braham *et al.* (1984) found that the proportion of white-colored versus grey-colored white whales (a

Table 2  
Selected estimates of vital rates for white whales and narwhals

Vital rates	White whales		Narwhals	
	Estimate(s)	Source(s) & Footnotes	Estimate(s)	Source(s) & Footnotes
Annual rate of calf production ( $r_0$ )	0.090–0.130	a, b	–	
	0.096–0.121	c, d		
	0.056–0.100	e		
Crude birth rate ( $b_0$ )	0.33–0.38	a, b		
Pregnancy rate ( $p$ )	0.41	b, g	0.39	h
	0.44	f	0.36	i
Proportion of mature females ( $P$ )	0.56–0.62	b		
Adult survival ( $q_x$ )	0.84–0.91	i	0.88–0.91	i
Fertility coefficient ( $B$ )	0.40–0.53	g		

a Brodie (1971)  
b Sergeant (1973)  
c Finley (1976)

d Heyland (1974)  
e Davis and Finley (1979)  
f Seaman and Burns (1981)

g Calculated by author, see text.  
h Finley and Miller (1982)  
i Ohsumi (1979; pers. comm.)

Table 3

Estimates of gross annual reproductive rate ( $r_0$ ) using published and calculated estimates of birth rate ( $b_0$ ) and proportion of mature females ( $P$ ) and equation (1)

$P$	$b_0$	
	0.33	0.38
0.50	0.083	0.095
0.56	0.092	0.106
0.62	0.102	0.118

minimum estimate of the proportion of adults) from ice-camp observations was 0.68. In 627 white whales which I observed off the west coast of Alaska, 9–20 May 1981, the frequencies of color categories were: white, 0.706; grey, 0.196; and calves, 0.097. This does not account for those white-colored animals that were not sexually mature, nor for grey-colored ones which were sexually mature. Differences also may exist among stocks. There may be inaccuracies in the estimate owing to the subjective nature of classifying animals in transition from grey to white (Braham *et al.*, 1984).

#### Coefficient of female fertility (B)

Using data in Tables 1 and 2, the maximum length of the breeding period is about 15 years for white whales or about one-half (0.40–0.53, Table 2) the life expectancy. Obviously, the accuracy of the age estimate of any one or more of the parameters will affect this estimate.

#### Gross Annual Reproductive Rate, GARR ( $r_0$ )

Many terms have been used to describe the annual rate of calf production (e.g. gross recruitment, annual recruitment, gross annual recruitment rate, crude birth rate, etc.). Whatever term one uses, this rate is a measure of recruitment into the total population rather than into a specific age-class and assumes that no mortality has taken place over the time of the estimate. This, of course, is generally not true, and thus one should view estimates of  $r_0$  from data taken during and after the calving season as underestimates, especially if taken several months thereafter.

Empirical estimates of  $r_0$  for white whales range widely, perhaps affected by the season, survey type, location, and environmental conditions. Sergeant (1973) observed the rate of calves to all others in the population to be 0.090–0.143; Finley (1976) observed 0.096–0.121; Davis and Finley (1979) 0.056–0.10; and I observed 0.097 in my 1981 survey.

Gross annual reproductive rate can be approximated, and an upper bound established, from the following equation:

$$r_0 = (b_0)(0.5)(P) \quad (1)$$

where:  $b_0$  is the crude birth rate, and  $P$  is the proportion of mature females in the population.  $P$  is multiplied by 0.5 to account for males in the population, assuming a 1.00:1.00 sex ratio. The range of estimates of  $r_0$  for white whales is 0.083–0.118 (Table 3) using data in Table 2. The value  $r_0 = 0.118$  is the upper limit using this method (line A, Fig. 2). However, I assumed no mortality (at a reduced initial population size) and equal sex ratio for all age classes, which would produce an overestimate of  $r_0$ .

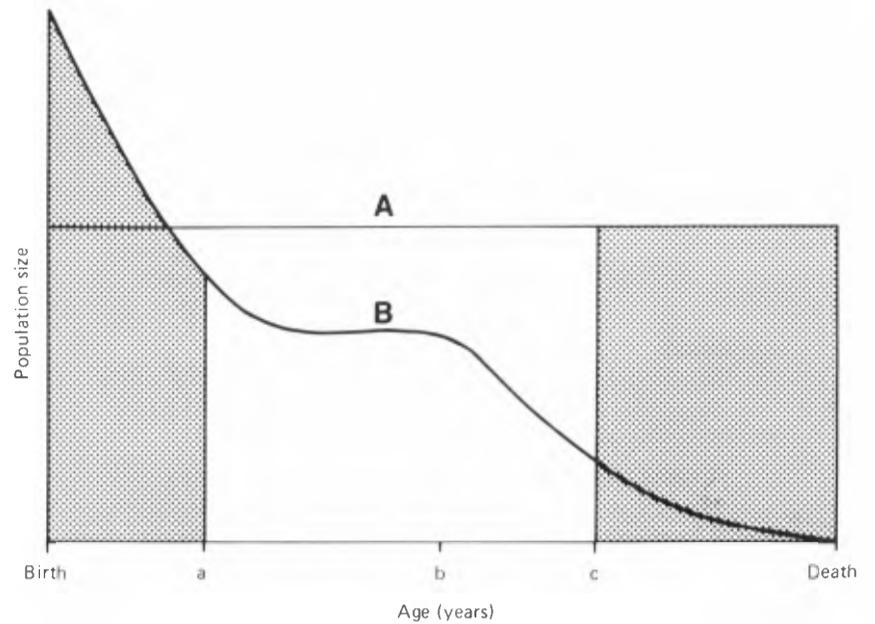


Fig. 2. Simplified age-structure model for white whales: a – age at first reproduction, b – age at reduced breeding success and increased adult mortality, c – age at breeding termination; A – model for no mortality among age-classes, and B – model for differential age-class mortality described by Caughley (1966) from birth to ‘a’ and proportional mortality and production among age classes to ‘b’ beyond which I assume that breeding success coupled with high adult mortality conforms to that presented by Sergeant (1973). Line B conforms to several mammal species summarized by Hutchinson (1978: 62–69).

Calf production in white whales, therefore, appears to be less than 0.12, assuming that line A of Fig. 2 represents the upper end of production, using existing data. This is supported by the literature. For example, Sergeant (1973, p. 1089) pointed out that mortality was high in animals greater than 15 years of age (b, Fig. 2) and stated that for three populations sampled in the 1950s and 1960s, ‘...[the] samples suggest that annual recruitment is small and survival variable [indicating] rather high mortality rates between ages 15–20 years.’ Sergeant’s work would support something approximating line B of Fig. 2.

#### Survivorship ( $q_x$ )

Virtually no empirical data are available on survival rates or age-specific survivorship in monodontids. An estimate of 0.905 for white whales for the first 6 months of life was questioned by Sergeant (1973) as being very low; however, Brodie *et al.* (1981) used Sergeant’s (1962) value of 0.955 from *Globicephala melaena* to estimate net recruitment in white whales.

Assuming for purposes of illustration that no major variation in mortality occurs among age-classes, which is doubtful, survivorship of the adult population in white whales on average or perhaps at its peak, would appear to be 0.91–0.92 (Allen and Smith, 1978) – or using Ohsumi’s (1979) reciprocal life span to mortality curve for survivorship, from 0.842 (2 GLGs/year) to 0.905 (1 GLG/year). Ohsumi’s (1979) maximum body length in males (average 425 cm) to mortality curve (assuming 2 GLGs/year) gives an approximate survival rate of 0.87.

It is, of course, difficult to view survival or mortality in any way other than as age specific (Michod and Anderson, 1980), but until better data are available, the estimate of survival rate varies from perhaps 0.84 to 0.92 (Table 2). The only estimates for  $q_x$  for (female) narwhals are 0.88 and 0.91 by Ohsumi (1979; pers. comm.).

Table 4

Projected summer stocks of white whales: estimates of present abundance and percent of initial population size; current average take (since about 1972); and present kill of current population (includes loss rate). Data summarized from IWC (1980, p. 120; 1981, p. 145; 1982, Tables 1, 2, 4), Boulva (1981), Ivashin and Mineev (1981), Davis and Evans (1982) and others

Summering stocks	Abundance estimate	Current percentage of initial	Estimated current take <sup>a</sup>	Percentage kill of stock size
<b>Canada</b>				
Mackenzie Delta	7,000–11,500	no est.	192	4
West Hudson Bay	5,000–9,000	50–90	182+	< 5
East Hudson Bay	> 1,000	< 10	507 <sup>b</sup>	< 50?
Ungava Bay	200–1,000	> 20	162	15–80
Frobisher Bay	250–300	no est.	7	2–3
Cumberland Sound	600	< 12	57 <sup>c</sup>	9–10
St Lawrence Estuary	350–400	< 10	38	10–12
<b>High Arctic</b>				
Canada	10,000–12,000	no est.	280	2–3
W. Greenland	2,000	no est.	100+	< 10
<b>USA</b>				
Cook Inlet	600–1,000 <sup>d</sup>		3–6 <sup>e</sup>	< 1
Bristol/Kuskokwim Bays	1,000–1,500	no est.	10–20 <sup>e</sup>	< 3
Yukon/Norton Sound	no est.	no est.	88–103 <sup>e</sup>	unknown
Kotzebue Sound	no est.	no est.	58 <sup>e</sup>	unknown
NW Alaska–US Beaufort	no est.	no est.	38–50 <sup>e</sup>	unknown
<b>USSR</b>				
Okhotsk Sea	< 10,000	no est.	0	0
Barents Sea	1,500–3,000	no est.	824	> 28–55
White Sea	500–1,000	no est.	256	26–51
Barent/Kara/Laptev Seas	1,000–2,000	no est.	186	9–18
Bering Sea–Anadyr Gulf	2,000–3,000	no est.	34	1–2
E. Siberia–Chukchi Seas	1,000–2,000	no est.	unknown	unknown
<b>World total</b>	<b>&gt; 40–55,000</b>		<b>&gt; 3,000</b>	

<sup>a</sup> Generally, averages over the last decade were used, or median values where appropriate; includes number landed plus a 33% killed but lost rate (loss rates are variable, and are not precise from 25–85% of total landed; IWC, 1980; 1982).

<sup>b</sup> May include some animals from Ungava Bay, James Bay and North Quebec Province. Average total take for area 1974–78 was 533 (Boulva, 1981).

<sup>c</sup> A quota of 40 was instituted in 1980; 43 were landed that year.

<sup>d</sup> Population likely to be twice the historical estimate according to Murray and Fay (1979); totals include those in the Gulf of Alaska as well.

<sup>e</sup> 1981 estimates (J. Burns, Alaska Department of Fish and Game, pers. commun.). Does not include loss rate estimates as in footnote <sup>a</sup> description. Some overlap in reporting between Bristol Bay and Yukon Delta occurred, hence the precise estimate of take by 'stock' may be different than reported here.

## STATUS OF STOCKS

### Stock management units: definitions

It has been proposed that white whales and narwhals conform to one of the following two stock-identity definitions (IWC, 1980, p. 117):

1. that wintering groups consist of a single interbreeding stock that disperses throughout the Arctic in spring and summer, or

2. that animals found in their summering areas represent separate stocks with wintering grounds that may be shared by more than one stock.

Because isolated resident stocks in some areas can be readily identified (e.g. Cook Inlet and Okhotsk Sea stocks of white whales, and East Siberian Sea-Chukchi Sea proposed narwhal group) and because some overwintering occurs in high latitudes, it was decided to identify management units as stocks according to their summer grounds. In support of this, 'management' is defined as the need for control over removal of individuals from a stock, and thus 'status' of these stocks is most influenced by hunting pressure. One problem with this concept is the question of whether these stocks are genetically separate. For example, mating apparently takes place from April

to June, which is prior to the time when most animals have reached their summering grounds. Each 'stock' may therefore be a subunit of a much larger gene pool.

Ognetev (1981) suggested that on the basis of body size, white whales in the White and Kara Seas are part of the same population. This may be true for other stocks or populations as well, but until this is resolved by using morphological, biochemical, or by other means, I chose to retain the stock-management construct as proposed by the IWC (1980).

Provisionally, 21 stocks of white whales (Table 4) and 4 stocks of narwhals (Table 5) were identified. As with most cetacean populations, estimates of abundance for these two species are generally crude, and none have confidence intervals.

### Abundance and removals

There are at least 40–55,000 white whales, worldwide. The most complete data are for the Mackenzie and eastern Canadian stocks, and the least complete are for the Alaskan and Soviet Union stocks. Seven stocks in Canada total 11–18,000 plus an additional 10–12,000 in the Canadian High Arctic-Baffin Bay (one stock?). The eastern High Arctic stock extends in winter to West

Table 5  
The stocks of narwhals: their abundance and harvest levels

Summering stocks	Abundance estimate	Current percentage of initial	Estimated current annual removal <sup>a</sup>	Percentage kill of stock size
High Arctic <sup>b</sup>	10,000–30,000 <sup>c</sup>	no est.	800 <sup>d</sup>	> 3–8
Canada <sup>e</sup>	—	—	369	—
W. Greenland <sup>f</sup>	—	—	425	—
W. Hudson Bay <sup>g</sup>	no est.	no est.	28	unknown
NW Europe to E Siberian Sea	several thousand <sup>h</sup>	no est.	unknown	unknown
E. Greenland–Spitzbergen <sup>i</sup>	no est.	no est.	low <sup>j</sup>	unknown

<sup>a</sup> Summarized from Davis *et al.* (1978); IWC (1980, 1982) and Meldgaard and Kapel (1981).

<sup>b</sup> Considered one stock in Canadian and W Greenland waters (Mitchell and Reeves, 1981).

<sup>c</sup> Mansfield *et al.* (1975) and Davis *et al.* (1978).

<sup>d</sup> Includes a 50% loss rate (Mansfield *et al.*, 1975) which is probably low (Davis *et al.*, 1980).

<sup>e</sup> Principally Lancaster Sound and northern bays.

<sup>f</sup> Includes Thule District.

<sup>g</sup> Includes Foxe Basin.

<sup>h</sup> Yablokov (1974) in Reeves and Tracey (1980).

<sup>i</sup> Nineteenth Century descriptions suggest that this stock was widespread and therefore probably large; presumably it did not undergo heavy exploitation other than coastal hunting by Greenlanders (D. Sergeant, Arctic Biological Station, Quebec, pers. comm.).

<sup>j</sup> Kapel (1977).

Greenland. The MacKenzie Delta stock (Table 4) comes from the Bering Sea, or the United States and perhaps the USSR (Anadyr and/or Chukchi) wintering stocks, but this estimate (7,000–11,500) represents the number of summering whales in the western Canadian Arctic (Fraker, 1980, pers. comm.; Davis and Evans, 1982).

Very few recent abundance data are available for the five or six US and USSR Bering Sea stocks, although the US stocks are all probably small (only a few thousand total).

Mitchell and Reeves (1981) provisionally concluded that one stock of narwhals occurs from Baffin Bay to Lancaster Sound (Davis, Richardson, Johnson and Renaud, 1978) and West Greenland (Meldgaard and Kapel, 1981). Virtually nothing is known of the other stocks in west Hudson Bay, USSR Arctic, and east Greenland–Spitzbergen (Reeves and Tracey, 1980; Mitchell and Reeves, 1981). The world population of narwhals exceeds the 10–30,000 estimate for the Canadian High Arctic (Table 5).

The stocks of narwhals collectively are probably producing young at a greater rate than they are being removed by hunters; but it is obvious from Tables 1, 2 and 5 that more information is needed. Many stocks of white whales, however, appear to be harvested at levels above replacement yield. Estimates of natural mortality for white whales are very crude at best (4–16%), as are estimates of calf production (8–12%). Any margin of error may be serious to one stock whose rate of production is lower than the available estimates.

Of the 18 white whale stocks known to be currently exploited, in 8 stocks harvest levels exceed net recruitment, which was estimated by Sergeant (1973, 1979, 1981) for the west Hudson Bay stock to be greater than 5% (Table 4). On the basis of estimates of yield similar to those of Sergeant (1979), Brodie, Parsons and Sergeant (1981) reported that a harvest quota of 40 animals in the Cumberland Sound stock would not exceed net recruitment. No replacement yield beyond 40 was provided for, however. Had a mortality estimate of

0.09 been used rather than 0.045 (0.045 was the extrapolated value from pilot whales, *G. melana*) or a lower GARR of 0.09 rather than 0.12, then no harvest quota would have been warranted.

#### CONCLUSIONS AND RECOMMENDATIONS

Because of the apparent biological similarities between white whales and narwhals, vital rates estimated for white whales might be applicable to narwhals. However, use of these estimates is hampered by the need for better precision (and possibly accuracy) in estimating age. Differences in exploitation among white whale stocks as well as between the two species also may mean that some vital rates have changed as population sizes changed. This weakens the argument of a clear comparison between species.

Catch limits have often been instituted in the absence of any specified management objective such as a desired level of population growth. With the proper information, however, decision as to the potential for a sustained yield is possible. To do so requires that three critical parameters be known or estimated: current population size; annual net recruitment; and rate of harvest removal including loss rate.

To reliably assess the status of white whale and narwhal stocks the following information is needed.<sup>2</sup>

- (1) knowledge of stock discreteness;
- (2) better population size estimates;
- (3) resolution of the question of age determination in white whales, especially;
- (4) better harvest data, including data on struck-and-loss rates and mortality of struck-and-lost animals: estimates of loss now range from 25–85%, depending upon the method of take (e.g. netting versus ice-edge hunt using high powered rifles); and
- (5) net recruitment, the most important parameter to

<sup>2</sup> These and other recommendations are covered in greater detail by Davis *et al.* (1980) and IWC (1980, 1981, 1982).

estimate; virtually no reliable estimates of mortality and only limited unbiased information are available on calf production.

Additional life history data for white whales and narwhals will help in their management in two ways. First, from an analysis of vital rates, greater insight can be gained into population growth and recovery. In addition, information on population growth from an assessment of recruitment will be essential for considering catch limits.

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**Appendix**  
**GLOSSARY**

<i>Crude Birth Rate</i> ( $b_0$ )	Annual rate of production of calves per mature female; how many calves, on average, a mature female will produce per annum.	<i>Gross Annual Reproductive Rate</i> , GARR ( $r_0$ )	The annual rate of calf production per entire population.
<i>Fertility Coefficient</i> ( $B$ )	Proportion of a mature female's life during which she can produce a calf.	<i>Pregnancy Rate</i> ( $p$ )	Proportion of pregnant females to all mature females.
<i>Generation Time</i>	Approximately, the average age of females giving birth in any one year; or a value larger than the average time from birth to age at first parturition. See Mertz (1971, p. 366) or Murray (1979, p. 22) for the mathematical expression.	<i>Reproductive Cycle or Interbrood Period</i> <i>Savssat</i>	Period of time between the onset of consecutive pregnancies. Small <i>polynya</i> of open water surrounded by pack ice which progressively closes during freeze-up, entrapping cetaceans which are unsuccessful at keeping it open as a breathing hole.
<i>GLGs</i>	Growth layer groups: the alternating light and dark lines in the dentine and cementum of teeth or accompanying mandible used to estimate age in odontocetes.	<i>Total Female Fertility</i>	The segment of a female's life during which she has the potential to reproduce; the difference between age of first and last parturition.



# Survey of Reproductive Data for the Beaked Whales (Ziphiidae)

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## ABSTRACT

Outside of *Berardius bairdii* and *Hyperoodon ampullatus*, the two species of ziphiids for which there have been commercial fisheries, little reproductive data are known. Mean length at birth ranges from 210 cm in *Mesoplodon europaeus* to 450 cm in *B. bairdii*. Maximum reported lengths range from a low of 430 cm for male *Mesoplodon hectori* to a high of 1,280 cm for female *B. bairdii*. Age at attainment of sexual maturity is known only for *H. ampullatus* and *B. bairdii* and ranges between 7 and 11 years. The maximum reported age of a ziphiid is 71 years for a male *B. bairdii*.

## INTRODUCTION

This is a survey of the literature for reproductive data on beaked whales (Ziphiidae). I have consulted one unpublished thesis (Ross, 1979) because of the bulk of data that it contained for the Southern Hemisphere species. I have consulted all of the papers dealing with beaked whale fisheries management and have tried to consult all of the papers dealing with stranded beaked whales. In addition I have used unpublished data on specimens contained in the United States National Museum (USNM) in Washington, D.C. and have used specimen data gathered by the Scientific Event Alert Network (SEAN) (Smithsonian Institution, Washington, D.C., 20560) and published in its monthly bulletin.

In dealing with the published data I have encountered a few minor problems. Most researchers do not specify whether the gonad weights are for one gonad or both gonads combined. I have interpreted them as being for one gonad. The maximum weight for ovaries appeared to be the weight with a corpus luteum. However, those weights that were obviously from an ovary with a corpus luteum were not included in the sample to obtain the mean ovary weight. There was no indication whether the testis weights were taken with the epididymus attached or trimmed off.

I could find no discussion or illustrations of the histology of the ovaries, testes or mammary glands in any beaked whale.

## DEFINITION OF TERMS

**Minimum length/age at sexual maturity:** This is the length/age of the smallest/youngest individual in the sample that was known to be sexually mature. In the case of limited samples that consisted of very short/young animals and very long/old animals, I left that category blank. If an animal seemed approximately the right length/age, a recently matured animal, or in the rare case where data were available on the number of corpora in the ovaries and there were only one or two, I included that animal in this category.

**Mean length/age at sexual maturity:** This category was restricted to fishery species, the only exception being *Mesoplodon europaeus*, where I had a large enough

sample of unpublished material to derive a meaningful average.

**Maximum length/age:** The maximum reported lengths and ages for a species. This category was left out if there were no data or if the data were for specimens young enough that they were not a good approximation of the maximum length/age that the species could be expected to attain.

**Length of the longest fetus and the shortest calf:** These are self-explanatory.

**Mean length at birth:** This is either the mean length at birth reported by other workers or a weighted average (taking into account other species of a genus) between the maximum reported fetal length and the length of the shortest calf.

**Gonad weights in general:** These are weights of a single gonad unless otherwise specified. For minimum gonad weights it is the weight of the smallest of the pair and for maximum gonad weights it is the weight of the largest of the pair. The testis weights on USNM specimens are with the epididymis removed.

**Gonad weights for immature animals:** These are weights of the gonads of juvenile animals. For fishery animals there was enough of a sample to yield a mean weight, but for stranded animals the weight is for the smallest gonad of a non-mature animal. In some cases this turned out to be a calf and in those cases it is lower than it should be to give an impression of the gonad weight of a juvenile.

**Minimum gonad weights at sexual maturity:** These were the minimum gonad weights of an animal that had just become sexually mature. In some cases where there were no data on the corpora in the ovaries, the lesser of the two gonad weights was chosen on a mature animal.

**Mean gonad weight at sexual maturity:** For fishery samples, this represents an actual mean. For stranded animals, it may represent the gonad weight of an animal that was presumed to be a 'typical' mature specimen.

**Maximum gonad weight:** This represents the maximum reported gonad weight of an individual. In females this is usually presumed to be an ovary with a corpus luteum attached. In males it may represent the combined weight of both testes in some cases, but it is intended to be the weight of the single largest testis.

**Age:** The ages of ziphiids are expressed in growth layer groups (GLGs; Perrin and Myrick, 1980: 48). As an

initial hypothesis, 1 GLG layer group can be assumed to represent 1 year's growth.

## RESULTS

### *Berardius arnuxii*

There are practically no reproductive data available for this species. Gaskin (1968: 44) gave a maximum length of 30 feet (900 cm) for males and Hale (1962: 231) gave the maximum length as 885 cm for females. The 885-cm female was pregnant but Hale gave no details of the fetus or the ovaries.

This species is restricted to the temperate and polar waters of the Southern Hemisphere, but is close enough morphologically to its northern relative to allow the assumption that reproductive parameters obtained for its *Berardius bairdii* can reasonably be applied to it as well. The lengths should be reduced by about 20% to make up for the lesser size of *B. arnuxii*.

### *Berardius bairdii*

Omura, Fujino and Kimura (1955) gave the bulk of the data on this species, based upon a sample of 924 animals caught off Japan. The minimum length at sexual maturity was 1,000 cm for females and 950 cm for males; the mean length at sexual maturity was 1,050 cm for females and 1,000 cm for males. Nishiwaki and Oguro (1971, p. 118), based on a sample of 701 animals caught off Japan, gave maximum lengths of 42 feet (1,280 cm) for females and 39 feet (1,190 cm) for males. The only record of a male longer than this is a specimen in the United States National Museum (USNM 49725) whose length is given as about 41 feet (1,250 cm) by True (1910, pp. 61, 63). I agree with Omura *et al.* (1955, p. 96) in questioning the sex and disallowing this record. Kasuya (1977, p. 15) gave the mean age at sexual maturity as 8–10 GLGs based on his age/length curve and the data on length at sexual maturity presented by Omura *et al.* (1955, pp. 113, 114), the maximum reported age for males at 71 GLGs (1955, pp. 3, 13) and that for females at 39 GLGs (1955, p. 3).

Omura *et al.* (1955, p. 113) gave testis weights as 1 kg in an immature specimen, 3 kg as the minimum weight at sexual maturity, and 5 kg as the mean weight at sexual maturity. Rice (1963, p. 186) gave 17.6 kg as the maximum testis weight. The only ovary weight was given by Pike (1953, p. 103) as less than two ounces (60 g) for a 29-foot 3-inch (890-cm) specimen. Ohsumi (1964, p. 134) concluded that there was no difference between the right and left ovaries as to age at maturity or accumulation of corpora.

The length of gestation was originally given as 10 months (Omura *et al.*, 1955, p. 114), based on an estimated growth curve of fetal lengths. Kasuya (1977, p. 17) gave 17 months based upon 'short cycles' (lunar months) observed in the prenatal dentine and the estimated fetal growth rate. I have chosen to adopt Kasuya's estimate. The length of the longest fetus was 14 feet (420 cm; Omura *et al.*, 1955, p. 115) and the length of the shortest calf was 481 cm (True, 1910, p. 64). Stejneger's notes on this animal (True, 1910, p. 64) said that he thought that there were remains of the umbilical cord present, but as the animal was in a state of advanced putrefaction, he was unsure of this. Omura *et al.* (1955,

p. 114) estimated the length at birth to be 15 feet (450 cm). The peak period of calving occurs in March and April, and the peak period of mating therefore occurs in October and November (Kasuya, 1977, p. 17).

### *Hyperoodon ampullatus*

This is another species that has been the object of a fishery and for which reproductive data are readily available. The samples that these studies were based on were 5,095 (Christensen, 1973), 129 (Benjaminsen, 1972) and an additional 74 from Labrador (Benjaminsen and Christensen, 1979). The minimum length at sexual maturity for females was 20 feet (600 cm) and 24 feet (730 cm) for males (Benjaminsen, 1972, p. 239); the mean length at sexual maturity was 22–23 feet (690 cm) for females and 24–25 feet (750 cm) for males (Benjaminsen, 1972, p. 238); maximum length for males was 32 feet (980 cm) (Benjaminsen, 1972, p. 238). Thompson (1846) recorded a female that was 28.5 feet (870 cm) long. Benjaminsen and Christensen (1979, p. 156) gave a minimum age of attainment of sexual maturity of 7 GLGs for both sexes, and a mean age at sexual maturity of 11 GLGs for females and 7–11 GLGs for males. Christensen gave maximum ages of 27 GLGs for females (1973, p. 335) and 37 GLGs for males (1973, p. 333).

The testis weight of an immature animal was 100 g per pair, minimal weight at attainment of sexual maturity was about 200 g per pair, mean weight at sexual maturity was about 1,200 g per pair, and maximum weight was 2,600 g per pair (Benjaminsen and Christensen, 1979, p. 156).

The gestation period was given as 12 months (Benjaminsen, 1972, p. 240) based upon a fetal length/month plot. The lactation period is estimated to be about 1 year based upon the presence of milk in the stomach of a 1-year old calf (Benjaminsen and Christensen, 1979, p. 158). The mean calving interval is estimated to be 2 years (Benjaminsen and Christensen, 1979, p. 158). The largest reported fetus was 12 feet (11.5 Norwegian feet; 361 cm; Ohlin, 1893, p. 8), the smallest calf was 11 feet 6 inches (350 cm; Fraser, 1934, p. 32) and the mean length at birth was reported to be around 10 feet (300 cm; Benjaminsen, 1972, p. 240). However, I feel that 360 cm is in better agreement with the data. The peak of calving is in April.

### *Hyperoodon planifrons*

There is a paucity of reproductive data for this animal. Zemskiy and Budylenko (1970, p. 201) gave a report of a 570-cm lactating female. Fraser (1964, p. 198) reported the largest specimen of this species, a 745-cm lactating female. Hale (1931, p. 294) reported the largest male, a 694-cm specimen. Ross (1979, p. 61) reported a 291-cm calf which he assumed, from the pigmentation (the presence of 'fetal folds'), had been recently born. The testis weights of the calf were 3.7 g and 3.2 g.

One has to use caution in extending the reproductive data from *Hyperoodon ampullatus* to *H. planifrons*. Although they are clearly related, there is a greater degree of osteological differentiation between them than there is between *Berardius arnuxii* and *B. bairdii*. In fact Moore (1968, p. 274) erected a new subgenus, *Frasercetus*, to include *H. planifrons*.

Table 1

Total body lengths in cm and ages in GLGs for ziphiids. Estimated lengths are marked with an \*

		<i>Berardius arnuxii</i>	<i>Berardius bairdii</i>	<i>Hyperoodon ampullatus</i>	<i>Hyperoodon planifrons</i>	<i>Mesoplodon bidens</i>	<i>Mesoplodon bowdoini</i>	<i>Mesoplodon carlhubbsi</i>	<i>Mesoplodon densirostris</i>	<i>Mesoplodon europaeus</i>	<i>Mesoplodon ginkgodens</i>	<i>Mesoplodon grayi</i>	<i>Mesoplodon hectori</i>	<i>Mesoplodon layardii</i>	<i>Mesoplodon mirus</i>	<i>Mesoplodon pacificus</i>	<i>Mesoplodon stejnegeri</i>	<i>Tasmacetus shepherdi</i>	<i>Ziphius cavirostris</i>	
Length	Minimum at sexual maturity	Females	1,000	600	570	—	—	—	—	—	—	—	—	—	—	—	—	—	527	
		Males	950	730	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Mean at sexual maturity	Females	1,050	690	—	—	—	—	—	450	—	—	—	—	—	—	—	—	580	
		Males	1,000	750	—	—	—	—	—	—	—	—	—	—	—	—	—	—	550	
	Maximum	Females	885	1,280	870	745	505	457	532	471	520	490*	533	443	615	510	—	525	660	754
		Males	900*	1,190	980	694	550*	—	532	473	456	477	564	430	584	533	—	525	700	700
Age	Minimum at sexual maturity	Females	—	—	7	—	—	—	—	9	—	—	—	—	—	—	—	—	—	
		Males	—	—	7	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Mean at sexual maturity	Females	—	8–10	11	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
		Males	—	8–10	7–11	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Maximum	Females	—	39	27	—	—	—	—	—	27	—	—	—	—	—	—	—	—	30
		Males	—	71	37	—	—	—	—	—	—	—	—	—	—	—	—	—	—	36
Length longest fetus		—	420	361	—	157	155	90	190	218	—	—	—	76	105	—	—	—	267	
Length shortest calf		—	481	350	291	245	—	247	261	196	—	242	210	280	233	—	—	—	269	
Mean length at birth		—	450	360	—	240	—	250	—	210	—	—	—	—	—	—	—	—	270	

### *Mesoplodon*

The 12 species of *Mesoplodon* make up a reasonably diverse yet clearly related assemblage. *M. carlhubbsi* seems to be so closely related to *M. bowdoini* that it may turn out to be a subspecies of it. Where there seem to be separate Northern and Southern Hemisphere populations (as in *M. mirus* and *M. hectori*) there appear to be consistent differences that indicate that interbreeding is relatively rare.

### *Mesoplodon bidens*

Despite being one of the most commonly stranded *Mesoplodon* species, there is surprisingly little reproductive data available. The maximum length of females was 505 cm (Jonsgård and Hoidal, 1957, p. 509) and of males 550 cm (18 feet; Isseling and Scheygrond, 1950). There are reports of males of 17 feet (520 cm; Andrews, 1870; title not seen, data from Flower, 1871, p. 210) and 16 feet (490 cm; Sowerby, 1804). (Data that are expressed in whole numbers of feet are likely to have been estimates.) The largest measured male was 15 feet 8 inches (478 cm; Turner, 1885, p. 145).

There are no gonad weights reported for *Mesoplodon bidens*.

The length of the longest fetus was 5 feet 2 inches (157 cm; Jonsgård and Hoidal, 1957, p. 509) and the smallest calf was 245 cm (Grieg, 1908). There were traces of the umbilical cord on the 245 cm calf, so I have estimated the length at birth at 240 cm.

### *Mesoplodon bowdoini*

There is one 457-cm physically mature female known (Tidemann, 1980, p. 64) and a 14-foot (420 cm) female that was carrying a 5-foot 2-inch (15 cm) fetus (McCann, 1976, p. 107; identified as *M. stejnegeri*).

### *Mesoplodon carlhubbsi*

The largest physically mature male and female specimens measured 532 cm (Mead, Walker and Houck, 1982, pp. 13, 20) The right ovary of that female weighed 13.2 g. The mean testis weight of a sexually mature male was 250 g (1982, p. 13). The largest fetus was 90 cm (1982, p. 8) and the smallest calf was 247 cm (1982, p. 6). The mean length at birth was estimated to be 250 cm (1982, p. 6) on rather tenuous grounds. Based upon the mean length at birth estimate, the calving season was estimated to be mid-summer (1982, p. 13).

### *Mesoplodon densirostris*

The maximum reported lengths were 473 cm for a male and 471 cm for a female (Ross, 1979, p. 316, table 27), and the minimum reported age at sexual maturity was 9 GLGs.

The testis of an immature male weighed 27 g (1979, p. 42). The minimum weight of the ovaries at sexual maturity was 12 g, the mean weight at sexual maturity was 14 g and the maximum weight was 25 g (1979, p. 317, table 24).

The length of the longest fetus was 190 cm and of the shortest calf 261 cm (1979, p. 313, table 24).

### *Mesoplodon europaeus*

Data on 7 mature females were available: 420 cm, ovary weights 18.5, 15.3 g (USNM 504349); 430 cm with a 196-cm calf (SEAN Bull., 3(5): 25); 14 feet (430 cm) with a 7-foot (210 cm) calf (Rankin, 1955, p. 26); 430 cm with a 162 cm fetus (USNM 550069); 458 cm, ovary weights 13.4, 12.0 g (USNM 504610); 473 cm, ovary weights 8, 12 g (USNM 504256); 17 feet (520 cm) with a 7-foot 2-inch (218 cm) fetus (Brimley, 1943, p. 199). The

Table 2  
Gonad weights in grams for Ziphiids

	<i>Berardius arnuxii</i>	<i>Berardius bairdii</i>	<i>Hyperoodon ampullatus</i>	<i>Hyperoodon planifrons</i>	<i>Mesoplodon bidens</i>	<i>Mesoplodon bowdoini</i>	<i>Mesoplodon carlhubbsi</i>	<i>Mesoplodon densirostris</i>	<i>Mesoplodon europaeus</i>	<i>Mesoplodon ginkgodens</i>	<i>Mesoplodon grayi</i>	<i>Mesoplodon hectori</i>	<i>Mesoplodon layardii</i>	<i>Mesoplodon mirus</i>	<i>Mesoplodon pacificus</i>	<i>Mesoplodon stejnegeri</i>	<i>Tasmacetus shepherdi</i>	<i>Ziphius cavirostris</i>
Immature																		
Females	—	60	—	—	—	—	—	—	—	—	—	—	—	—	—	2.6	—	5.2
Males	—	1,000	50	3.2	—	—	—	27	—	—	—	1.6	—	6.5	—	—	—	—
Minimum at sexual maturity																		
Females	—	—	—	—	—	—	—	12	12	—	—	—	—	11	—	12	—	16
Males	—	3,000	100	—	—	—	—	—	—	—	—	—	—	—	—	—	—	150
Mean at sexual maturity																		
Females	—	—	—	—	—	—	13	14	14	—	—	—	—	15	—	—	40	—
Males	—	5,000	600	—	—	—	250	—	—	140	—	—	—	—	—	—	—	4,000
Maximum																		
Females	—	—	—	—	—	—	—	25	18.5	—	—	—	—	49	—	—	—	57
Males	—	17,600	1,320	—	—	—	—	—	160	—	—	116	—	170	—	—	—	—

maximum reported length of a mature male is 456 cm (USNM 504738). The maximum reported age is 27 GLGs (USNM 504610; Perrin and Myrick, 1980, p. 8).

The minimum weight of an ovary that was considered to be mature was 12 g (the 8-g ovary of USNM 504256 is problematical and is ruled out for this consideration), the mean weight of sexually mature ovaries was 14 g, and the maximum weight was 19 g (18.5 g). The maximum reported weight of a mature testis was 160 g (USNM 504738).

The length of the longest reported fetus was 218 cm (Brimley, 1943, p. 199) and the length of the shortest reported calf was 196 cm (SEAN Bull., 3(5): 25). I have estimated the mean length at birth at 210 cm (the length of the calf that was reported by Rankin, 1955, p. 26).

#### *Mesoplodon ginkgodens*

The maximum reported length of a female was 16 feet (490 cm; Moore and Gilmore, 1965, p. 1239) and of a male 477 cm (Nishiwaki, Kasuya, Kureha and Oguro, 1972, p. 46).

The maximum reported weight of a mature testis was 140 g (Nishiwaki *et al.*, 1972, p. 48).

These data have to be used with caution because the sample size is extremely small (i.e. two).

#### *Mesoplodon grayi*

The maximum reported length of a female was 17 feet 6 inches (533 cm; von Haast, 1876, p. 457) and of a male 18 feet 6 inches (564 cm; Courtenay-Latimer, 1963, p. 122).

There are no reported gonad weights for this animal.

The shortest reported calf was 242 cm (SEAN Bull., 3(4): 14).

#### *Mesoplodon hectori*

The largest reported female was 443 cm and the largest male 430 cm (estimated), (Mead, 1981, pp. 430–1).

The weight of an immature testis was 1.6 g (1981, p. 431) and the maximum reported weight of a mature testis was 116 g (1981, p. 431).

The length of the shortest reported calf was 210 cm (1981, p. 431).

#### *Mesoplodon layardii*

These data have to be used with caution because the sample is extremely small (4).

This is the largest species of *Mesoplodon*, barring *M. pacificus* whose total length is unknown. The largest reported female was 615 cm and the largest male 584 cm (Ross, 1979, p. 298, table 10).

Gonad weights are unknown for this species.

The shortest reported calf was 280 cm (1979, p. 16) and the longest reported fetus 76 cm (Gaskin, 1968, p. 54).

#### *Mesoplodon mirus*

The largest reported female was 510 cm (Ross, 1979, p. 302, table 15) and the largest male 17 feet 6 inches (533 cm; Talbot, 1960, p. 406).

The testis weight for an immature male was 7 g (6.5 g) (Ross, 1979, p. 311, table 22) and the maximum weight of a testis was 170 g (USNM 504724). The minimum weight of a mature ovary was 11 g (Ross, 1979, p. 311, table 22), the 'mean' weight (derived by taking the lesser of the two ovary weights for USNM 504612) was 15 g and the maximum reported weight was 49 g (48.5 g; Ross, 1979, p. 311, table 22).

The length of the shortest reported calf was 233 cm (1979, p. 302; table 15) and the longest reported fetus was 105 cm (Ross, 1969, p. 585).

#### *Mesoplodon pacificus*

No known reproductive data. The only specimens of this species are two skulls found on beaches.

***Mesoplodon stejnegeri***

The largest reported female of this species was 17 feet 2.5 inches (525 cm; SEAN Bull., 2(10): 12) and the largest male 525 cm (Francis H. Fay, pers. comm.; the reported length of 16.5 feet (Anon. 1978, *Alaska*, 44(1): 20) was an error).

The ovaries of an immature female weighed 2.6 g (USNM 504330) and the minimum ovary weight of a presumably mature female was 12 g (11.6 g; SEAN 6497, SEAN Bull., 6(8): 9).

There are no reported fetuses or calves.

***Tasmacetus shepherdi***

The largest reported female was 660 cm (Mead and Payne, 1975, p. 213) and the largest male 23 feet (700 cm; Sorensen, 1940, p. 201). The gonads of the female weighed about 40 g each (Mead and Payne, 1975, p. 213) and were judged to be sexually mature.

These data must be used with caution because the sample size is extremely small (2).

***Ziphius cavirostris***

This is a more common ziphiid, perhaps the most common in terms of absolute numbers, and it has been the subject of a fishery in Japan. The shortest mature female was a 527-cm specimen with a 142-cm fetus (Filella, 1975, p. 49). The mean lengths of sexually mature individuals were 19 feet (580 cm) for females and 18 feet (550 cm) for males (Omura *et al.*, 1955, p. 117). The maximum reported length of a female was 24 feet 9 inches (754 cm; Fraser, 1946, p. 46) and of a male was 23 feet (700 cm; Nishiwaki and Oguro, 1972, p. 17). The maximum reported age was about 30 GLGs for a female and 36+ GLGs for a male (Ross, 1979, p. 46). This corresponds well to the maximum age of an unsexed tooth of 36+ GLGs and the maximum age of a male of 35 GLGs reported by Perrin and Myrick (1980, p. 6).

The ovary weight for a 269-cm calf was 5.2 g (USNM 504756). The minimum ovary weight at sexual maturity, taken as the lesser of the two weights in a mature female (USNM 504094), is 16 g. The maximum reported ovary weight was 57 g (56.7 g; Kenyon, 1961, p. 72). The minimum weight of a sexually mature testis was reported as 150 g (Ross, 1979, p. 48). This was for an animal that was physically mature and had at least 36 growth layers in the dental cementum. The weight seems rather low when compared to the maximum reported weight of 4 kg (Omura *et al.*, 1955, p. 117) and it may be that this represents a senescent animal whose testes have atrophied.

The length of the largest reported fetus was 267 cm (Tomilin, 1957, p. 438) and the shortest calf was 269 cm (USNM 504756). Accordingly I have taken 270 cm as an estimate for the mean length at birth.

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# Reproductive Parameters of Dolphins and Small Whales of the Family Delphinidae

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## ABSTRACT

The purposes of this review are to describe and critique methods used to estimate reproductive parameters, to summarize estimates in the literature and to examine patterns in the estimates and their implications. Reviewed are gestation period, fetal growth rate, size at birth, size and age at attainment of sexual maturity, average size and age of adults, maximum size, asymptotic length, ovulation rate, pregnancy rate, calving interval, length of lactation, weaning age, length of "resting" period, age and sex structure, and birth rates. Also discussed are the effects on the estimates of seasonality, schooling segregation, geographical variation and exploitation and the relationships between parameters.

## INTRODUCTION

Many populations of dolphins and small whales are exploited directly or incidentally (IWC, 1976–83) and must be assessed and managed. Most of the approximately 32 species (Mitchell, 1975) are poorly known, and the published information on them is scattered in a diverse and often obscure literature. For some species the literature contains widely varying estimates of parameters, a matter of some concern when scientists are asked to provide advice for management (e.g. see Smith, 1983).

The purposes of this review are several: to describe and critique methods used to estimate reproductive parameters, to summarize estimates in the literature and to examine patterns in the estimates and their implications.

It is not the purpose of this paper to review reproductive morphology, physiology, behavior or pathology, except to the extent that they are immediately relevant to estimation of parameters used in stock assessment and management. Broad reviews of reproductive morphology and function have been presented by Harrison (1969), Harrison, Brownell and Boice (1972) and others. Other relevant papers are contained in this volume.

## METHODS

In assembling parameter estimates we surveyed as much of the literature as was possible under the time constraints for publication of this volume. We do not believe that we have missed any major references and, while some length data may have been missed, the ranges of values presented here should be definitive of the present state of knowledge of the delphinids. We did not include data from the popular or semi-popular literature unless an obviously measured value was specified and the source of the information could be determined. We did not include lengths identified as estimates, but undoubtedly some of the supposed measurements are in fact estimates. We took considerable pains to avoid inclusion of the same data more than once but there likely is some duplication. We have taken into account information in other papers in this volume. However, because of considerations of timing this was not possible in all cases.

Body length can be measured in several ways: from the tip of the upper jaw to the notch in the flukes, or to the posteriormost extension of the flukes; in a straight line, or over the curvature of the body. We've tried to include only linear beak-tip-to-notch lengths, but some of the included lengths were probably taken in other ways, possibly contributing artificially to the range of length.

For derived estimates, such as average length of adults, we have included published estimates or have calculated the estimates ourselves where only raw data were published or for samples pooled across sources. We calculated standard deviations where sample size was adequate ( $\geq 25$ ).

Where specific identification was equivocal, we have omitted the data. It is possible that some early strandings of pilot whales in the eastern North Atlantic referred to *Globicephala melaena* were actually of *G. macrorhynchus* (see Duguay, 1968). Although two species of spotted dolphin (*Stenella* spp.) probably exist in the Atlantic (Perrin, Mitchell and van Bree, 1978), we included data only for specimens referred to *S. plagiodon*, because of the uncertain identity of animals referred to other nominal species (*S. frontalis* and *S. attenuata*).

## PARAMETERS

### Gestation Period and Fetal Growth Rate

#### Background and estimation methods

Gestation period is one of the least variable reproductive parameters on a within-species basis in delphinids and in mammals in general (Kiltie, 1982). Estimation of the gestation period is important to stock assessment and management because it comprises one segment of the calving interval. Fetal growth rates are important in determining the age of fetuses and in estimation of the length of gestation.

Estimates of gestation period, of some type, exist for 13 of the 32 delphinid species. Data of varying amounts and quality have been available for producing these estimates. Fetal growth rate has been estimated in only some of these cases. At least seven different methods have been employed. We group them here into three major categories: (a) direct observational estimates, (b) statistical

Table 1

Outline of the methods used to estimate gestation period for small cetaceans, with species for which the methods have been used

DIRECT		
I. Live captive		
<i>Tursiops truncatus</i>		<i>T. aduncus</i>
II. Embryology		
<i>Orcinus orca</i>		<i>Lagenorhynchus actus</i>
STATISTICAL		
III. Huggett and Widdas/Laws		
a. Within-population		
<i>Stenella attenuata</i>		<i>Globicephala melaena</i>
<i>Sotalia fluviatilis</i>		
b. Comparative		
<i>Pseudorca crassidens</i>		<i>Berardius bairdii</i>
<i>Pontoporia blainvillei</i>		
IV. Sacher and Staffeldt		
<i>Stenella longirostris</i>		<i>T. truncatus</i>
V. Comparative $G$ vs $L_n$		
a. Other delphinids		<i>S. longirostris</i>
b. Human growth curve		<i>G. melaena</i>
OTHER		
VI. Visual inspection of data		
<i>L. acutus</i>		<i>O. orca</i>
<i>Delphinus delphis</i>		<i>S. coeruleoalba</i>
VII. Not reported		
<i>O. orca</i>		<i>S. attenuata</i>
<i>G. melaena</i>		<i>D. delphis</i>
<i>G. macrorhynchus</i>		<i>L. acutus</i>
<i>P. crassidens</i>		<i>L. obliquidens</i>
<i>T. truncatus</i>		

estimates from series of specimens, and (c) 'other,' mostly non-rigorous methods (Table 1).

#### A. Direct observation

**Captive animals.** Estimates of this type are available for *Tursiops truncatus* only. The dates of conception and birth were observed for tank-held individuals. There are actually only a very few cases where conception date was known, with a larger series of observed births. Similar data may exist for other delphinids, but we did not find them.

**Embryology.** Guldberg and Nansen (1894) estimated gestation periods for *Orcinus orca* and *Lagenorhynchus acutus*. They gave detailed descriptions of the state of development of 'representative'-sized fetuses with collection dates and then inferred gestation periods qualitatively. This may have been an accurate technique, but Guldberg and Nansen's estimates have not to date been verified by direct observation or by statistical estimates based on data series.

#### B. Statistical estimates

All estimates in this category utilize standard regression techniques. Most require discrimination between modes in the distribution of fetal sizes by collection dates.

**Method of Hugget and Widdas (1951)/Laws (1959).** This the most commonly used technique for mammals in general, including delphinids. It utilizes the empirical concept that fetal growth in length ( $L$ ) or cube root of weight ( $W^{1/3}$ ) is directly related to time, and that two observable phases occur: a linear phase for most of the period, preceded by a briefer nonlinear phase (Fig. 1).

In estimating the total gestation period the gestation

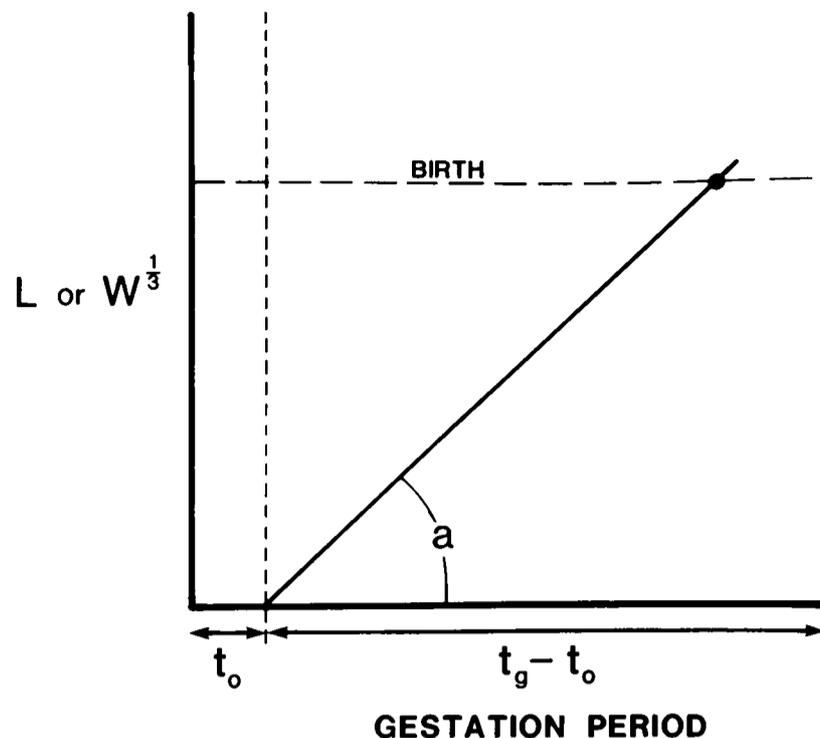


Fig. 1. Estimation of gestation period ( $t_g$ ) and fetal growth rate ( $a$ ) by the method of Hugget and Widdas (1951).  $L$  is total length,  $W$  is body weight,  $t_0$  is the early 'nonlinear' phase of growth.

time is divided into two phases. One phase ( $t_g - t_0$ ) extends to birth from the point where a straight line fitted to the data intersects the time axis. The other phase ( $t_0$ ) is from conception to the intersection. The linear phase is usually defined by a least-squares fit of time to modal points in  $L$  or  $W^{1/3}$ . The slope of the linear phase  $a$  is termed the fetal growth velocity. There is some indication that it is species-characteristic and varies with other measurable characters. The variables  $a$  and  $t_0$  are not the same for  $L$  and  $W^{1/3}$ , and the conversion from one set of units to the other is poorly defined. Work by Frazer and Hugget (1973) indicates that, at least for  $a$ , the relationship is not simply linear (i.e. not convertible by a common 'factor').

Estimation of ( $t_g - t_0$ ) requires a dependable estimate of length at birth. This in turn requires a series of specimens in sizes bracketing the true birth size. Length at birth can be estimated by interpolation as shown for *Stenella attenuata* by Perrin, Coe and Zweifel (1976) (also see below). In some cases a mean is calculated, in others the median is used. Both should be adequate if the real distribution of points is symmetrical. This method also requires an accurate separation of modes in size in a large data series. When modes are not distinct, this is undoubtedly a poor method. In some cases individuals are plotted rather than modes. This should be valid if breeding is distinctly seasonal.

Estimation of the early phase  $t_0$  is not straightforward or well defined. All applications refer back to Hugget and Widdas' (1951) simple breakdown of the proportion of gestation time in  $t_0$  by length of ( $t_g - t_0$ ). For example, for ( $t_g - t_0$ ) > 400 days, they said that  $t_0$  should be approximately  $0.1 \times t_g$ . Laws (1959) defined the relationship for length as being about 90% of that for weight. Both rules of thumb are arbitrary. Hugget and Widdas proposed the original scheme based on data from only seven species of terrestrial mammals. They extrapolated outside the limits of their data for the extreme values ( $t_g > 400$ ). Gestation periods for many delphinids lie outside the data range used by Hugget and Widdas.

A more precise definition of  $t_0$  is needed. As

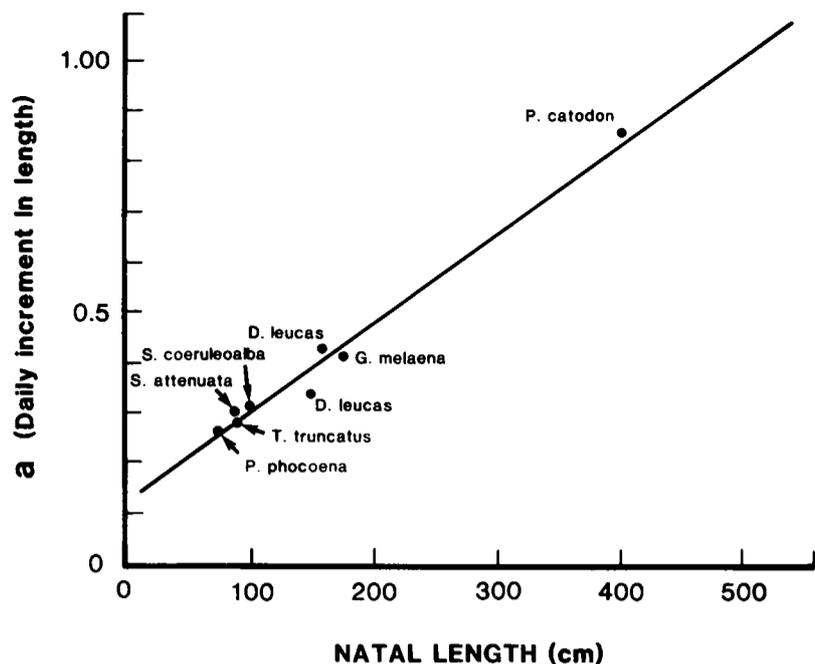


Fig. 2. Interspecific relationship between fetal growth rate ( $a$ ) and natal length, from Kasuya (1977).

mentioned above there appears to be a reasonably consistent relationship between  $a$ , (the slope of the linear phase) and size at birth. As shown in Fig. 2 (from Kasuya, 1977), the relationship appears to be linear, although the sample size employed is not large.

This relationship has been employed to estimate  $a$  for *Pseudorca crassidens* (Purves and Pilleri, 1978) and the non-delphinids *Pontoporia blainvillei* (Kasuya and Brownell, 1979) and *Berardius bairdii* (Kasuya, 1977). With this comparative slope estimate and an estimate of length at birth, the Hugget and Widdas procedure can be carried out. Unfortunately the large data series required for direct estimation of  $a$  is also generally required for a good estimate of natal length, so this relationship is of limited use.

**Method of Sacher and Staffeldt (1974).** The second type of statistical estimation is based on an empirically defined relationship between the duration of gestation and brain weight at birth, the ratio of birth to adult brain weight, and litter size. Sacher and Staffeldt examined a data series on 91 species of eutherian mammals. Variables included in the multiple-regression analysis were the above, plus (1) body weight at birth and (2) ratio of birth weight to adult body weight. The body-weight variables were not significantly related to gestation period. In applying this method one simply uses natal brain weight and litter size in the multiple-regression model. Our reservations about this procedure include the following:

- (1) Only two cetacean species were included in the 91 species from which the model was derived (*Tursiops truncatus* and *Phocoena phocoena*).
- (2) The use of data across many orders is useful in defining general patterns but probably does not provide good prediction within a particular order.
- (3) Use of ratios which include another predictor variable in the model is of questionable validity as a statistical technique.
- (4) Variables included in the original study were limited in scope; but  $R^2$  was high ( $> 0.9$ ).

**Comparative  $G$  vs  $L_n$ .** The third statistical approach utilizes the apparent relationship between duration of gestation ( $G$ ) and size at birth ( $L_n$ ) for other species within the Delphinidae (Fig. 3). Perrin, Miller and Sloan (1977)

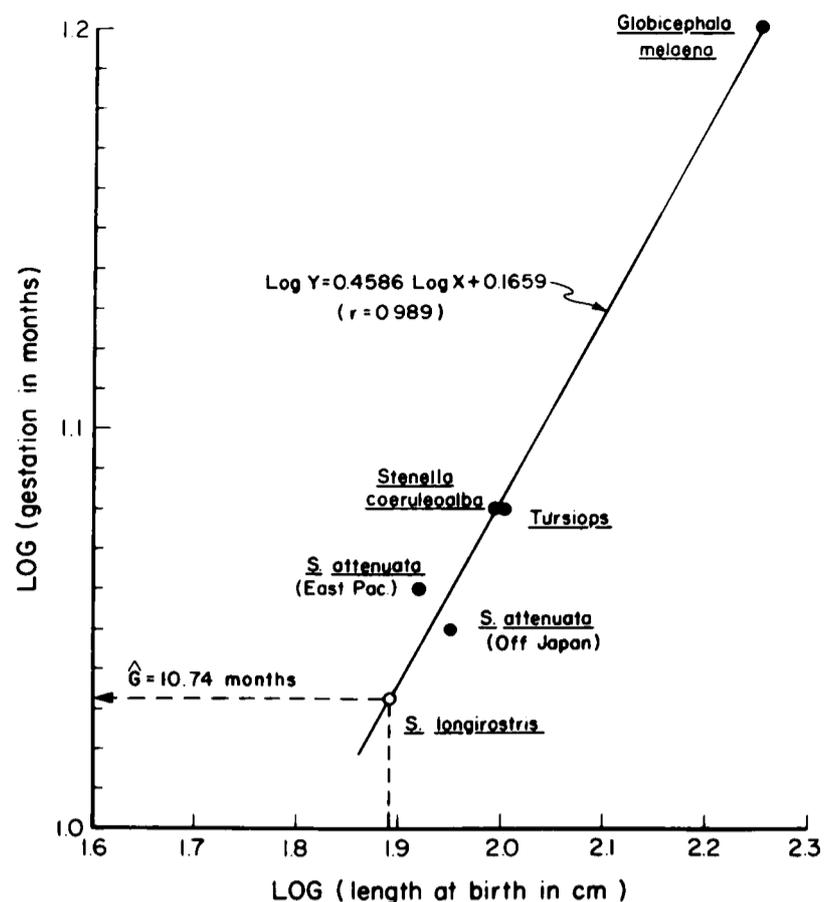


Fig. 3. Interspecific relationship between duration of gestation and size at birth, in four delphinid cetaceans, with extrapolation to predict length of gestation in the eastern spinner dolphin (from Perrin *et al.* 1977).

utilized this for *S. longirostris*. There was a fairly good fit by a straight line, but as with the other comparative relationship, the sample size available was not large.

### C. Other methods

These are generally visual fits to apparent modes in length frequencies or in frequencies of parturition or conception, e.g. *L. acutus* (Sergeant, St Aubin and Geraci, 1980) and *D. delphis* (Kleinenberg, 1956). This type of method may be a good first approximation for small data series but should be replaced by more quantitative, repeatable methods where possible.

Lastly, for nine species, estimates of gestation period were published with no accompanying information on data methods or sources.

### Available estimates

The published estimates of gestation period range from about 10 months to over 16 months (Table 2). As discussed above, there appears to be a relationship between length of gestation, fetal growth rate and birth size or brain weight at birth, such that larger delphinids (e.g. *Orcinus* and *Globicephala*) have longer gestation periods than do the smaller forms (*Stenella* or *Lagenorhynchus*).

There is an apparent contradiction between the results of Sacher and Staffeldt (1974) and those of the other statistical studies discussed here. They found no significant relationship between body size and gestation period. It would be of interest to pursue this disparity further, since the majority of comparative estimates (not just for delphinids) appear to utilize the body size/gestation relationship in some way.

Table 2

Gestation periods reported for delphinid cetaceans. Method types are defined in Table 1

Species	Estimate (months)	Method type	Source	Estimate (months)	Method type	Source	Estimate (months)	Method type	Source
<i>Sotalia fluviatilis</i>	10.0-10.3	III	Best and da Silva, 1984						
<i>Tursiops truncatus</i>	12	I	Essapian, 1963	12	I	McBride and Kritzler, 1951	12	I	Tavolga and Essapian, 1957
	13	IV	Perrin <i>et al.</i> , 1977						
('aduncus')	11.5-12	I	Ross, 1977						
<i>Globicephala melaena</i>	15.2	III	Sergeant, 1962	16.2	V	Sergeant, 1962	15.7	III	Frazer and Hugget, 1973
	15-16	VII	Harrison, 1969						
<i>G. macrorhynchus</i>	12	VII	Lowry, 1974						
<i>Stenella attenuata</i>	11.5	III	Perrin <i>et al.</i> , 1976	11.2	III	Kasuya <i>et al.</i> , 1974	9-10	VII	Harrison, 1969
<i>S. longirostris</i>	10.7	Va	Perrin <i>et al.</i> , 1977	9.5, 10.5	IV	Perrin <i>et al.</i> , 1977			
<i>S. coeruleoalba</i>	12	VI	Kasuya, 1972						
<i>Delphinus delphis</i>	10-11	VI	Kleinenberg, 1956	10	VII	Tomilin, 1957	11	VII	Harrison, 1969
	10	VII	Mal'm, 1932						
<i>Pseudorca crassidens</i>	15.5	III	Purves and Pilleri, 1978	11-12	VII	Harrison, 1969			
<i>Orcinus orca</i>	12-16	VI	Nishiwaki and Handa, 1953	12	II	Guldberg and Nansen, 1894	12	VII	Fraser, 1937
	12	VII	Grieg, 1889	11-12	VII	Harrison, 1969	12	VII	Christensen, 1984
'best'	15	I, VII	Perrin (ed.), 1982						
<i>Lagenorhynchus acutus</i>	10	II	Guldberg and Nansen, 1894	10	VII	Fraser, 1937	11	VI	Sergeant <i>et al.</i> , 1980
	11-12	VII	Geraci and St. Aubin, 1977						
<i>L. obliquidens</i>	10	VII	Harrison, 1969						
(Comparative estimates for other odontocetes)									
<i>Phocoena phocoena</i>	11	III	Laws, 1959	9	VII	Harrison, 1969			
<i>Pontoporia blainvillei</i>	11	III	Kasuya and Brownell, 1979	10.5-12	Va	Kasuya and Brownell, 1979			
<i>Berardius bairdii</i>	17	V	Kasuya, 1977	10	VII	Harrison, 1969			
<i>Delphinapterus leucas</i>	12	VII	Vladykov, 1944	14	III	Laws, 1959			
<i>Physeter macrocephalus</i>	16	III	Laws, 1959	16-17	VII	Harrison, 1969			

### Size at Birth

Estimates of size at birth are used in estimating the length of gestation and the time of birth. They are also the starting point for growth curves and ultimately contribute to estimates of the reproductive capacity of a population.

There are two basic categories of methods used to estimate length at birth. One quantitative method which has been employed for delphinids is termed '50% interpolation' in Table 3. In this method, the percentage of specimens which are postnatal is plotted for length categories or for length modes. The point on the length axis which corresponds to 50% postnatal from a linear regression is defined as the estimate of length at birth. The basic assumptions of the method are that (1) pregnant females (i.e. fetuses) and calves are equally available to the sampling procedure used, (2) both suffer natural mortality at the same rate, (3) naturally born calves are accurately distinguished from aborted, near-term fetuses, and (4) the sample size is adequate.

A second quantitative method used to determine size at birth is calculation of the mean length in a sample of apparently newborn calves. This method assumes that newborn calves are easily distinguishable from slightly older individuals. It will usually overestimate size at birth, especially if the calving season is protracted.

The other category of methods can be roughly termed 'qualitative' in that they don't use statistical techniques. One common method is to examine a relatively small series of fetuses and newborn calves, note the lengths and qualitatively infer a likely intermediate value for length at birth. Another is to use the length of the smallest postnatal specimen. (See Appendix 1 for smallest calf and largest fetal lengths reported.) For a number of other populations the methods used to arrive at the reported birth length were not reported. There is a total of 28 estimates available for 14 of 32 delphinid species (Table 3).

Of the methods discussed, the 50%-interpolation method is preferable. The assumptions of the method should be closely examined for each situation, however. Hohn and Hammond (1983) have discussed the basic methods for estimating length at birth in detail.

### Size and Age at Attainment of Sexual Maturity

Age at attainment of sexual maturity is an important parameter in stock assessment because it is thought to vary with exploitation, as part of the density-dependent response that theoretically yields a net reproductive rate greater than zero (Smith, 1983). Such change has not been observed but it has been inferred to have occurred in some

Table 3  
Body lengths at birth reported for delphinids

Species and region	Length at birth (cm)	Method	Source
<i>Sotalia fluviatilis</i>	75	Qualitative interpolation	Best and da Silva, 1984
<i>Stenella coeruleoalba</i>			
(Japan)	99.8	50% interpolation	Kasuya, 1972
(Japan)	100	50% interpolation	Miyazaki, 1977
<i>S. attenuata</i>			
(Japan)	89	Mean length of 'newborns' in drive fishery	Kasuya <i>et al.</i> , 1974
(E. trop. Pacific)	82.5	50% interpolation	Perrin <i>et al.</i> , 1977
<i>S. longirostris</i>			
(E. trop. Pacific)	77	50% interpolation	Perrin <i>et al.</i> , 1977
<i>Delphinus delphis</i>			
(E. trop. Pacific)	81.3	50% interpolation	Hui, 1977
(E.N. Pacific)	79.0	50% interpolation	Hui, 1977
(Black Sea)	80-90	Not reported	Tomilin, 1957
(All)	105	Not reported	Scott, 1949
<i>Globicephala melaena</i>			
(W.N. Atlantic)	177	50% interpolation	Sergeant, 1962
<i>G. macrorhynchus</i>			
(W. Pacific)	135-146	Range in size of 'newborns'	Yonekura <i>et al.</i> , 1980
(S. Africa)	140	Qualitative inference from small sample	Ross, 1979
<i>Lagenorhynchus acutus</i>			
(W. Atlantic)	110	Method not reported	Sergeant <i>et al.</i> , 1980
<i>L. albirostris</i>			
(E.N. Atlantic)	125	Method not reported	Tomilin, 1957
<i>Orcinus orca</i>			
(Japan)	276	Smallest postnatal specimen	Nishiwaki and Handa, 1958
(N. Atlantic)	210	Qualitative inference from fetal and calf lengths	Jonsgård and Lyshoel, 1970
(NE. Pacific)	246	Direct observations of five stranded newborn	Bigg, 1982
(N. Atlantic)	208-220	Qualitative extrapolation from fetal development	Guldberg and Nansen, 1894
(All?)	210-250	Not reported	Tomilin, 1957
<i>Pseudorca crassidens</i>			
(All?)	193	Mean length youngest calves	Purves and Pilleri, 1978
(S. Africa)	160	Qualitative inference from few specimens	Ross, 1979
<i>Tursiops truncatus</i>			
(W.N. Atlantic)	100	Not reported	Sergeant <i>et al.</i> , 1973
(W.N. Atlantic)	115	Average length of 'true neonates'	Hohn, 1980
(All)	980-1260	Range of reports	Harrison, 1969
(?)	130	Not reported	Scott, 1949
(S. Africa 'aduncus')	838-1120	Range of eight specimens	Ross, 1977
<i>Sousa chinensis</i>			
(S. Africa)	100	Qualitative inference from specimen series	Ross, 1979
<i>Grampus griseus</i>			
(All?)	150	Not reported	Tomilin, 1957
(Japan)	110-120	Qualitative inference from specimen series	Mizue and Yoshida, 1962

instances, based on comparison of populations of one species (*Stenella longirostris* - Perrin and Henderson, 1984) or populations of two species (*S. coeruleoalba* and *S. attenuata* - Kasuya, 1976) with different histories of exploitation.

Knowledge of size at maturation is useful because it allows estimation of maturity status of animals for which only length data are available.

#### Definition and criteria of sexual maturity

For females, the most accepted definition of sexual maturity is that the animal has ovulated at least once, as

evidenced by presence of at least one corpus luteum or corpus albicans in the ovaries. The assumption is made that scars of ovulation (whether or not followed by pregnancy) remain visible in the ovaries indefinitely (see Perrin and Donovan, 1984). An additional assumption commonly made is that presence of any scar or body in the ovaries means that ovulation has occurred (e.g. Perrin *et al.* 1976). This is not a valid assumption, because some scars may denote non-ovulatory events, e.g. lutealization of unerupted Graafian follicles (Perrin and Donovan, 1984).

For males the question of what constitutes sexual maturity is more complex. Several criteria have been used

in population studies. Presence of spermatozoa in the center of the testis was employed by Kasuya, Miyazaki and Dawbin (1974). Miyazaki (1977) defined immature, pubertal and mature males as those having, respectively, no spermatozoa, both spermatogonia and spermatocytes, and spermatozoa in the center of the testis. Perrin *et al.* (1976) defined puberty and maturity based on presence of spermatogenesis in the center of the testis, rapid change in diameter of seminiferous tubules, and presence of spermatozoa in the epididymis. Perrin *et al.* (1977) and Perrin and Henderson (1984) defined several levels of sexual 'maturity' based on presence of spermatogenesis and amount of sperm in the epididymis. Sergeant (1962) defined the onset of 'functional' maturity as the point at which gross examination of the epididymis shows presence of seminal fluid, which occurs at testis weights somewhat greater than those at which spermatogenesis can be detected histologically. Other workers have used various combinations of these criteria; this, as well as the use of various estimation procedures – described below – must be kept in mind when making comparisons of estimates of size or age at attainment of maturity across species or across studies.

An assumption made in the use of presence of sperm in the epididymis as a criterion of sexual maturity is that adult males produce sperm on a constant basis. This assumption is not valid, as it has been shown in at least some species that males may enter a resting phase, during which testis size decreases and sperm are absent from the epididymis (Hirose and Nishiwaki, 1971; Perrin and Henderson, 1984; Collet and St Girons, 1984).

#### Estimation methods

Length and age at attainment of maturity in females have been estimated in various ways:

- (a) *The mean length or age when 50% are mature*, by inspection of data tabulated by length or age interval (Mayarova and Danilevskiy, 1934; Sergeant, 1962) or by estimation of the 50%-mature length (or age) from a line fitted to a plot of % mature on length or age intervals (Kasuya, 1972; Perrin *et al.*, 1976; Perrin *et al.*, 1977). Perrin *et al.* (1976) noted that an estimate obtained in this way is an overestimate, because some of the smaller mature animals are those that have stopped growing at a shorter-than-average length, yielding an asymmetrical (left-skewed) maturity-length curve.
- (b) *The length or age at which the number of smaller or younger mature females equals the number of larger or older immature females*. Kasuya *et al.* (1974) pointed out that an estimate by this method is biased downward, because it does not take into account the effect of natural mortality in reducing the relative number of longer or older animals.
- (c) *The length or age corresponding to the age or length at which 50% are mature*, taken from an age-length key or growth curve (Kasuya *et al.*, 1974; Perrin *et al.*, 1976).
- (d) *The average greatest length at which females have not yet ovulated*, estimated by back-extrapolation to the origin of a body-length/corpus-count curve (Perrin *et al.*, 1976). Average age at maturity can then be estimated from a length/age curve.

- (e) *The length at first conception*, estimated in gravid females with only one ovarian corpus (a corpus luteum). A length increment (taken from a length/age curve) corresponding to the estimated time since conception as estimated from the length of the fetus (taken from a fetal length/age curve) is subtracted from body length (Perrin *et al.*, 1976). Average age at maturity can then be taken from a length/age curve. This is a probable underestimate, because it is based only on females that become pregnant at the first ovulation.

DeMaster (1984) has examined the properties of these estimates in more detail.

Average length and testis weight at age at attainment of sexual maturity in males have been estimated by some of the same methods used for females (*a*, *b* and *c* above). In more recent studies, e.g. Perrin *et al.* (1977) and Perrin and Henderson (1984), values have been estimated for several indices of 'maturity' (described above), with the caution that not enough is known about the breeding systems of these animals at any particular length, age, testis size, etc., to say that they are 'socially mature' in the sense of Best (1969a).

#### Available estimates

Estimates of age at attainment of sexual maturity are available for 11 of the roughly 32 species of delphinids (Table 4). They range from 3 (*Delphinus delphis*) to 16 years (*Orcinus orca*). (The former is almost certainly an underestimate, due to the effects of schooling segregation – see discussion below.) In many cases only a fairly broad range of estimates is available (e.g. 8–14 years for *Pseudorca crassidens*), which highlights the rudimentary state of knowledge of the life histories of most of the delphinids. Additional data on testis weight (of smallest 'adult' testis and of largest testis) and on body length (largest sexually immature and smallest mature animals) are included in Appendices 2 and 1, respectively. It should be noted that many species vary in these parameters from region to region (discussed below).

#### Average Size and Age of Adults

Average adult size and age are other parameters that may change under exploitation, with changes in age structure of the population caused by selective harvest or by increased reproductive rates. Average size and age are also useful parameters in cross-species comparisons and deductive modeling (discussion below). Available estimates of average adult length and age are given in Appendices 3 and 4, respectively.

#### Maximum Size and Age and Asymptotic Length

These parameters are useful in deductive modeling of life history. Asymptotic length is important in any model of growth. Values of maximum size based on adequate samples ( $n \geq 25$ ) are available in the literature for about half the delphinid species (Appendix 1). The wide geographical variation apparent in some species is discussed below. Maximum ages based on large samples are available for only a handful of species (Appendix 4) and in many cases are expressed in terms of dentinal or cemental growth-layer groups (GLGs, terminology of

Table 4

Estimates of average length and age at attainment of sexual maturity and ages of oldest immature and youngest immature for delphinids. Sample sizes in parentheses; values rounded off to nearest year (y) or GLG - terminology of Perrin and Myrick 1980 - (G)

Species and region (stock in parentheses)	Average length at attainment of sexual maturity		Average age at attainment of sexual maturity		Oldest immature animal		Youngest mature animal		Source
	Male	Female	Male	Female	Male	Female	Male	Female	
<i>Steno bredanensis</i>									
W. North Pacific							14G (9)	17G (9)	Miyazaki, 1980
<i>Peponocephala electra</i>									
W. South Pacific					3G (1)	4G (2)	7G (3)	12G (1)	Bryden <i>et al.</i> , 1977
<i>Pseudorca crassidens</i>									
E. North Atlantic	396-457	366-427	8-14y	8-14y					Purves and Pilleri, 1978
W. North Pacific		380-399							Kasuya and Izumisawa, 1981
<i>Orcinus orca</i>									
E. North Atlantic	~ 579	457-488	~ 16y	~ 10y					Christensen, 1982; Jonsgård and Lyshoel, 1970
<i>Globicephala melana</i>									
W. North Atlantic	490	365	12y	6-7y	15y (13)	6y (5)	11y (19)	5y (12)	Sergeant, 1962
<i>G. macrorhynchus</i>		380-390				14G (2)	12G (2)	11G (1)	Ross, 1979
<i>Lagenorhynchus obliquidens</i>									
E. North Pacific	170-180								Harrison <i>et al.</i> , 1972
<i>L. obscurus</i>									
E. South Atlantic								18y	Best, 1976
<i>L. actus</i>									
W. North Atlantic	230-240	201-222				12y (6)		6y (26)	Sergeant <i>et al.</i> , 1980
<i>Tursiops truncatus</i>									
Both coasts of Florida	245-260	220-235	~ 11y <sup>1</sup>	~ 12y <sup>1</sup>	20y (10)	14y (11)	12y (6)	9y (17)	Harrison <i>et al.</i> , 1972; Leatherwood <i>et al.</i> , 1978; Sergeant <i>et al.</i> , 1973
S.W. Indian Ocean ('aduncus')	210-240	213-230	9-11G		4G (7)	4G (6)	9G (11)	10G (6)	Ross, 1979
<i>Grampus griseus</i>									
S.W. Indian Ocean					3G (4)	5G (4)		> 9G (1)	Ross, 1979
<i>Stenella longirostris</i>									
Gulf of Mexico	~ 190	~ 188		7-10G	> 8G (3)	> 11G (7)	> 9g (8)	> 8G (4)	Mead <i>et al.</i> , 1980
E. trop. Pac. (eastern)	160-170	164	6-9y	4-5y	8-9y (106)	6-9y (94)	5-7y (106)	3-5y (153)	Perrin <i>et al.</i> , 1977
E. trop. Pac. (n. whitebelly)	165-170	167	6-8y	4-6y	11-16y (48)	7-11y (37)	4-5y (52)	3-4y (150)	Perrin and Henderson, 1984
<i>S. coeruleoalba</i>									
E. trop. Pacific	195-200								Gurevich and Stewart, 1979
W. North Pacific	219	216	9y	9y	12y (70)	13y (126)	7y (222)	5y (541)	Miyazaki, 1977
S.W. Indian Ocean	210-220				13+G (5)	3G (1)	12+G (2)	7G (2)	Ross, 1979
<i>S. attenuata</i>									
E. trop. Pac. (offshore)	~ 195	181	11G	8G	13G (55)	11G (100)	7G (42)	7G (209)	Perrin <i>et al.</i> , 1976
W. North Pacific	194	182	12y	9y	16y (81)	12y (69)	8y (49)	8y (124)	Kasuya, 1976; Kasuya <i>et al.</i> , 1974
<i>Delphinus delphis</i>									
Black Sea	170-180	150-170	3y	(a) 4y (b) 2y					Kleinenberg, 1956; Kleinenberg and Klevezal', 1962; Mayarova and Danilevskiy, 1934; Sleptsov, 1941
E. North Atlantic	200	190	5-7G	6-7G					Collet, 1981
E. trop. Pac. (cent. trop.)	200		6-7G						Gurevich and Stewart, 1978;
E. North Pacific			7-12y		12y (21)	14y (9)	9y (10)	8y (19)	Oliver, 1973
S.W. Indian Ocean					12G (3)	8G (6)	11+G (2)	10G (1)	Hui, 1977
									Ross, 1979

<sup>1</sup> From N.E. Florida.

Perrin and Myrick, 1980) that have not yet been calibrated to real time. The greatest ages reported in terms of years are for *Stenella attenuata* (40 years for males and 46 years for females) and in GLGs for *Peponocephala electra* (47 GLGs for males).

Adequate estimates of asymptotic length are available for even fewer species (Appendix 3). In most cases it has been estimated simply as the average length of physically mature specimens (those in which the vertebral epiphyses are fused to the centra and which are presumed to have stopped growing in length). In cases where the authors presented length data for physical maturity but did not estimate asymptotic length, we carried out the calculation and included the value in Appendix 3.

Perrin *et al.* (1976) estimated asymptotic length in *Stenella attenuata* as the average length of specimens in which the pulp cavity of the tooth was occluded. They used this estimate in fitting a Gompertz model of growth to their data. In similar development of a growth model, Perrin *et al.* (1977) estimated asymptotic length for *S. longirostris* (eastern form) as the average length of animals with 13 or more dentinal GLGs. Kasuya (1976) estimated asymptotic length in *S. attenuata* and *S. coeruleoalba* (later revised upward by Miyazaki, 1977) as the length at which growth rate levels off, based on growth curves fitted to length/age data by eye. Perrin and Henderson (1984) estimated asymptotic length for the northern whitebelly form of *S. longirostris* with iterative fits of Gompertz models to age/length data. This last method involves the fewest assumptions and is probably the most appropriate of those discussed here, providing that the sample includes adequate numbers of older animals.

### Ovulation Rate

#### Background and estimation methods

The ovaries of cetaceans are unusual in that scars (corpora albicantia, or CAs) resulting from ovarian events persist for years and probably indefinitely in at least some species. Early on, it was thought by some workers (e.g. Sleptsov, 1941) that CAs persist indefinitely in all delphinids, that they result only from regression of corpora lutea (CLs) of pregnancy, and that there is never more than one CL per pregnancy. This supposedly resulted in a permanent record of the number of pregnancies experienced by a particular female. The potential value of such a record, coupled with accurate age determination, in modeling population dynamics for stock assessment and management is obvious, but more recent research has shown that the genesis and significance of ovarian scars are more complex than earlier thought (see sections II A and B and Appendix B of Perrin and Donovan, 1984). CAs do apparently persist indefinitely in at least some species, e.g. *Globicephala macrorhynchus* (Marsh and Kasuya, 1984) and perhaps *G. melaena* (Sergeant, 1962). In *Tursiops truncatus*, CAs resulting from several successive infertile ovulations in females just entering sexual maturity may be resorbed (Harrison *et al.*, 1972). In *Stenella* spp. (*S. attenuata*, *S. longirostris* and *S. coeruleoalba*) the data are equivocal. Some apparently senescent females have withered ovaries containing fewer CAs than do the

ovaries of some other younger females still reproductively active, indicating that some CAs may eventually be resorbed, or at least not detected with the methods used to examine the ovaries in most studies (Perrin *et al.*, 1976; 1977; Kasuya, 1976; Perrin and Donovan, 1984). CAs of infertile ovulation may be more likely to be resorbed than those of pregnancy (Harrison *et al.*, 1972). In any case, for most delphinids there is no assurance that the CAs represent a complete history of ovarian activity.

All CAs do not represent pregnancies; some are the result of regression of CLs of infertile ovulation (Harrison *et al.*, 1972; Benirschke, Johnson and Benirschke, 1980). Although CAs of pregnancy may be more likely to persist indefinitely than those of simple ovulation, there is the problem of distinguishing between the two types of CAs. Some workers (e.g. Ivashin, 1984) maintain that this can be done based on histological criteria, but the balance of scientific opinion holds that CAs of pregnancy cannot be distinguished from those of infertile ovulation with present knowledge (Perrin and Donovan, 1984).

There may be more than one CL per pregnancy. Multiple CLs are common in some odontocetes (e.g. monodontids, Brodie, 1972) but rare in delphinids (*loc. cit.*).

Although ovarian scars do not provide a reliable record of fecundity, they are, at least for younger animals, a relative index of ovarian activity, i.e. estrus and ovulation, and thus potentially are still valuable in characterizing the structures, breeding systems and dynamics of populations. The somewhat controversial question of spontaneous vs induced ovulation is relevant to interpretation of CAs and estimation of ovulation rate. Harrison (1969) and Harrison *et al.* (1972) concluded that some delphinids (e.g. *Globicephala melaena*, *Pseudorca crassidens*, and perhaps *Stenella* spp. and *Lagenorhynchus obliquidens*) are probably spontaneous ovulators, but that others, in particular *Tursiops truncatus*, are reflex ovulators, i.e. require copulation and/or presence of a mature male to trigger ovulation. This and similar conclusions by Saayman and Taylor (1977) and Ross (1977) are based mainly on data for captive animals, i.e. observations that the ovaries of some captive females that have not been kept with adult males contain very few or no CAs despite having been of adult size and age for several years. In view of more recent work, however, it seems likely that these low rates or absence of ovarian activity may be related to other aspects of captivity. Longitudinal monitoring and experimentation have now shown clearly that both *Delphinus delphis* and *Tursiops truncatus* in captivity are spontaneous, albeit sporadic, ovulators (Kirby and Ridgway, 1984), and results of analyses of ovaries of *Stenella attenuata* and *S. longirostris* suggest that these dolphins ovulate spontaneously in the wild (Benirschke *et al.*, 1980), perhaps with more regularity than observed for other species in captivity. This endogenicity and regularity makes corpus-count data from wild populations potentially more valuable in modeling than would otherwise be the case.

Another important consideration in estimating ovulation rate from corpus-count data is that of variation with

age. Models of ovulation rate that employ a linear fit to corpus-count/age data (e.g. Kasuya, 1972, for *Stenella coeruleoalba*; Kasuya, 1976, for *S. coeruleoalba* and *S. attenuata*) assume no change in ovulation rate with age, but these linear fits are not good; inspection of the data shows systematic underestimation of rates in very young females and overestimation for old females. Curvilinear models (Perrin *et al.*, 1976; Perrin *et al.*, 1977; Perrin and Henderson, 1984) fit the data better and are consonant with data for captive animals, which indicate that young females may ovulate two or more times in relatively quick succession when entering sexual maturity (Harrison *et al.*, 1972). Data for old females indicate that some are reproductively senescent (Perrin *et al.*, 1976; Marsh and Kasuya, 1984). A typical pattern is that in *S. attenuata* (Perrin *et al.*, 1976) of 4 ovulations in the first year of sexual maturity, 2 in the second, and about 1 per year thereafter, until some time beyond about 13 years of reproductive age, when some individuals become senescent. In some other populations (e.g. *Stenella longirostris* – Perrin *et al.*, 1976) the rates for very young females are only slightly higher than for older females. As pointed out by Perrin *et al.* (1976) and Kasuya *et al.* (1974), estimates for ages beyond about 12 years have been unreliable because of underestimation of age caused by difficulty in interpreting very thin and convoluted dentinal GLGs in older animals.

Another source of error in corpus count/age data is the inclusion of corpora atretica and other scars of non-ovulatory events in the corpus-count (e.g. Perrin *et al.*, 1976 and 1977; Perrin and Henderson, 1984). The count should include only CLs and CAs (Perrin and Donovan, 1984).

In fitting models to corpus-count/age data to estimate ovulation rates, individual variation in age at attainment of sexual maturity must be taken into consideration. If the relationship of % mature to age is a symmetrical S-shaped curve and the curvilinear fit to corpus-count/age data is unweighted, this factor does not affect the analysis. In some instances, however, e.g. in the 'eastern' population of *Stenella longirostris* in the eastern Pacific (Perrin and Henderson, 1984), the maturation curve is quite skewed, and in such cases allowance for individual variation in age at maturation should be incorporated in the model. Perrin *et al.* (1976 and 1977) and Perrin and Henderson (1984) estimated average reproductive age  $\bar{A}$  for an age interval  $p$  as

$$\bar{A} = \left( \sum_{i=1}^p a_i b_i \right) \div c$$

where  $a_i$  = % maturing in  $i$ th interval (% mature in  $i$  minus % mature in  $i-1$ );  $b_i$  = average reproductive age in interval  $p$  of females mature in  $i$ ; and  $c$  = % mature in interval  $p$ . Average reproductive age in the  $i$ th interval of females maturing in  $i$  was set at 0.50.

Another method of estimating ovulation rate is based on estimated ages of CAs as indicated by size and other indices of degree of regression of the CL (Sergeant, 1962; Kasuya, 1972; Kasuya *et al.*, 1974). As pointed out by Kasuya (1976) and Miyazaki (1977), this method is not satisfactory for the delphinids because size of a CA is not a reliable index of its age, beyond the very early stages of regression of the CL.

Any use of estimates of ovulation rate in modeling (e.g. application to a corpus-count frequency distribution to obtain an age-frequency distribution) should only be done keeping in mind the very great individual variation in ovulation rate and resulting relatively low precision of the estimator. As can be seen in any scatterplot of corpus-count on age for a wild population (Kasuya, 1972; Kasuya *et al.*, 1974; Perrin *et al.*, 1976 and 1977; Sergeant *et al.*, 1980), variation can be sixfold or greater even among fully-mature females. Rates for adult captive animals of the same species kept under the same conditions can range from none to several ovulations per year (Wells, 1984; Kirby and Ridgway, 1984). Thus, corpus count is not a reliable predictor of age for individual animals, and any population index based on it will have an extremely large variance.

#### Available estimates

The available estimates of ovulation rates (Table 5) vary broadly among the delphinids. They also vary considerably within a species, depending on region and on the model employed. The curvilinear models are more consonant with the estimates based on direct observations than are the linear models. The difference between the estimates for the two stocks of *Stenella longirostris* is discussed below in the section on effects of exploitation.

### Pregnancy Rate and Calving Interval

#### Estimation methods

Annual pregnancy rate (APR) is usually estimated as the percentage of mature females pregnant (including those that are simultaneously pregnant and lactating) divided by the length of gestation (expressed in years). Several assumptions are implicit in this simple model:

- (a) There is no sampling bias caused by selectivity, i.e. the distribution of reproductive conditions in the sample is the same as in the population sampled. Factors that can invalidate this assumption include differential vulnerability (e.g. pregnant females easier to catch) and school or areal segregation by age or reproductive condition (e.g. more 'breeding' schools sampled than other types of schools). The latter factor is discussed below.
- (b) There is no sampling bias caused by seasonality of calving (also discussed below).
- (c) All pregnancies are detected. A very small embryo can be overlooked, especially in the field. If presence of a corpus luteum (CL) is used as a criterion of pregnancy, the estimate of APR is biased upward, because not all CLs derive from pregnancies and some pregnancies result in more than one CL (Perrin and Donovan, 1984).

APR can also be estimated as the reciprocal of calving interval (CI) calculated as the sum of independent estimates of the lengths of the component phases of the reproductive cycle: gestation, lactation (discussed below) and 'resting' (time spent neither pregnant nor lactating). The estimate of the length of the cycle obtained this way must be adjusted downward to take into account any overlap of lactation and pregnancy, by a factor equal to

Table 5  
Ovulation rates in delphinids

Species and region (stock in parentheses)	Rate (ovulations/year or GLG)	Model/method	Source
<i>Pseudorca crassidens</i>			
E. North Atlantic	Possibly several/y	—	Comrie and Adams, 1938
E. North Atlantic	About one/y	—	Purves and Pilleri, 1978
<i>Globicephala melaena</i>			
W. North Atlantic	2.4–2.5/y	—	Sergeant, 1962
<i>Lagenorhynchus obliquidens</i>			
E. North Pacific	High compared to other delphinids	—	Harrison <i>et al.</i> , 1972
<i>L. acutus</i>			
W. North Atlantic	> 1/y	—	Sergeant <i>et al.</i> , 1980
<i>Tursiops truncatus</i>			
W. North Atlantic	~ 1/GLG after ~ 15 GLGs	—	Sergeant <i>et al.</i> , 1973
Not given (captive)	None to several/y	Direct observations	Kirby and Ridgway, 1984
<i>Stenella longirostris</i>			
E. trop. Pacific (eastern)	~ 1/GLG, declining slightly with age	$Y = 1.39X^{0.79}$	Perrin <i>et al.</i> , 1977
E. trop. Pacific (eastern)	Same	$Y = 13.68(i - e^{-0.099x})$	Perrin and Henderson, 1984
E. trop. Pacific (n. whitebelly)	~ 3/first GLG, 2/second, falling off rapidly to < 1/GLG.	$Y = 6.80(i - e^{-0.654x})$	Perrin and Henderson, 1984
Central Pacific (captive)	Several/y	Direct observations	Wells, 1984
<i>S. coeruleoalba</i>			
W. North Pacific	0.69/y (0.25 to 1.6)	$Y = 0.69X - 5.16$	Kasuya, 1972
W. North Pacific	0.59/y, between 10 and 15y	$Y = 0.590X - 4.875$	Kasuya and Miyazaki, 1975
W. North Pacific	0.41/y, between 5 and 25y	$Y = 0.414X - 2.40$	Kasuya, 1976
	0.12/y, between 26–43y	$Y = 0.115X - 6.55$	Kasuya, 1976
W. North Pacific	~ 3/y (1.5 to 12)	Ovary diagram	Miyazaki, 1977
<i>S. attenuata</i>			
W. North Pacific	0.43, increasing slightly with age	$Y_i = 0.00327X_i + 0.4286$	Kasuya <i>et al.</i> , 1974
W. North Pacific	0.41/y	$Y = 0.412X - 1.97$	Kasuya <i>et al.</i> , 1974
E. trop. Pacific (offshore)	~ 4/first GLG, 2/second, falling off to ~ 1/GLG	$Y = 4.06X^{0.51}$	Perrin <i>et al.</i> , 1976
<i>Delphinus delphis</i>			
E. North Pacific (captive)	None to several/y	Direct observations	Kirby and Ridgway, 1984

the percentage of lactating females also pregnant (Perrin *et al.*, 1977).

An approximate variance of the APR has been estimated (e.g. Perrin *et al.*, 1977) as

$$\text{var}(\text{APR}) = \text{APR}(1 - \text{APR})/n$$

which is the variance of a simple proportion. Since the basic APR estimate includes adjustment of the proportion pregnant ( $P$ ) by the gestation period in years ( $T_G$ ), the above method will generally underestimate var(APR). A better approximation of var(APR), using the delta method (Seber, 1973), is

$$\text{var}(\text{APR}) = (-P/T_G^2)^2 \text{var}(T_G) + (1/T_G^2) P(1 - P)/n_p,$$

where  $n_p$  is the sample size used to estimate  $P$ . This assumes that  $P$  and  $T_G$  are independently estimated, i.e.  $\text{cov}(P, T_G) = 0$  and, on a more practical level, that an estimate of the variance of  $T_G$  exists. While gestation period is one of the least variable vital parameters, estimation of  $T_G$  is usually not straightforward and variances have not been estimated in most cases (see 'Gestation period and fetal growth rate,' above).

The above does not hold for APR estimated as the reciprocal of the sum of the component phases of the reproduction cycle. This estimate of APR and its variance are more complex and dependent upon unbiased estimates of not only the proportion pregnant, but those

lactating and in gestation. Also, pregnancy rate estimated by this second method is systematically negatively biased (L. L. Eberhardt, personal communication to WFP, 2/13/80).

The variance of the calving interval estimate can also be derived using the delta method. With  $\text{CI} = 1/\text{APR}$ , the approximate variance is

$$\text{var}(\text{CI}) = (\text{APR}^{-4}) \text{var}(\text{APR}).$$

#### Available estimates

Estimates of APR are available for only a few species (Table 6). They range from 12% (from the data of Jonsgård and Lyshoel, 1970, for *Orcinus orca* in the North Atlantic) to about 75% (*Tursiops truncatus* and *Delphinus delphis* in the Black Sea). In some cases where two or more estimates are available for the same population, they vary by a factor of about two or more (*Orcinus orca*, *Stenella coeruleoalba* and *Delphinus delphis*). At least some of this variation must be due to violation of the above-listed assumptions. In the case of the Black Sea (*Tursiops truncatus* and *Delphinus delphis*), Kleinenberg (1956) pointed out that calving females apparently leave the area of the fishery and remain apart during early lactation, thus causing a downward bias in the estimated length of lactation and an upward bias in APR. The estimate of APR for the Black Sea population

Table 6

Estimates of annual pregnancy rate (APR) and calving interval (CI) for delphinids. Criterion of pregnancy noted as fetus present (F) or corpus luteum present (CL). Method for estimating APR noted as percentage of mature female pregnant P divided by gestation period G expressed in years (P/G); as reciprocal of sum of separately estimated reproductive phases (S); or as inferred from several lines of evidence (I). Estimates of calving interval CI noted as reciprocal of APR or of sum of phases S

Species and Region (stock or years in parentheses)	Mature females (no.)	Percent pregnant P (and criterion) (%)	Annual pregnancy rate APR (and method) (%)	Calving interval CI (and method) (years)	Source of estimates or data
<i>Pseudorca crassidens</i>					
E. North Atlantic	(59)	14.0 (F)	—	—	Purves and Pilleri, 1978
W. North Pacific	(38)	21.1 (F)	—	—	Kasuya and Izumisawa, 1981
<i>Orcinus orca</i>					
E. North Atlantic	(430)	13.7 (F)	12.0 (P/G of 15 months)	8.3	(1/APR) IWC, 1982 (Jonsgård and Lyshoel, 1970)
E. North Atlantic	(161)	34.9 (F)	28.9 (P/G of 15 months)	3.5	(1/APR) IWC, 1982 (Christensen, 1981)
E. North Atlantic	(51)	39.2 (CL)	32.8 (P/G of 15 months)	3.0	(1/APR) IWC, 1982 (Christensen, 1982)
Antarctic	(91)	27.5 (F)	13.7 (P/G, adj. for season)	7.3	(1/APR) IWC, 1982 (Mikhalev <i>et al.</i> , 1981)
<i>Globicephala melaena</i>					
W. North Atlantic	(500) <sup>1</sup>	39.8 (F)	30.0 (1/S)	3.3	(S) Sergeant, 1962
E. North Atlantic	(30)	40.0 (F)	—	—	Purves and Pilleri, 1978
<i>Tursiops truncatus</i>					
Black Sea	(24)	63.0 (—)	63.0 (P/G of 12 months)	1.3–1.5	(1/APR) Danilevskiy and Tyutyunnikov, 1968
W. North Pacific	(140)	43.6 (F)	43.6 (P/G of 12 months)	—	— Kasuya and Izumisawa, 1981
<i>Grampus griseus</i>					
W. North Pacific	(13)	30.8 (F)	—	—	— Kasuya and Izumisawa, 1981
<i>Stenella longirostris</i>					
E. trop. Pacific (eastern, 1973–81)	(569) <sup>2</sup>	30.8 (F)	34.9 (P/G of 10.6 months)	2.9	(1/APR) Henderson <i>et al.</i> , 1980; Oliver <i>et al.</i> , 1983
E. trop. Pacific (n. whitebelly, 1973–81)	(435) <sup>2</sup>	29.0 (F)	32.8 (P/G of 10.6 months)	3.0	(1/APR)
E. trop. Pacific (s. whitebelly, 1973–81)	(132) <sup>2</sup>	26.5 (F)	30.0 (P/G of 10.6 months)	3.3	(1/APR) Perrin and Oliver, 1982
<i>S. coeruleoalba</i>					
E. trop. Pacific (all stocks)	(23)	30.4 (F)	30.4 (P/G of 12 months)	3.3	(1/APR) Perrin and Oliver, 1982
W. North Pacific (1968–71)	(361)	29.9 <sup>4</sup> (F)	29.9 (P/G of 12 months)	~ 3	(S) Kasuya, 1972
W. North Pacific (1952–58)	(321)	40.5 <sup>4</sup> (CL)	40.5 (P/G of 12 months)	4.2 (est. initial) to 1.8 (1973)	(1/APR) Kasuya and Miyazaki, 1975
W. North Pacific (1961–68)	(301)	33.6 <sup>4</sup> (CL)	33.6 (P/G of 12 months)		
W. North Pacific (1970–73)	(950)	55.6 <sup>4</sup> (CL)	55.6 (P/G of 12 months)		
W. North Pacific (1971–75)	(165)	70.9 <sup>4</sup> (—)	70.9 (P/G of 12 months)		
<i>S. attenuata</i>					
E. trop. Pacific (n. offshore, 1973–78) <sup>3</sup>	(522) <sup>2</sup>	36.0 (F)	37.6 (P/G of 11.5 months)	2.7	(1/APR) Henderson <i>et al.</i> , 1980; Oliver <i>et al.</i> , 1983; Perrin and Oliver, 1982
E. trop. Pacific (n. offshore, 1979–81)	(493) <sup>2</sup>	28.4 (F)	29.6 (P/G of 11.5 months)	3.4	(1/APR)
E. trop. Pacific (s. offshore, 1973–80)	(277) <sup>2</sup>	39.4 (F)	40.0 (P/G of 11.5 months)	2.5	(1/APR) Perrin and Oliver, 1982
W. North Pacific (1970–73)	(250)	26.8 <sup>4</sup> (—)	28.7 (P/G of 11.2 months)	3.5	(1/APR) Kasuya <i>et al.</i> , 1974
W. North Pacific (1970–76)	—	— (—)	25.4 <sup>5</sup>	3.9	(1/APR) Kasuya, 1976
<i>Delphinus delphis</i>					
Black Sea (1936–39)	(1179)	—	75.0 (I of preg. in 3 out of 4 years)	1.3	(1/APR) Sleptsov, 1941
Black Sea (1946)	(934)	80.4 (—)	75.0	1.3	(1/APR) Kleinenberg, 1956
Black Sea (1949)	(231)	40.7 (—)	46.4 (P/G of 11.5 months)	2.2–2.3	(1/APR) Sokolov, 1962
E. trop. Pacific (all stocks)	(365)	36.2 (F)	37.8 (P/G of 11.5 months)	2.6	(1/APR) Henderson <i>et al.</i> , 1980; Oliver <i>et al.</i> , 1983; Perrin and Oliver, 1982

<sup>1</sup> Excludes 29 'anoestrous or infertile'.

<sup>2</sup> Excludes senescent.

<sup>3</sup> Includes only specimens from sets in which 40 or more killed.

<sup>4</sup> Values differ from those in sources because all PL (simultaneously pregnant and lactating) included here, rather than only  $\frac{1}{2}$ .

<sup>5</sup>  $\frac{1}{2}$  PL included.

of *Delphinus delphis* of 75% reflects a conclusion by Sleptsov (1941) that adult females become pregnant 3 years running and skip the fourth year. The inference was also based on modal progression of fetal and calf length and on regression of ovarian corpora, but mainly on the proportion of pregnant females in the catch. For *Stenella coeruleoalba* in the western North Pacific, Miyazaki and Nishiwaki (1978) have posited similar segregation by reproductive condition and pointed out that the various types of schools have not been equally sampled, causing an overestimate of APR in some studies (e.g. Kasuya and Miyazaki, 1975, and Kasuya, 1976).

For some species, e.g. *S. attenuata* and *S. longirostris*, the range of estimates is fairly small. Where sample size allowed, Henderson, Perrin and Miller (1980) adjusted for bias caused by differential capture vulnerability with age in *S. attenuata* by including data only from purse-seine sets in which 40 or more dolphins were killed; these samples are thought to be more accurately representative of the population than are small-kill samples. The effect is to adjust APR upward. Perrin and Oliver (1982) discussed other biases in the data. The estimates for *S. attenuata* (n. offshore, 1973–78) by the two methods described above (37.6% and 32.3%) are not statistically different from each other (at  $\alpha = 0.05$ ) nor are the estimates of APR for three populations of *S. longirostris* in the eastern tropical Pacific. The 'Method-2' estimates of APR of Perrin *et al.* (1977), Perrin and Henderson (1979) and Henderson *et al.* (1980) are invalid for reasons discussed below in the section on lactation.

The estimate of 13.7% for *Orcinus orca* in the Antarctic (IWC, 1982, from data in Mikhalev, Ivashin, Zavusin and Zelemaya, 1981) is based on division of fetuses into yearly cohorts based on length. This correction is necessary because gestation lasts more than a year and possible because breeding is sharply seasonal.

### Length of Lactation and Age at Weaning

The lactation period is the most variable component of the calving cycle. As such, it is important in any model or hypothesis of change in reproductive rate in a population. It can change in two ways: through change in average age at weaning, or through change in differential calf mortality (mortality of nursing calves minus mortality of lactating females). In the former case, the average lactation time per weaned calf decreases with decreased lactation time, but in the latter case it increases (because the lactation time spent on calves that die before weaning must be added to that spent on calves that survive to weaning age).

### Estimation methods

(a) *Ratio of lactating to pregnant.* The most common method of estimating length of lactation is based on the assumption that the proportion of a sample of mature females that is in a particular reproductive condition is directly proportional to the relative length of time spent in that condition. Thus, if an estimate of length of gestation is available, length of lactation can be estimated as

$$T_L = T_G \cdot L/P$$

where  $T_G$  = length of gestation;  $L$  = proportion of sample lactating;  $P$  = proportion of sample pregnant

(including animals both lactating and pregnant). This estimation is based on the same assumptions and subject to the same potential biases as discussed above for the estimation of pregnancy rate.

(b) *Cow-calf method.* This method estimates age at weaning. Age at weaning is not equivalent to length of lactation, because it does not take into account differential calf mortality. However, it has often been used as an estimate of lactation time. The cow-calf method assumes that for each lactating cow in a sample there should be also a suckling calf present. The age of the longest calf thus assumed suckling is an estimate of maximum age at weaning. The method assumes that at least some calves reach weaning age. It contains both a downward bias because the longest suckling calf could be expected to continue suckling for some unknown length of time, and an upward bias because it does not consider individual variation in length with age. The method is very sensitive to random error because dispersion of length in the longer calves assumed to be suckling is relatively great and growth at these lengths is relatively slow, meaning that a small difference in length yields a relatively large difference in age estimated from a growth curve.

The cow-calf estimate has been used inappropriately as an estimate of average age at weaning ('Method 2' calculation in Perrin *et al.* (1977) Perrin and Henderson, 1979 and Henderson *et al.* (1980)); the overestimation of lactation time is in addition to that caused by the differential calf mortality (discussed below) that is known to exist in the dolphin population involved in the tuna purse-seine fishery in the eastern tropical Pacific (Perrin and Oliver, 1982). Miyazaki (1977) modified the cow-calf method in an attempt to estimate average weaning age. After assigning calves to suckling or non-suckling categories in each of 19 samples (based on length of the assumed oldest suckling calf in that sample), he used the age at which 50% of all the calves in the pooled sample were estimated to be still suckling as an estimate of average age at weaning. This procedure may improve the accuracy of maximum weaning age as an estimate of length of lactation, but it does not address the problem of differential calf mortality.

In the simplest situation, that of no differential calf mortality (Fig. 4), the accuracy of maximum age at weaning ( $w_{\max}$  in Fig. 4a) as an estimate of length of lactation depends on the total length of suckling and on the variance of average weaning age ( $\bar{w}$ ). With the addition of differential calf mortality (in Fig. 4b), lactation can cease in two ways (because of weaning or because of death of the calf with survival of the mother), and weaning age ( $w_{\max}$ ) becomes still more of an overestimate of length of lactation ( $\bar{l}$ ). Sensitivity to amount of differential mortality is high ( $B$  and  $C$  in Fig. 4). A countervailing factor causing underestimation of maximum weaning age (by  $w_{\max}$  in Fig. 4b) from tuna-fishery data is the fact that too many suckling calves are present in the sample in relation to the number of lactating cows (calves are more vulnerable to capture), causing the length of the longest suckling calf to be underestimated. In the extreme case of complete differential mortality, i.e. no survival to weaning age ( $D$  in Fig. 4), the estimate of weaning age by the cow-calf method becomes actually an estimate of maximum length of lactation corresponding to maximum age to which

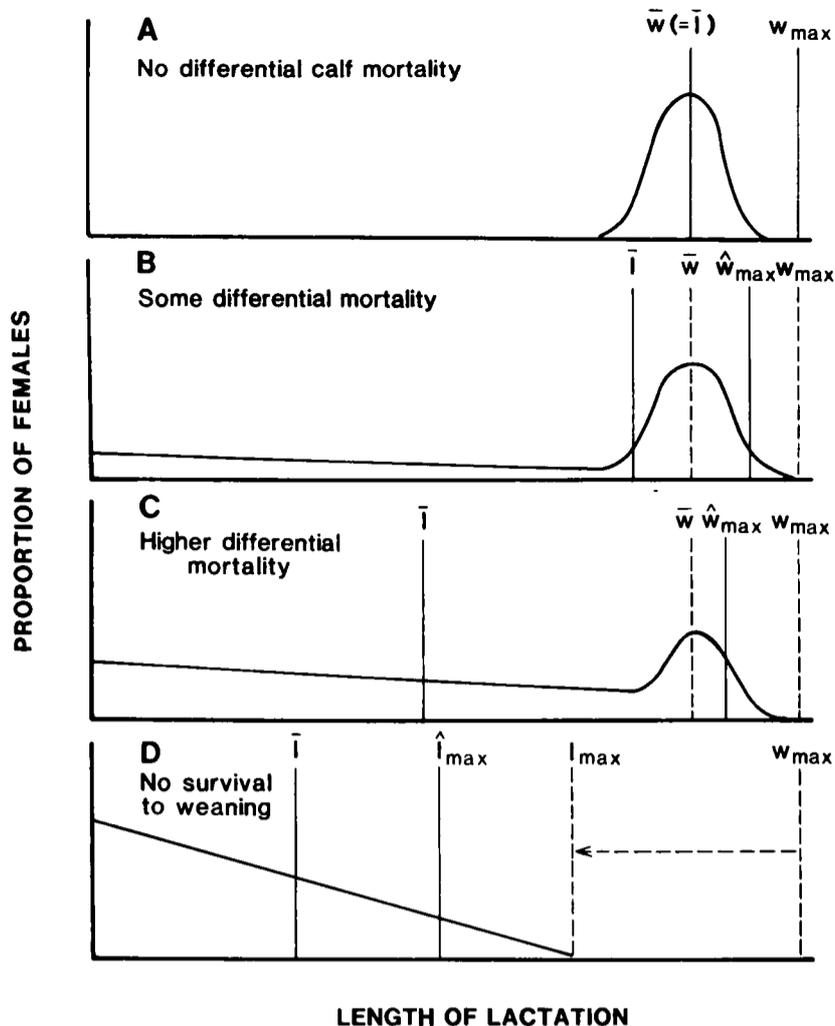


Fig. 4. Conceptual model of relationships between length of lactation ( $l$ ), age at weaning ( $w$ ) and differential calf mortality.

calves survive ( $l_{\max}$ ). The complete relationships between estimates of weaning, estimates of length of lactation and differential calf mortality have not been quantitatively modeled, so the usefulness of the cow-calf method at this point is problematical.

(c) *Stomach contents*. Although the examination of stomach contents allows direct determination of a shift from milk to solid food plus milk, (e.g. Perrin *et al.*, 1976) estimation of age at weaning by this method is open to question because of the difficulty of detecting small quantities of milk mixed with solid food. Odontocetes may continue to suckle for long periods, in some cases years after a major shift to solid food. The extended duration of cow-calf bonding may serve some non-nutritional function (Brodie, 1969). P. B. Best (personal communication to WFP) has employed a chemical test for lactose in his examination of sperm-whale stomachs. The color reagent used can detect sperm-whale milk at a 30-fold dilution. Without data on suckling rates and milk volume consumed during the latter stages of nursing lasting for years and data on the rate of digestion of milk, it is not possible to know whether this test is sufficiently sensitive to allow estimation of weaning age from stomach contents.

If mortality rates for weaned and unweaned calves are different, an estimate of average age at weaning based on a 50% -weaned criterion for a sample of animals would be biased. For example, if weaned calves have higher mortality, the estimate of average weaning age would be biased upward.

(d) *Behavioral observations*. Individual nursing calves can be observed in captivity or in the wild. This method has resulted in a general consensus that *Tursiops truncatus* calves usually nurse about 18 months, with a lot

of variation. For other species that are rare in captivity or difficult to observe in the wild, a sample-size problem is soon encountered. There is also the question of the effect of captivity. A bottlenose dolphin in an oceanarium in South Africa developed a habit of squirting milk at the glass at an observation post to startle visitors. This animal suckled for 38 months, possibly because of the learned behavior (Ross, 1979).

#### Available estimates

The available estimates of length of lactation (Table 7) range from 8 months (*Stenella coeruleoalba* off Japan during the period 1970-73) to 27 months (*S. attenuata* off Japan, 1970-76). The modal value appears to be 18-20 months (8 of the 21 estimates in Table 7). The relatively low values for *S. coeruleoalba* off Japan (8-20 months) and *Delphinus delphis* in the Black Sea (14-19 months) reflect the segregation of calving females discussed above for both cases. The possible effects of exploitation on length of lactation (thought to have operated, for example in the western Pacific population of *S. coeruleoalba* and the eastern Pacific populations of *S. longirostris*) are discussed below in the section on the topic.

The range of estimates of age at weaning is greater (5 months to 34 months) than for length of lactation. The lowest value of 5-6 months for *D. delphis* in the Black Sea again reflects segregation of lactating females. The estimates of weaning age for the three populations of *S. longirostris* (11, 19 and 34 months) are inversely correlated with the three estimates of length of lactation (19, 18 and 15 months); this inconsistency is discussed below in the section on effects of exploitation.

Solid food is taken in the first year of life in delphinids; the six estimates range from 3-6 months to 4-11 months with the mean at about 6 months. Maximum length of suckling is at least 2 years; the six estimates range from 24 months to 48-60 months.

#### Length of 'Resting Period'

In estimating reproductive rates, mature females are usually classified into four categories: pregnant only ( $P$ ), pregnant and lactating ( $PL$ ), lactating only ( $L$ ) and 'resting' ( $R$ ) (all those neither pregnant nor lactating). In some analyses, e.g. Perrin *et al.* (1976), Perrin *et al.* (1977) and Henderson *et al.* (1980), senescent females (those neither pregnant nor lactating and with small withered ovaries containing no recent corpora) were not included in the resting category. In most studies, the category is a catchall and includes females in estrus, those between ovulation cycles, senescent females, those that have recently aborted and those pregnant with very small embryos missed in dissection. The length of the 'resting' period is calculated in the same manner and is subject to the same potential biases as the estimates of length of lactation or length of gestation:

$$T_R = T_G \cdot R/P$$

where  $T_G$  = gestation time,  $R$  = proportion resting and  $P$  = proportion pregnant.

In alternative estimates of annual pregnancy rates based on independent estimates of gestation and weaning age (the 'Method 2' estimates of Perrin *et al.* (1977)

Estimates of length of lactation, age at weaning and length of 'resting period' in delphinids. Methods noted: observed in wild, observed in captivity, determined from stomach contents, determined from eruption of teeth, estimated by cow-calf method (C-C), estimated from ratio of lactating to pregnant (L/P) and estimated from ratio of 'resting' to pregnant

Species and region (stock or year in parentheses)	LACTATION				WEANING				'Resting' (by R/L) (months)	Source of estimate or data
	Mature females (no.)	Length (by L/P) (months)	Age at first solid food (months)	Oldest nursing (months)	Age at weaning (months)	Method	Method	Method		
<i>Pseudorca crassidens</i> W. North Pacific	(38)	18 <sup>1</sup>	—	—	—	—	—	—	—	Kasuya and Izumisawa, 1981
<i>Orcinus orca</i> E. North Pacific	—	—	—	—	≥ 12	—	—	(ob. wild)	—	IWC, 1982
<i>Globicephala melana</i> E. North Atlantic	(485)	22	6-9	—	—	—	—	—	8	Sergeant, 1962
<i>Lagenorhynchus acutus</i> E. North Atlantic	(32)	18 <sup>2</sup>	—	—	—	—	—	—	—	Sergeant <i>et al.</i> , 1980
<i>Tursiops truncatus</i> All regions	(31)	19 <sup>3</sup>	4-11	38	18-20	(ob. cap. and wild)	(ob. cap. and wild)	—	5	Kasuya and Izumisawa, 1981; Leatherwood <i>et al.</i> , 1978; McBride and Kritzer, 1951; Prescott, 1977; Ridgway and Benirschke, 1977; Ross, 1977, 1979, Saayman and Taylor, 1977; Sergeant, 1962
<i>Stenella longirostris</i> E. trop. Pacific (eastern, 1973-81)	(569)	19	—	—	11 <sup>4</sup>	—	—	(C-C)	6	Henderson <i>et al.</i> , 1980;
E. trop. Pacific (n. whitebelly, 1973-81)	(435)	18	—	—	19 <sup>4</sup>	—	—	(C-C)	9	Oliver <i>et al.</i> , 1983;
E. trop. Pacific (s. whitebelly, 1973-81)	(132)	15	—	—	34 <sup>4</sup>	—	—	(C-C)	15	Perrin and Oliver, 1982
<i>S. coeruleoalba</i> E. trop. Pacific (all stocks)	(28)	14 <sup>3</sup>	—	—	—	—	—	—	10	Perrin and Oliver, 1982
W. North Pacific (1968-71)	(361)	12 <sup>3</sup>	~ 6	24	≥ 15	(erupt. teeth)	(—)	(C-C)	5	Kasuya, 1972
W. North Pacific (1952-58)	(321)	17 <sup>3</sup>	—	—	—	—	—	—	4	Kasuya and Miyazaki, 1975
W. North Pacific (1961-68)	(301)	20 <sup>3</sup>	—	—	—	—	—	—	5	Kasuya and Miyazaki, 1975
W. North Pacific (1970-73)	(950)	8 <sup>3</sup>	—	—	—	—	—	—	2	Kasuya and Miyazaki, 1975
W. North Pacific (1971-75)	(—)	13 <sup>3</sup>	—	~ 36	—	(—)	(—)	—	4	Kasuya, 1976
W. North Pacific (1972-73)	(—)	—	3-6	36	18	(stom.)	(C-C)	(C-C) <sup>5</sup>	—	Miyazaki, 1977
<i>S. attenuata</i> E. trop. Pacific (n. offshore, 1973-78)	(522) <sup>6</sup>	17	5-7	33	20	(stom.)	(C-C)	(C-C)	5	Henderson <i>et al.</i> , 1980;
E. trop. Pacific (n. offshore, 1979-81)	(493)	26	—	—	—	—	—	—	6	Oliver <i>et al.</i> , 1983;
E. trop. Pacific (s. offshore, 1973-80)	(277)	13	—	—	—	—	—	—	5	Perrin <i>et al.</i> , 1976;
W. North Pacific (1970-73)	(250)	26	3-6	48-60	—	(stom.)	(C-C)	—	7	Perrin and Oliver, 1982
W. North Pacific (1970-76)	(—)	27	—	—	—	—	—	—	9	Kasuya <i>et al.</i> , 1974 Kasuya, 1976
<i>Delphinus delphis</i> Black Sea (1931-33)	(~ 800)	14 <sup>7</sup>	—	—	—	—	—	—	—	Mayarova and Danilevskiy, 1934
Black Sea (1936-39)	(—)	—	—	—	5-6 <sup>8</sup>	—	—	(—)	—	Sleptsov, 1941
Black Sea (1946)	(934)	—	—	—	6 <sup>8</sup>	—	—	(—)	—	Kleinenberg, 1956
Black Sea (1949)	(231)	19 <sup>7</sup>	—	—	—	—	—	—	4	Sokolov, 1962
E. trop. Pacific (all stocks)	(365)	19 <sup>7</sup>	—	—	—	—	—	—	4	Henderson <i>et al.</i> , 1980; Oliver <i>et al.</i> , 1983; Perrin and Oliver, 1982

<sup>1</sup> Assumed gestation of 16 months.

<sup>3</sup> Assumed gestation of 12 months.

<sup>5</sup> Modified as described in text.

<sup>6</sup> Includes only specimens from net hauls in which 40 or more were killed (see text, under *Pregnancy rate*).

<sup>7</sup> Assumed gestation of 11.5 months.

<sup>2</sup> Assumed gestation of 11 months.

<sup>4</sup> For 1973-78 only ( $n = 521, 366$  and  $123$ ).

<sup>8</sup> But see text.

and Henderson *et al.* (1980)), *R/P* estimates of length of the 'resting' portion of the calving cycle were used.

The available estimates (Table 7) range from 2 months (for the reportedly depleted population of *S. coeruleoalba* off Japan) to 15 months (for the southern whitebelly population of *S. longirostris* in the eastern tropical Pacific). The modal value is 4–5 months (9 of the 18 estimates).

### Age and Sex Structure

#### Background and methods

Sex ratios and age structure are usually estimated from series of specimens captured in fisheries or collected from strandings. Rather than follow a single age class throughout its life (which has not been possible for delphinids) to determine sex ratios, age structures and mortality/survival rates, the usual method is to estimate these parameters using a sample from one time period. These techniques are adapted from human demography and fisheries and wildlife sciences (e.g. Keyfitz, 1968; Ricker, 1975; Caughley, 1977).

Assumptions involved in making sex- and age-structure inferences from specimen series include (1) age and sex are accurately determined; (2) the sample is representative of the population; and (3) the population is stationary in structure. The difficulty of testing these assumptions increases in the order in which they are listed.

Sex is more easily determined than age for dead specimens, and estimates of sex ratio are therefore generally more reliable than those of age structure. Both sex and age are often very difficult to determine for live specimens in studies that do not involve capture. Species with marked sexual dimorphism (e.g. *O. orca*) are exceptions to this, at least for sex ratio of adults.

Recent developments in age determination are reviewed in Perrin and Myrick (1980). In some cases, ovarian-corpora frequencies have been used to represent age in adult females on the assumption that ovulation is a regular event. Since this assumption is probably not valid (see discussion above), age estimates from corpus frequencies are not reliable.

While it is probably not possible to determine with a great deal of certainty that an observed age series is representative of the population, some simple methods can identify strongly biased samples. For example, there should in general be fewer individuals in older age classes. Distributions which have peak frequencies at ages over 0–1 indicate under-representation of juveniles. This type of age distribution has been observed for many delphinid populations (see below).

To date, stationarity has not been demonstrated for any delphinid population. Again, this would in fact be very difficult to do. Any information suggesting recent changes in overall population size would invalidate this assumption.

Common methods used to estimate adult mortality rates in fisheries and wildlife sciences include log-linear regression (e.g. Ricker, 1975) and the Chapman–Robson (1960) method. Regression methods were used by Kasuya *et al.* (1974) and Kasuya (1976) for *S. attenuata*, and by Sergeant (1962) for *G. melaena*. In some instances it is possible to factor out influences from population growth and mortality via exploitation from the total mortality

represented by an observed age structure (e.g. see Ohsumi, 1979).

#### Available estimates

In every case for which data exist on sex and age structure of a delphinid population, two patterns have surfaced. First, the ratio of males to females appears to decline with age (Table 8). Second, a certain segment of the population, roughly 'juvenile' in age, appears to be under-represented in the samples. This second observation suggests that any reproductive parameter estimated from relative frequencies of age classes (mortality rate, ages at sexual maturity and first birth, relative pregnancy by age) may be biased. In some cases there are also sex differences in the under-representation of juveniles, e.g. in *Stenella attenuata* of the eastern tropical Pacific (J. Barlow, A. Hohn and A. Myrick, pers. comm. to SBR), *Globicephala melaena* near Newfoundland (Sergeant, 1962), and *Stenella coeruleoalba*, near Japan (Miyazaki and Nishiwaki, 1978).

A wide range in sex ratios for entire populations has been reported (Table 8): from 5.5:1 for *Lagenorhynchus acutus* in Norway down to 0.5:1 for *Tursiops truncatus* off North Carolina (Townsend, 1914). Within the Black-Sea *Delphinus* data alone, the range is from 0.64:1 to 2.85:1, depending upon the month during which the nearshore schools were captured. This variation is most likely due in great part to age/sex segregation, which has been shown to be seasonal in the Black Sea (Kleinenberg, 1956; Tomilin, 1957; Mayarova and Danilevskiy, 1934). The same is true for *Tursiops truncatus* off the eastern US (True, 1891). Segregation by sex and/or age has been observed both within and between groups in studies of free-ranging *Tursiops truncatus* (Lear and Bryden, 1980; Wells, Irvine and Scott 1980; Würsig, 1978), *Stenella longirostris* (Norris and Dohl, 1980a; Pryor and Kang, 1980), *Stenella attenuata* (Pryor and Kang, 1980), *Sousa* sp. (Saayman and Tayler, 1979), *Lagenorhynchus obliquidens* (Norris and Prescott, 1961), *L. obscurus* (Würsig and Würsig, 1980) and *Orcinus orca* (Bigg, 1982; Balcomb, Boran and Heimlich, 1982; Condy, van Arde and Bester, 1978). Age/sex segregation has been reported from studies of captured schools for *Stenella attenuata* (Kasuya, 1976; Kasuya *et al.*, 1974) *S. coeruleoalba* (Kasuya, 1972, 1976; Miyazaki and Nishiwaki, 1979), *Delphinus delphis* (Mayarova and Danilevskiy, 1934; Kleinenberg, 1956; Tomilin, 1957; Hui, 1973), *Tursiops truncatus* (True, 1891; Mead, 1975b), *Lagenorhynchus acutus* (St Aubin and Geraci, 1979) and *Globicephala melaena* (Sergeant, 1962). The implications of age and asexual segregation on estimating delphinid population parameters are profound. As discussed above, unbiased estimation of many vital rates requires representative age-structure samples. Since age and/or sex segregation may be the rule rather than the exception for delphinids, data should be scrutinized closely before calculation of vital-rate statistics.

Estimates of natural mortality have been made for only three delphinid cetaceans: *G. melaena* (0.115: Sergeant, 1962), *S. coeruleoalba* (0.137: Kasuya, 1976) and *S. attenuata* (0.161: Kasuya, 1976), as reviewed and evaluated by Ohsumi (1979). In each case the original authors made more than one estimate. Values reported

Table 8  
Sex ratios reported for delphinids, listed here as ♂:♀, with female values scaled to 1.0. Data from studies which selected by sex are not listed here

Species and region	Data type	Age class and sample size	♂:♀ ratio	Age class and sample	♂:♀ ratio	Age	♂:♀ ratio	Source
<i>Orcinus orca</i> (Pacific N.W., U.S.) (Pacific N.W., U.S.) (Marion Island)	Live observation	Adult (43)	0.48:1	—	—	—	—	Balcomb <i>et al.</i> , 1982
	Live observation	Adult (132)	0.83:1	—	—	—	—	Bigg, 1982
	Live observation	Adult (478)	1.34:1	—	—	—	—	Condy <i>et al.</i> , 1978
<i>Globicephala macrorhynchus</i> (Florida) (California)	Mass stranding	All (135)	0.53:1	—	—	—	—	Irvine <i>et al.</i> , 1979
	Mass stranding	All (27)	0.28:1	—	—	—	—	Hall <i>et al.</i> , 1971
<i>G. melana</i> (Nova Scotia) (Newfoundland)	Mass standing	All (99)	1.91:1	—	—	—	—	Geraci and St. Aubin, 1977
	Drive fishery	Newborn (250)	1.43:1	6-10 years (87)	0.85:1	8-22 years (213)	0.32:1	Sergeant, 1962
<i>Pseudorca crassidens</i> (Scotland) (Scotland)	Mass stranding	All (72)	0.85:1	—	—	—	—	Purves and Pilleri, 1978
	Mass stranding	All (62)	0.82:1	—	—	—	—	Peacock <i>et al.</i> , 1936
<i>Feresa attenuata</i> (Japan)	Mass stranding	All (14)	1:1	—	—	—	—	Nishiwaki <i>et al.</i> , 1956
<i>Steno bredanensis</i> (Florida)	Mass stranding	All (10)	1.5:1	—	—	—	—	Layne, 1965
<i>Lagenorhynchus acutus</i> (New England) (Norway)	Mass stranding	'Young' (16)	1.67:1	'Intermed.' (30)	1.72:1	'Adult' (56)	0.22:1	Sergeant <i>et al.</i> , 1980
	—	All (22)	5.5:1	—	—	—	—	Guldberg and Nansen, 1894
<i>Tursiops truncatus</i> (N. Carolina) (Florida) (Florida) (N. Carolina) (Black Sea)	Drive fishery	All (157)	1.14:1	—	—	—	—	True, 1890
	Live capture	All (61)	1:1	—	—	—	—	Sergeant <i>et al.</i> , 1973
	Live capture	All (47)	0.96:1	—	—	—	—	Irvine <i>et al.</i> , 1981
	Drive fishery	All (51)	0.5:1	—	—	—	—	Townsend, 1914
	Drive fishery	All (53)	1:1	—	—	—	—	Danilevskiy and Tyutyunnikov, 1968
<i>Stenella longirostris</i> (Florida) (ETP: 1973-75)	Mass stranding	All (25)	0.85:1	—	—	—	—	Mead <i>et al.</i> , 1980
	Tuna seine	— (294)	1.1:1	1.3-1.6 m (631)	0.99:1	Adult (1,330)	0.94:1	Perrin <i>et al.</i> , 1976
(ETP: 1979-80) (ETP: 1981)	Tuna seine	All (734)	0.98:1	—	—	—	—	Perrin and Oliver, 1982
	Tuna seine	All (305)	1.15:1	—	—	—	—	Oliver <i>et al.</i> , 1983
<i>S. attenuata</i> (ETP)	Tuna seine	Neonate (412)	1:1	'2-tone' (1,367)	0.95:1	'Speckled' (1,275)	0.91:1	Perrin <i>et al.</i> , 1976
	—	Mottled (1,298)	0.73:1	'Fused' (5,019)	0.75:1	—	—	Perrin <i>et al.</i> , 1976
(ETP: 1976) (ETP: 1979-80) (ETP: 1981) (Japan)	Tuna seine	All (6,225)	0.8:1	—	—	—	—	Perrin <i>et al.</i> , 1977
	Tuna seine	All (2,246)	0.75:1	—	—	—	—	Perrin and Oliver, 1982
	Tuna seine	All (830)	0.73:1	—	—	—	—	Oliver <i>et al.</i> , 1983
	Drive and harpoon fishery	Juv. (149)	1.16:1	'Puberal' (167)	2.21:1	'Mature' (422)	0.38:1	Kasuya <i>et al.</i> , 1974

Table 8 (continued)

<i>S. coeruleoalba</i> (Japan)	Drive and harpoon	Juv. school (276)	3.07:1	Mixed school (653)	1.06:1	Adult school (1,638)	0.78:1	Miyazaki and Nishiwaki, 1978
(Japan)	Drive and harpoon	Fetus (661)	1.13:1	'Suckling' (744)	1.07:1	Others (7,967)	1.19:1	Kasuya and Miyazaki, 1975
(Japan)	Drive and harpoon	0-1.5 year (251)	1.09:1	2.5-8.5 years (1,438)	1.55:1	9.5-13.5 years (847)	0.93:1	Miyazaki, 1977
(Japan)	Drive and harpoon	14.5+ year (747)	0.77:1					
	Drive and harpoon	'Prenatal' (115)	1:1	'Postnatal' (1,048)	0.73:1			Miyazaki, 1977
<i>Delphinus delphis</i> (ETP: 1973-78)	Tuna seine	All (140)	0.95:1					Henderson <i>et al.</i> , 1980
(ETP: 1979-80)	Tuna seine	All (363)	0.85:1					Perrin and Oliver, 1982
(ETP: 1981)	Tuna seine	All (117)	1.05:1					Oliver <i>et al.</i> , 1983
(Black Sea: 1930s)	Drive fishery	All (82, 843)	1.12:1					Tomilin, 1957
(ETP: north)	Tuna seine	All (286)	0.87:1					Hui, 1977
(ETP: south)	Tuna seine	All (799)	0.85:1					Hui, 1977
(Black Sea: 1931)	Drive-or-gun fishery	All (395)	1.5:1					Danilevskiy and Tyutyunnikov, 1968
(Black Sea: 1931, Jan.)	Drive-or-gun fishery	All (212)	0.64:1					Mayarova and Danilevskiy, 1934
(Black Sea: 1931, Feb.)	Drive-or-gun fishery	All (176)	2.85:1					Mayarova and Danilevskiy, 1934
(Black Sea: 1931, Mar.)	Drive-or-gun fishery	All (589)	1.44:1					Mayarova and Danilevskiy, 1934
(Black Sea: 1931, Apr.)	Drive-or-gun fishery	All (687)	1.56:1					Mayarova and Danilevskiy, 1934
(Black Sea: 1931, May)	fishery	All (277)	2.12:1					Mayarova and Danilevskiy, 1934
(Black Sea: 1931, Jul.)	fishery	All (384)	1.56:1					Mayarova and Danilevskiy, 1934
(Black Sea: 1931, Aug.)	fishery	All (440)	1.17:1					Mayarova and Danilevskiy, 1934
(Black Sea: 1931, Sept.)	fishery	All (135)	0.69:1					Mayarova and Danilevskiy, 1934
(So. Calif: 1971)	Tuna seine	0-4 (68)	—	5-10 (28)	0.70:1	11+(19)	0.9:1	Hui, 1973
(ETP: 1977)	Tuna seine							Gurevich and Stewart, 1978

Table 9  
Annual birth rates reported for populations of delphinids

Species and region/stock	b or GARR	Notes	Source
<i>Sousa chinensis</i> Indian Ocean	0.10(b)	Visual obs. % calves in population	Saayman and Tayler, 1979
<i>Orcinus orca</i> Puget Sound, WA.	0.04–0.05	Visually obs. preg. rate × % female adult	Dahlheim, 1980
Vancouver Is., B.C.	0.046(b)	No. calves/no. all others ('cropped' population)	IWC, 1982
Vancouver Is., B.C.	0.032	'Uncropped' state	IWC, 1982
Puget Sound, WA.	0.026(b)	Obs. no. calves/no. all others	IWC, 1982
<i>Globicephala melaena</i> Newfoundland	0.132	% female × % mature female preg. divided by gestation (exploited)	Sergeant, 1962 Harrison, 1969
<i>Tursiops truncatus</i> Florida	0.082(b)	% calves visually counted (non-exploited)	Irvine <i>et al.</i> , 1981
N. Gulf of Mexico	0.077(b)	% calves visually counted (exploited)	Leatherwood, 1977
Argentina, S. Atlantic	0.096(b)	% calves visually counted (non-exploited)	Würsig, 1978
E. Australia	0.012(b)	% calves visually counted (non-exploited)	Lear and Bryden, 1980
Black Sea	0.30?	% female × % female mature × % preg. (biased sampling suspected) (exploited)	Danilevskiy and Tyutyunnikov, 1968
<i>Stenella longirostris</i> Eastern stock, ETP	0.08	% female × % female mature × % preg. (exploited)	Perrin <i>et al.</i> , 1977
	0.075	% female × % female mature × % preg. (exploited)	Perrin and Henderson, 1984
Northern whitebelly stock, ETP	0.094	% female × % female mature × % preg. (exploited)	Perrin and Henderson, 1984
Southern whitebelly stock, ETP	0.067	% female × % female mature × % preg. (exploited)	Henderson <i>et al.</i> , 1980
<i>Stenella coeruleoalba</i> All stocks, ETP	0.109	% female × % female mature × % preg. (exploited)	Henderson <i>et al.</i> , 1980
Japan	0.11	% female × % mature × % preg. (exploited) (calculation from data given)	Kasuya, 1972
Japan	0.103	% female × % mature × % preg. (exploited) (calculation from data given)	Kasuya, 1976
<i>Stenella attenuata</i> Japan	0.103	% female × % mature × % preg. (exploited) (calculated from data in both papers)	Kasuya, 1976 and Kasuya <i>et al.</i> , 1974
Northern offshore stock, ETP	0.117	% female × % mature × % preg. (exploited) (calculated from data in both papers); 1973–1978 data	Henderson <i>et al.</i> , 1980
Northern offshore stock, ETP	0.109	% female × % mature × % preg. (exploited); 1973–1975 data	Perrin <i>et al.</i> , 1977
Southern offshore stock, ETP	(0.195)	(M1)	Henderson <i>et al.</i> , 1980
<i>Delphinus delphis</i> ETP	0.096	(Exploited) (M1)	Henderson <i>et al.</i> , 1980
Northern stock, E. Pac.	0.087	No. preg./total population	Hui, 1977
Southern stock, ETP	0.066	No. preg./total population	Hui, 1977
Black Sea	0.106 <sup>1</sup>	% all female preg. × % female (exploited)	Danilevskiy and Tyutyunnikov, 1968

<sup>1</sup> Adjusted for 10-month gestation =  $(12/10) \times (22/35) \times 0.35 \times 0.4 = 0.106$ . Unadjusted =  $0.22 \times 0.4 = 0.088$ .

here are those which Ohsumi (1979) concluded to be the most appropriate. All of these estimates are tentative, incorporating unresolved problems in age determination and possibly sampling biases. Direct observations of *O. orca* in Puget Sound indicated a relatively low adult natural mortality rate of  $M = 0.01$  (Balcomb *et al.*, 1982).

Ohsumi (1979) and Ralls, Brownell and Ballou (1980) have reviewed the available data on mortality rates for delphinid cetaceans (among other taxa). Ralls *et al.* found that the degree to which males have higher mortality increases with the degree of sexual dimorphism. Ohsumi (1979) investigated the relationships between  $M$ , life span and asymptotic body size. He found that, in general, larger, longer-lived taxa have lower natural mortality

rates. Since his data included mysticete as well as odontocete species, it is not clear how accurate his predictions of  $M$  would be for species not included in the original analysis.

### Reproductive Rates

There are two types of population reproductive rates of interest in stock assessment and management. These can be generally categorized as gross and net rates, differing roughly by annual natural mortality. Each category encompasses a number of specific types of estimates and each has been addressed in more than one way. These are summary parameters, usually estimated from combina-

Table 10  
Net annual reproductive rates reported for delphinids

Species and region	Net repro. rate	Notes	Source
<i>Orcinus orca</i>			
Vancouver Is., B.C.	0.031	Observed net pod change 'cropped' state	IWC, 1982
Vancouver Is., B.C.	0.017	Observed net pod change 'uncropped' state	IWC, 1982
Puget Sound, WA	0.023	Observed net pod change 'cropped' state	IWC, 1982
<i>Stenella coeruleoalba</i>			
Japan	0.031-0.032	Computed in complex manner, observed $F$ , assumed $M$ , est. $N$ , $CI$ , sex ratio	Kasuya and Miyazaki, 1975
Japan	0.023-0.024	Above data re-evaluated from new age determinations and catch data	Kasuya, 1976
Japan	0.044	'Intrinsic' rate, extrapolated from series of $r_t$ , $N_t$	Kasuya, 1976

tions of other, directly measured (or assumed) statistics. It is generally assumed that one or both categories vary in a density-dependent manner such that net reproduction increases as density decreases from the so-called carrying capacity level. Such a change in net reproduction was estimated to have occurred for *Stenella coeruleoalba* near Japan (Kasuya, 1976).

The general category of 'gross' rates (Table 9) includes estimates of crude birth rates ( $b$ ) (Keyfitz, 1977) and gross annual reproductive rates (GARR) (Perrin *et al.*, 1976; Smith, 1983). Ideally the crude birth rate is estimated as  $b = \int_{x=0}^{\infty} c_x m_x dx$ , where  $m_x$  is the probability that a female aged  $x$  will give birth during each time period, and  $c_x$  is the proportion of the population composed of mature females aged  $x$  (Keyfitz, 1977). In practice the crude birth rate has been calculated as the estimated number of newborn calves divided by the estimated total population (e.g. Saayman and Taylor, 1977; Leatherwood, 1977, Würsig, 1978). This is usually a biased estimate since (1) it doesn't consider calf mortality from birth to the census time; (2) calving is usually diffusely seasonal and some births may take place after the census; and (3) cow mortality is not considered. The degree of inaccuracy is related to the degree of calving seasonality, the timing of the census in relation to the calving pulse, and the differentials in mortality between newborn calves, reproductive females and the rest of the population. The most accurate estimate of this type would be made from a census taken just following the completion of a very sharply-defined annual calving period. Even then it would be an overestimate, not considering cow mortality during the previous time period. (Such mortality is implicitly considered in the 'ideal' formulation given above).

The other type of gross rate, 'GARR', is usually estimated as the product of the proportion of the population that is female, the proportion of females sexually mature and the annual pregnancy rate (APR). GARR has been shown to be very sensitive to the method of estimation of APR (Perrin and Henderson, 1984; Henderson *et al.*, 1980). Estimation of GARR by the product method also requires the assumption of unbiased estimates of sex ratio and the proportion of females which are sexually mature; it is therefore sensitive to problems in estimating these parameters (as discussed above). However, GARR can also (more simply) be estimated as the proportion of pregnant

females in the total population, with adjustment for length of gestation. While subject to some of the same assumptions this method is more straightforward than the product method.

The 'Method-2' estimates of GARR of Perrin *et al.* (1977) are invalid for reasons discussed above in the section on lactation.

GARR and the crude birth rate differ in that the latter includes integration of mortality of cows while GARR does not. Both statistics can be useful indices of relative population status. Especially with GARR, within-population comparisons over time are more informative than between-population comparisons. Polacheck (1982) has shown that age-structure effects alone can confound between-population comparisons of GARR estimates, obscuring any looked-for trend in GARR with population level (e.g. see Perrin and Henderson, 1984).

Net reproductive rates represent reproduction in excess of mortality for a population as a whole. They are extremely difficult to obtain for cetaceans, as demonstrated by the paucity of points in Table 10. In the strict context of human demography, the term 'net reproduction' refers to  $R_0$ , which is the number of female offspring expected to be born to a female given existing rates of age-specific survival and reproduction (Keyfitz, 1977). In practice, for delphinids, the more general definition given above is usually the one used. One method of estimating net reproduction which has been considered is the subtraction of population natural mortality from GARR (Smith, 1983). This is incorrect, as the natural mortality should be subtracted from crude birth rate to estimate net increase. Unfortunately, natural mortality is also very difficult to measure and (in the case of *Stenella* spp.) must be assumed from comparison with other populations. In this case, the GARR of an assumedly unexploited stock has been taken as equivalent to natural mortality for that stock. This second GARR has then been subtracted from that for the exploited population. This systematically overestimates net recruitment for the exploited population (personal communication to SBR from D. Goodman).

The most accurate way to measure net reproduction is to observe net changes in total population size in the absence of (or concomitant with a known level of) removals by humans. So far this has been feasible only for small groups of killer whales in the Pacific Northwest in which nearly all individuals are identifiable (Table 10).

Another method which has been employed to estimate net reproduction of a delphinid population is that utilized by Kasuya (1976) and Kasuya and Miyazaki (1975) for *Stenella coeruleoalba* off Japan. Theirs is a fairly complex series of computations which is based upon observed fishing mortality, estimated sex ratio, age structure, population size and an assumed natural mortality rate (i.e. a version of GARR – M, which doesn't explicitly compute GARR enroute).

No variances are listed for gross or net rates in Tables 9 or 10. This is because they were usually not reported in the source literature. It would be possible to derive and compute them in most cases. The ranges reported (0.026–0.144 gross and 0.017–0.032 net) reflect different estimation methods and different amounts and quality of data and represent populations in a variety of states: heavily, lightly or not exploited. Consequently it is not appropriate to draw any general inferences from the ranges except perhaps as indications of reasonable limits for these parameters.

## DISCUSSION

### Effects of Seasonality

Seasonality of mating and calving has been demonstrated for all delphinids that have been studied in any depth, although the degree of seasonality (intensity of breeding peaks) varies greatly. The impact of seasonality on estimating parameters depends on the degree of seasonality (Fig. 5) and also on the length of gestation and lactation. For example, if pregnancy and lactation each last about a year and breeding peaks are moderately diffuse (as in *S. attenuata* in the eastern Pacific – Perrin *et al.*, 1976), seasonality can be expected to have negligible effect on estimates of reproductive parameters. On the other hand, if pregnancy lasts about a year and a third (as in the pilot whales and the killer whale – Table 2), even moderate seasonality can lead to considerable bias in estimates. Barlow (1984) discusses the nature and impact of seasonal bias.

### Effects of Schooling Segregation

Estimates of reproductive parameters based on samples from a catch assume that the samples accurately represent the population at large in terms of age, sex and reproductive condition, and initial population studies of several delphinids relied on this assumption (*Delphinus delphis* – Mayarova and Danilevskiy, 1934; Sleptsov, 1941; *Stenella coeruleoalba* – Kasuya, 1972; *S. attenuata* and *S. longirostris* – Perrin *et al.*, 1976 and 1977, Perrin and Henderson, 1984; Henderson *et al.*, 1980). More recent work, however, has indicated that schooling segregation of one sort or another may be a general feature of delphinid life history and must be taken into account in estimating reproductive parameters (Norris and Dohl, 1980a and b; Würsig and Würsig, 1980; Miyazaki and Nishiwaki, 1978). As discussed above, Kleinenberg (1956) discovered that female common dolphins, *D. delphis*, in the Black Sea to some extent school separately during calving and early lactation in an offshore area not usually involved in the dolphin fishery, leading to erroneously high estimates of pregnancy rate and low estimates of length of lactation based on samples of the catch. The estimate of the length of the calving cycle is now about twice the earlier estimates, about 2 years rather than about 1 year (Sokolov, 1962), a difference obviously of great import to assessment and management. The most recent parameter estimates for *S. coeruleoalba* off Japan (Miyazaki, 1984; Kasuya, 1984) take into account the now-well-documented existence of several kinds of schools that are sampled differentially by the fishery (Miyazaki and Nishiwaki, 1978). The most recent information on age structure of the northern offshore population of *S. attenuata* in the eastern Pacific (personal communication, A. A. Hohn, A. C. Myrick, Jr. and J. Barlow) indicates that a substantial portion of females just at or below the average age at attainment of sexual maturity are not represented in the samples of dolphins killed incidentally in the tuna fishery and probably school separately in schools that for some reason are not associated with tuna, throwing all the published estimates of reproductive parameters in the population (cited above) into question.

Clearly schooling segregation is possibly a general phenomenon in delphinids, and it should not be assumed to not exist or not be of importance in any population. In some cases, the sampling problems caused by it may be insoluble but they cannot be denied.

### Effects of Geographical Variation

As can be seen in the various tables and in the appendices to this report, estimates of life-history parameters often vary sharply between populations of the same species. Several reasons for this are possible:

- (1) Sample sizes were inadequate, and the differences are ascribable to statistical error.
- (2) The samples were biased in one case or the other and were not accurately representative of the population(s).
- (3) Different analytical methods were used to arrive at the estimates.
- (4) The differences reflect real differences in the status

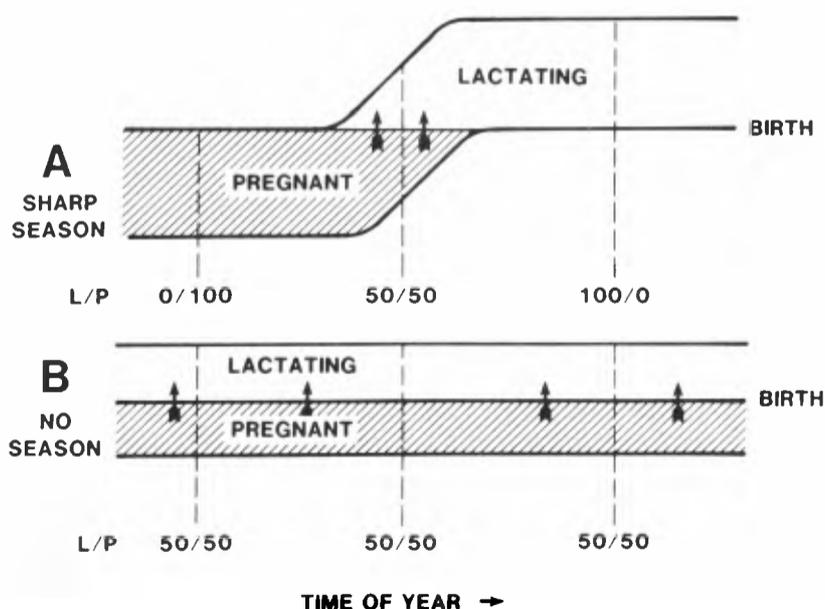


Fig. 5. Effect of sharp breeding seasonality on estimates of pregnancy and lactation. A hypothetical extreme case in which pregnancy and lactation each last six months.

of the populations, e.g. change in carrying capacity or density (discussed in next section).

- (5) The differences are real and inherent, i.e. genetically determined geographical variation.

For dynamic parameters such as age at attainment of sexual maturity, pregnancy rate and length of lactation, it is difficult or impossible to determine whether reasons 2, 4, or 5 are responsible for differences in estimates. For example, the differences between estimates for *Stenella attenuata* in the eastern Pacific and the western Pacific (Tables 4, 6 and 7) could be due to differential bias known to exist (but not measured – Perrin and Oliver, 1982; Miyazaki, 1977) in the two kinds of fisheries involved, to the differential status *vis-a-vis* exploitation (Smith, 1983) or, at least partially, to inherent differences in basic life-history features. It is interesting to note, however, that where problems of sampling bias are thought to be uniform and analytical methodologies are the same for two or more populations of the same species, e.g. *S. attenuata* and *S. longirostris* in the eastern Pacific, differences in most or all estimates of dynamic parameters are statistically insignificant.

Some parameters, such as maximum size and average size of adults, vary geographically independent of dynamic factors. *Tursiops truncatus* is a notable example. The range of variation in adult length (Appendix 1) is enormous, from 202 cm for the smallest female to 381 cm for the largest male, nearly a two-fold difference. The sample sizes for adult female bottlenose dolphins from two regions, Florida and the western North Pacific (Appendix 3), are sufficiently large to allow determination that the difference in average length (239 cm vs 288 cm) is real ( $P < 0.001$ ). The differences in maximum size, length of largest immature and length of smallest mature animals (Appendix 1) between samples from several other regions suggest that there are probably real differences among them as well (eastern North Atlantic, Black Sea, western North Atlantic, Gulf of Mexico, eastern North Pacific, and Indian Ocean – the ‘*aduncus*’ form). This pattern of wide geographical variation in the best-known delphinids and similar patterns in other species for which large volumes of data have been available for two or more regions (e.g. *Stenella longirostris*, and *Delphinus delphis*, Appendices 1 and 3) suggest that considerable

geographical variation in size is to be expected in any broadly distributed small cetacean and should be taken into account in any deductive modeling of relationships among parameters (discussed below).

### Effects of Exploitation

Population and management models that incorporate the concept of net production (sustainable yield available for harvest, or population growth increment) are based on the assumption that reproductive rates and/or natural mortality rates change with population density (Perrin and Donovan, 1984; Smith, 1983). The reproductive parameter estimates tabulated here can be examined for correlation with population status (present size/pre-exploitation size). The species for which large amounts of data exist for one population through time (or for more than one population of the same species for which the analytical methods are the same) and any sampling biases can be expected to be the same, are *Stenella longirostris* (in the eastern tropical Pacific) and *S. coeruleoalba* (in the western North Pacific). In a simple comparison of trends in reproductive parameters with population status (Table 11), the estimates do not behave entirely as would be predicted by the assumption of density-dependent response. For *S. longirostris*, age at attainment of sexual maturity is greater in the less exploited southern whitebelly population, as expected, and the ranking in pregnancy rate parallels status in the expected way, but length of lactation shows a trend the reverse of what would be expected, i.e. it is longest in the most-exploited population and shortest in the least-exploited population (due to the same trend in length of the ‘resting period’ Table 7). Perrin and Henderson (1984) found that estimated gross reproductive rate is not different (at  $\alpha = 0.05$ ) in the eastern and northern whitebelly populations, although the former is probably at less than 25% of its original size and the latter at more than 75% of original (Smith, 1983).

For the heavily exploited population of *S. coeruleoalba* off Japan, Kasuya and Miyazaki (1975) estimated that pregnancy rate has increased and length of lactation decreased over the period 1952 to present but the lowest estimate of pregnancy rate and highest estimate of

Table 11

Comparison of trends in reproductive-parameter estimates to trends in status of populations in two delphinids. Rankings are of estimates from Tables 4, 6 and 7

	Percent of pre-exploitation size (rank: 1 is largest)	Age at attainment of sexual maturity (rank: 1 is highest)	Annual pregnancy rate (rank: 1 is lowest)	Length of lactation (rank: 1 is longest)
<i>Stenella longirostris</i>				
E. trop. Pacific				
S. whitebelly	1	—	1	3
N. whitebelly	2	1	2	2
Eastern	3	2	3	1
<i>S. coeruleoalba</i>				
W. Pacific				
1952–1958	1	—	2	2
1961–1968	2	—	1	1
1970–1973	3	—	3	3

length of lactation are for an intermediate period, 1961–68.

These simple comparisons suggest that reproductive parameters may behave in unexpected ways in a population under exploitation (see also section above on net reproductive rate).

### Relationships Between Parameters

Ohsumi (1979) has extensively reviewed the topic of deductive modelling to estimate reproductive parameters. In the context of the present review, two cautionary points suggest themselves.

In any comparison across species or populations, care should be taken to use similarly derived estimates. For example, in modeling a relationship between size and other parameters (mortality rate, maximum net reproductive rate, etc.), the possible choices of measures of size include length at attainment of sexual maturity in males or females, average size of adult males or females, asymptotic length and other indices. Whatever the index used, it should be of the same parameter and calculated in the same way throughout. Further, and perhaps more difficult to ensure, any morphological or quantitative criteria used in estimating, e.g. the histological criteria of sexual maturity in males, should be comparable.

Another important point is that geographical variation should be taken into account in any analysis based on specimens that come from more than one location, or that come from only one population when considerable geographical variation is known to exist. Thus the results of an analysis relating mortality rate to body size across several species might be different (and probably more useful) if the component estimates included estimates for two or more populations of *Tursiops truncatus* than if they included only a pooled *Tursiops* estimate or an estimate for only one population. In a deductive analysis involving several parameters, it is, of course, essential that the estimates of input parameters for a species come from the same or similar populations of the species.

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[Appendices 1-4 are on the following 8 pages]

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Appendix 1  
Length data for dolphins. Sources listed for tabulated values; other sources consulted (which contributed to sample sizes) are included in Literature Cited

Species and region (stock in parentheses)	Largest fetus		Smallest individual		Largest immature animal		Smallest mature animal		Largest individual		Source						
	cm	(n)	cm	(n)	cm	(n)	cm	(n)	Male			Female					
									cm	(n)		cm	(n)				
<i>Steno bredanensis</i> All regions	87	(4)	—	—	216	(28)	212	(14)	265	(68)	255	(65)	Cadenat, 1949; Layne, 1965; Lütken, 1889; Perrin and E. Walker, 1975				
<i>Sotalia fluviatilis</i> Coastal Riverrine	59 71	(1) (3)	92 83	(13) (28)	157 138	(3) (9)	170 132	(4) (7)	187 152	(7) (17)	182 149	(8) (11)	Best and da Silva, 1984; Carvalho, 1963; Harrison and Brownell, 1971; van Utrecht, 1981				
<i>Sousa chinensis</i> All regions	—	—	97	(9)	—	—	—	—	320	(6)	244	(5)	Blanford, 1888-91; Ross, 1979				
<i>Sousa teuszii</i> E. trop. Atlantic	—	—	—	—	—	—	—	—	248	(3)	235	(3)	Cadenat and Paraiso, 1957; Cadenat, 1959				
<i>Peponocephala electra</i> All regions	65	(1)	112	(8)	212	(2)	229	(3)	264	(3)	257	(1)	Bryden <i>et al.</i> , 1977; Perrin, 1976				
<i>Feresa attenuata</i> All regions	53	(2)	82	(16)	—	—	—	—	216	(2)	221	(2)	Best, 1970; Nishiwaki <i>et al.</i> , 1965; Perrin and Hubbs, 1969; Pryor <i>et al.</i> , 1965; Ross, 1979				
<i>Pseudorca crassidens</i> All regions	183	(10)	157	(429)	366	(12)	364	(10)	372	(28)	349	(54)	Mizue and Yoshida, 1961; Purves and Pilleri, 1978; Ross, 1979; Scott and Green, 1975; Tomilin, 1957				
<i>Orcinus orca</i> All regions North Atlantic North Pacific South Pacific Indian Ocean Antarctic	274 255 193 140 — 250	(272) (239) (1) (1) — (16)	183 183 228 200 381 320	(2,741) (693) (134) (12) (37) (1,229)	617 559 520 — — —	(4) (—) (2) — — —	488 488 — — — 370	(16) (10) — — — (1)	520 660 760 — — —	(6) (—) (1) — — —	457 457 560 — — 540	(215) (111) (1) — — (91)	975 975 829 805 884 910	(2,306) (1,239) (56) (5) (25) (652)	853 853 698 670 792 762	(1,744) (822) (52) (6) (12) (577)	Allen, 1977; Anon. 1982b; Best and Ross, 1977; Carl, 1945; Christensen, 1982; Condy, van Aarde and Bester, 1978; Fiscus and Niggol, 1965; Ivashin, 1981; Jonsgård and Lyschoel, 1970; Mikhaliev <i>et al.</i> , 1981; Nishiwaki and Handa, 1958; Pike and MacAskie, 1969; Ridgway, 1979; Scheffer, 1967; Tomilin 1957
<i>Globicephala melana</i> All regions E. North Atlantic W. North Atlantic New Zealand Tasmania	195 195 190 — —	(308) (2) (306) — —	137 137 165 177 187	(3,629) (206) (3,399) (14) (95)	472 — 472 — —	(65) — (65) — —	386 238 386 — —	(471) (5) (466) — —	48 — 48 — —	(5) — (5) — —	351 375 351 — —	(89) (5) (84) — —	762 762 617 600 620	(1,398) (88) (1,378) (7) (40)	570 570 511 500 555	(2,086) (56) (2,020) (5) (55)	Anon., 1981a and 1982a; Budker, 1968; Duguay 1973-82; Duguay and Budker, 1972; Fraser, 1974; Gray, 1846; Guiler, 1978; Paulus, 1960; Sergeant, 1962
<i>G. macrorhynchus</i> All regions W. North Atlantic E. North Pacific W. North Pacific Indian Ocean	140 — 104 140 —	(25) — (2) (17) —	135 162 135 182 168	(661) (369) (64) (153) (95)	437 383 352 — 437	(16) (1) (2) — (1)	396 334 336 — 396	(17) (3) (8) — (2)	508 — — — 508	(3) — — — (3)	335 335 396 — 405	(6) (2) (3) — (1)	610 535 590 491 610	(231) (95) (23) (51) (49)	525-550 478 480 392 525-550	(344) (146) (32) (102) (35)	Alagarwami <i>et al.</i> , 1973; Hall <i>et al.</i> , 1971; Harrison <i>et al.</i> , 1972; Layne, 1965; Lowery, 1974; Perrin and Myrick, 1980; Ross, 1979; SEAN, 1977; van Bree <i>et al.</i> , 1978; Walker, 1975; Yonekura <i>et al.</i> , 1980

North Pacific	102	(7)	124	(269)	198	(13)	216	(28)	170	(8)	170	(> 13)	230-234	(> 162)	236	(> 115)	Fiscus and Niggol, 1965; Harrison <i>et al.</i> , 1972; Harrison and McBrearty, 1977; Kasuya and Izumisawa, 1981; Scheffer and Slipp, 1948
<i>L. acutus</i>	114	(> 59)	108	(233)	210	(16)	222	(6)	244	(4)	194	(51)	275	(> 99)	243	(> 83)	Sergeant <i>et al.</i> , 1980; Tomlin, 1957; van Utrecht, 1959
<i>L. obscurus</i>			92	(37)			130	(1)			170	(3)	211	(10)	193	(21)	Allen, 1977; Anon., 1978; Best, 1976; Brownell, 1974
<i>L. cruciger</i>			110	(3)											183	(2)	Brownell, in press; Fraser, 1966; Lrouville, 1913; Nichols, 1908
<i>L. albirostris</i>	125	(> 6)	119	(> 152)	257	(2)	249	(5)	251	(2)	250	(9)	315	(> 36)	305	(> 53)	Duguy, 1982; Fraser, 1974; Tomlin, 1957; van Utrecht, 1981; Weber, 1887
<i>L. australis</i>	45	(3)	95	(23)	184	(3)	231	(2)	264	(1)	226	(> 4)	264	(6)	264	(12)	Kellogg, 1941
<i>Tursiops truncatus</i>	122	(78)	84	(> 3,338)	314	(91)	295	(72)	202	(51)	190	(194)	381	(~ 1,400)	367	(~ 1,400)	Allen, 1977; Cadenat, 1959; Cornell, 1977; van Deinste, 1946; Duguy, 1974, 1976, 1980; Fraser, 1934, 1953; Guenter, 1942; Harmer, 1927; Harrison <i>et al.</i> , 1972; Harrison and Fanning, 1973; Harrison and McBrearty, 1977; Kasuya, 1973; Kasuya and Izumisawa, 1981; Kleinenberg, 1956; Leatherwood <i>et al.</i> , 1972; Norris and Prescott, 1961; Ross, 1977, 1979; SEAN, 1976, 1977, 1979; 1981; Sergeant <i>et al.</i> , 1973; Tomlin, 1957; True, 1889; Walker, 1981; Zeiler, 1977
All regions	91	(2)	116	(235)	314	(1)	295	(1)			312	(3)	381	(> 74)	350	(50)	
E. North Atlantic			140	(25)	160	(1)					300	(1)	330	(14)	320	(6)	
Mediterranean			122	(> 1,450)							226	(> 4)	310	(~ 700)	234	(4)	
Black Sea			92	(305)	210	(3)					232	(6)	310	(121)	339	(132)	
W. North Atlantic <sup>1</sup>	117	(6)	92	(305)	210	(3)					232	(6)	310	(121)	339	(132)	
Florida coasts	112	(8)	95	(284)	277	(32)	238	(22)	242	(10)	225	(38)	290	(127)	276	(143)	
Gulf of Mexico <sup>1</sup>	122	(7)	91	(123)	269	(3)	239	(1)	218	(3)	229	(13)	380	(43)	367	(46)	
E. North Pacific			110	(50)	269	(3)	264	(1)	263	(7)	276	(6)	340	(20)	330	(27)	
(all forms)																	
E. North Pacific (onshore)					269	(1)	255	(4)	297	(4)			333	(8)	307	(9)	
E. North Pacific (offshore)			114	(14)	234	(2)	264	(5)	263	(3)	276	(3)	310	(5)	290	(9)	
E. tropical Pacific	88	(2)			236	(5)	242	(7)	244	(7)	243	(2)	266	(12)	256	(9)	
W. North Pacific	120-129	(60)			292	(18)	280-289	(8)	288	(12)	250-259	(107)	335	(194)	320-329	(258)	
Indian Ocean (all forms)	60	(2)	84	(84)	278	(18)	280	(15)	202	(13)	190	(12)	327	(56)	280	(33)	
Indian Ocean ('aduncus')	60	(2)	84	(89)	235	(16)	220	(14)	202	(13)	190	(12)	254	(44)	252	(41)	
Indian Ocean ('truncatus')			270	(7)	278	(3)	280	(1)					327	(5)	280	(2)	
E. tropical Atlantic													368	(11)	350	(7)	
<i>Grampus griseus</i>	166	(10)	135	(> 243)	297	(15)	280-284	(14)	262	(10)	260-264	(22)	383	(> 81)	366	(69)	
All regions			135	(62)							298	(1)	360	(11)	310	(10)	
Mediterranean			173	(78)	244	(1)					320	(3)	383	(29)	366	(27)	
E. North Atlantic			158	(25)							305	(5)	340	(9)	318	(12)	
W. North Atlantic	90-94	(4)	180-184	(43)	297	(11)	280-284	(10)	262	(9)	260-264	(13)	307	(20)	285-289	(23)	
S. W. Indian Ocean	84	(2)	163	(19)	243	(2)	257	(4)			291	(1)	325	(9)	277	(6)	
<i>Stenella longirostris</i>	84	(331)	70	(5,001)	192	(9,249)	190	(1,067)	160	(766)	152	(1,054)	235	(2,340)	204	(2,621)	
All regions	81	(2)	90	(41)	158	(1)	190	(7)	173	(17)	177	(17)	208	(18)	204	(22)	
Tropical Atlantic									181	(2)	193	(3)	216	(2)	203	(3)	
E. tropical Pacific (Costa Rican)																	
E. tropical Pacific (eastern)	84	(169)	70	(2,566)	192	(594)	182	(608)	160	(356)	152	(536)	195	(1,102)	187	(1,297)	
E. tropical Pacific (n. whitebelly)	82	(159)	72	(2,218)	191	(330)	188	(433)	160	(319)	157	(425)	203	(1,063)	195-199	(1,155)	
E. tropical Pacific (s. whitebelly)			85-89	(123)					167	(69)	162	(63)	235	(142)	190-194	(119)	

## Appendix 1 (continued)

Species and region (stock in parentheses)	Largest fetus		Smallest individual		Largest immature animal				Smallest mature animal				Largest individual				Source
	cm	(n)	cm	(n)	Male		Female		Male		Female		Male		Female		
					cm	(n)	cm	(n)	cm	(n)	cm	(n)	cm	(n)	cm	(n)	
<i>S. clymene</i> Atlantic	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	Perrin <i>et al.</i> , 1981
<i>S. plagiodon</i> Atlantic	—	—	120	(40)	—	—	—	—	—	—	—	—	—	—	—	—	Caldwell and Caldwell, 1966; SEAN, 1975, 1981
<i>Stenella coeruleoalba</i> All regions	108	(114)	80	(6,236)	—	—	—	—	—	—	—	—	—	—	—	—	Duguy, 1980; Duguy <i>et al.</i> , 1978; Gurevich and Stewart, 1979; Kasuya, 1972; Miyazaki, 1977; Perrin and Oliver, 1982; Ross, 1979; SEAN, 1979
Mediterranean	—	—	80	(232)	—	—	—	—	—	—	—	—	—	—	—	—	
North Atlantic	—	—	116	(72)	—	—	—	194	—	—	—	—	—	—	—	—	
E. trop. Pacific	80	(13)	90	(202)	—	—	—	—	—	—	—	—	—	—	—	—	
W. North Pacific	108	(99)	95	(5,493)	—	—	—	—	—	—	—	—	—	—	—	—	
S. W. Indian Ocean	—	—	—	—	240-250	(~127)	230-240	200-210	200-210	218	(5)	200	(5)	256	(16)	228	(10)
<i>S. attenuata</i> All regions	106	(562)	75-79	(6,347)	202	(~259)	209	(440)	162	(~820)	167	(~1,462)	257	(~3,566)	240-244	(~3,235)	Allen, 1977; Best, 1969; Kasuya <i>et al.</i> , 1974; Nishiwaki <i>et al.</i> , 1965; Perrin, 1975a; Perrin <i>et al.</i> , 1976; Perrin and Oliver, 1982; Ross, 1979
E. tropical Pacific (coastal)	—	—	90-94	(128)	—	—	—	—	203	(37)	184	(76)	257	(43)	240-244	(85)	
E. tropical Pacific (n. and s. offshore)	90	(468)	75-79	(5,348)	201	(~150)	193	(307)	179	(~724)	167	(~1,127)	225-229	(~3,141)	220-224	(~2,792)	
Central Pacific	—	—	—	—	180	(1)	160	(1)	182	(6)	189	(3)	202	(8)	203	(4)	
W. North Pacific	—	—	89	(959)	202	(103)	209	(132)	162	(44)	173	(253)	234	(~300)	220	(~344)	
S. W. Indian Ocean	—	—	89	(9)	198	(3)	—	—	216	(2)	215	(1)	220	(5)	215	(5)	
<i>Delphinus delphis</i> All regions	108	(~446)	70	(~45,650)	206	(33)	222	(~1,973)	171	(~5,090)	141-150	(~8,583)	260	(~27,211)	230	(~26,368)	Allen, 1977; Aloncle, 1964; Anon., 1981a; Cadena, 1957; 1959; 1976; 1981; 1981b; 1981c; 1981d; 1981e; 1981f; 1981g; 1981h; 1981i; 1981j; 1981k; 1981l; 1981m; 1981n; 1981o; 1981p; 1981q; 1981r; 1981s; 1981t; 1981u; 1981v; 1981w; 1981x; 1981y; 1981z; 1982; 1983; 1984; 1985; 1986; 1987; 1988; 1989; 1990; 1991; 1992; 1993; 1994; 1995; 1996; 1997; 1998; 1999; 2000; 2001; 2002; 2003; 2004; 2005; 2006; 2007; 2008; 2009; 2010; 2011; 2012; 2013; 2014; 2015; 2016; 2017; 2018; 2019; 2020; 2021; 2022; 2023; 2024; 2025; 2026; 2027; 2028; 2029; 2030; 2031; 2032; 2033; 2034; 2035; 2036; 2037; 2038; 2039; 2040; 2041; 2042; 2043; 2044; 2045; 2046; 2047; 2048; 2049; 2050; 2051; 2052; 2053; 2054; 2055; 2056; 2057; 2058; 2059; 2060; 2061; 2062; 2063; 2064; 2065; 2066; 2067; 2068; 2069; 2070; 2071; 2072; 2073; 2074; 2075; 2076; 2077; 2078; 2079; 2080; 2081; 2082; 2083; 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**Appendix 2**  
Testis data for delphinids

Species and region (stock in parentheses)	Minimum weight of 'adult' testis		Maximum weight of testis		Source
	g	(n)	g	(n)	
<i>Steno bredanensis</i>					
W. North Pacific	175	(9)	1,150	(9)	Miyazaki, 1980
<i>Sotalia fluviatilis</i>					
Amazon basin	27	(7)	1,060	(10)	Best and da Silva, 1984; Harrison and Brownell, 1971
<i>Peponocephala electra</i>					
W. trop. Pacific	674	(3)	685	(3)	Bryden <i>et al.</i> , 1977
Central trop. Atlantic	~ 1,100 <sup>1</sup>	(1)	~ 1,100 <sup>1</sup>	(1)	Goodwin, 1945
<i>Feresa attenuata</i>					
Central trop. Pacific	321	(1)	377	(1)	Pryor <i>et al.</i> , 1965
<i>Pseudorca crassidens</i>					
W. North Pacific	~ 1,700 <sup>1</sup>	(21)	~ 7,400 <sup>1</sup>	(31)	Kasuya and Izumisawa, 1981
<i>Orcinus orca</i>					
All regions	—	—	23,100	(64)	Ross, 1979; Allen, 1977; Mikhalev <i>et al.</i> , 1981; Harrison <i>et al.</i> , 1972
Antarctic	—	—	23,100	(57)	Mikhalev <i>et al.</i> , 1981
<i>Globicephala melaena</i>					
E. North Atlantic	575	(12)	7,200	110)	Sergeant, 1962
<i>G. macrorhynchus</i>					
S.W. Indian Ocean	770	(4)	3,540	(4)	Ross, 1979
E. trop. Pacific	264 <sup>2</sup>	(7)	548 <sup>2</sup>	(10)	Walker, 1981
W. North Pacific	~ 50 <sup>1</sup>	(12)	~ 700 <sup>1</sup>	(29)	Kasuya and Izumisawa, 1981
W. South Pacific	505	(1)	572	(8)	Ross, 1979
S.W. Indian Ocean (' <i>aduncus</i> ')	318	(5)	800	(5)	Ross, 1979
<i>Grampus griseus</i>					
E. North Pacific	3,130	(3)	6,360	(3)	Orr, 1966; Harrison <i>et al.</i> , 1972
W. North Pacific	~ 350 <sup>1</sup>	(9)	~ 5,300 <sup>1</sup>	(20)	Kasuya and Izumisawa, 1981
<i>Lagenorhynchus obliquidens</i>					
E. North Pacific	548	(16)	559	(16)	Harrison <i>et al.</i> , 1972
W. North Pacific	~ 170 <sup>1</sup>	(25)	~ 390 <sup>1</sup>	(87)	Kasuya and Izumisawa, 1981
<i>L. obscurus</i>					
E. South Atlantic	—	—	800	(—)	Best, 1976
<i>L. acutus</i>					
W. North Atlantic	180	(5)	370	(21)	Sergeant <i>et al.</i> , 1980
<i>Lagenodelphis hosei</i>					
W. North Pacific	990	(1)	990	(1)	Tobayama <i>et al.</i> , 1973
S.W. Indian Ocean	1,280	(1)	1,280	(2)	Ross, 1979
<i>Tursiops truncatus</i>					
All regions	~ 50 <sup>1</sup>	(45)	983	(98)	Below, and Harrison and Fanning, 1974, Allen, 1977 and Leatherwood, 1978

<sup>1</sup> Estimated as  $\frac{1}{2}$  combined testis weight.

<sup>2</sup> Includes epididymis.

## Appendix 2 (continued)

Species and region (stock in parentheses)	Minimum weight of 'adult' testis		Maximum weight of testis		Source
	g	(n)	g	(n)	
Florida and Gulf of Mexico	280	(6)	532	(19)	Harrison <i>et al.</i> , 1972; Sergeant <i>et al.</i> , 1973; Harrison and Ridgway, 1971; Walker, 1981
E. North Pacific (onshore)	536	(4)	983	(5)	
E. North Pacific (offshore)	248	(3)	530	(5)	Walker, 1981
<i>S. attenuata</i>					
E. trop. Pacific (offshore)	100 <sup>2</sup>	(> 207)	~ 1,200 <sup>1, 2</sup>	(> 415)	Harrison, 1969; Harrison <i>et al.</i> , 1972; Perrin <i>et al.</i> , 1976
W.N. Pacific	66	(142)	~ 650 <sup>1</sup>	(> 138)	Kasuya <i>et al.</i> , 1974; Kasuya, 1976
S.W. Indian Ocean	—	—	121	(5)	Ross, 1979
<i>Stenella longirostris</i>					
Gulf of Mexico	320	(9)	980	(12)	Mead <i>et al.</i> , 1980; Layne, 1965
E. trop. Pacific (eastern)	20–30 <sup>2</sup>	(50)	800–900	(826)	Perrin <i>et al.</i> , 1977; Perrin and Henderson, 1984
E. trop. Pacific (n. whitebelly)	60–80 <sup>2</sup>	(92)	1,354 <sup>2</sup>	(695)	Perrin and Henderson, 1984
Centr. trop. Pacific	—	—	330	(8)	Harrison <i>et al.</i> , 1972; Allen, 1977;
E. trop. Atlantic	—	—	925	(2)	Cadenat and Doutre, 1959
<i>S. coeruleoalba</i>					
E. trop. Pacific	—	—	~ 157 <sup>1, 2</sup>	(38)	Gurevich and Stewart, 1979
W. North Pacific	8	(> 222)	~ 250 <sup>1</sup>	(> 437)	Kasuya, 1976; Miyazaki, 1977; Hirose and Nishiwaki, 1971
S.W. Indian Ocean	94	(2)	136	(2)	Ross, 1979
<i>Delphinus delphis</i>					
Black Sea	300	(—)	1,000	(2,138)	Sleptsov, 1941
E. North Atlantic	100	(9)	800	(20)	Collet and St. Girons, 1984
E. North Pacific (offshore)	465	(12)	1,672	(31)	Harrison, 1969; Harrison <i>et al.</i> , 1972; Ridgway and Green, 1967
E. trop. Pacific (centr. trop.)	129	(12)	853	(42)	Oliver, 1973
S.W. Indian Ocean	1,815	(3)	4,085	(3)	Ross, 1979
E. trop. Atlantic	—	—	883	(7)	Cadenat, 1959
<i>Lissodelphis borealis</i>					
E. North Pacific	705	(2)	705	(3)	Harrison <i>et al.</i> , 1972; Sullivan and Houck, 1979
<i>Cephalorhynchus hectori</i>					
W. South Pacific	—	—	465	(1)	Baker, 1978

<sup>1</sup> Estimated as  $\frac{1}{2}$  combined testis weight.<sup>2</sup> Includes epididymis.

Appendix 3

Average length of adults and asymptotic length in delphinids. Minimum sample size for inclusion is at least 2 for at least one column. Standard deviation given for sample size of 25 or more, where possible

Species and region (stock in parentheses)	Average length of sexually mature animals						Asymptotic length				Source	
	Males			Females			Males		Females			
	cm	(n)	SD	cm	(n)	SD	cm	(n)	cm	(n)		
<i>Steno bredanensis</i>												
W. North Pacific	232	(24)	—	231	(11)	—	—	—	—	—	—	Miyazaki, 1980
E. trop. Atlantic	227	(3)	—	234	(1)	—	—	—	—	—	—	Cadenat, 1959
<i>Sotalia fluviatilis</i>												
Coastal	177	(4)	—	176	(4)	—	—	—	—	—	—	van Utrecht, 1981
Riverine	146	(6)	—	145	(7)	—	—	—	—	—	—	Best and da Silva, 1984; Carvalho, 1963
<i>Sousa teuszii</i>												
E. trop. Atlantic	200	(3)	—	—	—	—	—	—	—	—	—	Allen, 1977
<i>Peponocephala electra</i>												
E. South Pacific	268	(3)	—	—	—	—	—	—	—	—	—	Bryden et al., 1977
<i>Pseudorca crassidens</i>												
E. North Atlantic	532	(4)	—	447	(14)	—	541	(3)	452	(10)	—	Peacock et al., 1936; Purves and Pilleri, 1978
W. North Atlantic	520	(1)	—	458	(2)	—	—	—	—	—	—	Odell et al., 1980
W. North Pacific	—	—	—	430	(92)	27.1	—	—	—	—	—	Kasuya and Izumisawa, 1981; Mizue and Yoshida, 1961
W. South Pacific	—	—	—	400	(18)	—	—	—	—	—	—	Scott and Green, 1975
<i>Orcinus orca</i>												
E. North Atlantic	945	(1)	—	566	(110)	65.5	—	—	—	—	—	Christensen, 1982; Gray, 1846; Jonsgård and Lyshoel, 1970
Antarctic	—	—	—	645	(91)	56.6	—	—	—	—	—	Mikhalev et al., 1981
<i>Globicephala melaena</i>												
W. North Atlantic	545	(12)	—	381	(85)	11.5	~ 550	(> 4)	~ 460	(> 19)	—	Sergeant, 1962
<i>G. macrorhynchus</i>												
W. North Atlantic	—	—	—	345	(2)	—	~ 470	(—)	~ 360	(—)	—	Harrison et al., 1972; Irvine et al., 1979
E. North Pacific	—	—	—	466	(2)	—	—	—	—	—	—	Harrison et al., 1972
W. North Pacific	453	(13)	—	358	(72)	14.2	—	—	330-360	—	—	Yonekura et al., 1980
<i>Lagenorhynchus obliquidens</i>												
E. North Pacific	190	(8)	—	192	(12)	—	—	—	—	—	—	Fitch and Brownell, 1968; Harrison et al., 1972; Ridgway and Green, 1967
<i>L. acutus</i>												
W. North Atlantic	250	(4)	—	224	(30)	6.0	—	—	—	—	—	Sergeant et al., 1980
<i>L. obscurus</i>												
E. South Atlantic	188	(2)	—	191	(1)	—	—	—	—	—	—	Best, 1976
<i>L. albirostris</i>												
E. North Atlantic	260	(2)	—	259	(9)	—	—	—	—	—	—	Duguy, 1982; van Bree and Husson, 1964; van Utrecht, 1981
<i>Lagenodelphis hosei</i>												
All regions (4)	236	(3)	—	235	(7)	—	234	(7)	241	(4)	—	Perrin et al., 1973; Ross, 1979; SEAN, 1978; Tobayama et al., 1973
<i>Tursiops truncatus</i>												
Black Sea	275	(—)	—	233	(—)	—	—	—	—	—	—	Kleinenberg, 1956
W. North Atlantic <sup>1</sup>	—	—	—	252	(6)	—	—	—	—	—	—	Leatherwood et al., 1972
Florida (both coasts)	258	(13)	—	239	(45)	8.7	270	(7)	250	(13)	—	Cornell, 1977; Harrison et al., 1972; Harrison and McBrearty, 1977; Sergeant et al., 1973; Zeller, 1977
Gulf of Mexico <sup>1</sup>	241	(4)	—	251	(12)	—	—	—	259	(1)	—	Gunter, 1942; Harrison et al., 1972; Harrison and McBrearty, 1977, Schmidly, 1978
E. N. Pacific (onshore)	—	—	—	312	(4)	—	—	—	—	—	—	Walker, 1981
E. N. Pacific (offshore)	283	(3)	—	282	(3)	—	—	—	—	—	—	Walker, 1981
E. trop. Pacific	256	(7)	—	250	(2)	—	—	—	—	—	—	Walker, 1981
W. North Pacific	—	—	—	288	(138)	13.4	—	—	—	—	—	Kasuya and Izumisawa, 1981
Indian Ocean ('aduncus')	239	(15)	—	237	(26)	—	239	(5)	241	(14)	—	Allen, 1977; Harrison and Fanning, 1973; Harrison and McBrearty, 1977; Ross, 1979

Appendix 3 (continued)

Species and region (stock in parentheses)	Average length of sexually mature animals						Asymptotic length						Source
	Males			Females			Males			Females			
	cm	(n)	SD	cm	(n)	SD	cm	(n)	SD	cm	(n)	SD	
<i>Grampus griseus</i> E. North Atlantic	—	—	—	332	(5)	—	370	(1)	—	342	(1)	—	Flower, 1872; Fraser, 1934, 1946; Harmer, 1927; Murie, 1870; Tomilin, 1957 Kasuya and Izumisawa, 1981
W. North Pacific	288	(9)	—	276	(13)	—	—	—	—	—	—	—	—
<i>Stenella longirostris</i> Gulf of Mexico	192	(15)	—	189	(17)	—	201	(1)	—	201	(1)	—	Mead <i>et al.</i> , 1980; Layne, 1965 Perrin, 1975a
E. trop. Pacific (Costa Rican)	192	(2)	—	—	—	—	—	—	—	—	—	—	—
E. trop. Pacific (eastern)	176	(594)	6.0	171	(560)	6.1	180	(12)	—	171	(60)	—	Perrin <i>et al.</i> , 1977, 1979; Perrin and Oliver, 1982
E. trop. Pacific (n. whitebelly)	179	(319)	7.0	176	(425)	6.8	180	(21)	—	175	(28)	—	Perrin and Henderson, 1984
E. trop. Pacific (s. whitebelly)	181	(69)	6.6	178	(63)	7.3	—	—	—	—	—	—	Perrin <i>et al.</i> , 1979; Perrin and Oliver, 1982
<i>S. clymene</i> Atlantic	185	(3)	—	—	—	—	—	—	—	—	—	—	Perrin <i>et al.</i> , 1981
<i>S. coeruleoalba</i> E. trop. Pacific	—	—	—	—	—	—	205	(3)	—	200	(2)	—	Gurevich and Stewart, 1979
W. North Pacific	227	(157)	—	220	(151)	—	238	(214) <sup>2</sup>	—	225	(584) <sup>2</sup>	—	Miyazaki, 1977
S.W. Indian Ocean	235	(5)	—	218	(5)	—	244	(1)	—	217	(2)	—	Ross, 1979
<i>S. attenuata</i> E. trop. Pacific (coastal)	228	(32)	10.7	209	(70)	9.0	—	—	—	—	—	—	Perrin, 1975a; Perrin and Oliver, 1982
E. trop. Pacific (n. and s. offshore)	201	(730)	8.5	187	(1,123)	7.0	200	(—)	—	190	(—)	—	Harrison <i>et al.</i> , 1972; Perrin <i>et al.</i> , 1979; Perrin and Oliver, 1982
W. North Pacific	204-207	(80)	—	192-195	(251)	—	207	(—)	—	194	(135) <sup>2</sup>	—	Harrison <i>et al.</i> , 1972; Kasuya, 1976; Kasuya <i>et al.</i> , 1974; Nishiwaki <i>et al.</i> , 1974 Best, 1969; Ross, 1979
S.W. Indian Ocean	217	(3)	—	215	(2)	—	—	—	—	215	(1)	—	—
<i>Delphinus delphis</i> Black Sea	178	(890)	—	(a) 170 (b) 175	(1,809) (25)	—	—	—	—	—	—	—	Mal'm and Trotskaya, 1932; Mayarova and Danilevskiy, 1934; Stepstov, 1941; Sokolov, 1962 Collet, 1981; Fischer, 1881; Fraser, 1934; Slijper, 1936; van Utrecht and Husson, 1968 Mercer, 1973; Ulmer, 1981 Evans, 1975
E. North Atlantic	219	(17)	—	193	(23)	—	243	(1)	—	211	(3)	—	—
W. North Atlantic	—	—	—	211	(2)	—	—	—	—	—	—	—	—
E. trop. Pacific (centr. trop.)	208	(40)	—	196	(48)	—	—	—	—	—	—	—	—
W. South Pacific	219	(5)	—	201	(3)	—	—	—	—	—	—	—	Allen, 1977; van Utrecht, 1981
S.W. Indian Ocean	242	(4)	—	212	(1)	—	—	—	—	212	(1)	—	Ross, 1979
E. trop. Atlantic	210	(9)	—	208	(5)	—	—	—	—	—	—	—	Cadenat, 1959
<i>Lissodelphis borealis</i> E. North Pacific	263	(7)	—	217	(9)	—	—	—	—	—	—	—	Leatherwood and Walker, 1979; SEAN, 1981; Sullivan and Houck, 1979
<i>Cephalorhynchus commersonii</i> W. South Atlantic	136	(1)	—	—	—	—	130	(6)	—	139	(2)	—	Lockyer <i>et al.</i> , 1981; Spotte <i>et al.</i> , 1979

<sup>1</sup> Exclusive of Florida.<sup>2</sup> Total in analysis, mature and immature.

Appendix 4

Average age and maximum age of sexually mature delphinids, in years (y) or GLGs - terminology of Perrin and Myrick 1980 - (G)

Species and region (stock in parentheses)	Average age of sexually mature				Maximum age of sexually mature				Source
	Males		Females		Males		Females		
	y or G	(n)	y or G	(n)	y or G	(n)	y or G	(n)	
<i>Steno bredanensis</i>									
W. North Pacific	20y	(24)	21y	(10)	32y	(24)	30y	(11)	Miyazaki, 1980
<i>Peponocephala electra</i>									
W. South Pacific	27G	(2)	12G	(1)	47G	(2)	12G	(1)	Bryden <i>et al.</i> , 1977
<i>Feresa attenuata</i>									
S.W. Indian Ocean	14G	(2)	—	—	14G	(2)	—	—	Ross, 1979
<i>Pseudorca crassidens</i>									
E. North Atlantic	16y	(3)	17y	(3)	20y	(33)	22y	(40)	Purves and Pilleri, 1978
<i>Orcinus orca</i>									
All regions	—	—	—	—	35G	(56)	34G	(68)	Christensen, 1980; Mitchell, 1980; Ross, 1979
<i>Globicephala melaleuca</i>									
W. North Atlantic	> 11y	(58)	> 13y	(203)	26G, 14y	(165)	> 19G, > 20y	(296)	Perrin and Myrick, 1980; Ross, 1970; Sergeant, 1962
<i>G. macrorhynchus</i>									
W. North Atlantic	—	—	—	—	21G	(6)	49G	(11)	Perrin and Myrick, 1980; Ross, 1979
W. North Pacific	—	—	—	—	30G	(7)	> 29G	(3)	
S.W. Indian Ocean	13G	(2)	14G	(1)	15G	(2)	14G	(1)	
<i>Lagenorhynchus obscurus</i>									
E. South Atlantic	—	—	—	—	7y	(1)	21y	(2)	Best, 1976
<i>L. acutus</i>									
W. North Atlantic	—	—	12G	(26)	22G	(14)	27G	(38)	Sergeant <i>et al.</i> , 1980
<i>Tursiops truncatus</i>									
All regions	19y, > 12G	(17)	> 26y, > 11G	(26)	25y, 25G	(158)	> 30y, 27G	(166)	Hohn, 1980; Ross, 1977, 1979;
W. North Atlantic	19y	(6)	> 19y	(17)	25y, 25G	(90)	> 30y, 27G	(98)	Sergeant <i>et al.</i> , 1973
S.W. Indian Ocean	> 12G	(11)	> 11G	(6)	> 17G	(11)	13G	(6)	
( <i>'aduncus'</i> )									
<i>Grampus griseus</i>									
S.W. Indian Ocean	—	—	> 13G	(2)	> 13G	(2)	> 17G	(2)	Ross, 1979
<i>Stenella longirostris</i>									
Gulf of Mexico	9G	(2)	12G	(2)	10G	(3)	12G	(4)	Mead <i>et al.</i> , 1980; Perrin <i>et al.</i> , 1977; Perrin and Henderson, 1984
E. trop. Pacific (eastern)	7-10y	(39)	—	—	12-15y	(182)	15-21y	(250)	
E. trop. Pacific (n. whitebelly)	8-12y	(57)	—	—	13-19y	(170)	16-23y	(270)	
<i>S. coeruleoalba</i>									
E. trop. Pacific	—	—	—	—	16G	(38)	15G	(48)	Gurevich and Stewart, 1979;
									Miyazaki, 1977
W. North Pacific	14y	(222)	14y	(541)	29y	(222)	28y	(541)	
<i>S. attenuata</i>									
E. trop. Pacific (n. offshore)	> 11G	(42)	—	—	> 17G	(42)	> 17G	(209)	Kasuya, 1976; Perrin <i>et al.</i> , 1976
W. North Atlantic	—	—	—	—	40y	(158)	46y	(200)	
<i>Delphinus delphis</i>									
Black Sea	—	—	15y	(17)	22y	(—)	20y	(17)	Kleinenberg and Klevezal', 1962
E. North Atlantic	—	—	—	—	> 12G	(5)	> 9G	(4)	Collet and St. Girons, 1984
<i>Cephalorhynchus commersonii</i>									
W. South Atlantic	—	—	—	—	15G	(13)	11G	(7)	Lockyer <i>et al.</i> , 1981



# Reproduction in the Porpoises (Phocoenidae): Implications for Management

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## ABSTRACT

The population biology of most phocoenid species is still rather poorly understood. It is important that we improve our knowledge in view of concerns which have been expressed in recent years about the status and long-term viability of some populations. A survey of the literature suggests that it would be unwise to assume that an unknown life-cycle parameter of a phocoenid species would necessarily be similar to that of another species, simply on the basis of taxonomic relationship. Each population and species has experienced a unique evolutionary history in a different ecological regime, and selective influences will have moulded life cycle parameters accordingly.

Most quantitative published data relate to *Neophocaena phocaenoides* (coastal waters of eastern Asia), *Phocoenoides dalli* (boreal – temperate North Pacific), and *Phocoena phocoena* (boreal – temperate N. Pacific and N. Atlantic, and Black Sea). *Phocoena dioptrica* (southern South America and the New Zealand subantarctic), *P. sinus* (Gulf of California), and *P. spinipinnis* (temperate – subtropical waters of South America) are not well known yet. Body-size variation within the family is relatively limited: 65–192 cm (*N. phocaenoides*); 100–225 cm (*P. dalli*); 67–190 cm (*P. phocoena*); and gestation periods are very similar in these three species: 11 months (*P. phocoena* and *N. phocaenoides*) and 11.4 months in *P. dalli*. Far greater differences are apparent in estimates of the age at sexual maturity, the life span, the duration of weaning, and the mean calving interval. It is important to determine if such differences result from misinterpretations or if they relate to radically different evolutionary adaptations (among animals of about the same body size) which have arisen in response to different environmental histories and ecological constraints.

The age at which sexual maturity is attained in *N. phocaenoides* is not yet known. The maturation process seems to be complete between 4–5 and 5–6 years of age in the western North Atlantic and North Sea populations of *P. phocoena*, respectively, and at about 7 years in *P. dalli*. The mean calving intervals appear to be 2 years in *N. phocaenoides*, 3 years in *P. dalli*, and variable in *P. phocoena* from 1–3 years, depending perhaps on nutritional levels. The duration of weaning is not well known in *N. phocaenoides* (estimated between 6–15 months). It could be as short as a few months (6–8) in *P. phocoena* and as long as 2 years in *P. dalli*. As with other odontocetes, controversies exist concerning the accuracy of age determination, but all direct evidence points to *P. phocoena* being relatively short-lived, to a maximum of about 12–13 years. On the basis of age determined from dentinal or cementum layers, *P. dalli* and *N. phocaenoides* have longer life spans than this; at least 16–17 years and 23 years respectively. Attempts to correlate numbers of corpora albicantia with body length have generally not been very successful.

## INTRODUCTION

Three genera are recognized in the family Phocoenidae:<sup>1</sup> *Neophocaena* with a single species *N. phocaenoides* (G. Cuvier, 1829); *Phocoenoides* with a single species *P. dalli* (True, 1885) (having two colour morphs ‘dalli’ and ‘truei’ Andrews, 1911); and *Phocoena* with four species, *P. phocoena* (Linnaeus, 1758); *P. dioptrica* Lahille, 1912; *P. sinus* Norris and McFarland, 1958; and *P. spinipinnis* Burmeister, 1865. All species have distributions which are essentially coastal in nature except *P. dalli*, which ranges widely across the pelagic North Pacific. While phocoenids are relatively familiar animals to coastal observers in the temperate zones of Europe, North and South America, their biology is not that well known, and probably about 90% of published literature relates to *P. phocoena*. The population biology of *P. dioptrica*, *P. sinus*, and *P. spinipinnis* is best described as virtually unknown.

Concern has been expressed for the long-term viability of some populations of *P. phocoena* (Wołk, 1969; Andersen, 1972; 1974; IWC, 1977), and the single population of *P. sinus* may be in immediate danger (Brownell, 1983). Like other shallow-water small cetaceans, phocoenids are particularly vulnerable to incidental capture in gill nets and other set fishing gear. Directed fisheries exist for several species in various parts of the world (Mitchell, 1975), but at present the incidental net

captures probably represent not only the major threat to several phocoenid species, but may also prove to be the most frustrating and intractable obstacle to any successful management programs for these animals.

## MATERIALS AND SOURCES

### *Neophocaena phocaenoides*:

Published data by Chi Ping (1926), Mizue, Yoshida and Masaki (1965), Harrison and McBrearty (1973–74) and Kasuya and Kureha (1979).

### *Phocoenoides dalli*:

Published data by Okada and Hayashi (1951), Wilkie, Taniwaki and Kuroda (1953), Mizue and Yoshida (1965), Mizue, Yoshida and Takemura (1966), Koga (1969), Kuzin and Perlov (1975), Houck (1976), Kasuya (1976a; 1978) and Morejohn (1979).

### *Phocoena phocoena*:

One hundred and eighty-one specimens obtained directly or indirectly by the authors from the western North Atlantic between 1969 and 1981; published data by Fraser (1934; 1953; 1974), Møhl-Hansen (1954), Ropelewski (1957), Wołk (1969), Fisher and Harrison (1970), Harrison (1970), Andersen (1972, 1974), Nielsen (1972), van Bree (1973), Gaskin, Arnold and Blair (1974), Gaskin and Blair (1977), Smith and Gaskin (1974), Watson

<sup>1</sup> Some workers prefer use of a subfamily Phocoeninae.

(1976), Yurick (1977), van Utrecht (1978) and Yasui (1980).

#### *Phocoena dioptrica*:

Published data by Lahille (1912), Bruch (1916), Hamilton (1941), Praderi (1971), Praderi and Palerm (1971), Brownell (1975) and Baker (1977).

#### *Phocoena sinus*:

Published data by Norris and McFarland (1958), Noble and Fraser (1971) and Brownell (1983).

#### *Phocoena spinipinnis*:

Published data by Allen (1925), Pilleri and Gühr (1972), Aguayo (1975), Würsig, Würsig and Mermoz (1977), and Brownell and Praderi (1982).

### REPRODUCTIVE SYSTEMS OF PHOCOENIDS

The urinogenital systems of both sexes are quite typical for odontocetes, perhaps with the exception of the very large proportional size of the testes in the sexually active male (see General Discussion). The right ovary is usually permanently submature in appearance, and non-functional. Descriptions of all or part of male systems of phocoenids can be found in Hepburn and Waterston (1904), Braun (1907), Meek (1918), Chi Ping (1926), Fisher and Harrison (1970) and Harrison (1970); and of the female systems in Klaatsch (1886), Daudt (1898), Wislocki (1933), Harrison (*loc. cit.*), and Fisher and Harrison (*loc. cit.*). The most recent and comprehensive descriptions specifically relating to morphology and histology of ovary and testis have been given by Fisher and Harrison for *P. phocoena*.

### LIFE HISTORY PARAMETERS

#### Age

##### *The status of age determination in phocoenids*

Kasuya (1978) estimated age in *P. dalli* from dentinal layers using decalcified sections stained with haematoxylin. A layer of enamel persists in the teeth of this species after the decalcification treatment. Growth layers were found to be irregular and unclear in postnatal dentine after the first layer, with a pulp cavity rapidly narrowing with age. Teeth in this species are proportionately smaller than in *P. phocoena*. Layering in dentine in older specimens was indistinguishable, or had ceased. In some cases, no distinct layers could be recognized at all. Cementum layers were present and useful to some extent, but the thickness was greatly variable from one individual to another, and accessory layers were often present. Independent counts on the same teeth produced discrepancies of up to 20%. Precise determination of age in this species is not yet possible (Kasuya, 1978).

Age, based on analysis of dentinal growth layers, has been estimated in *P. phocoena* by Nielsen (1972), Gaskin and Blair (1977) and van Utrecht (1978). Nielsen worked with decalcified, hematoxylin-stained transverse and longitudinal sections, the other authors with untreated, unstained longitudinal axial sections. All concurred in the

conclusion that two laminations, one opaque and one translucent (with respect to transmitted light), were deposited to form a single growth layer each year. Nielsen reported that she was unable to distinguish growth layers in the osteodentine of older animals, but van Utrecht made no mention of such a problem, and Gaskin and Blair suggested that Nielsen's chance of recording animals older than about 8 years was limited by the small sample size at her disposal.

Studies of age determination in *N. phocaenoides* are still in progress (Kasuya and Kureha, 1979); the problem has yet to be addressed in the case of *P. dioptrica*, *P. sinus* and *P. spinipinnis*.

#### *Age at sexual maturity*

The mean regressions of body length on age in the two species for which sufficient data are available (*P. dalli* and *P. phocoena*) are presented in Fig. 1.

Kasuya (1978) concluded that the maturing process occurred rapidly in both sexes of *P. dalli*. He estimated that 50% of the males of *P. dalli* were mature by about 7.7 years of age, and 50% of the females by 7.0 years. By using his data and applying the method of DeMaster (1981), we calculated a value of about 7.3 for the average age at which first birth occurs (Table 1). Given the difficulty of interpreting the status of maturing testis tissue however, the two methods obviously yield a similar result. The data base available for *P. phocoena* is not really large enough to apply Kasuya's method to that species.

Van Utrecht (1978) and Yurick (1977) drew attention to differences in growth curves for both sexes of *P. phocoena* in the eastern and western North Atlantic; data for the Bay of Fundy and southern North Sea populations of *P. phocoena* are plotted separately in the figure. The degree of overlap between the individual points (not shown) is considerable, however, and the differences can only be shown statistically, not as absolutes which separate any two individuals from these populations at a given age. The unbroken section of each curve indicates those age classes in which significantly more than 50% of specimens sampled have clearly attained sexual maturity. The curve published by Nielsen (1972) for *P. phocoena* is included for comparison, but since she plotted males and females together, and lacked samples from reproductive organs, the age at sexual maturity of animals in the Baltic population cannot be indicated.

Both males and females of *P. phocoena* appear to reach maturity earlier in the western North Atlantic than in the North Sea. Males and females are mature in the Bay of Fundy population at three to four years of age (Gaskin and Blair, 1977); in the North Sea however, van Utrecht (1978) found males maturing at age five and females at six. Previous suggestions that *P. phocoena* might mature at about 14 or 15 months of age (Møhl-Hansen, 1954; Slijper, 1962) have already been discounted by Fisher and Harrison (1970), and we are in full agreement with this conclusion.

Much less information is available for the other phocoenid species. Kasuya and Kureha (1979) found a male of *N. phocaenoides* 141 cm in length to have testes still in the 'early pubertal stage', while other specimens of 148 cm and upwards were sexually mature. Two females of *P. dioptrica* 186 and 191 cm long were pregnant; two males 200 and 204 cm long were physically

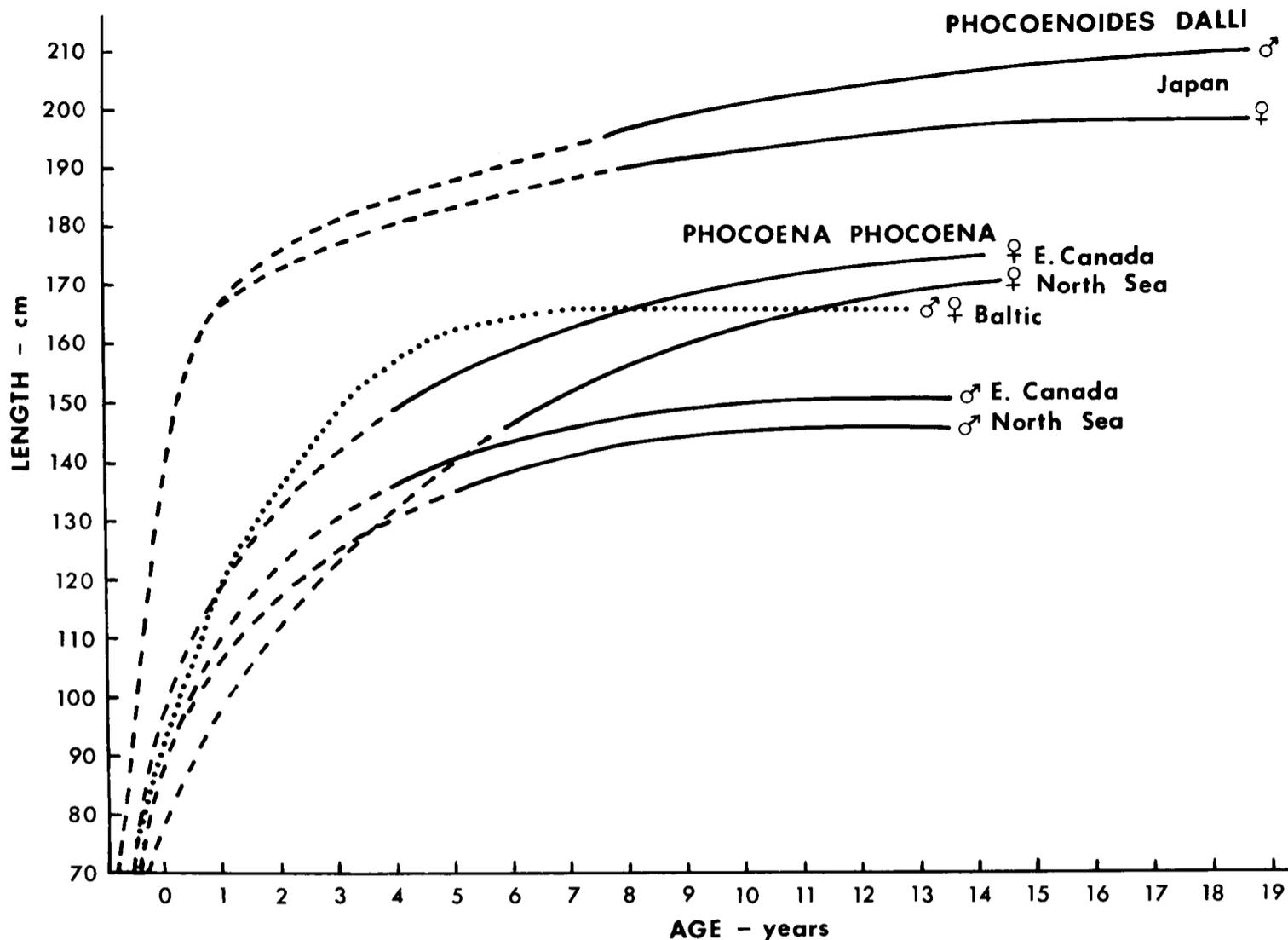


Fig. 1. Relationship between body length and age in years (based on dentinal layers), of specimens of *Phocoenoides dalli* from the vicinity of Japan, and males and females of three populations of *Phocoena phocoena* (Baltic data from Nielsen (1972), North Sea data from van Utrecht (1978) and eastern Canadian data from Gaskin and Blair (1977)).

Table 1

Calculation of the average age of first birth of *Phocoenoides dalli* (data from Kasuya, 1978) using the method of DeMaster (1981)

Age in years (x)	No. females observed n(x)	No. females pregnant t(x)	Proportion of reproductive ♀ z(x)	P (give birth at or before age x) r(x)	P (1st birth at P age x) xr(x)	
2	23	0	0	0	0	0
3	17	0	0	0	0	0
4	26	1	0.038	0.038	0.038	0.152
5	24	2	0.083	0.118	0.080	0.400
6	22	4	0.182	0.279	0.161	0.966
7	27	16	0.593	0.707	0.428	2.996
8	13	3	0.231	0.775	0.068	0.544
9	9	5	0.556	0.900	0.125	1.125
10	9	4	0.444	0.944	0.044	0.440
11	4	1	0.250	0.958	0.014	0.154
12	3	1	0.333	0.972	0.014	0.168
13	1	1	1.000	1.000	0.024	0.312
14	1	1	1.000	1.000	0	0
15	1	1	1.000	1.000	0	0
16	0	0	0	0	0	0
17	1	1	1.000	1.000	0	0
						7.257 <sup>a</sup>

<sup>a</sup> Average age of 1st birth in this sample = 7.257 years.

*Life span*

mature (Brownell, 1975). Only two female specimens of *P. sinus* 139 and 150 cm long have been reported; both appeared to be physically mature (Brownell, 1983). A male of *P. spinipinnis* 180 cm long had active testes according to Brownell and Praderi (1982).

Accurate estimation of life span, both maximum and average, remains a contentious and difficult problem in phocoenid biology, and obviously any simulations of long-term population production are suspect until this issue is resolved. Kasuya and Kureha (1979) reported

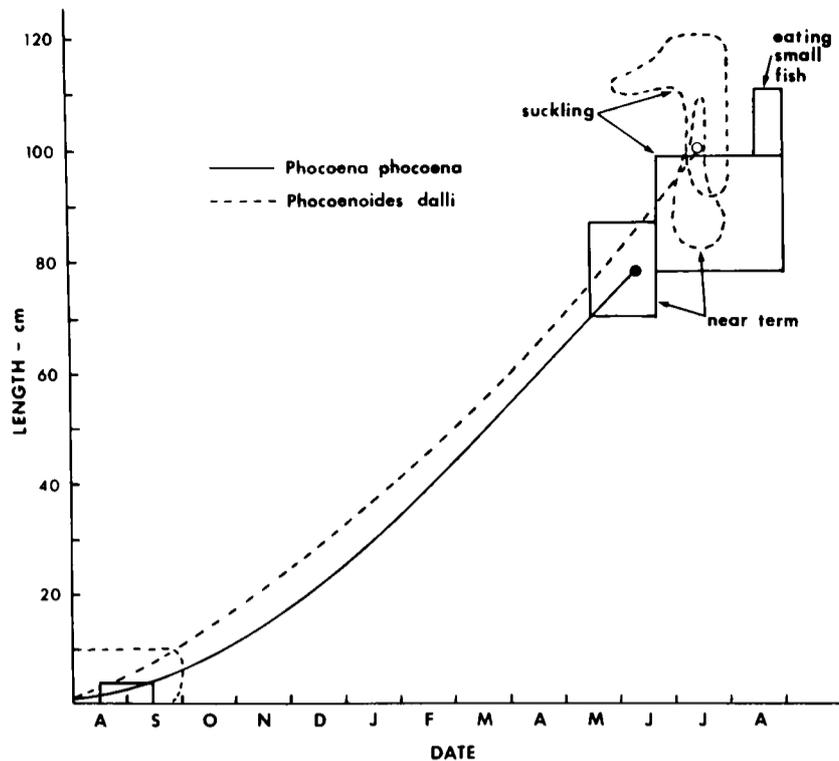


Fig. 2. Foetal development, time of birth, and neonatal development in *P. dalli* (broken lines and areas) and *P. phocoena* (solid lines and boxes). The circles at the end of each line represent best estimate of mean size at birth from Kasuya (1978) and Mizue *et al.* (1966) for *P. dalli*, and from our data, and data in Fisher and Harrison (1970), Harmer (1927), Møhl-Hansen (1954) for *P. phocoena*. Time of recognition and size range of early embryos, near-term foetuses and sucklings in *P. dalli* are drawn from Okada and Hayashi (1951), Mizue *et al.* (1966) and Kasuya (1978). The same stages in *P. phocoena* are from sources in our own data, Fisher and Harrison (1970), and Baltic and Norwegian data summarized by Møhl-Hansen (1954).

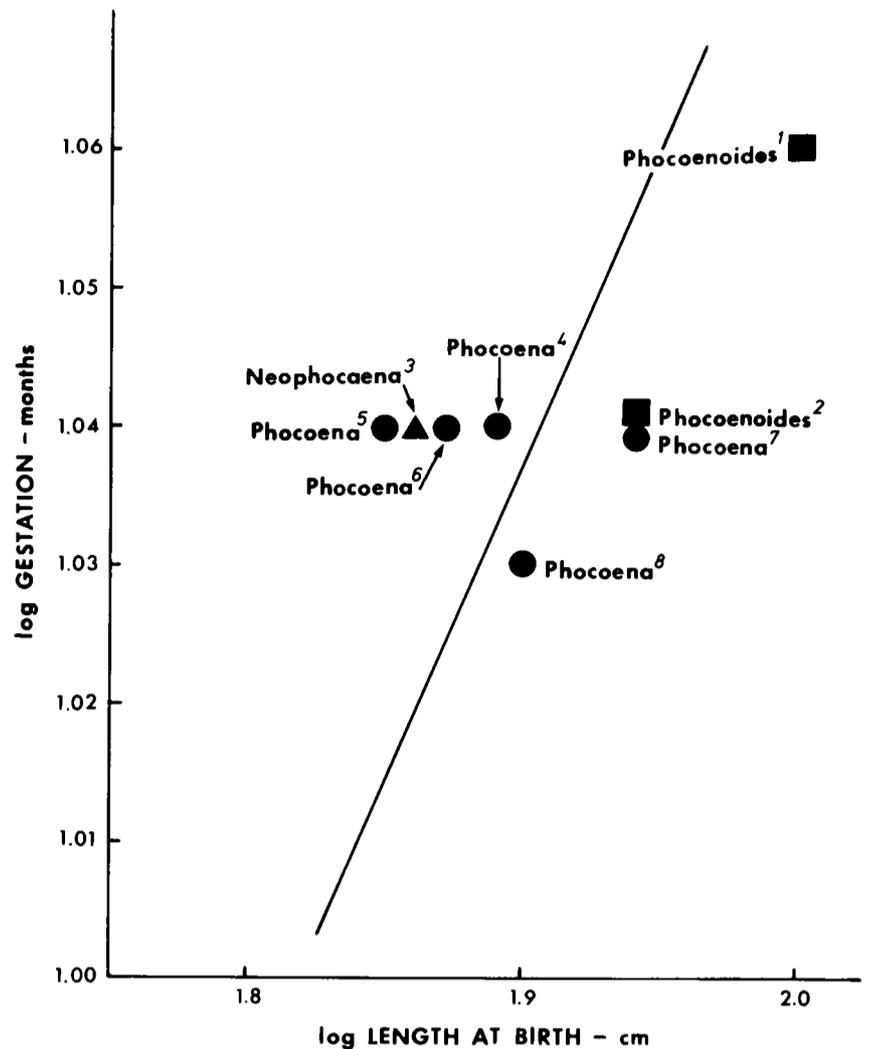


Fig. 3. The relationship in phocoemids of log gestation (in months) with log size at birth (cm), after the diagram of Perrin *et al.* (1977). Data drawn from: 1. Kasuya (1978); 2. Mizue *et al.* (1966); 3. Kasuya and Kureha (1979); 4. Data of present authors; 5. Harmer (1927); 6. Møhl-Hansen (1954); 7. Fisher and Harrison (1970); 8. Van Utrecht (1978, replotted). See note in text concerning data for *P. dalli* of Okada and Hayashi (1951).

specimens of *N. phocaenoides* with up to 23 dentinal growth layers in their samples from coastal Japan; as in most other odontocetes, one growth layer appeared to be deposited each year. Kasuya (1978) had a very few males and females of *P. dalli* in his samples between the ages of 14–18 and 14–16 years respectively, but based on (debatable) assumptions about the magnitude of bias in the fishery for animals of different age groups, he extrapolated regression lines from the right-hand peak of the catch curve (from the Sanriku coast harpoon fishery) that suggested that males and females of *P. dalli* could attain maximum ages of approximately 40 and 35 years, respectively, i.e. somewhat less than, but comparable to, the life span of *Stenella coeruleoalba* as estimated by Kasuya (1976b; 1978, Fig. 25).

Gaskin and Blair (1977) and van Utrecht (1978) reported several specimens of *P. phocoena* with 10–13 annual layers in the dentine. The former workers suggested that catch curves of animals shot more or less at random at sea (sex ratio nearly 1:1 and all size classes well represented) pointed to the maximum life span of this species in western North Atlantic waters being from 12–13 years, somewhat less than the maximum of 15 years suggested by Slijper (1962). However, Yurick (1977) reported that the results of his study, and the studies of Gaskin and Blair (1977) and Nielsen (1972) indicated that few harbour porpoise live beyond 7–8 years of age. There is no published information on the possible life span of *P. dioptica*, *P. sinus*, or *P. spinipinnis*.

## Growth

### Foetal growth rates

Foetal growth rates have been described by Kasuya (1978) for *P. dalli* and for the Baltic, eastern North Atlantic and North Sea populations of *P. phocoena* by Møhl-Hansen (1954), who re-plotted data gathered by earlier authors, and van Utrecht (1978). With few exceptions, only foetuses at a very early stage were available to Fisher and Harrison (1970), Gaskin *et al.* (1974) and Gaskin and Blair (1977) during studies of the western North Atlantic population. We have summarized information for this species and *P. dalli* in Fig. 2, in the form of a pair of mean foetal growth curves extrapolated to the times of year at which near-term foetuses and the smallest sucklings have been recorded.

Perrin, Holts and Miller (1977) explored the relationship between length at birth ( $\log x$ ) and duration of the gestation period ( $\log y$ ) in delphinids. Van Utrecht (1978) redrew this figure and added *P. phocoena* based on data drawn from the southern North Sea population. Unfortunately, as a result of an arithmetical or plotting error ( $\log 10.66$  is 1.028, not 1.04), *P. phocoena* appears to fall right on the theoretical line in his figure. This is not the case. In Fig. 3, we have replotted his value, together with estimates drawn from our own data and those of other authors, and compared these with equivalent values for *P. dalli* given by Okada and Hayashi (1951). Based on their data the point for that species lies

Table 2  
Reproductive parameters of Phocoenidae

Species	Locality	Mating season	Gestation period	Size at birth	Parturition season	Duration of lactation	Comments
<i>Neophocanea phocaenoides</i>	Inland Sea of Japan	Late August-early September <sup>1*</sup>	11 months <sup>2</sup>	65-85 + cm <sup>2, 3</sup>	March-June, <sup>2</sup> with peak in April-May <sup>2</sup> August-September <sup>7*</sup>	Poorly known, 6-15 months <sup>2</sup> ( $\bar{x}$ < 12) 0.5 to 3.5 years <sup>7</sup> ( $\bar{x}$ = 2.07 years)	* Considered to be erroneous estimate <sup>2</sup> * Peak in late August <sup>7</sup>
<i>Phocoenoides dalli</i>	Coastal waters of Japan	Mid-August-late October <sup>7</sup> with peak in September	11.4 months <sup>7</sup>	99.7 cm <sup>7</sup>	April-May <sup>4*</sup>	About 2 years	* Considered by Kasuya (1978) <sup>7</sup> to be in error; he believed peak of pairing to be in September in all N.W. Pacific-Bering Sea regions.
	Sea of Okhotsk and Sea of Japan	Late June-early July <sup>4*</sup> , mid-August-October <sup>7</sup>	7-9 months <sup>4*</sup>	—	—	—	—
	Bering Sea and N. Pacific	July and August <sup>5, 6</sup>	11 months <sup>6</sup>	100 cm <sup>6</sup>	Peak in late August <sup>6, 8</sup>	About 2 years <sup>7</sup>	—
	Coastal waters of western United States	All year round <sup>9</sup>	—	—	All year round <sup>9</sup>	—	Morejohn (1979) <sup>9</sup> presents data to challenge the concept of a unimodal birth peak in the N. Pacific, and believed that the Japanese conclusions resulted from using samples taken during limited seasonal fisheries.
<i>Phocoena sinus</i>	Gulf of California	Not known <sup>10</sup>	Not known <sup>10</sup>	74 cm <sup>10</sup>	April <sup>10</sup>	Not known <sup>10</sup>	—
<i>Phocoena diopttrica</i>	Coastal waters of southern South America, and N.Z.	August-? <sup>11*</sup>	Not known	48.4 + cm <sup>12</sup>	Not known	Not known <sup>11</sup>	* Apparent near-term foetuses recorded in July and August <sup>11</sup>
<i>Phocoena spinipinnis</i>	Southern South America	Not known <sup>13</sup>	Not known <sup>13</sup>	44 + cm <sup>13</sup>	Austral fall? <sup>13</sup>	Not known <sup>13</sup>	—
<i>Phocoena phocoena</i>	Northern European waters	August-September <sup>14*</sup>	—	—	June-July <sup>14</sup>	—	* Considered to be in error, and inconsistent with same author's comments on sizes of foetuses in August <sup>19</sup>
	Norwegian waters	—	8-10 months <sup>15, 16</sup>	70-85 cm <sup>17</sup>	March-July <sup>15, 16</sup>	8 months <sup>16</sup>	—
	Norwegian waters	—	c. 10 months <sup>18</sup>	80-86 cm <sup>18</sup>	May-July <sup>18</sup>	—	—
	West Baltic Sea	July-August <sup>19</sup>	11 months <sup>19</sup>	$\bar{x}$ = 75 cm <sup>19</sup>	June-July <sup>19</sup>	8 months <sup>19</sup>	—
	United Kingdom waters	June-August <sup>20</sup>	10 + months <sup>20</sup>	$\bar{x}$ = 71 cm <sup>20</sup>	June onwards <sup>20</sup>	—	—
	Netherlands waters	June-August <sup>22*</sup> (-October) <sup>17</sup>	(11 months) <sup>23, 24</sup>	(76.2-99.1 cm) <sup>25-27</sup>	(June-July) <sup>23, 24</sup>	—	—
	North Atlantic in general	June-August <sup>28</sup>	10.66 months <sup>22</sup>	67-80 cm <sup>22</sup>	June-early July <sup>22</sup>	—	* Judged by birth data given by this author <sup>22</sup>
	Bay of Fundy region, Canada	June-August <sup>23</sup>	11 months <sup>23</sup>	(70 cm) <sup>17</sup>	July <sup>22</sup>	—	—
	Northwest coast of U.S.A.	July-August <sup>29</sup>	11 months <sup>28, 30</sup>	$\bar{x}$ = 78 cm <sup>29</sup>	June-early August <sup>28, 29, 30, 31</sup>	8 months*	* Estimated from age-length data in <sup>30</sup> and lengths at which solid food starts to be recorded <sup>29</sup>
	Northwest coast of U.S.A.	July-August <sup>32</sup>	c. 10 months <sup>32</sup>	80-86 cm <sup>32</sup>	May-July <sup>32</sup>	—	—

References: <sup>1</sup> Mizue *et al.* (1965); <sup>2</sup> Kasuya and Kureha (1979); <sup>3</sup> Harrison and McBrearty (1973-74); <sup>4</sup> Okada and Hayashi (1951); <sup>5</sup> Mizue and Yoshida (1965); <sup>6</sup> Mizue *et al.* (1966); <sup>7</sup> Kasuya (1978); <sup>8</sup> Koga (1969); <sup>9</sup> Morejohn (1969); <sup>10</sup> Brownell (1983); <sup>11</sup> (1975); <sup>12</sup> Bruch (1916); <sup>13</sup> Brownell and Praderi (1982); <sup>14</sup> Collett (1912); <sup>15</sup> Grieg (1891); <sup>16</sup> Slijper (1898); <sup>17</sup> Grieg (1898); <sup>18</sup> Guldberg and Nansen (1894); <sup>19</sup> Møhl-Hansen (1954); <sup>20</sup> Harmer (1927); <sup>21</sup> Van Diense (1946); <sup>22</sup> Van Utrecht (1978); <sup>23</sup> Fisher and Harrison (1970); <sup>24</sup> Harrison (1974); <sup>25</sup> Fraser (1970); <sup>26</sup> (1946); <sup>27</sup> (1953); <sup>28</sup> Gaskin *et al.* (1974); <sup>29</sup> Smith and Gaskin (1974); <sup>30</sup> Gaskin and Blair (1977); <sup>31</sup> Gilpin (1875); <sup>32</sup> Scheffer and Slipp (1948).

very far below the regression line, somewhere between 0.84 and 0.95 on the  $x$  axis. Like Kasuya (1978), we consider their estimate to be wrong. As can be seen from the figure, the spread among the three species is not great, even allowing for variation and some uncertainty about the exactitude of mean values for gestation period and size at birth, inevitable at this stage of our knowledge of these animals.

#### *Size at birth in phocoenids*

Probably no phocoenid is less than about 60 cm long at birth, judging from the body size of adults. Statements by Bruch (1916) that a 48.4 cm foetus in a specimen of *P. dioptrica* was 'near-term' should be treated with considerable caution. Even the value of 60 cm for a 'near-term' foetus of *N. phocaenoides* seems to be on the low side. For this species, *P. phocoena* and *P. dalli*, the size spectrum appears to lie between about 67–100 cm, with the average in *Phocoena* and *Neophocaena* perhaps not far from 75 cm. The estimates for each species in the literature are summarized in Table 2.

#### *Postnatal growth*

Sexual dimorphism is a characteristic of phocoenids, although few data are available for some species. The largest known male and female specimens of *N. phocaenoides* were 192 and 175 cm, respectively (Kataoka, Furuta and Kitamura, 1974; Kataoka, Kitamura, Yamamoto, Manabe and Sekida, 1969). Similarly in *P. dalli*, males are larger than females, with the largest male and female reported by Kasuya (1978) to be 219 cm ( $n = 485$ ) and 209 cm ( $n = 399$ ), respectively. In harbour porpoises, however, it is the female which is larger. Data on growth in body length in the latter two species are summarized in Fig. 1. Almost no data exist on total length differences between sexes for *P. dioptrica*, *P. sinus* and *P. spinipinnis*.

Yurick (1977) found that sexual dimorphism is present in *P. phocoena* from birth, with neonatal skull length greater in females than in males. This dimorphism is maintained throughout life, being present at the onset of sexual maturity (Fisher and Harrison, 1970), upon reaching physical maturity (Gaskin and Blair, 1977; Møhl-Hansen, 1954), and in the annual growth increment estimated for female and male harbour porpoises

stranded on the California coast, 95 and 55 mm/year respectively, by Stuart and Morejohn (1980). The maximum body length reached by both sexes in different parts of the range are presented in Table 3. The 178-cm male from the Bay of Fundy was exceptional in our extensive experience with this population. No other male in the Fundy sample ( $n = 66$ ) was longer than 150 cm; several females however, were greater than 160 cm in length. Further details are not available to us for the 191-cm male from the English Channel, but it is no doubt the largest harbour porpoise ever recorded. Despite these two apparently unusual males, Yurick (1977), using data from 473 specimens, found that female *P. phocoena* were larger on average than males throughout the range of this species.

Population differences have been recognized in *P. phocoena*; growth curves for both sexes from eastern Canada and the North Sea are presented separately in Fig. 1. Differences between the males at any age are minimal, and the length/age relationship also converges in the females of the two populations with increasing age. Van Utrecht (1978) claimed that linear regression of length and weight also revealed some differences in growth rates between the North Sea and Baltic Sea populations as he had indicated in an earlier paper (van Utrecht, 1960). The differences, however, are quite small, and possibly not significant when the standard errors about the two regressions are compared (without the raw data, we were unable to do this). Yurick (1977) also suggested that the Baltic population might be morphometrically distinct, but did not carry out a detailed comparison because of numerous statistical objections and different sample sizes.

#### *Reproductive cycles in phocoenids*

##### *Mating seasons*

Mating seasons of cetacean species can be inferred (assuming a discrete season actually exists) from direct observations of mating behaviour, from the distribution of the annual peak of births and from studies of the state of the testes of adult males. Even reasonably good data from such sources may not necessarily permit us to define a mating season with great precision, often because sampling is limited to a particular time of the year.

Table 3  
Maximum body length attained by male and female harbour porpoises

Location	Females	Males	Source
N.E. Pacific	176 (27) <sup>a</sup>	161 (22)	Stuart and Morejohn (1980)
	179 (16)	163 (5)	Yurick (1977)
Bay of Fundy	175 (50)	178 (66)	Yurick (1977)
Baltic	180 (164)	164 (225)	Møhl-Hansen (1954)
	180–189 (357)	160–169 (296)	Van Bree (1973)
	173 (10)	152 (17)	Yurick (1977)
Irish coast	178 (22)	178 (14)	Yurick (1977)
North Sea	168 (32)	168 (29)	Yurick (1977)
(English coast)			
English Channel	183 (17)	191 (27)	Yurick (1977)
North Sea	186 (62)	151 (43)	Van Utrecht (1978)
(Dutch coast)	164 (21)	149 (12)	Yurick (1977)

<sup>a</sup> Length in cm followed, in parentheses, by sample size.

Published data on the timing and duration of mating season of phocoenid species are summarized in Table 2, by species and locality. In virtually all cases the season occurs in the high summer months in boreal-temperature species and appears to have a duration of about two months on average, although sexual behaviour in *P. phocoena* has been noted by us between May and September (but sometimes between small (apparently immature) animals). From published accounts of *P. phocoena* (Table 2), mating seems to take place later in Baltic and Scandinavian waters than in those off the United Kingdom and the Netherlands. It is noteworthy that the observations published by Morejohn (1979) are in direct contradiction to Japanese reports about mating and calving periods in *P. dalli* (see General Discussion).

#### *Gestation period*

The duration of gestation is known with reasonable accuracy in three species of phocoenid: *N. phocaenoides*, *P. dalli*, and *P. phocoena* (Table 2; Figs 2 and 3). In each case, it appears to be close to 11 months.

#### *Parturition season*

This is relatively well known for the same three species listed above; earlier in *N. phocaenoides* than in *P. dalli* or *P. phocoena* in the Northern Hemisphere, yet also earlier in *P. phocoena* in Norwegian than in western European waters (Table 2). Mother-calf pairs of *P. phocoena* begin to arrive in Bay of Fundy coastal waters in June, or rarely in late May. They have the calves with them when they arrive, so we assume (Watson, 1976) that birth takes place away from the near-shore region. Very small sucklings can still be observed in the beginning of August, and a 78-cm specimen was taken in early August in 1971 off southern New Brunswick. Morejohn (1979) argued that calving in the population of *P. dalli* off the west coast of the United States could occur at any time of the year.

#### *Duration of lactation and mean age at weaning*

The duration of lactation is perhaps the least known of this group of life-cycle parameters. Kasuya and Kureha (1979) considered the mean duration in *N. phocaenoides* to be about 12 months, but the error around the mean was large, with estimates ranging from six to 15 months. A similar problem was encountered by Kasuya (1978) when studying the Japanese coastal population of *P. dalli*; the mean period was long, as in larger odontocetes, about 2.07 years, with the low estimate at 0.5 years and the high of 3.5 years.

There is general agreement among workers on both sides of the North Atlantic that lactation in *P. phocoena* appears to last for no more than 8 months. Females taken by our group in the Bay of Fundy in early mid-summer (July) which were accompanied by small animals (but not the size of calves) usually showed some residual fluid production in the mammary gland, but not milk. Watson (1976) observed the progress of a nursing mother of this species, recognizable by a large scar across her back, from mid-July to early September, a period of about 8–9 weeks. In July, and through to the first week of August, the calf stayed very close to the caudal peduncle of the mother, hardly ever leaving this position. By the last two weeks of August and into September, growing independence was observed in the behaviour of this calf; by the end of

the observation period, it was frequently 'foraging' 5–10 m away from the female, sometimes diving with her, sometime moving away independently, and sometimes being temporarily left at the surface as she dived, presumably to feed.

We found milk in the stomachs of 10 calves of *P. phocoena* (82–99 cm in length) taken between 8 July and 20 August in the Bay of Fundy, and to these can be added another five (90–110.5 cm) collected by Fisher in the same area between 2 August and 28 September. A small (104 cm) animal examined by us in mid-August had the remains of small fish in its stomach (Smith and Gaskin, 1974), indicating that solid food can be taken as early as about eight weeks after birth. Møhl-Hansen (1954) found fish in stomachs of juveniles in the Baltic in November, and, based on the state of tooth eruption and the presence of parasites, concluded that they were taking much solid food by five months of age. There seems little doubt (Fisher and Harrison, 1970; Nielsen, 1972; Gaskin and Blair, 1977) that calves of *P. phocoena* attain body lengths of 100–110 cm by the end of their first summer of life, and there is little or no evidence to support the idea of an extended lactation period in this species. It seems unlikely that intensive lactation lasts much more than five to six months, and it is probably complete within eight months. There is some evidence, however, that young may stay with the mother until the birth of the next calf and perhaps for a month or so after that, judging by the number of mother+calf+juvenile combinations sighted in July–August in the Bay of Fundy. Kasuya and Brownell (1979) have recently reported a lactation period of similar duration in another very small cetacean, *Pontoporia blainvillei* (Gervais and d'Orbigny, 1844), off the coast of Uruguay.

#### *Changes in the testes*

Little published information is available on testis size and weight in *N. phocaenoides*. Harrison and McBrearty (1973–74) reported that two males 130 and 150 cm long had single testis weights (including the epididymis) of 78.3 and 603 g respectively. The latter specimen was believed to be mature and was captured (December) during the breeding season. Mean testis weights in *P. dalli* increase with age (Kasuya, 1978, Fig. 11) and also with body length (Kasuya, 1978, Fig. 14). Kasuya also examined the relationship between the mean diameter of seminiferous tubules and testis weight in that species, and correlated testis weight and tubule diameter with the ratios of immature and mature animals determined from histological samples.

Fisher and Harrison (1970) examined testes of 26 male specimens of *P. phocoena*, some with incomplete data. Their histological material was very limited, but they collected some useful volumes and weights. The present authors collected another 66 specimens; paired weights for mature animals in the combined sample ranged from 971–3,740 g in May and June ( $\bar{x} = 1,971$  g) and from 165–538 g in August ( $\bar{x} = 403$  g). The series of 66 specimens taken by us were examined histologically; 26 were immature and 40 mature. The immature males were all 3 years of age or less and had seminiferous tubules ranging in diameter from 37.0 to 63.9  $\mu\text{m}$  (mean: 48.0  $\mu\text{m}$ ; Table 4). A significant increase in tubule diameter was found with increasing body length,

Table 4

Comparison, by age and body length, of seminiferous tubule diameters, percentage of tubules containing sperm, and single testis volumes from a sample of 74 harbour porpoises, *P. phocoena*, collected in coastal waters of eastern Canada (9 July–2 September)

Age	Sample size	Body length cm	Tubule diameter $\mu\text{m}$	% tubules with sperm	Single testis volume, cc
0	9	86.0–103.5 (94.8)	37.0–56.3 (42.9, 8)*	—	7.8
1	15	109.0–124.5 (116.9)	37.0–62.6 (49.4, 14)	—	8.8–26.2 (15.8, 7)
2	4	116.5–134.0 (126.9)	52.2–63.9 (58.1, 3)	—	18.3–40.3 (29.3, 2)
3	3	126.0†–142.0 (132.0)	54.0†–156.4 (101.9, 3)	0–100 (60)	96.3–538.2 (317.3, 2)
4	6	137.0–155.0 (145.9)	100.4–140.6 (118.6, 5)	10–100 (77)	99.5–651.2 (239.3, 5)
5	20	134.0–158.0 (142.2)	96.8–176.3 (128.4, 17)	0–100 (66)	92.3–539.1 (254.0, 14)
6	5	125.0–145.5 (138.0)	100.7–163.5 (119.3, 5)	0–80 (33)	118.8–415.1 (216.9, 5)
7	6	132.0–178.0 (148.1)	91.0–150.2 (110.0, 5)	0–95 (64)	114.9–412.7 (226.2, 3)
8	4	137.0–150.0 (144.9)	107.7–141.8 (129.7, 4)	0–100 (64)	104.1–175.8 (138.6, 3)
10	1	141.5	105.4	55	—
13	1	137.0	168.6	95	—

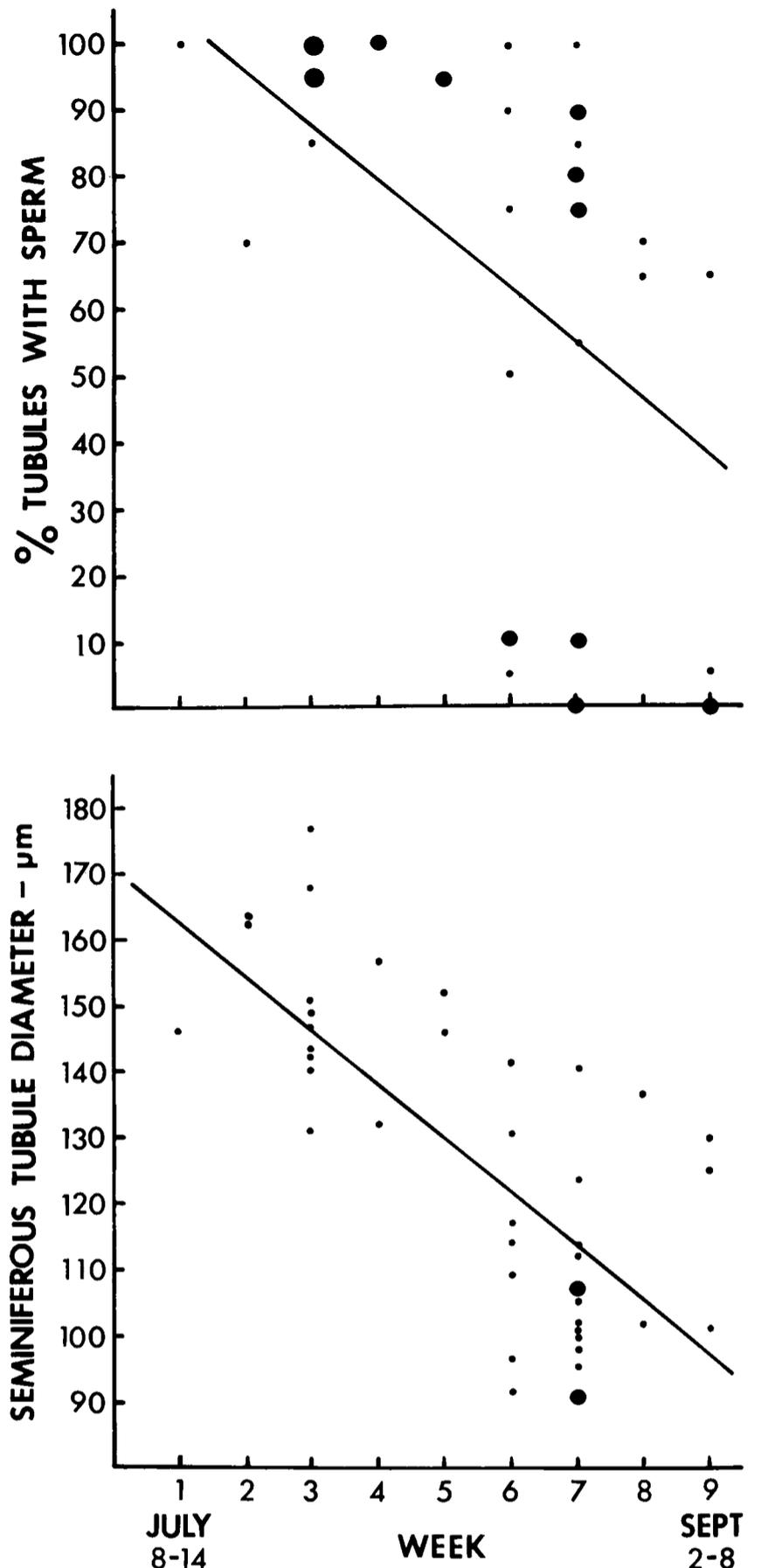
\* Mean, followed by number of animals examined.

† This animal immature.

expressed by  $y = 0.34x + 10.4$  (d.f. = 24, and  $0.01 < P < 0.001$ ). This relationship is indicative of normal growth and development of the testes relative to increase in body size. The mature males were 3 to 13 years old and had tubules 91.0 to 176.3  $\mu\text{m}$  in diameter (mean: 124.2  $\mu\text{m}$ ; Table 4). No correlation was found between tubule diameter and age, nor between percentage of tubules with sperm and age. Both of these parameters, however, were correlated significantly with date of capture (Figs 4 and 5). The decreasing percentage of seminiferous tubules containing sperm during the summer months (Fig. 4) could be described by  $y = -9.72x + 120.9$  (d.f. = 39, and  $P < 0.001$ ); and the decreasing diameter of seminiferous tubules over time (Fig. 5) by  $y = -7.95x + 170.3$  (with d.f. = 38, and  $P < 0.001$ ).

The statistically significant relationship of declining tubule diameter and the percentage of tubules containing sperm with date of capture seems indicative of a seasonal cycle of spermatogenesis and agrees with data presented by Fisher and Harrison (1970), who concluded that testicular activity in North Atlantic harbour porpoises increased from May onwards (reaching a peak in the latter half of July) and then decreased dramatically by mid-August.

The possibility that declining activity could also be reflected by decreasing testicular volume was investigated by plotting bi-monthly mean volumes for mature males from the Bay of Fundy (Fig. 6). Mean volume during the first half of September was nearly 50% less than that calculated for the latter half of July. In conjunction with the aspermatogenic state of some of the samples in late August and early September, this is further evidence of



Figs 4, 5. Evidence of an annual sexual cycle in male harbour porpoises indicated by declining testicular activity during a 9 week period in summer. Decreasing percentage of seminiferous tubules containing sperm (Fig. 4) is described by the equation  $y = -9.27x + 120.9$ , where  $y$  is the percentage of tubules containing sperm and  $x$  is the date in sequential weeks (week 1 = 8–14 July). Decreasing diameter of the seminiferous tubules (Fig. 5) is described by the equation  $y = -7.95x + 170.3$ , where  $y$  is the diameter in  $\mu\text{m}$  and  $x$  is the date in sequential weeks (as above). Levels of significance and d.f. values given in text. The three sizes of circles represent one, two and three observations.

the existence of an annual reproductive cycle in the male harbour porpoise. We also found that immature and mature males of *P. phocoena* may be easily differentiated during the summer months on the basis of single testis volume: 7.8–40.3 cc, mean 17.7 cc,  $n = 10$ ; compared to 92.3–651.2 cc, mean 236.4 cc,  $n = 32$ , respectively.

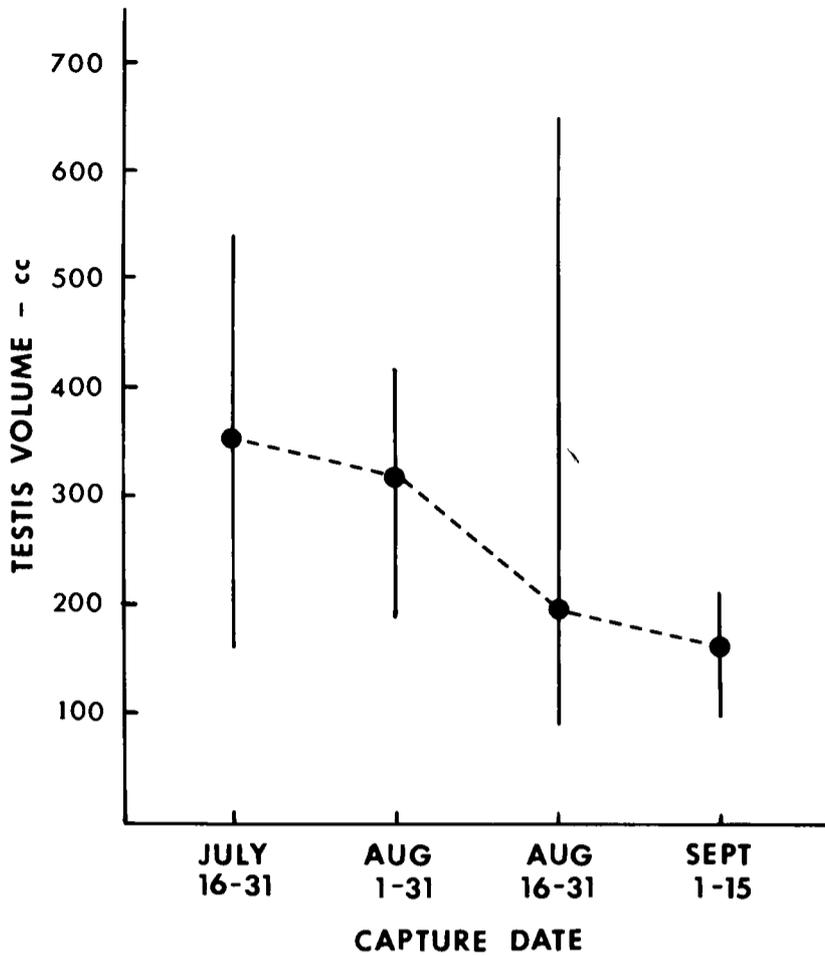


Fig. 6. The single testis volumes (calculated as ellipsoids) for 32 mature harbour porpoises collected in eastern North American waters. The closed circles represent the mean volume for each 2 week period and the ranges are defined by the vertical lines.

*Changes in the ovary*

In this section, we have restricted ourselves to terminology used by Harrison, Boice and Brownell (1969) and Perry (1971) to describe ovarian features; we adopt the terms Type I and Type II for two kinds of corpora albicantia described in delphinids by Harrison *et al.* (*loc. cit.*) and Fisher and Harrison (1970).

*Follicular development and ovulation.* Kasuya (1978) presented little information on follicles in *P. dalli*, nor has follicular growth been well-studied in *P. phocoena*, in both cases primarily because of the lack of material from all months of the year. Ovarian activity is almost exclusively sinistral, although Fisher and Harrison (1970) reported one specimen with a corpus albicans in the right ovary. In our series of summer-caught specimens of *P. phocoena*, we found both primary and secondary follicles ranging in size from one to six mm. The largest follicle was found in the ovary of a female taken in early July. Fisher and Harrison (*loc. cit.*) reported follicles from 1.0–4.5 mm in diameter in specimens from the same area; Graafian follicles were not found in either species. The timing of ovulation is not really understood in phocoenids, nor has the question of possible/probable multiple ovulations been satisfactorily resolved. Fisher and Harrison found up to 9 corpora albicantia in several of their smaller females and speculated that ovarian activity had become established out of phase with, or in the absence of, males. In our material, we counted up to 15 corpora albicantia in females 4 and 5 years of age, suggesting that multiple ovulations without fertilization occur regularly in younger females of *P. phocoena* before they are fully incorporated into the breeding population.

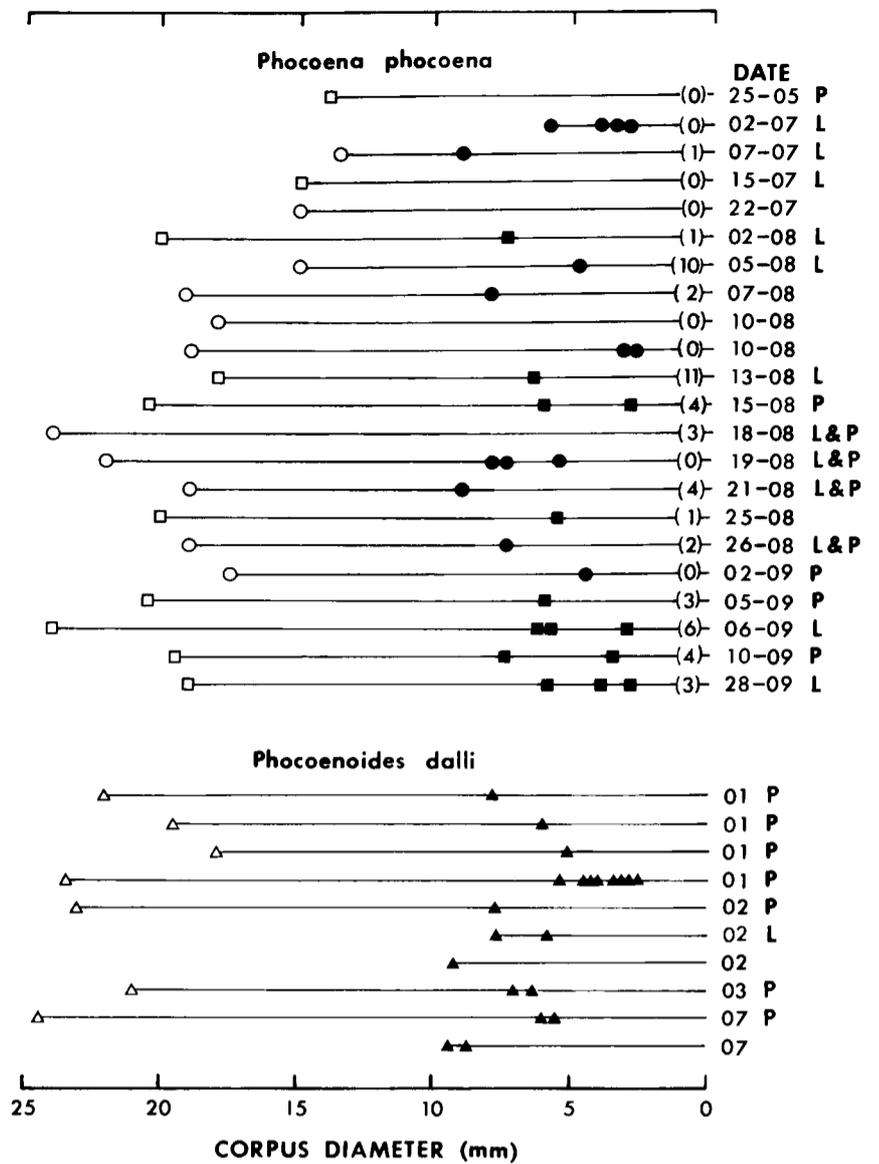


Fig. 7. Relationship between size of corpora lutea (open symbols) and corpora albicantia of Type I (i.e. containing much acellular material) of Fisher and Harrison (1970) (closed symbols) and time of year, for *P. phocoena* (above), and *P. dalli* (below). Circles are data of the present authors, squares represent data drawn from Fisher and Harrison (1970), and triangles from Kasuya (1978). The numbers of Type II corpora albicantia noted in parentheses. P = pregnant; L = lactating; blanks = resting or not examined; date = day-month (*P. phocoena*), month (*P. dalli*).

Kasuya *et al.* (1974) established that a polyoestrus cycle of one month occurred in *Stenella attenuata*, and that the largest follicles were found in resting or lactating females.

*Corpora lutea.* We have no confidence that corpora lutea of pregnancy and corpora lutea of ovulation can be satisfactorily distinguished in phocoenids. Kasuya, Miyazaki and Dawbin (1974) tentatively suggested that in *Stenella attenuata* those less than about 15–16 mm in diameter might be from ovulation, while those about 19 mm in diameter might be corpora lutea of pregnancy (see end of this section with respect to *P. phocoena*). They did not point out, however, that five of the females in the former sample were lactating. In *P. dalli*, Kasuya (1978) noted that the diameters of 20 corpora lutea of pregnancy ranged from 17.2–24.6 mm with a mean of 21 mm, with no accessory corpora lutea being observed. We have compared the size range of corpora lutea (and corpora albicantia) in *P. dalli* and *P. phocoena* against time of year in Fig. 7.

Since material of *P. phocoena* was collected by Fisher and Harrison and ourselves during the summer months in the Bay of Fundy, one would expect to find corpora of both ovulation and pregnancy. In our series of mature

animals, three females with corpora lutea were pregnant, three were lactating, and five were in neither condition. The corpora lutea in the latter must surely be the result of unfertilized ovulation. We are in agreement with Fisher and Harrison (1970) that the corpus luteum in lactating females always shows some signs of regression (see those authors for a histological description). An ANOVA test of this Bay of Fundy material revealed no statistically significant differences between the mean diameters of the corpora lutea of pregnant, lactating, simultaneously pregnant and lactating, and resting female harbour porpoises.

*Corpora albicantia.* As pointed out by Harrison *et al.* (1969) and Fisher and Harrison (1970), two kinds of corpora albicantia can be differentiated histologically in delphinids and phocoenids. The first (which we designate Type I) is typically 5–10 mm in diameter and consists of a firm mass of connective tissue with sparsely distributed cellular elements and large obliterated blood vessels around the periphery. Narrow radiating septa of fibrous connective tissue are present. The second (Type II) is smaller, only 3–5 mm in diameter, contains numerous closely-packed obliterated and degenerate arteries, and characteristically lacks the acellular material found in quantity in Type I.

Fisher and Harrison (*loc. cit.*) suggested that Type I bodies were derived from corpora lutea of pregnancy, while Type II bodies might result from corpora lutea of ovulation, or even represent the remains of large lutealized follicles (corpora atretica). They speculated that the largest Type I corpora found in animals taken in August were associated with pregnancies that had come to term about 13 months previously. In this respect their argument for the above associations of the two types was logically developed, especially considering the larger size of Type I bodies. Unfortunately, we found in our series of *P. phocoena* two females that provide some contradictory evidence which must be considered. The first was the youngest pregnant animal recorded by us, 133 cm in length, with only two dentinal growth layers. This animal not only had a corpus luteum in the left ovary, but also a single Type I corpus albicans and six Type II albicantia. Three alternative explanations can be considered: (i) this specimen was more than two years of age, or (ii) was reproductively abnormal and had had a previous pregnancy in its first year of life, or (iii) Type I corpora are not invariably associated with pregnancy. Several members of our group aged this animal independently and arrived at the same conclusion about its age; the layers are distinct and in no way unusual, and the body length is normal for that age class. Nor was there any indication of obvious abnormality other than the relatively small size of the animal at maturity. Option iii, therefore, provides the most parsimonious explanation. Further support for this hypothesis was provided by another animal in our series, a 153.5-cm four-year-old pregnant female with a corpus luteum and no less than three Type I corpora albicantia. We can only conclude that neither type of corpus albicans can be specifically related to pregnancy or ovulation in *P. phocoena*.

The regression and ultimate fate of corpora albicantia in general is not well understood in phocoenids. We attempted to plot the regression of numbers of corpora

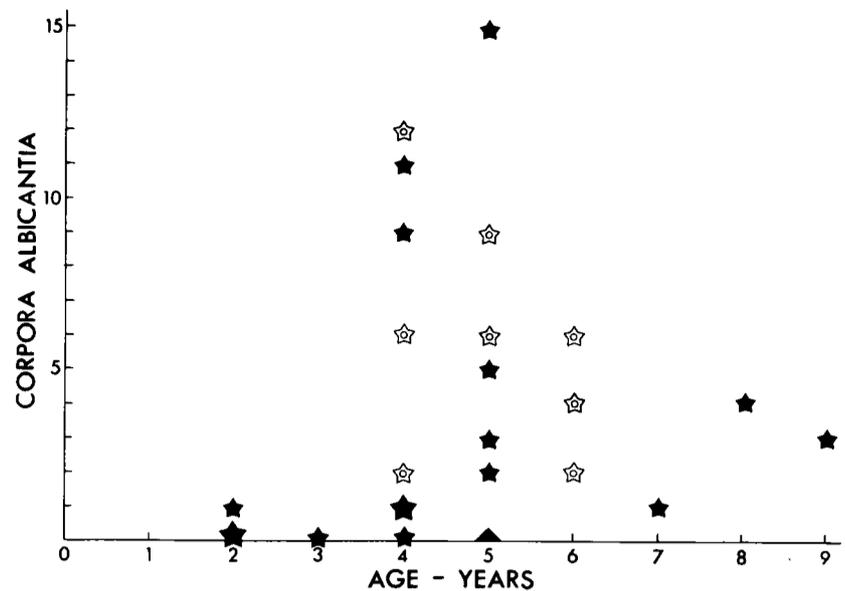


Fig. 8. Relationship between number of corpora albicantia of both types and age in years (based on dentinal growth layer groups – GLGs) in *P. phocoena* from the Bay of Fundy. Closed stars are data of the present authors; open stars are data from Fisher and Harrison (1970) with number of GLGs estimated from the relationship:

$$d = \left[ \frac{b}{(-0.84b + 156.15)} \right]^{-1}$$

where  $d$  is the number of GLGs and  $b$  is body length in cm (Gaskin and Blair, 1977). The large closed stars represent two specimens and the triangle includes four specimens examined by the present authors and one by Fisher and Harrison.

albicantia on age in Bay of Fundy female *P. phocoena* (Fig. 8); no relationship was found – the same negative result obtained by Gaskin and Blair (1977) with a smaller sample. A similar plot for *P. dalli* was also considered to be inconclusive (Kasuya, 1978, Fig. 23). Fisher and Harrison (1970) offered no explanation for the fate of Type I bodies, but suggested that they might eventually become totally indistinguishable. We agree with this postulation; in our series of animals the greatest numbers of both types of corpora were found in four- and five-year-old females. In two females estimated to be eight and nine years old, four Type I albicantia only (with no corpus luteum) were present in the former (pregnant) specimen, but only three Type II in the latter animal, which was simultaneously lactating and pregnant. Although the evidence is by no means conclusive, both types appear to be resorbed.

Some guide as to what occurs during the ovarian cycle in these animals might be obtained from the studies on *Stenella attenuata* by Kasuya *et al.* (1974) and *S. coeruleoalba* by Miyazaki (1977), with the caution that the former is a largely tropical species and the latter subtropical, in contrast to the boreal-temperate distributions of *P. phocoena* and *P. dalli*. Kasuya *et al.* recorded corpora albicantia as small as 1 mm, and speculated that they might persist throughout life in *S. attenuata*. Their size appeared to decrease significantly after parturition, reaching a 'mean final diameter' perhaps some 70 months after that event. Miyazaki (1977) produced a clear and interesting figure (1977, Fig. 11) based on examination of 206 pregnant females of *S. coeruleoalba*. He demonstrated a steady reduction in the size of the corpus luteum prior to parturition, from about 27 mm some five months before parturition to about 23.5 mm immediately prior to the event. He was also able to plot a curve to show actual decrease in size of the mean modal sizes of the largest

corpora albicantia from about 12 mm after parturition to barely 5 mm 27–28 months after parturition. Neither Miyazaki nor Kasuya *et al.* concerned themselves with histological differences among corpora albicantia, other than the latter (p. 202) indicating that they did not include in their counts 'corpora atretica' considered to result from atretic lutealized follicles as described in ovaries of *Tursiops truncatus* by Harrison and Ridgway (1971). The latter authors reported that *all* corpora lutea in *T. truncatus* related to pregnancy events, and not to infertile ovulations. They considered that ovulation was induced, not cyclic.

*Post-partum and post-lactum oestrus.* Post-partum oestrus is characterized (Perry, 1971) by regression of the corpus luteum of pregnancy immediately before parturition, and the maturation of one or more follicles, which 'ripen' and rupture within 24 h of parturition. Kasuya (1978) was able to present little information on this aspect of reproduction in *P. dalli*. Fisher and Harrison (1970) found no females in their sample of *P. phocoena* from the Bay of Fundy that were simultaneously pregnant and lactating; they concluded that harbour porpoises did not necessarily become pregnant every year, even though Møhl-Hansen (1954) had presented some evidence for post-partum pregnancy in the Baltic population of that species. In a sample of 36 Bay of Fundy mature females, we found 3 were pregnant, 5 were simultaneously pregnant and lactating, and 7 were lactating. These catch data suggest that the percentage of animals experiencing post-partum pregnancy is 14% of all mature females, and 62.5% of all pregnant females. It is also worth noting that three recognisable marked females studied by Watson (1976) in the Fish Harbour region of New Brunswick not only returned several years in succession (3 years, 2 years and 2 years), but in each year had newborn calves with them. At the beginning of at least four of these seasons they were also accompanied for a time by a larger juvenile assumed to be the offspring from the previous season. We are therefore left to wonder if Fisher and Harrison (1970) missed some very small embryos in some of their lactating specimens (easy to do, since the earliest embryos are almost impossible to find by routine gross inspection, and we suspect we missed some in our own series during field examination). The size of corpora lutea quoted by them in one or two animals might support this suspicion (Fig. 7).

#### GENERAL DISCUSSION AND CONSIDERATIONS

While it may be useful to draw parallels between phocoenids and other small cetaceans, especially delphinid species for which much more reproductive material has been examined, this should be tempered by the realization that phocoenids may perhaps be quite different mammals in many respects.

Although it is dangerous to assume that taxonomic affinity necessarily implies similarity in life cycles, the body size, life zone and behaviour of *P. dalli* are such that we would nevertheless formulate any first hypothesis on the basis that its life cycle parameters probably would be more similar to those of *P. phocoena* than to those of tropical *Stenella* species.

As in other cetaceans, the problem of accurate age determination, so critically important for population analysis, remains vexing. Most workers seem to be agreed that one growth layer is laid down in a single year in those phocoenids so far examined, but evidence relating to their average life span – and hence lifetime calf production by females – is far from satisfactory. We have, for example, produced data here and elsewhere to support our contention that *P. phocoena* is relatively short-lived for its body size, and this seems to be borne out by the recent paper by van Utrecht (1978) on the North Sea population. A short life span, with no more than about three or four calves produced on average by each mature female, is certainly not out of the question, especially if this species, as a small cold-water cetacean, has an elevated metabolic rate (Kanwisher and Sundnes, 1965). Such a reproductive pattern renders the species highly vulnerable to excessive additional mortality through exploitation.

Kasuya (1978) went to great length to estimate possible fishing bias in the harpoon fishery for *P. dalli* in the western North Pacific. That some level of bias exists in the fishery is not disputed, nor is the possibility of segregation of some social categories (such as lactating females) to other areas, thus preventing their full representation in the catch. What does worry us is that while Kasuya develops a sophisticated argument to support the hypothesis that this animal can live to much greater ages than indicated by dentinal or cemental layers, the basic fact of the matter remains that no animal in his samples could be *confirmed* as being more than 16–18 years of age. He considered a whole series of hypotheses, and adopted a compact mathematical method (1978, p. 51) to estimate mortality fractions in the population, and another series of hypotheses to examine catch bias and measure its impact (p. 45). We believe that one should also examine such situations from the most conservative viewpoint. This would involve re-examining four possibilities: (i) That mortality rates in this phocoenid population remain rather steep, and that the life span of the average *P. dalli* is in fact not much greater than the values suggested by tooth sections and, furthermore, that many assumptions related to the age composition of *Stenella attenuata* are valid only if Kasuya's (1976b) re-evaluation of the life span of that species is valid. (ii) That scarcity of individuals over seven years of age results not just from catch selection or inability to age the material accurately, but simply because there are not that many animals beyond age seven in the population. (For example, he did not find older animals in any quantity in the salmon gill net fishery either, yet we have taken some of our oldest specimens of *P. phocoena* from nets.) (iii) That the possibility of a male sexual cycle in phocoenids, coupled with the limited season of capture, may have led to misinterpretation of the real percentage of mature males from age 4 onwards, since 'maturing' testis is so difficult to assess in these animals. The mean age at maturity could then be significantly lower than he suggested. (iv) Contagious distribution of animals on the hunting grounds (which would include areas where nets were being set for fish, because the porpoises would also be concentrating for prey) could disguise a significant decline in population size until it was far advanced. While Kasuya may well have provided a reasonably accurate,

Table 5  
 Estimation of gross annual reproductive rate (GARR) of *P. phocoena* from three life history studies

	Baltic (Møhl-Hansen, 1954)	Bay of Fundy	
		(Fisher and Harrison, 1970)	(This study)
Proportion female	0.38 <sup>c</sup>	0.50	0.50
Proportion of females reproductive	0.47	0.42	0.52
Proportion of reproductive females pregnant	0.84	0.45	0.22 <sup>d</sup>
Duration of pregnancy (years)	0.92	0.92	0.92
Annual pregnancy rate <sup>a</sup>	0.91	0.49	0.24
GARR <sup>b</sup>	0.16	0.10	0.06

<sup>a</sup> Annual pregnancy rate calculated by dividing the proportion pregnant by the duration of pregnancy (0.92 yr).

<sup>b</sup> GARR = (proportion female) × (proportion reproductive) × (annual pregnancy rate); method of Perrin *et al.* (1977).

<sup>c</sup> Preponderance of males attributed to catch bias; if equal numbers of each sex is true for this population, GARR would be 0.21.

<sup>d</sup> See text for explanation of low proportion pregnant.

optimistic picture of the status of the western North Pacific population of *P. dalli*, it seems to us that his conclusions rest on a series of rather fragile assumptions.

The argument put forward by Morejohn (1979) to support the possibility of *P. dalli* having diffuse mating and calving seasons (at least in the coastal waters of the western United States) merits attention, since it is completely at variance with the findings of the Japanese workers. He noted that large testes could be present in both winter and summer, but the case for continuous activity is weakened by the statement that the largest testes observed were rather flaccid and in a non-reproductive state. We can see no reason to assume, as he did, that 114.9-cm and 118-cm juveniles taken in July and February respectively were necessarily born months apart; although Mizue *et al.* (1965) noted growth rates of about 5 cm/month, these are only averages, with wide variance. The stronger points of his case are certainly (i) a record of a stranded animal with a near-term foetus in November (although one could ask how near term was it, cf. Bruch's (1916) record for a 48.4-cm foetus in *P. dioptrica* as 'near-term'), and (ii) an 87.6-cm foetus found in April. There is suspicion, therefore, that Dall's porpoise on this coast are not necessarily breeding in synchrony with their western Pacific counterparts.

The possibility that a male sexual cycle exists in phocoenids is interesting and would seem to be at odds with the situation in larger odontocetes. Best (1969) and Gambell (1968; 1972) considered that there was little real evidence for a seasonal change in the male testis of the sperm whale. Best noted that 'There is no enlargement of the testes of mature males during the female breeding season, no increase in the diameter of the seminiferous tubules, and no increase in the incidence or number of spermatozoa per tubule. These facts fail to demonstrate the presence of a seasonal cycle of spermatogenic activity, but the enlargement of Leydig cells during the female breeding season could be indicative of an increase in testis androgen production, which might produce significant changes in the social and sexual behaviour of mature males at this time of year.'

Why then might such a cycle exist in *P. phocoena* (and the evidence is not totally conclusive) but not in other species? The answer may be related to the large

proportional size of the active testes in phocoenids. In *P. phocoena*, according to the data of Fisher and Harrison (1970) and the present authors, peak paired testes weights of adults can range up to 3.5% of total body weight. In the sperm whale, assuming an animal of about 30,000 kg and combined testes weights of about 3 kg, the equivalent percentage is only about 0.01%. The difference is very great, and since the harbour porpoise is relatively small, it seems to make sense in energetic terms for selection to have occurred leading to minimization of the surplus tissue during the non-productive part of the year.

Like Kasuya (1978) working with *P. dalli*, we were unable to derive any workable estimates of ovulation rates or true pregnancy rates for *P. phocoena* from our limited samples. It is, therefore, nearly impossible at this time to arrive at accurate estimates for birth rates even in the Bay of Fundy population. Based on sighting data for the period 1970–78 collected in the western Bay of Fundy, the average proportion of calves in the population is 10.3%. This value is supported by the proportion of animals of year class 0 in the sample collected for age determination by Gaskin and Blair (1977), which comes to almost exactly 10%. It is possible that fluctuations can be detected in the extensive sighting data, but these data are still under investigation by Yurick.

For a randomly collected sample ( $n = 95$ ) and a subsample of 36 mature females (see Section 3.6.4), we estimated the gross annual reproductive rate (GARR) of this population using the method of Perrin *et al.* (1977) and compared it to GARR values calculated by A. J. Read (personal communication) from the data of Møhl-Hansen (1954) for the Baltic population and for the Bay of Fundy population in the 1950s (Fisher and Harrison (1970)) (Table 5). The GARR of 0.06 for the recent Bay of Fundy population is lower than that in the 1950s and much lower than that calculated for the Baltic population. It is also less than estimates for *Stenella* spp. (0.08–0.14), *Delphinis delphis* (0.14), *Globicephala melaena* (0.10–0.13) and *Delphinapterus leucas* (0.12) calculated by Perrin *et al.* (op. cit.). We suspect (as noted in section 3.6.4) that we underestimated the proportion of adult females that were pregnant by failing to find a few very tiny embryos during routine autopsies in the field. Unlike

Møhl-Hansen's specimens which were collected from November to February when he found fetuses 14 cm to 45 cm long, the females we examined were mostly captured in the period June to September; embryos discovered ranged from 0.8 cm to 1.0 cm in length. It is quite possible that additional embryos of microscopic size were overlooked. If in the sample of 36 females we had found five more that were pregnant, the GARR would be 0.10, perhaps a more realistic value in light of the observed proportion of calves (10.0–10.3%). Alternatively, a decline in reproductive rate may have taken place in the Bay of Fundy population of *P. phocoena* between 1950–55 and 1970–80.

It is difficult to provide any discussion of approaches to management of phocoenids at this stage, given the impoverished state of our knowledge about life-cycle parameters of even the commercially exploited species. Initiation of scientific collecting in all months of the year in specific areas is easy to recommend, but would not necessarily produce the desired results. For example, because of the nature of its migration and behaviour, *P. phocoena* is only readily available for systematic biological sampling in the western North Atlantic during the summer, from May to September.

In the case of this species, however, we do believe that we are dealing with a short-lived animal that may already be maximizing its productivity, and the reproductive flexibility of *P. phocoena* is, therefore, likely to be limited, especially if more than half of the breeding females already appear to be producing calves in successive seasons.

The obvious recommendations that must be made, however, are for strict control or reduction of the directed catches of phocoenids until we have better knowledge of population sizes and production, and for all efforts to be made to reduce the magnitude of incidental catches in all kinds of fishing gear to which the porpoises are vulnerable.

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# Review of Reproduction in Platanistid Dolphins

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## ABSTRACT

Length at birth is about 75–80 cm in *Pontoporia*, about 80 cm or greater in *Inia* and *Platanista*, and 95 cm or greater in *Lipotes*. Gestation is 10.5 months and the lactation period is eight to nine months in *Pontoporia*; both are unknown in the other genera. The calving interval is two years in *Pontoporia* and assumed to be the same or greater in the other genera. Some *Inia* and *Pontoporia* females are known to be lactating and pregnant at the same time. Males and females of *Pontoporia* attain sexual maturity on the average at lengths of about 131 and 140 cm, respectively. The smallest known sexually mature females of *Pontoporia*, *Inia*, *Platanista* and *Lipotes* are 137, 183, 200 and 202 cm long, respectively. The smallest known sexually mature males of *Pontoporia*, *Platanista*, *Lipotes* and *Inia* are 121, 199, 206 and 209 cm, respectively. The age at the attainment of sexual maturity is two to three years for both sexes in *Pontoporia*. It is unknown in the other genera but is probably two to three times greater than in *Pontoporia*. The total number of corpora albicantia accumulated in the ovaries in all five species is small. The corpora albicantia appear to persist in all the platanistids, as in other cetaceans, and are found in both ovaries.

Females are clearly larger than males in *Pontoporia*, *Platanista* and *Lipotes*, but the reverse is the case in *Inia*. Available data indicate that the life span of *Pontoporia* may be only 15 to 20 years. This may explain why *Pontoporia* has a lower corpora count than *Platanista* and *Lipotes*. Few data are available for the other genera but one male specimen of *Inia* has lived in captivity for over 18 years. One male specimen of *Platanista* and one female specimen of *Inia* had 28 dentinal growth-layer groups.

## INTRODUCTION

Little was known about reproduction in the platanistid dolphins until the early 1970s. Recent data on the ovaries, testes, and reproduction in the franciscana (*Pontoporia blainvillei*) were reported by Harrison, Brownell and Boice (1972); Brownell (1975); Kasuya and Brownell (1979); and Harrison, Bryden, McBrearty and Brownell (1981). Data on the gonads of the boutu (*Inia geoffrensis*) were published by Harrison and Brownell (1971). Harrison (1972), Kasuya (1972) and Harrison *et al.* (1972) reported on new reproductive materials and summarized what is known about the Ganges and Indus susus, *Platanista gangetica* and *P. minor*. Brownell and Herald (1972) reviewed knowledge on the beiji (*Lipotes vexillifer*). Other more recent information on reproduction in *Lipotes* can be found in Chen and Chen (1975); Zhou, Qian and Li (1977); and Chen, Liu and Lin (1982). In addition, reproduction in *Lipotes* is reviewed by Chen, Liu and Lin (1984), and in *Inia* by Best and da Silva (1984).

## MATERIALS AND METHODS

Between 1964 and 1970, specimens of *I. geoffrensis* were obtained from rivers near Iquitos, Peru; Leticia, Columbia; Manaus, Brazil; and from San Fernando de Apure, Venezuela. Specimens of *P. blainvillei* were collected offshore between Punta del Diablo and Playa La Coronilla, Uruguay between 1969 and 1973. Three specimens of the Indus susu, *P. minor*, were collected in November 1968 near Sukkur, Pakistan. Specimens of *I. geoffrensis* and *P. minor* were caught for display at various aquariums in the United States. Some of the boutus died on capture or during transport; others survived in captivity for periods of only a few days to over 18 years (as of November 1983). The three susus only lived 24 to 44 days. All the franciscanas were taken dead in shark gillnets (Table 1). Additional data for all

Table 1

Samples of postnatal specimens of *Pontoporia blainvillei* by month between 1969 and 1973

Month	Females	Males	Total
January	63	87	150
February	20	10	30
March	15	15	30
April	0	0	0
May	1	4	5
June	5	10	15
July	25	22	47
August	17	16	33
September	15	11	26
October	15	6	21
November	6	2	8
December	45	37	82
Total	227	220	447

three genera and *Lipotes* were taken from the literature.

The total length (straight line from the tip of the rostrum to the notch between the flukes) of each dolphin was measured. Reproductive tracts were examined and foetal sizes recorded. Mammary glands were visually examined for evidence of lactation. The gonads were removed from the carcasses and fixed in 10% formalin. They were subsequently photographed, weighed and sectioned by hand to count corpora lutea and corpora albicantia. The presence of one or more corpora in one or both ovaries was used as the criterion of female sexual maturity and probable ovulation.

Slices of selected ovaries and testes were embedded in paraffin, sectioned and stained with haematoxylin and eosin (H and E). The determination of sexual maturity in male franciscanas was based on the examination of all the available seminiferous tubules in a slide, usually a cross section of the entire testis. An individual was classified as mature if all the tubules contained spermatids

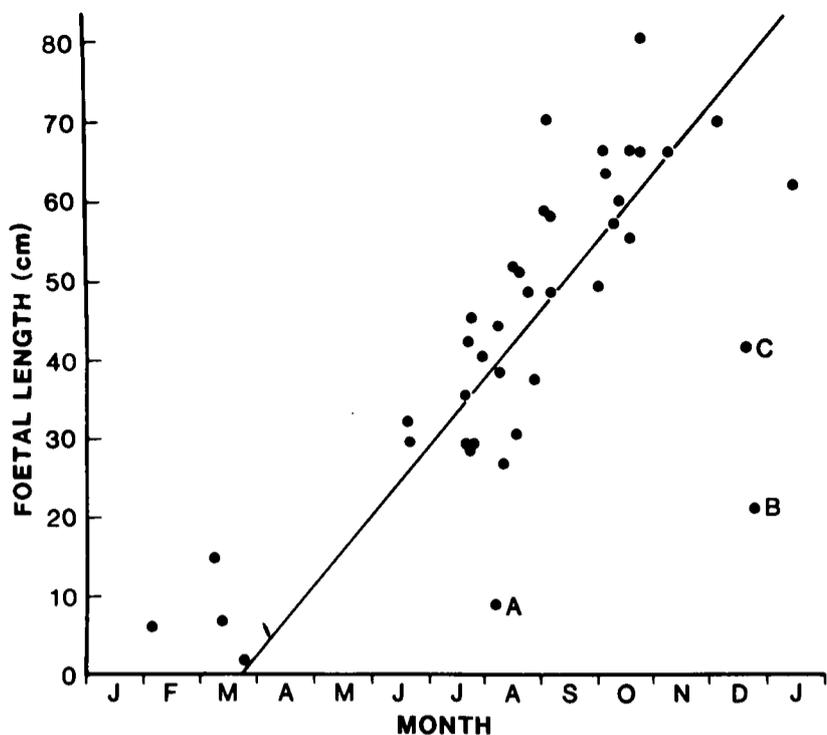


Fig. 1. Linear regression analysis of lengths of foetal specimens of *Pontoporia blainvillei* collected between June and December. The foetuses marked A, B and C were not used in the analysis. Data from Harrison *et al.* (1981) plus one 82 cm specimen.

or spermatocytes, immature if no tubules contained them, and pubescent if some of the tubules contained them.

Age determination of *Pontoporia* specimens was based on counting the growth layers of dentine and cementum in longitudinally ground sections of teeth (see Kasuya and Brownell, 1979, for details).

## RESULTS

### Length of gestation

There are insufficient data available to calculate foetal growth curves for *Inia*, *Platanista* and *Lipotes*.

*Pontoporia* – All available foetal length data are plotted against collection date in Fig. 1. The data points for the months June through December were fitted using a linear regression of foetal length on time. There were insufficient data to calculate an accurate foetal growth curve throughout gestation. The deviant points marked A, B and C were omitted from this calculation.

*Platanista* – Anderson (1879) reported that his informants regarded the gestation period to be 8 to 9 months.

### Length and weight at birth

*Pontoporia* – The largest female and male foetuses were 82 and 70 cm long, respectively. Five other male foetuses were 68, 66, 65, 65 and 62 cm long, and a female foetus was 66 cm long. The next largest foetuses were 63 and two 60 cm females and a 62 cm male. One 60 cm female foetus weighed 3.7 kg. The three smallest calves, all males, were 84, 84.5 and 85 cm long and weighed 10, 10.9 and 10.5 kg, respectively. Lengths and weights of all available foetuses and the smallest postnatal specimens (less than 100 cm) are plotted in Fig. 2, along with the few available specimens from the other genera. Based on these data the weight of a newborn calf between 75 and 80 cm long would range between 7.3 and 8.5 kg.

*Inia* – The largest foetus was only 66 cm long (Best and da Silva, 1984). The smallest calf encountered was a 76-cm male and weighed 6.8 kg. The two next largest calves were

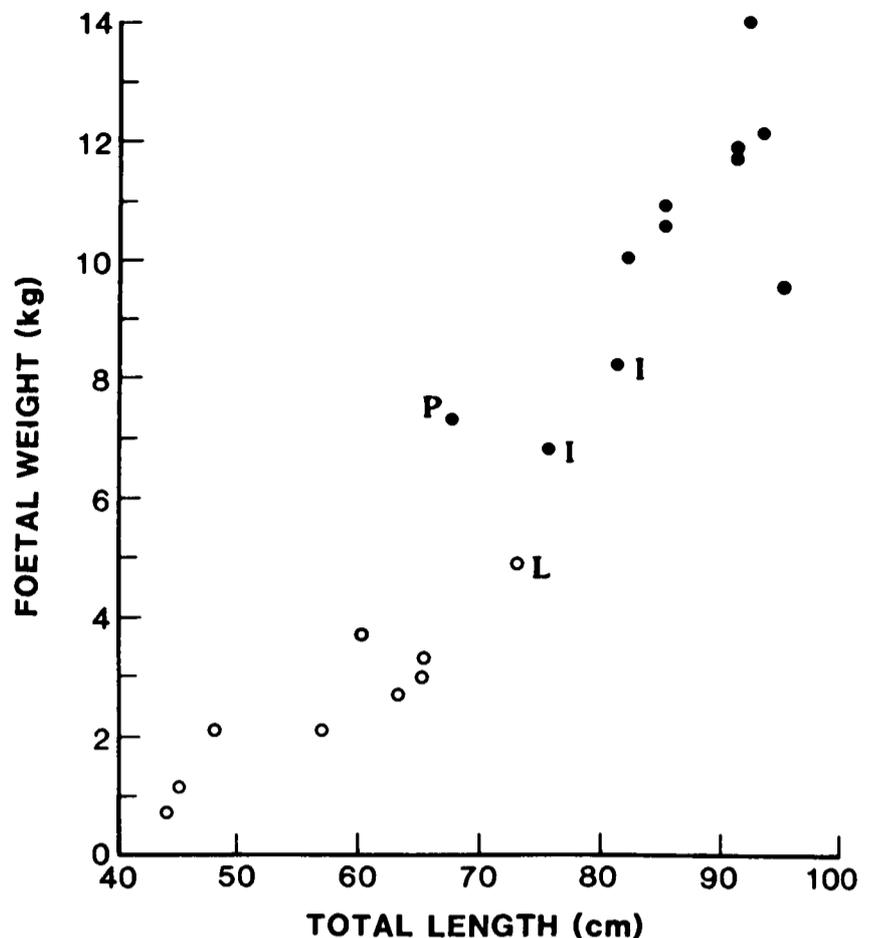


Fig. 2. Lengths and weights of all available foetuses and the smallest postnatal platanistid specimens (less than 100 cm in length). Closed circles represent postnatal specimens and open circles foetuses. All specimens are *Pontoporia blainvillei* except for those marked I, L and P, which stand for *Inia geoffrensis*, *Platanista* spp. and *Lipotes vexillifer*.

both 80 cm males without weight data. A female calf of 81 cm weighed 8.2 kg (Best and da Silva, 1984). The mean length of six newborn calves, including these four, was 79.4 cm (Best and da Silva, 1984).

*Platanista* – Four foetuses were between 42.5 and 54.7 cm long (Harrison, 1972). Anderson (1879) reported the largest near-term foetus was 70.5 cm long. The smallest free-swimming calf was a female 67.4 cm in length which weighed 7.3 kg (Kasuya, 1972).

*Lipotes* – Only three foetuses are known: a 41.5-cm male, a 54.5-cm male, and a 73-cm female (Chen and Chen, 1975; Zhou *et al.*, 1977). The largest male and the female weighed 2.5 and 4.5 kg, respectively. Chen *et al.* (1984) reported a neonatal female 95 cm in length and 9.5 kg in weight. The lengths of the next smallest known postnatal male and female were 141 and 150 cm, respectively (Zhou *et al.*, 1977). The male weighed 42 kg.

### Lactation

*Pontoporia* – Harrison *et al.* (1981) reported 16 lactating dolphins in their sample. Based on the ovarian characteristics of those specimens they suggested that lactation may last at least nine months, assuming a mean birth date in the second half of November.

*Inia* – Seven lactating dolphins all over 183 cm in length were collected in March, April, September and December (Layne, 1958; Harrison and Brownell, 1971; Gewalt, 1978; Best and da Silva, 1984).

*Platanista* – No lactating specimens have been reported.

*Lipotes* – A lactating specimen 202 cm in length was taken in December (Brownell and Herald, 1972).

**Age, length and weight at weaning**

*Pontoporia* – As noted above, Harrison *et al.* (1981) estimated a nine-month lactation period. Stomach contents were available from only four juveniles (Kasuya and Brownell, 1979). The smallest specimen was a 84.5 cm male about 0.2 year old, with milk in its stomach. Remains of some small unidentified discs about 0.3 mm in diameter were also present. These may have been derived from solid food. The three other individuals were between 90.5 and 104.5 cm in length and between 0.3 to 1.1 years of age. Remains of fish, squid and shrimp were found in their stomachs. No milk was noted. These data suggest that the *Pontoporia* calf starts taking solid food at about 3 months of age. Animals of about 100 cm in length weigh about 13 or 14 kg.

*Inia* – Harrison and Brownell (1971) reported two lactating females taken in April. These were 196 and 191 cm long with calves of 115 and 114 cm long, respectively. Best and da Silva (1984) collected two lactating females in September. The adults were 196 and 183 cm and the calves 133 and 108.5 cm long, respectively. A 188 cm lactating female with an 80 cm calf was collected in March (Gewalt, 1978).

*Platanista* and *Lipotes* – No lactating female/calf pairs have been reported for these genera.

**Age, length and weight at attainment of sexual maturity in females**

*Pontoporia* – The youngest sexually mature female was 2 years old, and the oldest immature was 4 years old. Kasuya and Brownell (1981) calculated the mean age at attainment of sexual maturity as 2.7 years. The smallest sexually mature and the largest immature females were 137 and 146 cm long, respectively. The smallest sexually mature animal weighed about 30 kg and all females were sexually mature at a body weight of 34 kg. The largest recorded female was 174 cm long and weighed 40 kg (Lahille, 1899). The heaviest non-pregnant dolphin examined was 171 cm long and weighed 53.3 kg (RLB 803). The oldest female was 13 years old (Kasuya and Brownell, 1979). The female life span may be only about 15 years.

*Inia* – The smallest sexually mature female was 183 cm long and weighed 71 kg (RLB 303). The largest female was 228 cm long (Trebbau, 1975). The heaviest non-pregnant female weighed 96.5 kg with a total length of 196 cm (Best and da Silva, 1984). Kamiya and Kasuya (1982) reported a 204 cm sexually mature female with 28 growth layers (GLGs).

*Platanista* – Few sexually mature female specimens are reported in the literature; the smallest I found was a 200-cm specimen (Harrison, 1972). The largest known female was 252 cm long. The weights of two pregnant animals 200 and 240 cm long were 66 and 83.5 kg, respectively. The smallest sexually mature female (also pregnant) weighed 51 kg and was 203 cm long (Harrison, 1972). No weights of non-pregnant sexually mature animals are available. Kasuya (1972) estimated the age of sexual maturity to be 10 years or less in both sexes, but no sexually mature females have been aged.

*Lipotes* – The smallest and largest sexually mature females were 202 and 253 cm long, respectively (Brownell and Herald, 1972; Zhou *et al.*, 1977). A 199 cm female,

of unknown maturity, weighed 87 kg, and a 238-cm non-pregnant specimen weighed 166.5 kg (Chen *et al.*, 1984). No material has been aged.

**Age, length and weight at attainment of sexual maturity in males**

*Pontoporia* – Body lengths of the smallest sexually mature and the largest immature males were 121 and 137 cm, respectively. The combined weight of both testes for the largest immature animal was 7.6 g and for the smallest mature specimen was 4.6 g. Pubertal testes weighed between 3.1 and 8.7 g. The weight of the heaviest immature male was 24.5 kg, and the lightest mature male was 29.0 kg. The largest known male was 158 cm long and weighed 32 kg (Lahille, 1899). The heaviest known male was 42.7 kg with a total length of 145 cm (RLB 709). The oldest male was 16 years (Kasuya and Brownell, 1979) and the life span may only be about 18 to 20 years. Males attain sexual maturity at an age between 2 and 3 years (Kasuya and Brownell, 1979).

*Inia* – Males 159 to 221 cm in length had histologically inactive tests (Harrison and Brownell, 1971). Combined testes weights for dolphins with lengths of 159, 185, 190, and 219 cm were 14.3, 27.6, 613, and 356.5 g, respectively. The diameters of the seminiferous tubules in these same specimens were 80, 85, 100, and 150  $\mu$ . Another male 228 cm in length had active testes that weighed 1,447 g. The tubules averaged 200  $\mu$  in diameter and spermatozoa were found in the epididymis. Best and da Silva (1984) reported that males of 209 cm or larger had enlarged testes with combined weights greater than 520 g. However, their judgements of sexual activity were based only on weight. The largest male examined by Best and da Silva was 255 cm long and weighed 128.7 kg. The largest known male was 255 cm long (Best and da Silva, 1984). No specimens have been aged. However, one male has survived in captivity for 18 years (as of November, 1983), and another male survived over 16 years in captivity.

*Platanista* – Kasuya (1972) suggested that males may become sexually mature at about 170 cm in length or less, when they are 10 years old or slightly younger. This conclusion was based on a 171.5 cm male with an age of 10 dentinal growth layer groups (GLGs). The testes in this specimen were too decomposed to weigh, but Kasuya estimated the weight of the testes might have been approximately 40 to 140 g based on the size of the tunica compared to that in two other sexually mature males. Two males, 180 and 185 cm in length, collected in December, had single testis (with epididymis) weights of 123 and 155 g, respectively (Harrison, 1972). One animal had inactive testes, the other showed 'signs of slight activity in the seminiferous epithelium: there were no free spermatozoa in the testicular tubules and none in the epididymis' (Harrison, 1972). The seminiferous tubules averaged 170  $\mu$  in diameter and almost all of them possessed a lumen in both specimens. Based on these samples, Harrison could not say for certain whether these males were approaching sexual maturity or were showing a seasonal decline in spermatogenesis. Kasuya (1972) reported a specimen 199 cm in body length that was sexually mature based on histological observation of the testis. The testes in this individual weighed 250 g. Another specimen, 200 cm in length, was identified as

sexually mature based on the weight of its testes, 1,110 g (Kasuya, 1972). The 199 cm specimen weighed 84 kg. The largest known male was 211 cm long (Anderson, 1879). The two sexually mature specimens with lengths of 199 and 200 cm had 28 and 16 dentinal growth layer groups, respectively (Kasuya, 1972).

*Lipotes* – Chen and Chen (1975) referred to one specimen 170 cm in length as an adult male. No data were provided to support this conclusion and I believe they were in error. Chen *et al.* (1984) reported on three adult males with the following total lengths and weights: 191 cm (80 kg), 194 cm (87.5 kg), and 206 cm (95 kg). The details on these males are sketchy at best, but the smallest animal was said to have every stage of differentiation of the spermatocytes present in sections of the testis. The weights of these testes, together with the epididymis, were 7.0 (left), 35.0 (both), and 30 g (right), respectively. The largest and heaviest known specimen, also referred to as an adult, was 229 cm in length and weighed 135 kg (Brownell and Herald, 1972). No specimens have yet been aged.

### Length of reproductive cycle

A two-year breeding cycle has been reported for *Pontoporia* (Kasuya and Brownell, 1979; Harrison *et al.*, 1981). Postpartum ovulation can occur, but it is not known whether this is followed by conception. Nothing is known about the length of the reproductive cycle in *Inia*, *Lipotes*, or *Platanista*.

### Seasonality

*Pontoporia* – Harrison *et al.* (1981) reported that the mean parturition peak is the second half of November to the second half of December, depending on the estimate of neonatal length used. No seasonal change was noted in the testes weights examined by Kasuya and Brownell (1979). However, this could be because their sample contained so few adult animals.

Little is known about the seasonality of reproduction in the other platanistids. Zhou, Pilleri and Li (1980) reported that *Lipotes* calves are born in March and April. The calving peak for *Inia* is between October and November (Best and da Silva, 1984). The parturition season appears to last for a long time in *Platanista*, or there might be two peaks, one in early winter and the other in early summer (Kasuya, 1972).

### Simultaneous lactation and pregnancy

Two pregnant and simultaneously lactating females of *Pontoporia* were reported by Kasuya and Brownell (1979). A lactating specimen of *Inia* with a 15.5 cm foetus was caught in April (Harrison and Brownell, 1971). However, it is not certain whether conception immediately follows parturition or occurs a year later.

### Sex ratios

*Pontoporia* – The foetal sex composition for specimens over 20 cm long was 48.1% males and 51.9% females (Table 2). The overall postnatal sex composition of the sample was 49% males and 51% females (Table 2). One

Table 2

Length frequency and sex ratios in 27 foetuses and 447 neonatal-to-adult specimens of *Pontoporia blainvillei*. Foetal samples are limited to foetuses longer than 20 cm

Stages	Length (cm)	Sample size (no.)	Females		Males		Sex ratio M/F
			No.	%	No.	%	
Foetuses	> 20	27	14	51.9	13	48.1	0.93
Neonates	80–89	4	1	25.0	3	75.0	3.00
to adults	90–99	16	4	25.0	12	75.0	3.00
	100–109	46	23	50.0	23	50.0	1.00
	110–119	74	30	40.5	44	59.5	1.47
	120–129	90	33	36.7	57	63.3	1.73
	130–139	92	42	45.7	50	54.3	1.19
	140–149	63	38	60.3	25	39.7	0.66
	150–159	38	34	89.5	4	10.5	0.12
	160–169	21	21	100	0	0	—
	> 170	3	3	100	0	0	—
	Total	474	243	51.3	231	48.7	0.95
* Dec. 1972– Jan. 1973	Total	95	51	53.7	44	46.3	0.86

\* Unbiased samples, see text for explanation.

Table 3

Length frequency and sex ratios in 100 postnatal specimens of *Inia geoffrensis*

Length (cm)	Sample size (no.)	Females		Males		Sex ratio M/F
		No.	%	No.	%	
70–79	1	0	0	1	100	—
80–89	3	1	0	2	100	2.00
90–99	0	0	0	0	0	—
100–109	1	1	0	0	0	—
110–119	4	3	100	1	0	0.33
120–129	4	0	0	4	100	—
130–139	6	5	83	1	17	0.20
140–149	5	4	75	1	25	0.25
150–159	10	3	30	7	70	2.33
160–169	5	1	20	4	80	4.00
170–179	4	0	0	4	100	—
180–189	10	6	60	4	40	0.67
190–199	20	11	45	9	55	0.82
200–209	11	7	64	4	36	0.57
210–219	7	2	29	5	71	2.5
220–229	6	1	33	5	67	5.00
230–239	1	0	—	1	—	—
240–249	1	0	—	1	100	—
250–259	1	0	—	1	—	—
Totals	100	45	45	55	55	1.22

Data from: Best and da Silva (1984); Trebbau (1975); Gewalt (1978); Layne (1958); Pilleri and Gühr (1969; 1977a); RLB, unpublished.

local fisherman agreed to collect a limited number of dolphins during my absence. I asked him to collect specimens greater than 135 cm long. This biased the sample towards females. The sample was also biased towards December and January (austral summer) because of the seasonal nature of the shark fishery. An unbiased sample of 95 dolphins was examined during December 1972 and January 1973. This sample was 54% males and 46% females.

*Inia* – The overall sample of 100 postnatal animals was 55% males (Table 3). Almost all of these specimens were

Table 4

Length frequency and sex ratios in 47 postnatal specimens of *Platanista* spp.

Length (cm)	Sample size (no.)	Females		Males		Sex ratio M/F
		No.	%	No.	%	
60-69	1	1	100	0		—
70-79	0	0	—	0	—	—
80-89						
90-99						
100-109						
100-109	6	4	67	2	33	0.50
110-119	16	7	44	9	56	1.29
120-129	10	5	50	5	50	1.00
130-139	1	0	—	1	100	—
140-149	0	0	—	0	—	—
150-159						
160-169						
170-179						
170-179	1	0	0	1	100	—
180-189	2	0	0	2	100	—
190-199	1	0	0	1	100	—
200-209	4	3	75	1	25	0.25
210-219	1	0	0	1	100	—
220-229	1	1	100	0	0	—
230-239	1	1	100	0	0	—
240-249	1	1	100	0	0	—
250-259	1	1	100	0	0	—
Totals	47	24	51	23	49	0.96

Data from Pilleri and Gihl (1977b); Herald *et al.*, (1969); Harrison (1972); Kasuya (1972); Anderson (1879); and RLB, unpublished.

taken live for display in the United States or Europe. Any capture biases are unknown. However, 73% of the specimens were under 2 m in length, which may mean that these animals are easier to capture than are larger adults.

*Platanista* – Data on length and sex are available for 47 postnatal specimens (Table 4). Twenty-three were males and 24 were females. Only two animals between 130 and 180 cm in length have been collected.

*Lipotes* – Data on postnatal specimens are only available for 14 males and 17 females (Table 5). Nothing is known about any possible capture biases; few neonatal and small postnatal animals have been collected.

Table 5

Length frequency and sex ratios in 31 postnatal specimens of *Lipotes vexillifer*

Length (cm)	Sample size (no.)	Females		Males		Sex ratio M/F
		No.	%	No.	%	
90-99	1	1	100	0	0	—
100-109	0	0	—	0	—	—
110-119						
120-129						
130-139						
140-149	3	0	0	3	100	—
150-159	5	2	40	3	60	1.33
160-169	1	0	0	1	100	—
170-179	2	0	0	2	100	—
180-189	1	0	0	1	100	—
190-199	4	2	50	2	50	1.00
200-209	4	3	75	1	25	0.33
210-219	1	1	100	0	0	—
220-229	2	1	50	1	50	1.00
230-239	1	1	100	0	0	—
240-249	3	3	100	0	0	—
250-259	3	3	100	0	0	—
Totals	31	17	55	14	45	0.82

Data from Zhou *et al.* (1977); Chen *et al.* (1984); Liu and Lin (1982).

**Length-weight relationships**

Length-weight relationships were determined using postnatal males and non-pregnant, postnatal females of each species by using linear regressions of log weight on log length (Table 6).

**Histology of corpora**

*Pontoporia* – The information on corpora lutea and corpora albicantia given here is based on Harrison *et al.* (1981). Only one corpus luteum was present in each pair of ovaries in 33 animals known to be pregnant. There was much individual variation in the relationship between the mean diameter of the corpus luteum and foetal length, but in general the corpus luteum increased in size slightly during gestation.

The fully developed corpus luteum contained two morphologically distinct cell types. Both cell types are apparently functional. Large, polygonal, acidophilic cells

Table 6

Length/weight parameters based on linear regressions of form  $\log W = a + b \log L$  (exponential form  $W = c \times 10^{-a} L^b$ ). Pregnant females were excluded

Species	Sex	N	Size range (cm)					Correlation coefficient (r)
				a	b	c	d	
<i>P. blainvillei</i>	M	75	84-145	-1.847	1.518	1.42	2	0.78
	F	56	97-171	-3.895	2.512	1.27	4	0.95
<i>I. geoffrensis</i>	M	17	114-255	-4.285	2.725	5.19	5	0.94
	F	16	81-208	-3.846	2.501	1.43	4	0.95
<i>P. gangetica</i>	M	14	108-199	-4.729	2.881	1.87	5	0.96
	F	4	118-127	-5.195	3.089	6.38	6	0.69
<i>L. vexillifer</i>	M	12	141-229	-3.647	2.445	2.25	4	0.91
	F	8	192-245	-7.864	4.218	1.37	8	0.90

with large, pale-staining nuclei probably develop from the granulosa cells, and smaller, more basophilic fusiform cells may arise from the theca interna. No foetus was found in a number of dolphins which had a fully developed corpora luteum. There does not seem to be any morphological difference between corpora lutea of pregnancy and those which are not associated with pregnancy.

Almost all the corpora albicantia were visible on the ovarian surface as slightly raised areas forming small excrescent discs. In longitudinal section they were either elliptical or cuneiform in shape. Macroscopically, the maximum number visible on any pair of ovaries was four.

Four distinct stages in the size and histological appearance of the corpus albicans were recorded, and these were thought to be related to their age (Harrison *et al.*, 1981):

Type I. Large corpus albicans, mean diameter 9–11 mm. These were vascular structures with many thin-walled blood vessels within their substance. Blood vessels in the periphery had thicker walls than similar vessels in the corpus luteum. Luteal cells were present, and most contained pycnotic nuclei, although their cytoplasm was unstained in H and E sections. The degree of degeneration and fibrosis was different in different parts of the structure.

Type II. Mean diameter 6–8 mm. There was advanced hyaline degeneration of the peripheral parts and fibrosis of the centre. Blood vessels within the organ had markedly thickened walls, but many of the peripheral vessels still had a large lumen. Less than half the cell ghosts had nuclei, and the nucleated cells present were confined to small clumps.

Type III. Mean diameter 4–6 mm. Extensive hyaline degeneration had occurred. The few blood vessels within the structure were occluded, and only isolated cells contained nuclei.

Type IV. Mean diameter 2–4 mm. The structure was completely avascular, and consisted of hyaline and fibrous tissue. Barely any cells were recognizable and no nuclei were present. A few small, occluded blood vessels were seen around the periphery.

A gradation in size and histological appearance of the corpora albicantia as reported above was found in all ovaries. Only in a few ovaries (particularly those with four corpora albicantia) were there two or more corpora albicantia of the same order of size and microscopic appearance.

*Inia* – Details of corpora lutea and albicantia found in five pairs of ovaries were presented by Harrison and Brownell (1971). A pregnant specimen (197 cm) with a 3.0 cm foetus had a corpus luteum of 25 × 20 mm in the left ovary. This corpus luteum was enclosed within the structure of the ovary and not pedunculate as in most odontocetes (Harrison, Boice and Brownell, 1969). Another corpus luteum was found in the left ovary (35 × 30 mm) of a lactating and pregnant female (202 cm) with a 15.5 cm foetus.

Two other adult females (201 and 210 cm) had two and four small (2 to 3 mm) corpora albicantia, respectively. Histologically these appeared to be of two types. One was a small raised scar (8 × 4 mm) with a mass of relatively acellular connective tissue and was arranged in lobules divided by fibrous septa with obliterated and degenerated blood vessels distributed about the periphery and in the septa. This type is considered to be a corpus albicans of pregnancy. The second type was smaller (3 × 2 mm) and the surface scar was depressed and darkly coloured. The cut surface exhibited a yellow pigmentation. The corpora consisted of coiled, obliterated blood vessels embedded in dense fibrous tissue. The organization of the second type generally suggested that it could have been derived

from a corpus luteum less well established than one of pregnancy and may have been from an infertile ovulation or from a lutealized follicle.

*Platanista* – Harrison (1972) reported on the details of ovaries from four pregnant specimens of *P. gangetica*. Foetal lengths were between 42.5 and 54.7 cm. The average diameter of the corpus luteum of pregnancy was between 14 and 18 mm. The largest corpus luteum was associated with the longest foetus. The corpora lutea were somewhat pedunculate and were well established and well vascularized. However, the luteal cells showed signs of involution in that they were heavily vacuolated. Corpora albicantia of diminishing size were present and suggested that the corpus luteum persists after parturition, as in other odontocetes (Harrison, 1969), as raised, spherical knobs or as raised, wrinkled scars.

There were ten definite corpora albicantia which formed a series with comparable features and these could be grouped by size and histological characteristics as: (a) two recent, 9–10 mm in average diameter; (b) six medium size, 5–8 mm; and (c) two small, 3 mm.

The largest corpora albicantia retained some cellularity and vestiges of the form of the fully developed corpus luteum. The general appearance of these two specimens, compared to those in other small odontocetes (Harrison *et al.*, 1972), strongly suggested that these corpora were those of previous pregnancies. It is not clear if all the other corpora albicantia were also derived from corpora lutea of pregnancy. This argument would depend on the persistence only of corpora of pregnancy and would be invalidated by the persistence of corpora of a cycle, pseudopregnancy, or abortion or by the persistence of accessory lutealized follicles. Several small (1 mm) pigmented areas were also present in most ovaries and these are most likely to be the remains of lutealized follicles.

*Lipotes* – Chen *et al.* (1984) provided a brief account on the ovaries from four sexually mature females. Two of the specimens were pregnant with foetal lengths of 54.5 and 73 cm. The largest corpus luteum of pregnancy was 45 mm and was associated with the larger foetus. The other corpus luteum had no fibrous core and the largest granulosa luteal cells were 46  $\mu$  in diameter. Three adults had fifteen corpora albicantia that ranged in size from 6 × 0.5 to 10 × 0.8 mm.

### Corpus accumulation

*Pontoporia* – The distribution of corpora between left and right ovaries is presented in Table 7. The first corpus occurs in the left ovary 93% of the time. Subsequent corpora are found in the left ovary at the same rate or higher. All females with three or more corpora had corpora in only the left ovaries. None of the 43 specimens had corpora in both ovaries and the maximum number of corpora recorded was only five. Some of these observations may be due to the small sample size. This is clearly a case of Type III corpus accumulation as discussed by Ohsumi (1964), where for a relatively long time, ovulation occurs only from the left ovary and then some corpora accumulate in the right.

*Inia* and *Platanista* – Corpus data were available for nine pairs of ovaries (Table 7). Although the total number of accumulated corpora was small, they were found in both ovaries. Both species can be classified as Type I

Table 7

Location of corpora (corpora lutea and corpora albicantia) in ovaries of 43 specimens of *Pontoporia blainvillei*, 5 of *Inia geoffrensis*, 4 of *Platanista gangetica* and 4 of *Lipotes vexillifer*

Genus	Number of corpora	Sample size	Location of corpora		
			Left ovary only (%)	Right ovary only (%)	Both ovaries (%)
<i>Pontoporia</i>	1	14	93	7	0
	2	13	92	8	0
	3	11	100	0	0
	4	3	100	0	0
	5	2	100	0	0
	Total	43			
<i>Inia</i>	1	1	100	0	0
	2	2	0	0	100
	3	1	0	0	100
	4	1	0	100	0
	Total	5			
<i>Platanista</i>	1	0	0	0	0
	2	1	0	0	100
	3	2	0	50	50
	4	0	0	0	0
	5	0	0	0	0
	6	1			
	Total	4			
<i>Lipotes</i>	1	0	0	0	0
	2	1	0	0	100
	3	1	0	0	100
	4	0	0	0	0
	5	0	0	0	0
	6	1	0	0	100
	7	0	0	0	0
	8	1	0	0	100
	Total	4			

The source of these data are: *P. blainvillei* (Harrison *et al.*, 1981); *I. geoffrensis* (Harrison and Brownell, 1971); *P. gangetica* (Harrison, 1972 not *P. indi* as noted in error [typo] in table 2, p. 73); and *L. vexillifer* (Chen *et al.*, 1984).

(Ohsumi, 1964), where both ovaries mature at the same time and ovulation occurs equally from both ovaries.

*Lipotes* – Chen *et al.* (1984) reported corpora from both ovaries in four pairs. These data are included in Table 7. Therefore, *Lipotes* ovaries can also be classified as Type I (Ohsumi, 1964).

**Postreproductive females**

No adult female specimens of *Inia* or *Pontoporia* showed any evidence of being postreproductive or 'senile' (see criteria in Perrin, Holts and Miller, 1977), nor is there anything in the literature on reproductive senescence in any of the other river dolphins.

**DISCUSSION**

All observed and estimated reproductive parameters are given in Table 8. *Pontoporia* is clearly the best known of the platanistids because of the larger sample size, which is approximately 10 times that for *Platanista* and *Lipotes* and 4 times that for *Inia*. The problems associated with the values and estimates in Table 8 are discussed below.

Harrison *et al.* (1981), estimated the duration of gestation was a little over 10 to 12 months, with a mean birth date during the second half of November. This estimate was based on the length at birth in *Pontoporia* at 70 cm, the largest foetal length in the sample. Fig. 1 includes the same data as Harrison *et al.* (1981) plus one additional female foetus, 82 cm in length, collected on 19 October (RLB 913). Kasuya and Brownell (1979), using two other methods, calculated neonatal lengths of 72.6 and 81.6 cm for *Pontoporia* and gestation periods of 10.5 and 11.1 months, respectively. The value of 72.6 cm was an arithmetic error and should have been 75.7 cm, which gives a slightly longer gestation period of 10.8 months. These values compare favorably with the range of 10.5 to 12 months estimated by Harrison *et al.* (1981). A captive newborn specimen of *Platanista gangetica* grew

Table 8

Reproductive parameters of platanistids. Estimated values are shown with an asterisk.

	<i>Pontoporia</i>	<i>Inia</i>	<i>Platanista</i>	<i>Lipotes</i>
Mean length at birth (cm)	75.7	79.4(76-83.6)	—	—
Range length at birth (cm)	70.9*-88.3*	92.5*-120*	< 100*-124*	95-125*
Range weight at birth (kg)	—	6.8-8.2	—	14.1*-
Mean sexually mature body length (cm)	♂♂ 131 ♀♀ 140	—	—	—
Range sexually mature body length (cm)	♂♂ 121-158 ♀♀ 137-174	209-255 183-228	185*-211 < 199-252	206-229 < 202-253
Mean body weight at sexual maturity (kg)	♂♂ 25-29 ♀♀ 33-34	—	—	—
Range body weight of sexually mature animals (kg)	♂♂ 29-42.7 ♀♀ 29.9-52.3	71-159.5 67.4-96.5	—84 51-83.5	95-135 142.5-166.5
Gestation period (months)	10.5	—	—	—
Lactation period (months)	8-9	—	—	—
Mean age at sexual maturity (years)	♂♂ 2.3 ♀♀ 2.7	—	—	—
Longevity (years)	♂♂ 16 ♀♀ 13	18+ 28	28 —	— —
Sample size of postnatal specimens	447	100	47	31

Layne (1958) reported the largest male and female specimens of *Inia* as 274 and 244 cm in total length, respectively. I have excluded these measurements because they probably were not standard total lengths. Some geographical variation in body length probably exists in *Inia* because of its widespread distribution in several major river systems.

8.6 cm in two months (Kasuya, 1972). A young specimen of *Pontoporia* collected on 28 December had a total length of 84.5 cm and an estimated age of 0.2 years. If this franciscana was born in mid-October and grew at the same rate as the Ganges susu, its estimated size at birth would be 74.2 cm. The range of available estimates for the neonatal length in *Pontoporia* is thus 75–80 cm. Further improvement of the gestation period estimate will depend on better knowledge of the neonatal length. To obtain more data on neonatal length, additional specimens must be collected in October and November (see Table 1).

The estimate of an 8–9 month gestation for the Ganges susu from Anderson (1879) has been frequently cited but there is nothing in Anderson's account to substantiate this value. It seems too short compared to the gestation periods of *Pontoporia* and other small odontocetes. The general trend in both mammals as a whole and in odontocetes is that the gestation period increases with species size (Eisenberg, 1981; Perrin and Reilly, 1984).

Judging from the adult size, the neonatal length of 67.4 cm reported by Kasuya (1972) for *Platanista* seems too low. The neonatal length should be higher in *Platanista* than in *Pontoporia* because of the larger size at sexual maturity in females and the greater total length attained. Ohsumi (1966) derived an allometric relationship between neonatal length,  $y$  in m, and the mean length of females at sexual maturity,  $x$  in m, from the values of these parameters in eight species of odontocetes. An estimated neonatal length for the Ganges susu, using Ohsumi's equation of  $y = 0.532x^{0.916}$  and 180 cm as the mean length of females at the attainment of sexual maturity is 91.1 cm. The total length estimate of 180 cm is based on an estimate for *Inia*, which has a maximum female size similar to that of *Platanista* (244 and 252 cm, respectively). The range of neonatal lengths for six specimens of *Inia* was 76 to 83.6 cm with a mean of 79.4 cm. Based on Ohsumi's (1966) equation, a newborn length for *Inia* of 82 cm would indicate an adult female length of 160 cm. This may be possible but does not seem probable. Only one immature female was available in the size class from 160 to 179 cm. Three of the *Inia* calves used in calculating the mean of 79.4 cm were born in captivity and may have been premature, so it is possible that this value is too low. Alternatively, Ohsumi's equation, which was based on only eight species of odontocetes, may not yield an accurate prediction.

In *Lipotes*, the ratio of largest foetal length (73 cm) to adult female length (250 cm) is only 0.292. Using the smallest known sexually mature female of *Lipotes* of 202 cm, a neonatal length of 101 cm is obtained from Ohsumi's (1966) equation. Based on the data from other genera of platanistids in Fig. 2, the weight of a newborn calf 101 cm long would be 13.6 kg ( $y = -11.0 + 0.244x$ , when  $x =$  total length). Chen *et al.* (1984) reported a neonatal female 95 cm in length which weighed 9.5 kg and was collected on 29 May. They assumed that this calf could have been born about two months earlier. This assumption was based on observations of young animals closely associated with large individuals of *Lipotes* during April and May. Most of these calves were estimated to be 100 cm in length with body weights between 10 and 15 kg. Based on Ohsumi's (1966) allometric relationship,

a 95 cm calf would be produced from a female 190 cm in length.

The mean age at attainment of sexual maturity in the female sample of *Pontoporia* was 2.7 years. This is the lowest age at sexual maturity of any small cetacean. Gaskin, Smith, Watson, Yasui and Yurick (1984) reported that sexual maturation in the harbour porpoise (*Phocoena phocoena*) seems to be complete between 4 to 5 years of age in the western North Atlantic and that the maximum life span seems to be about 12 to 13 years. Females of the other platanistids all become sexually mature at a much greater total length (ca 170 to 190 cm) than *Pontoporia*. *Inia*, *Platanista* and *Lipotes* are similar in size to other small cetaceans which become sexually mature between 6 and 9 years of age and have longer lifespans than *Pontoporia* (Perrin and Reilly, 1984).

The maximum ages (GLGs of dentine or cementum) in female and male specimens of *Pontoporia* were 13 and 16, respectively. The only other upper ages for platanistids are 18 years in captivity for a male bottlenose and 28 GLGs in a male Ganges susu and a female bottlenose. The general trend in mammals as a whole and in odontocetes is that the life span increases with size (Eisenberg, 1981; Perrin and Reilly, 1984). In addition, Ohsumi (1979) estimated the maximum life span ( $T$ ) of the Ganges susu as between 33 and 35 years. I believe that *Lipotes* and *Inia* should have life spans similar to that estimated for *Platanista* because of their similar maximum body lengths. Ohsumi (1979) noted that there was no evidence of any large difference in  $T$  value between the sexes in cetaceans. Therefore, I propose use of a  $T$  value of 15 years for *Pontoporia* and 30 for the other platanistids.

The available data suggest that the major factor that could produce differences in the lifetime reproductive capabilities of platanistids is the number of potential reproductive years. Based on the estimated age data, females of *Pontoporia* can potentially reproduce for a maximum of 12 years and females of the other platanistids, *Inia* and *Platanista*, for about 22 years. If the other female platanistids have, like *Pontoporia*, a two-year breeding cycle but become sexually mature at about 8 years of age, they could potentially produce 9 to 11 calves during their life compared to a maximum of 6 for *Pontoporia*. The *Pontoporia* population I studied in Uruguay is the most exploited of all platanistid populations; the effect this has had on its reproductive rate is unknown. Few corpora albicantia accumulate in the ovaries of any platanistid, but *Inia*, *Lipotes* and *Platanista* all accumulate more corpora than *Pontoporia*. *Inia* can accumulate twice the number of corpora found in *Pontoporia*. Low corpus counts in *Pontoporia* may be related to its relatively short life span.

As Gaskin *et al.* (1984) noted, 'it is dangerous to assume that taxonomic affinity necessarily implies similarity in life cycles, the body size, life zone, and behaviour.' Considerable variation in such traits is known to occur within families of terrestrial mammals (Eisenberg, 1981). Furthermore, the Platanistidae may not be a group of closely related species. The family Platanistidae has had a very unstable taxonomic history because of the degree of morphological difference between genera assigned to the family. All possible combinations of *Inia*, *Lipotes*, *Pontoporia* and *Platanista*

have been proposed, from placing the four genera together in a single family Platanistidae (Simpson, 1945; Slijper, 1962) to placing each genus in its own family (Zhou, 1982).

In a review of mammals in which females are larger than males, Ralls (1976) pointed out that no single hypothesis can account for all known cases. She concluded that the most common selective pressures favouring large size in females are probably those associated with the fact that a big mother is often a better mother and those resulting when females compete more intensely for some resource, such as food, than do the males. Whether or not these selective pressures can account for the cases within the platanistids is unknown (females of *Pontoporia*, *Lipotes* and *Platanista* are larger than males).

Females tend to be larger than males in the smallest cetaceans. In addition to the river dolphins, this is also true in the best studied small cetacean, *Phocoena phocoena* (Gaskin *et al.*, 1984) and *Sotalia fluviatilis* (Best and da Silva, 1984). *Phocoena phocoena* has a similar life history strategy to *Pontoporia* (i.e. few corpora, relatively short life span, early age at sexual maturity). Little is known about reproductive parameters in *Sotalia*. Data on sexual dimorphism are not yet available for the other extremely small cetaceans, such as the other *Phocoena* spp. and *Cephalorhynchus* spp. Among other toothed cetaceans, males are usually larger, except for some species of beaked whales. The only obvious common factor among the toothed cetaceans where females are larger is an apparently very simple social structure (i.e. small school size).

Females are also larger in baleen whales (Ralls, 1976; Lockyer, 1984). Norris (1967) suggested that this size difference might be attributable to the metabolic needs of mother and young during the long migration. Downhower (1976) applied this hypothesis to vertebrates in general and stated it more precisely: if resources for reproduction are derived from energy reserves stored at some other time, for example, before migration to the breeding grounds, then large females will have an advantage because they will have more reserves left to devote to reproduction. Like the toothed cetaceans where females are larger than males, baleen whales seem to have a relatively simple social structure (Gaskin, 1982).

Based on the corpus accumulation classification of Ohsumi (1964), *Lipotes*, *Inia* and *Platanista* are Type I. Other species with Type I accumulation rates are the sperm whales, some ziphiids and the baleen whales. *Pontoporia* corpora accumulation fits Ohsumi's Type III. Some other Type III species are *Phocoenoides dalli*, *Lagenorhynchus obliquidens*, *Tursiops truncatus* and *Stenella* spp.

### RESEARCH NEEDS

More specimens of *Pontoporia* should be aged to confirm the short life span in this species. Samples from other species of river dolphins should be aged to determine the age at attainment of sexual maturity, especially in females. Additional data need to be collected on calving intervals in river dolphins.

The main problem of working with river dolphins is

that the attainable sample sizes are usually only in the tens of animals, compared to the 100s or 1,000s available in *Stenella* spp. or other delphinids that have been studied during the past two decades. The population of *P. minor* in the Indus River between the Sukkur and Guddu Barrages is the smallest of the platanistid populations: only 241 dolphins were counted in this area in 1977 (Pilleri and Bhatti, 1978). This entire population is only a fraction of the 2,675 eastern spinner dolphins, *Stenella longirostris*, studied by Perrin *et al.* (1977). Recently, the population of *Lipotes* along a 170 km section of the Chang Jiang (Yangtze River) between Nanjing and Taiyangzhou is believed to be decreasing (Zhou *et al.*, 1980). Much remains to be learned about the platanistids before they are gone.

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**Session II**  
**Problems and New Approaches in Methodology**



# Statistics of Reproductive Rate Estimates, and their Implications for Population Projection

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## ABSTRACT

Errors in population predictions can arise through errors in direct measurement of population parameters, discrepancies between reality and assumptions used in collapsing parameters to obtain a simplified model, and departures of the time trajectory of parameter values from their expected course. In this paper, we consider one aspect of each of these phenomena. We discuss the consequences of measurement errors in terms of the sensitivity of the population growth rate to the measured parameters. We illustrate the problem of collapsing parameters with the calculation, from census data, of parameter values for a geometric series population model. We treat the matter of variability over time by developing some new theory regarding the biases introduced by using average reproductive rates in a stochastic projection.

As an illustration, these ideas are applied to a population model with parameter ranges typical of estimates for the spotted dolphin, *Stenella attenuata*. We observe that the present uncertainty regarding mortality rates is the most critical deficiency in our data, as expected. Two other findings are perhaps less expected. We find that the obviously unrealistic assumption of no senescent decline need not distort the value of the population growth computed from a geometric series model; and we find that use of time-averaged reproductive rates will necessarily cause us to overestimate the achieved population growth rates and to underestimate the severity of the consequences of incidental adult mortality and the biases increase with the actual degree of random variation in reproductive rates over time. Finally, we present some values for the confidence limits on the population growth rate estimates for the spotted dolphin, under the presently available data.

## INTRODUCTION

It is commonly remarked in connection with predictions about human population that the predictions are often distinctly at variance from what actually transpires. Human demographers, of course, have at their disposal far more, and better, data than is our lot in marine mammal population dynamics; possibly we are only saved from embarrassment by not even having enough data to reveal how imprecise our previous estimates were. In part, the failure of predictions may be no one's fault, since the vicissitudes of nature can result in changes in parameter values that are, of necessity, beyond the scope of the predictive powers of a purely demographic analysis. Some sorts of error, by contrast, are avoidable, and others though unavoidable are at least statistically predictable, so we can attempt to minimize error, and in any case can estimate the confidence limits for our predictions. The purpose of this paper is to examine three sorts of error which may be relevant in the estimation of a population growth rate from measurements including reproductive rates.

The three sorts of error which will concern us are (1) errors which arise directly in measurement or sampling, (2) errors which arise during the course of calculating the parameters of a simplified model to be applied in a situation of constant vital rates, and (3) errors which arise owing to specific peculiarities of random multiplicative processes which apply where vital rates may vary over time. Not only do these three sorts of error differ in their origins, they are also quite different in regard to the nature of the error itself.

In the case of measurement and sampling errors, we are dealing with an inherent feature of the measurement and sampling process. Such error will always be present, manifested as a distribution of the estimate about the true

value, for any finite data-gathering effort. What we can hope to achieve in this regard is a realistic appraisal of the nature of the distribution, and an allocation of our data gathering resources over the component determinations in such a way that the resulting error in the computed value of greatest importance is minimized. Since the calculation of sampling error is elementary, this component of error is often computed in population assessments; but the error so computed does not necessarily encompass all the error in an estimate.

Errors associated with model parameterization have to do either with discrepancies between reality and the simplified representation given in a model, or with actual mathematical misconceptions about the process in question. Real systems are usually too complicated to be treated in all their detail, and, indeed, the details of a system will far exceed our ability to gather data. When a rarefied abstraction of the system is proposed as a simplification which, nevertheless, captures the essential behavior of the real system, the demands for data are reduced, but they may also be somewhat transformed. The things we measure directly pertain to the real system, whereas the parameter values which are used as input to a model may themselves require some preliminary mathematical manipulation, analagous to the process of abstraction whereby the model was abstracted from the more complex reality. Thus errors may arise either in the process of reducing data to parameters, or through incomplete isomorphism between the model and the system it is taken to portray. We note that these errors are substantially different from the strictly statistical errors of sampling or measurement, in that we are now concerned with a reality which is beyond our model, so we do not have standard formulae for calculating the error.

Population dynamics, in essence, depend on a number

of multiplicative processes operating sequentially in time. Therefore, the relevant summary statistic often will be a statistic based on multiplication, such as a geometric mean, rather than the more familiar sort of average, which is based on addition of a set of values. Use of the inappropriate average (arithmetic mean) will introduce a bias in that application, for the geometric mean is necessarily smaller than the arithmetic mean of the same numbers. A more fundamental difficulty arising under random multiplicative processes is that they tend to generate strongly skewed distributions, where the mode (the most likely single outcome) is very different from the mean (the average realized outcome). Resolution of this problem requires reconsideration of the mathematical necessity for density dependence in a population history, leading us to discover that a second sort of bias, involving harmonic means, will result from use of simple average reproductive rates in computing population growth rates.

The following sections will treat each of these three sorts of error separately and will include a numerical example based on data for the northern offshore population of spotted dolphins, *Stenella attenuata* in the eastern Pacific.

### I. CONFIDENCE LIMITS ON POPULATION GROWTH RATES COMPUTED FROM UNCERTAIN BUT CONSTANT DEMOGRAPHIC DATA

The asymptotic growth rate of an age-structured population is a derived statistic, computed from vital rates – mortalities and fecundities – which are measured for each age class. One motivation for this procedure, as opposed to a direct measurement based on successive censuses of the entire population, is to ensure that the measured growth rate is not biased by transient distortions in the population's age distribution (especially the frequency of young individuals which often are most sensitive to environmental variation) at the time of the censusing. In some instances, it may also be the case that age-specific vital rates, owing to their nature as *per-capita*, and therefore relative quantities, will be measurable with greater accuracy than could be achieved with a direct census (cf. Goodman, 1979). One disadvantage of indirect computation of the growth rate is that the amount of mathematics which intervenes between the actual measurements and the desired statistic makes somewhat obscure the relation between the degree of certainty of the data and the degree of certainty of the final result. In this section we describe the theory of the dependence of the growth rate on the respective vital rates, and present results of a numerical simulation which accumulates a distribution for the computed asymptotic growth rate under specified random variation in the component vital rates.

The growth rate, the estimation of which we are concerned with, is presumed constant over time. The errors and uncertainties arise as sampling and measurement problems only. The complementary problem of fluctuations of vital rates over time will be dealt with in Section III.

The dependencies of the population growth rate on the vital rates can be investigated in the abstract by examining the first derivative of the growth rate with

respect to the vital rate of interest. This may be done with respect to the age-specific vital rates or with respect to the collapsed parameters of a more aggregated model such as the geometric series model (namely:  $\alpha$ , the age at first reproduction;  $l_\alpha$ , survivorship to the age of first reproduction;  $p$ , mean survival rate of individuals aged  $\alpha$  and older; and  $m$ , the mean effective fecundity rate of individuals in the reproductive age classes). It is known, from such investigation, that the growth rate for a typical marine-mammal life history is very sensitive to the average mortality rate, is less sensitive to changes in the average fecundity or in the survivorship to age of first reproduction, and is insensitive to the age at first reproduction (Goodman, 1980; 1981), as has been shown in numerical studies (Eberhardt and Siniff, 1977) and from algebraic considerations (Lewontin, 1965). Accordingly, we would expect this same pattern of sensitivities to govern the propagation of error in vital rates to error in the computed growth rate.

For more details of the distribution of the growth rate, under various sorts of uncertainty in vital rates, we will use a Monte Carlo simulation program capable of generating a set of random variables, with specified means, variances, and covariances. The growth rate we shall be concerned with will be expressed as a multiplicative factor of increase,  $\lambda$ . We shall compute it from the geometric series parameters as the one real, positive root of the polynomial equation:

$$\lambda^\alpha - p\lambda^{\alpha-1} - ml_\alpha = 0 \quad (1)$$

The theory of this parametrization, and the possibility of error owing to the parametrization itself, will be discussed in Section II.

There can be uncertainties in all four parameters of the geometric series approximation, and, further, there can be relations among the errors in the respective parameters, all of which will affect the distribution of  $\lambda$ .

The sources of uncertainty, which we will express as variances in the parameters, will be sampling error, measurement error, spatial or temporal dependencies which bias individual samples, and random departures from assumptions in the models employed in censusing, ageing, and other measurements. All of those should be combined for a total variance in each parameter. Covariances between parameters will originate in two ways. First, some pairs of parameters will share an underlying parameter. For example,  $\alpha$  and  $l_\alpha$  are obviously so related, giving rise, in this case, to a negative correlation between the two, if there are errors in determining reproductive status but not in ageing. The second source of covariance will operate when parameters are not measured from independent samples. Then causal relations in the way vital rates respond to environmental conditions will tend to give rise to negative correlations between fecundity and mortality, and between fecundity and age at first reproduction, and positive correlations between mortality and age at first reproduction.

Considerable thought must be devoted in any instance to thorough reflection on the sources of variance and covariance so that these may be estimated properly. As an example in the use of this program of calculation for associating a confidence interval with a computed population growth rate, we show, in Table 1 the input conditions for a simulation based on judgements

Table 1

Input parameter specifications for a Monte Carlo simulation of random error in demographic parameters used in a geometric series calculation of population growth rate

Parameter specifications:		Limits of uniform interval – High		Low	
Age at first reproduction		7.0000		5.0000	
Survivorship to first reproduction		0.7351		0.2725	
Adult survival rate		0.9500		0.8500	
Adult fecundity rate		0.2500		0.1667	
		Mean		Standard deviation	
Age at first reproduction		6.0000		0.5774	
Survivorship to first reproduction		0.5038		0.1335	
Adult survival rate		0.9000		0.0289	
Adult fecundity rate		0.2084		0.0240	
		Correlation matrix			
		(A)	(L)	(P)	(M)
Age at first reproduction	(A)	1.0000	-0.5000	0.0000	0.0000
Survivorship to first reproduction	(L)	-0.5000	1.0000	0.2500	0.0000
Adult survival rate	(P)	0.0000	0.2500	1.0000	0.0000
Adult fecundity rate	(M)	0.0000	0.0000	0.0000	1.0000

concerning the vital rates of the northern offshore stock of the spotted dolphin, *Stenella attenuata*. The discussions at the Status of the Porpoise Stocks Workshop (Smith, 1979) were the source of the estimates of the ranges for the vital rates. Some of these estimates have come under dispute, and some are in the process of being recalculated using more recent data, so their inclusion here is merely for illustration and not to argue for the correctness of particular parameter values.

Some of the dolphins in the incidental kill of the purse-seine tuna fishery have been aged by counting tooth layers, and some of the females were dissected to determine reproductive status. These observations serve as the origin for estimates that the age at first reproduction is 5 to 7 years and the calving interval is 2 to 3 years (Perrin, Coe and Zweifel, 1976; Perrin, Miller and Sloan, 1977). Since there is only one calf per litter, the fecundity in female births per female is  $(1/2)/2$  to  $(1/2)/3$ , not including the survival component which converts births to effective fecundity (we will absorb this component into the calculation of  $l_\alpha$ ).

A natural mortality rate of 10% per year for the adult spotted dolphin has been estimated from comparison of reproductive rates in exploited and unexploited populations, assuming both are in equilibrium (Kasuya, 1976). An unexploited population of spinner dolphins is calculated to have a mortality rate of 6.8%. Empirical regression of mortality rate on body size in a suite of cetaceans (where these mortality rates are determined by various means) predicts a value of 14% for the spotted dolphin (Ohsumi, 1979). All told, these estimates suggest a range of 85 to 95% as reasonable adult survival rates.

No direct evidence is available concerning survivorship to age of first reproduction. If annual mortality rates of independent immatures are comparable to those of adults, and if mortality rates of dependent young represent a simple compounding of this same probability of death of the parent and death of the young, conditional on survival of the parent, then high and low

limits on the survivorship to age at first reproduction may be computed by applying the range of adult survival rates through the appropriate number of years. The formula is  $l_\alpha = p^{\alpha+1}$ , where one factor of  $p$  is included to convert from births to effective fecundity, another is included to take account of the probability of the mother's survival during the calf's first year, and the remaining  $(\alpha - 1)$  are the usual number to account for the probability of calf mortality from age 1 to age  $\alpha$ , excluding parental effects. Thus our high estimate is 0.7351 and the low estimate is 0.2725.

Note that the calculation procedure creates a dependence of the estimate for  $l_\alpha$  on the values chosen for  $\alpha$  and  $p$ . However, the linkage between  $l_\alpha$  and  $p$  is grounded in an actual biological mechanism only with respect to the parental mortality component of  $l_\alpha$ . The remainder of the dependence in the above calculation was based on an arbitrary (but not entirely unreasonable) assumption that the fundamental mortality rate of immatures is the same as the adult mortality rate, and this assumption itself may be in error. Accordingly, the correlations between the actual errors in our estimates of  $l_\alpha$  and  $p$  will be smaller than the correlations between the estimates themselves. For purposes of illustration, we will assume that the correlation in the error in  $l_\alpha$  and  $p$  is 0.25. There is a tighter mechanistic connection between  $l_\alpha$  and  $\alpha$ , and for this reason, in this illustration, we assign this correlation a value of -0.5 (i.e. twice the absolute magnitude of the correlation of  $l_\alpha$  and  $p$ ).

The parameter ranges agreed upon at a 1979 workshop (Smith, 1979) were not associated with particular central, 'best' estimates, indeed consecration of central estimates was explicitly avoided. In this spirit, we will, for purposes of the Monte Carlo simulation, assume that variation in each parameter value has a uniform distribution within the stated respective range. (This is not to say that the workshop discussions contemplated such an assumption).

If we ignore the interactions and compute the factor of

Table 2

Results of Monte Carlo simulation of 10,000 trials sampling uniform distributions for parameters, as specified in Table 1

Realized parameter statistics	Mean	Standard deviation			
Age at first reproduction	5.9936	0.7054			
Survivorship to first reproduction	0.5052	0.1344			
Adult survival rate	0.8997	0.0287			
Adult fecundity rate	0.2083	0.0242			
Correlation matrix		(A)	(L)	(P)	(M)
Age at first reproduction	(A)	1.0000	-0.4601	-0.0015	-0.0100
Survivorship to first reproduction	(L)	-0.4601	1.0000	0.2335	0.0140
Adult survival rate	(P)	-0.0015	0.2335	1.0000	0.0116
Adult fecundity rate	(M)	-0.0100	0.0140	0.0116	1.0000

After 10,000 trials,  
the mean factor of increase is 1.002182  
the standard deviation is 0.030903

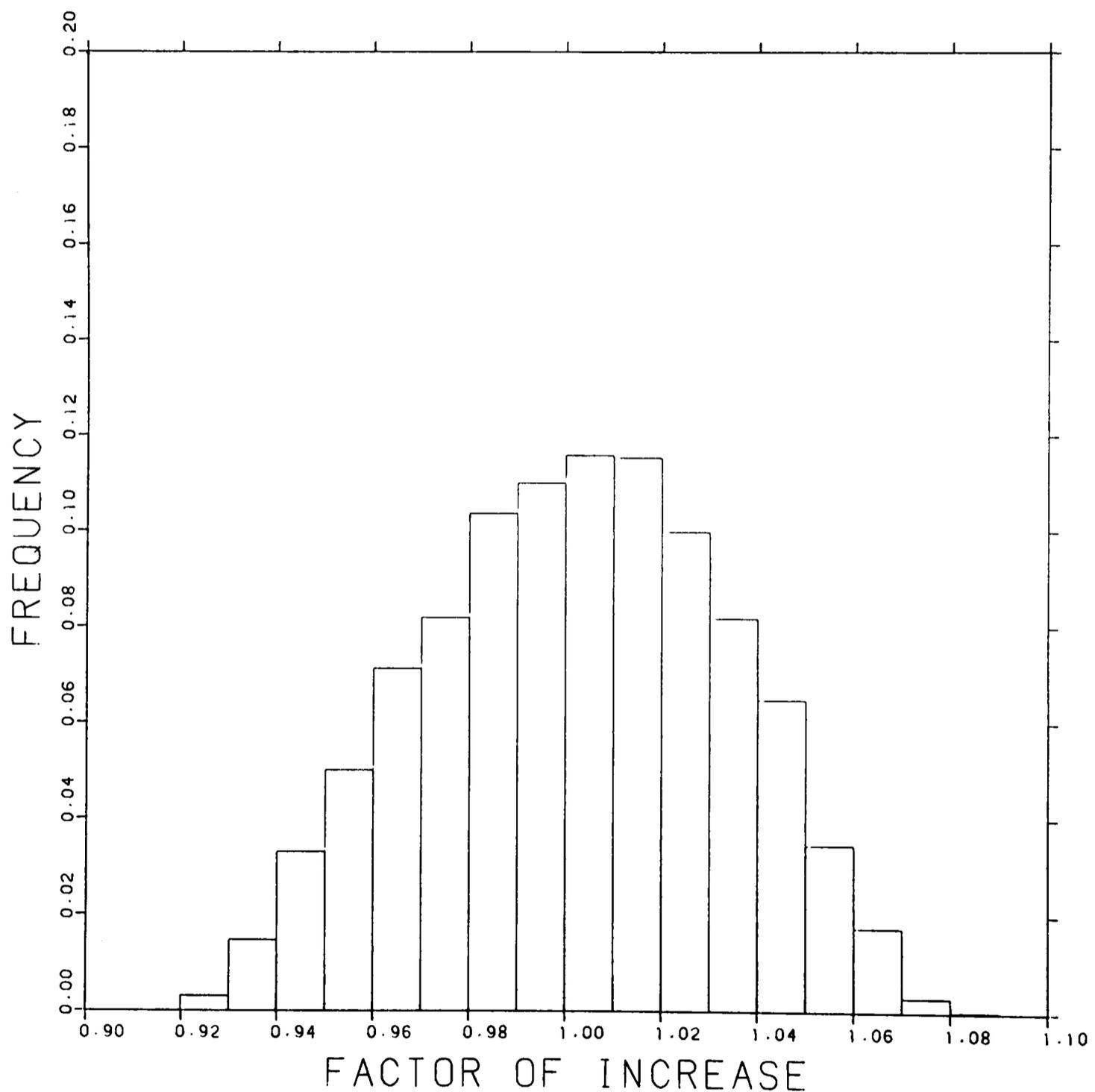


Fig. 1. Histogram of values for population growth rate resulting from the Monte Carlo simulation reported in Table 2.

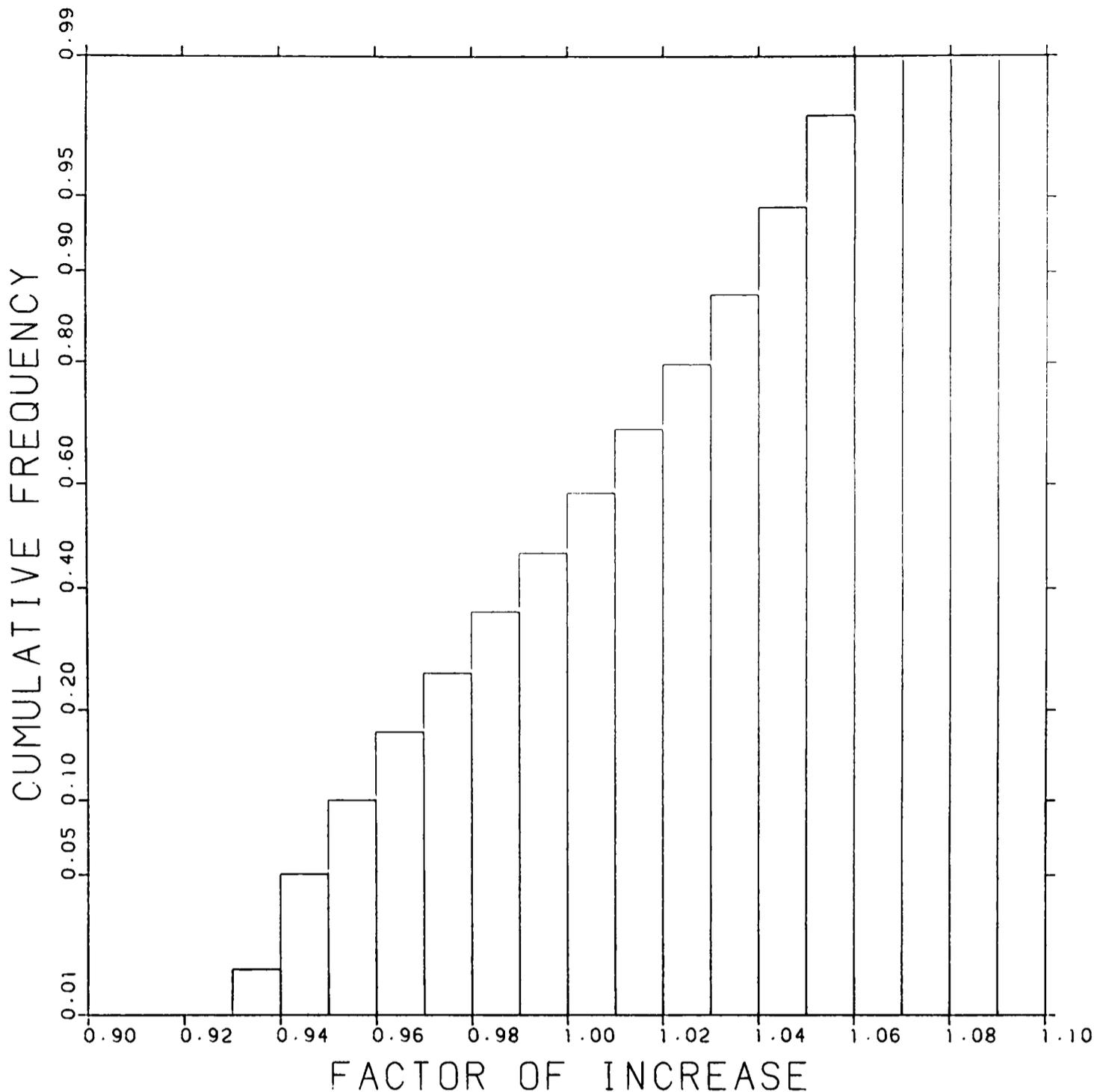


Fig. 2. Cumulative distribution of values for population growth resulting from the Monte Carlo simulation reported in Table 2, plotted on a probability scale which transforms a normal distribution to a straight line.

increase associated with a life table where each of the parameters is simply the median of the respective range described above, we obtain a value of 1.003 (i.e. a growth rate of 0.3% annually in the absence of any incidental kill). The partial derivatives of the factor of increase with respect to the parameters at these parameter values are

$$\frac{\partial \lambda}{\partial p} = \frac{1}{\alpha \left(1 - \frac{p}{\lambda}\right) + \frac{p}{\lambda}} = 0.66 \quad (2)$$

$$\frac{\partial \lambda}{\partial m} = \frac{l_{\alpha}}{\lambda^{\alpha-1}} \frac{\partial \lambda}{\partial p} = 0.33 \quad (3)$$

and

$$\frac{\partial \lambda}{\partial l_{\alpha}} = \frac{m}{\lambda^{\alpha-1}} \frac{\partial \lambda}{\partial p} = 0.14 \quad (4)$$

The formula for the sensitivity to change in the age at first reproduction depends on whether we wish to include an effect of age at first reproduction on the value for survivorship to age at first reproduction. If we are merely concerned with influences of error in parameter values, and in ignoring interactions choose to ignore possible

correlation between error in  $\alpha$  and in  $l_{\alpha}$ , the effect of age at first reproduction on survivorship would not be included. If we are concerned with the biological effect of a change in  $\alpha$ , it would be more realistic to include the concomitant effect on  $l_{\alpha}$ . In this case, the formula is

$$\frac{\partial \lambda}{\partial \alpha} = \frac{-\lambda}{\alpha + \left(\frac{p}{\lambda - p}\right)} (\mu_{(\alpha)} + \ln \lambda) = 0.007 \quad (5)$$

where  $\mu_{(\alpha)}$  is the instantaneous mortality rate at age  $\alpha$  (assumed to be  $-\ln p$  for the above calculation). For the sensitivity in the absence of the effect on  $l_{\alpha}$ , the formula would omit the term  $\mu_{(\alpha)}$ , and in the present example would result in an even smaller value.

So, as predicted, the factor of increase associated with this life history, composed of the median values for the parameters, is most sensitive to small changes in the adult survival rate, is approximately half as sensitive to the adult fecundity, is about one quarter as sensitive to the survivorship to age of first reproduction, and displays almost no response to small changes in age of first reproduction.

The specifications for the Monte Carlo simulation of variation in parameter estimates are given in Table 1. The resulting statistics from the simulation are given in Table 2. The distribution of the computed population growth rate is shown in histogram form in Fig. 1, and as a cumulative distribution, plotted on a probability scale, in Fig. 2.

We see that, despite the use of uniform distributions for the vital rates, the distribution of the growth rate is rather like a Gaussian distribution. There is only about a 50% certainty that the population growth rate is positive in the absence of harvest. Ninety-five percent of the distribution lies below 1.05, and 95% lies above 0.95, which is to say that, based on this input information, we are 90% certain that the population growth rate is between plus 5% and minus 5%. Or, to put it another way, our confidence that the population cannot withstand an incidental kill of 5% is 95%.

To investigate the manner in which variation in each parameter contributed to the resultant uncertainty in the growth rate, the simulation was repeated holding first one parameter constant (at its respective mean), then another. Fixing the adult survival rate reduced the variance in  $\lambda$  by 57%. Fixing the survivorship to first reproduction reduced the variance by 55%; fixing the fecundity rate reduced the variance by 7%, and fixing the age at first reproduction made less than 1% difference. Simply setting to zero the correlations between survivorship to first reproduction, age at first reproduction and the adult survival rate reduced the variance in the growth rate by 18%. These variances are of course the results of convolution of the sensitivity, as given in equations (2) through (5), and the range of uncertainty in the vital rate parameter. Thus, for example, the uncertainty in growth rate owing to uncertainty in  $l_x$  is substantially larger than that owing to uncertainty in  $m$  because the initial uncertainty in  $l_x$  is that much larger than the uncertainty in  $m$ , etc.

We see, therefore, that the weakest link in the present estimate of the dolphin population growth rate is the adult mortality. Not only is the growth rate most sensitive to marginal changes in this parameter, but the present range of uncertainty in the adult mortality contributes a greater fraction of the variance in estimates of growth than does uncertainty in any other parameter. The next largest fraction of the variance is due to the uncertainty in the survivorship to age of first reproduction (which is estimated entirely by analogy, whereas the adult mortality rate is at least supported by some data). The present uncertainties in fecundity or age at first reproduction are, in comparison, inconsequential.

## II. ERRORS IN MODEL PARAMETRIZATION

One of the burdens of age-structured models is the large number of measured values which enter into the calculation. Excessive detail is especially bothersome in our present application, inasmuch as the values assigned are in any case insecure. Since many of these values will share certain statistical properties – that is to say, for example, that the preponderance of the biases affecting the estimated fecundities will be much the same for all age classes in a given instance, etc. – it makes sense to lump the age-specific values into a few aggregate parameters, provided this can be done in such a way that all the

quantities lumped in a particular parameter really are subject to much the same sources of error and uncertainty, and provided the lumped parameter is capable of conveying the same essential information relative to the calculation of a population's growth rate.

The parametrization we shall adopt here is the geometric-series approximation to the life table (Goodman, 1978). In this approach, the life table is represented as four parameters: age at first reproduction, survivorship to first reproduction, mean adult survival rate, and mean adult fecundity rate. The implicit assumption that reproductive maturity is achieved all at once, and that all the reproductive age classes have the same fecundity and mortality, does not, of course, exactly match reality, but this approximation, nevertheless, does remarkably well at modeling the dynamics of many sorts of long lived organisms, most especially where growth is determinate, as in birds and mammals (Goodman, 1974).

Where information is sparse, the data may from the onset be structured in terms of the four parameters of interest. Where more information is available (i.e. where the vital rates are known with more detailed age specificity) we may use some simple formulae to calculate the corresponding four parameters, depending on the manner in which the demographic data were obtained. Under some circumstances, which we shall consider, explicit calculation of the collapsed parameters from the age-specific data will result in more accurate estimates for purposes of population projection.

We shall adopt the notational conventions for discrete time data as presented in Goodman (1978 and 1982), where the fecundities are effective fecundities measured as female offspring censused at the end of the interval per female censused at the beginning of the interval, and the age classification begins with class 1 which includes all individuals of ages from birth to 1. Leaving aside for the moment the optimal choice of  $\alpha$ , the age of first reproduction, the calculation of the other parameters is straightforward.

### (a) Theoretical parameter values

The survivorship to nominal age of first reproduction,  $l_x$ , is taken directly from the survivorship schedule. Next, the population growth rate, expressed as a factor of increase,  $\lambda$ , is calculated from the age-specific rates according to the characteristic equation:

$$\sum_{x=1}^{\infty} \lambda^{-x} l_x m_x = 1 \quad (6)$$

where  $m_x$  is the fecundity of age class  $x$ , and  $l_x$  is the survivorship to age class  $x$ , computed from the age-specific survival rates,  $p_x$ , according to

$$l_x = \prod_{j=1}^{x-1} p_j \quad (7)$$

Next the stable age distribution is calculated in the usual manner,

$$c_x = \frac{\lambda^{-x} l_x}{\sum_{y=1}^{\infty} \lambda^{-y} l_y} \quad (8)$$

where  $c_x$  is the fraction of the ultimate population that will be in age class  $x$ .

Now, the mean adult fecundities and survival rates may

be calculated exactly by distributing the population's births and the nominally adult deaths over the fraction of the population that is nominally adult in the stable age distribution:

$$p = \frac{\sum_{x=\alpha}^{\infty} c_x p_x}{\sum_{x=\alpha}^{\infty} c_x} \quad (9)$$

and

$$m = \frac{\sum_{x=\alpha}^{\infty} c_x m_x}{\sum_{x=\alpha}^{\infty} c_x} \quad (10)$$

With these four parameters  $\alpha$ ,  $l_\alpha$ ,  $m$  and  $p$  in hand, we may use the geometric series summation formula, to which the characteristic equation reduces in this special case, to calculate the population growth rate, as per the equation given in Section I.

Interestingly, the growth rate so calculated will agree exactly with the growth rate calculated from the detailed life table, regardless of our choice of  $\alpha$ . On reflection, this is not so remarkable, since we used the value of the growth rate to calculate the schedule of  $c_x$ , which in turn was used to calculate the values of the parameters  $m$  and  $p$ .

Of course, this does not imply that we are at liberty to choose any value of  $\alpha$  we please. The value of  $\alpha$  should, for present purposes, coincide with an age near the onset of reproduction, so that we may be realistic in our appraisal of the uncertainties in assessing that age. Furthermore, the value of  $\alpha$  will determine the generation time associated with the life table, and so it will determine the principal oscillatory transients in the population dynamics. This suggests one rationally defensible means for choosing  $\alpha$ : it should be the integer value which yields a generation time which is as close as possible to the population generation time associated with the detailed life table. The population generation time is defined as

$$T = \sum_{x=1}^{\infty} x \lambda^{-x} l_x m_x \quad (11)$$

which in the geometric series approximation reduces to

$$T = \alpha + \frac{\frac{p}{\lambda}}{1 - \frac{p}{\lambda}} \quad (12)$$

With this adjustment, which must be done iteratively, since parameters  $l_\alpha$ ,  $m$ , and  $p/\lambda$  must be computed from  $\alpha$  before the generation time can be computed for comparison with the desired value, the parametrization is complete.

The geometric series equation for the population growth rate (eq. 1) does not require mathematically that the age  $\alpha$  be an integer. We may adopt a fractional age

$$\alpha = \alpha_i + \alpha_f \quad (13)$$

where  $\alpha_i$  is the integer part of  $\alpha$  and  $\alpha_f$  is the fractional part. This can represent a situation where a fraction of the population matures at age  $\alpha_i$  and the rest mature at age  $\alpha_i + 1$ . With the fractional age at first reproduction, more care is required in calculating the other parameters in terms of age-specific vital rates which are defined, in

discrete time notation, only for integer ages. One internally consistent set of adjustments which will yield the correct growth rate exactly is as follows:

$$l_\alpha = l_{\alpha_i} p_{\alpha_i}^{(1-\alpha_f)} \quad (14)$$

$$m = \frac{\sum_{x=1}^{\infty} c_x m_x}{g + \sum_{x=\alpha_i+1}^{\infty} c_x} \quad (15)$$

and

$$\rho = \frac{g p_{\alpha_i} + \sum_{x=\alpha_i+1}^{\infty} c_x p_x}{g + \sum_{x=\alpha_i+1}^{\infty} c_x} \quad (16)$$

where

$$g = c_{\alpha_i} \left( \frac{1 - \left( \frac{\lambda}{p_{\alpha_i}} \right)^{(1-\alpha_f)}}{1 - \frac{\lambda}{p_{\alpha_i}}} \right) \quad (17)$$

Because of the mixing of continuous and discrete time calculations, the above treatment of non-integer age at first reproduction, though formally correct, is excessively contrived from the standpoint of interpretation. If we have data indicating that the transition to reproductive status does not occur all at one age, and if we wish to have a collapsed-parameter model that retains this property, it will probably be preferable to adopt a slightly less collapsed Leslie matrix model. This would be a projection matrix, of  $\beta$  rows and  $\beta$  columns, which is identical to the Leslie matrix out to age  $\beta - 1$ , but in column  $\beta$  has a collapsed parameter  $m$  in row 1 and a collapsed parameter  $p$  in row  $\beta$  (i.e. there is a non-zero value in one position on the main diagonal, unlike the Leslie matrix). The values for  $m$  and  $p$  are calculated from equations analogous to (9) and (10):

$$p = \frac{\sum_{x=\beta}^{\infty} c_x p_x}{\sum_{x=\beta}^{\infty} c_x} \quad (18)$$

and

$$m = \frac{\sum_{x=\beta}^{\infty} c_x m_x}{\sum_{x=\beta}^{\infty} c_x} \quad (19)$$

If  $\beta$  is the first age of full recruitment to the reproductive class, but there are prior ages with non-zero fecundity, this procedure will result in a model which has fewer parameters than the full Leslie matrix but which still represents the fact of partial recruitment to reproductive status in some of the ages younger than  $\beta$ . The geometric series model can be seen as a special case where the age at first reproduction is also the first age at full recruitment.

The polynomial equation for the growth rate in this gradual recruitment model is

$$\lambda^\beta \left( 1 - \frac{p}{\lambda} \right) \left( 1 - \sum_{x=1}^{\beta-1} \lambda^{-x} l_x m_x \right) - m l_\beta = 0 \quad (20)$$

using equation (7) for the  $l_x$  expressions.

**(b) Estimating parameter values**

The theoretical equations for collapsing a full life-table model to the four parameters of a geometric-series model depend on detailed information which might not be accessible in practice. Thus we must inquire into the means for estimating the parameters from the sorts of data which are likely to be available.

Note that we cannot consider one parameter, such as fecundity, in isolation. A value of  $m$  is not in itself true or false. The criterion for the 'truth' of such a value will be whether it yields a correct value for the calculated growth rate,  $\lambda$ , when used in combination with a set of mutually consistent parameter estimates in a life-table model. Thus our emphasis must be on defining consistent combinations of parameters. For example, the summations taken to infinity in equations (8), (9), (10), (15), (16), (18) and (19) may equally well be truncated at the last reproductive age in the life history. If this age is different from the oldest age in the population, the resulting set of collapsed parameters will have different values than they would have if the summations were not truncated, but provided the truncation is adhered to consistently, the combination will still yield a correct computed value for the population growth rate.

At the time when we gather data from a population, the population's age distribution may or may not conform reasonably closely to the stable age distribution of its life table, depending on the history of recent disturbances to the population or changes in its vital rates. If the population age distribution departs considerably from the stable age distribution, then there is no valid alternative to obtaining estimates for all the age-specific fecundity rates,  $m_x$ , and survival rates,  $p_x$ , using these to compute  $\lambda$  via the characteristic equation, and then using  $\lambda$  to compute the correct stable age distribution, from which the mean *per capita* values,  $p$  and  $m$ , may be computed as per the theoretical equations given above.

Obviously, this is an unsatisfactory situation, as the fine subdivision by age classes will greatly reduce the number of observations supporting the estimation of any one of the age-specific rates. In particular, if the survival rates are obtained from a tag-and-recovery program, or catch curve, each survival rate will be computed from a ratio, with error in both the numerator and denominator. Unfortunately, the expectation of a ratio of random numbers is not equal to the ratio of their expectations. If the errors are independent, the expectation of the ratio will be the ratio consisting of the arithmetic mean of the numerator divided by the harmonic mean of the denominator. Since the harmonic mean is necessarily smaller than the arithmetic mean of the same set of numbers, the denominator will be biased downward, and thus the survival rate so obtained will tend to be an overestimate of the true value. The discrepancy between harmonic and arithmetic means increases with the variance, so the bias will be of appreciable magnitude when the small sample size associated with each age-specific survival rate results in unstable values.

The problem is of lesser severity in the estimation of age-specific fecundities. This estimation might be carried out by distributing the observed recruitment to the first age class over the female population of the prior season in proportion to some measure of relative fecundity (such

as age-specific pregnancy rates). Then the age-specific fecundity is computed as

$$m_x = \frac{B_{t+1}}{N_{x,t}} \left( \frac{f_x N_{x,t}}{\sum_{y=1}^{\infty} f_y N_{y,t}} \right) = f_x \left( \frac{B_{t+1}}{\sum_{y=1}^{\infty} f_y N_{y,t}} \right) \quad (21)$$

where  $B_t$  is the number of recruits to the youngest age class in year  $t$ ,  $f_x$  is the age-specific relative measure of fecundity, and  $N_{x,t}$  is the abundance of females in age class  $x$  in year  $t$ . Since  $B$  and the vector  $N$  are measured at different times, the errors involved in scaling them as absolute numbers of individuals (i.e. they can not be obtained simply as ratios of the respective age classes in the same sample) will to an extent be independent. Thus we again are faced with a ratio where there is error both in numerator and denominator. In this case, however, the excessive variance attributable to the small sample size resulting from age stratification is confined to the estimate of  $f_x$  in the numerator. The relative fecundities in the vector  $f$  can be obtained at the same time as  $N$ , and since all elements of  $f$  are summed in the denominator, the denominator will not be nearly so unstable. Thus, there will be a tendency to overestimate age-specific fecundities via this method, but the magnitude of the bias probably will not be nearly so great as with the age-specific survival rates. Systematic errors owing to differing efficiencies in sampling adults and recruits may be very serious, but this is a specific empirical problem and not inherent in the statistics of our parametrization.

If we can assume that the population is in its stable age distribution, though it may be increasing or decreasing, parameter estimation becomes much simpler. For example, the value of  $m$  would be given simply as the mean *per capita* fecundity observed in that segment of the population which is nominally reproductive. This may be based on the mean frequency of pregnancies corrected by an estimate of foetal and neonate survival rates to the time of first census. The estimate of the frequency of pregnancies is not intrinsically biased, since it is a simple fraction of a sample. The survival correction, depending on how it is measured, may be biased, owing to its being a ratio with uncertainty in both the numerator and denominator, but since age stratification is not necessary, the feasible sample size can be large, thus reducing the variances, and so reducing the bias. Alternatively, the mean *per capita* fecundity may be calculated simply as the ratio of recruitment (to age class 1) to the size of the population aged alpha and older in the prior time period, by collapsing the formula for the age-specific estimate, on the assumption that the population is in stable age distribution. This will continue to be an overestimate, but for substantial sample sizes the bias should be slight.

Adult mortalities in a population in stable age distribution may be estimated from a single determination of the age distribution. If we rewrite the expression for the stable age distribution in terms of the age-specific survival rates

$$c_x = \frac{\prod_{j=1}^{x-1} \left( \frac{p_j}{\lambda} \right)}{\sum_{y=1}^{\infty} \lambda^{-y} l_y} \quad (22)$$

and substitute this expression into our theoretical formula for  $p$ , we obtain

$$p = \frac{\sum_{x=\alpha}^{\infty} p_x \prod_{j=1}^{x-1} \left(\frac{p_j}{\lambda}\right)}{\sum_{x=\alpha}^{\infty} \prod_{j=1}^{x-1} \left(\frac{p_j}{\lambda}\right)} = \lambda \left(1 - \frac{c_\alpha}{\sum_{x=\alpha}^{\infty} c_x}\right) \quad (23)$$

Thus, if the population is in stable age distribution, we may estimate  $p/\lambda$  as

$$\frac{p}{\lambda} = 1 - \frac{n_\alpha}{n} \quad (24)$$

where  $n_\alpha$  is the number of individuals that are age  $\alpha$  in a sample of  $n$  individuals that are age  $\alpha$  or older.

This remarkably simple statistic, which in the zero-growth form was first proposed by Heincke (1913), is unbiased, for there is random error (relative to the sample size,  $n$ ) only in the numerator of the ratio. The sampling error associated with that one term is simply the variance of a binomial with parameters  $(n, E[n_\alpha/n])$ , so the sampling variance of our estimate of mean *per capita* survival discounted by the growth rate is

$$V_{AR}\left(\frac{p}{\lambda}\right) = \frac{V_{AR}(n_\alpha)}{n^2} = \frac{E(n_\alpha) \left(1 - \frac{E(n_\alpha)}{n}\right)}{n^2} \quad (25)$$

and so from the prior relation, the expectation of the variance in  $p/\lambda$  is

$$E\left(V_{AR}\left(\frac{p}{\lambda}\right)\right) = \frac{\frac{p}{\lambda} \left(1 - \frac{p}{\lambda}\right)}{n} \quad (26)$$

which will have an acceptably small value for reasonable sample sizes.

It may seem a statement to have estimated  $\rho/\lambda$ , when we wanted an estimate of  $\rho$  in order to calculate the unknown  $\lambda$ , but note that the polynomial equation (1) for  $\lambda$  may be written

$$\lambda^\alpha \left[1 - \left(\frac{p}{\lambda}\right)\right] - ml_\alpha = 0 \quad (27)$$

whence we see that the value of the ratio  $\rho/\lambda$  can be used in a calculation to obtain a value for  $\lambda$  even if we don't have a separate estimate for  $\rho$ .

The other traditional methods for calculating an 'average mortality' are not generally satisfactory for our purposes. Where the mortality rates of the reproductive age classes do not vary with age (i.e. where  $p_x = p$ , for  $x > \alpha$ ), the ideal method is that of Chapman and Robson (1960), which like our estimate is unbiased and has an even smaller sampling variance. This is a maximum likelihood method, where the likelihood function for an observed distribution in the sample is given by a multinomial distribution, which has the form

$$\Pr(\mathbf{n}) = k_1 \prod_{x=\alpha}^{\infty} (c_x)^{n_x} \quad (28)$$

where  $n_x$  is the observed number of individuals of age class  $x$  in the sample and  $k_1$  absorbs both the combinatorial correction for the number of possible orderings of ages with that distribution and the scale factor which normalizes the expression so that the sum over all outcomes is one.

For  $x > \alpha$  we note that  $c_x$  is proportional to  $\prod_{j=\alpha}^{x-1} (p_j/\lambda)$ , so substituting this above, we obtain

$$\Pr(\mathbf{n}) = k_2 \prod_{x=\alpha}^{\infty} \left[ \prod_{j=\alpha}^{x-1} \left(\frac{p_j}{\lambda}\right) \right]^{n_x} = k_2 \prod_{x=\alpha}^{\infty} \left(\frac{p_x}{\lambda}\right)^{\left(\sum_{y=x+1}^{\infty} n_y\right)} \quad (29)$$

where  $k_2$  now absorbs the proportionality constant  $k_1$ , and the remainder of the expression is a weighted geometric mean of the age-specific survival rates from age  $\alpha$  and older, with the survival rate of each age class weighted by the abundance of all older age classes in the sample. This contrasts with the mean *per capita* survival rate we really are looking for, which is a weighted arithmetic mean, with the survival rate of each age class  $\alpha$  and older weighted by its own abundance.

In the special case where the survival rates of all age classes  $\alpha$  and older are the same (we will designate this value  $\hat{p}$ ), the unusual averaging in the Chapman–Robson method is immaterial, and the expression reduces to

$$\Pr(\mathbf{n}) = k_2 \prod_{x=\alpha}^{\infty} \left(\frac{\hat{p}}{\lambda}\right)^{\sum_{y=x+1}^{\infty} n_y} = k_2 \left(\frac{\hat{p}}{\lambda}\right)^{\sum_{x=\alpha}^{\infty} \sum_{y=x+1}^{\infty} n_y} = k_2 \left(\frac{\hat{p}}{\lambda}\right)^{\sum_{x=\alpha+1}^{\infty} n_x(x-\alpha)} = k_2 \left(\frac{\hat{p}}{\lambda}\right)^{n(\bar{x}-\alpha)} \quad (30)$$

where  $n$  is the size of the sample of individuals age  $\alpha$  and older, and  $\bar{x}$  is the arithmetic mean age in that sample.

Unfortunately, if survival rates are age dependent, the mean age in the sample will not yield a correct value for the likelihood function, and the Chapman–Robson formula for the mean mortality

$$\frac{p}{\lambda} = \frac{1}{1 + \frac{1}{\bar{x}-\alpha}} \quad (31)$$

then 'averages' the mortality rates in a way that is not appropriate for obtaining a mean *per capita* value. Numerical experiments indicate that a decrease in age-specific mortalities at some early age (within the set of age  $\alpha$  or greater) will cause the Chapman–Robson statistic to underestimate the true mean *per capita* mortality, whereas an increase in age-specific mortalities at some late age will cause the Chapman–Robson statistic to overestimate the true *per capita* mean.

The other common techniques, such as linear

regression on log transformed abundances against age, or nonlinear regression to fit an exponential, are substantially worse than the Chapman–Robson statistic when the true mortality rates are not age dependent, and worse yet when there is a pattern of age dependence (Barlow, 1982). In reading this literature, it is well to bear in mind that some of the methods were indeed developed for analysis of the age distribution of a sample taken at one time, but some were developed for analysis of the catch curve of a cohort over time, and others were developed for analysis of the time sequence of recaptures of a marked subpopulation which was not necessarily a cohort. Clearly, the assumptions will differ in each case. For our purposes it is important to note that methods developed for catch-curve or recapture analysis must be revised to include the distortions due to population growth, if these are to be applied in analysis of an age distribution.

There remains the problem of estimating the value of  $l_\alpha$ , the survivorship to age  $\alpha$ , to complete the set of parameter values for the geometric-series life-table model. This may be accomplished either by a tagging program or by analysis of the relative frequencies of age classes 1 and  $\alpha$ . For the latter, we obtain the measure

$$\frac{l_\alpha}{\lambda^{\alpha-1}} = \frac{n_\alpha}{n_1} \quad (32)$$

The fact that the measure is for  $(l_\alpha/\lambda^{\alpha-1})$  rather than  $l_\alpha$  again is not an obstacle, for the polynomial equation for  $\lambda$  may be rearranged as

$$\lambda = \frac{1 - \left(\frac{p}{\lambda}\right)}{m \left(\frac{l_\alpha}{\lambda^{\alpha-1}}\right)} \quad (33)$$

We are, however, faced with a ratio measure, where there will be bias owing to random error in numerator and denominator, though the random component can be reduced by sufficiently large sample sizes. Graver practical difficulties may be encountered in the search for a sampling technique which is not selective between ages 1 and  $\alpha$ .

For these reasons, a tagging program may be preferable, though it must be understood that to compute a useable  $l_\alpha$ , the recovery, at age  $\alpha$ , of individuals which were marked at age 1, must be scaled in absolute numbers of individuals in the population. In other words, a good estimate of the recovery efficiency will be necessary. This is seldom available. Were that not the case, estimates of population size would not pose such a challenge.

Given that survivorship to age  $\alpha$  is so refractory to estimation, it is no wonder that very few independent estimates of this quantity are available for wild populations. We may consider ourselves fortunate that the population growth rate for most cetaceans is not inordinately sensitive to this parameter, at least by comparison with the sensitivity to adult mortalities; though, as we saw in the dolphin example, the uncertainty in it may be so great that it becomes important to the calculation of growth rate despite the rather modest sensitivity.

We note, in passing, that these comments on parametrization apply with equal force to the partially collapsed Leslie model mentioned in Section II (a). In this

model, age-specific fecundity and survival rates are retained up till some age  $\beta$ , but at this age and beyond a geometric series is assumed. The choice of age  $\beta$  will rest either on judgements regarding sufficiency of the sampling to support age-specific parameters for all younger age classes, or on evidence that the vital rates do become constant with age at some point. In either case, the geometric series parameters,  $m$  and  $p$ , then represent fecundities and survival rates that are means *per capita* of the population age  $\beta$  and older. The model may be used as a projection matrix of order  $\beta$ , or the characteristic polynomial may be formed directly, as in equation (20), and solved for the asymptotic growth rate using common computer algorithms, such as in Newton's method.

### III. POPULATION PROJECTION WITH TIME-VARYING VITAL RATES

When the actual age-specific survival rates and fecundity rates vary from one time period to the next, perfect data concerning past rates are no longer sufficient for perfect projection of the population. There will be an unavoidable uncertainty about future vital rates, but we may decide that the means, variances and covariances which described these parameters in the past will apply for the future. Then we might ask whether we can arrive at some statistical description of the population projection.

#### (a) Projection of uncertainty

If we allow the age-specific survival and fecundity rates to have distributions which are time-invariant, we may readily construct a Leslie matrix model for projecting the population. The projection of a given initial vector, describing the number of individuals in each age class, is carried out by multiplication by a matrix which is a sum of two matrices, one of which is the matrix composed of means of the respective vital rates, and the other is determined by the variances and covariances. The solution for the means and variances of the elements of the population vector at some time in the future is given by formulae developed by Sykes (1969) from the matrix model.

The expectation of the number of individuals in each age class in the future population is simply the number that results from applying the Leslie matrix of parameter means to the initial population vector. This is to say that projecting the 'mean' outcome under this model of random variation in the parameters of the life table can readily be accomplished just by constructing a Leslie matrix, the elements of which are the respective time averages of the time-varying fecundities and survival rates.

The projection of the variance associated with the abundance of each age class in the population at time  $t$  is much more cumbersome. A computer program which carries out these operations is available at the National Marine Fisheries Service, Southwest Fisheries Center (Gerrodette, Goodman, and Barlow, 1982). The variances compound with time, and for a projection beyond the very near term the uncertainties are large, so much so that we need to be circumspect in our interpretation of these distributions and the mean rates associated with the projection process.

**(b) Ensemble averages and path averages**

Consider a simple multiplicative process, where a time-varying factor of increase,  $\lambda_t$ , is applied each time period. The variation in the factor of increase is random, with no correlation between values in different time periods, and with the same distribution governing the values in each time period. Let the mean of the distribution of the factor of increase be designated  $\bar{\lambda}$ , which is the same for any time and which may be estimated by the average of the factors of increase recorded in a history of a realization of the process. This is a path average.

Oddly, the path average, when raised to the power of the time elapsed along that path, does not describe the realized growth along that path. Since we are dealing with a multiplicative process, it is the geometric mean of the factors of increase realized along a path which describes correctly the net increase. The geometric mean of a set of numbers is necessarily smaller than the arithmetic mean. Thus the path average will necessarily give an inflated picture of the growth actually achieved.

But, of course, the growth achieved along a path for which we have a record is in any case known. What can be said about a projection into the future, on the basis of a statistic, such as  $\bar{\lambda}$ , which may be estimated from a past history? Since for the future there is random variation, which we can characterize only in terms of a distribution, the correct metaphor for projection of the growth process to time  $t$  is the distribution of values resulting at that time under a large number of independent realizations of the growth process from the initial time (the last known value) to time  $t$ . It is as if we had a large number of populations starting at the same size but growing under independent random variation (but with this random variation being governed by a common distribution), and then we recorded the distribution of the final population sizes at the end of the process (at time  $t$ ), by which time the independent trajectories will have diverged, taking separate paths. The mean of this group of final values is an ensemble average.

The ensemble average population size is correctly described by  $\bar{\lambda}$  (which is estimated by the path average) raised to the power of the time elapsed, for the mean of a product of two independent terms is the product of the respective means of the two terms. It is for this reason that in the age-stratified model referred to above, the 'mean' for the projected population vector is given by application of the Leslie matrix of mean rates. But this contrasts uncomfortably with our statement that the path-average factor of increase did not correctly describe the growth along the historical path. How can it be that a statistic which does not describe net growth along a realized historical path will nonetheless describe the mean outcome of projected growth?

The answer lies in the observation that for each path in the set of future projections there will be a different path average and indeed a different final population size. Along each such path, the geometric mean of that path's factors of increase will determine the net growth, and that geometric mean will not be the same as the path average. Owing to the law of large numbers, the path averages of the respective paths will be much the same if they are of sufficient length, but the geometric means of the

respective paths will not be so similar, for geometric means are not stabilized by large sample sizes. (Recall that one small number can make a product small, whereas its inclusion in a sum of many numbers would have negligible impact). On the other hand, the modal outcome (that is, the mode in the distribution of final population sizes) is given by the mode of the geometric means among the ensemble of paths, and this is simply the geometric mean of the distribution of the factors of increase.

This may be envisioned more easily by log transforming, so that the growth process (in units of the log of population size) can be represented as addition rather than multiplication. Then, since the increments in each time interval are independent, the central limit theorem applies, from which we conclude that after sufficient time has elapsed the distribution of the logarithms of the ensemble's population sizes will be normal, which is to say that the distribution of the ensemble is lognormal. The lognormal is an asymmetric distribution whose mode is located at the mean of the symmetric normal distribution which is obtained upon log transformation. The mean of the lognormal is computed from the parameters of the normal to which it may be transformed as

$$\bar{x} = e^{\mu + \frac{\sigma^2}{2}} \quad (34)$$

or, perhaps more revealingly,

$$\ln \bar{x} = \mu + \frac{\sigma^2}{2} \quad (35)$$

where  $\bar{x}$  is the mean of the lognormal (in this case the expectation of the projected population size),  $\mu$  is the mean of the log-transformed distribution (i.e., the geometric mean, or in this case the logarithm of the modal projected population size), and  $\sigma^2$  is the variance of the log-transformed distribution.

Thus the modal outcome of the projection departs from the mean by an amount which increases with the variance in the distribution, and since the variance compounds with time, the discrepancy for a long-term projection can be vast. Indeed, this sort of process can give rise to a projection where the expectation of the population size grows exponentially with time, whereas the probability of extinction (e.g. the fraction of the ensemble which is below some specified small value) approaches 100% with time.

**(c) Stationarity and density dependence**

The discouraging features of the above model, namely the endlessly compounding variance and the growing divergence between the mean and the modal outcome, are aspects of the non-stationarity of the distribution of the projected population distribution. Real populations which persist do not behave that way, for biological persistence implies bounds on the mean and variance of the population distribution. It has been proven by Royama (1977) that for a random multiplicative process to remain bounded, the growth factors cannot be independent. In terms of mechanisms, this means that the random factors of increase must display some density

dependence, or the long-term behavior of the model will not make biological sense.

Thus the real answer to the seeming paradoxes generated by the simple model described above is that the model was not appropriate to the phenomenon we had in mind. In order to deal adequately with the statistics of population projection with time-varying vital rates, the projection model must incorporate density dependence. Then, the projected population distribution can be stationary, and the mean outcome will coincide with the mode. Now we ask what sort of statistic of the time-varying vital rates in the density-dependent model will be the correct descriptor of the mean outcome.

For simplicity, let us consider only time variation in the fecundity rates. This is not unreasonable, for fecundity rates are generally more sensitive to environmental fluctuations than are adult survival rates in the sorts of long-lived animals which are our concern, and variation in survival rates of the young can be represented equally well by absorbing these into the variation in fecundity without doing violence to the essential properties of the model. Let the density dependence operate through a linear effect due to the total adult population size, and let the fecundity rate of all adults be independent of age, though the survivorship function can be general. Then the basic matrix model for projecting the population vector,  $\mathbf{n}$ , from time  $t$  to  $t+1$  is

$$\mathbf{n}_{t+1} = A\mathbf{n}_t + (q(\bar{N} - N_t) + \epsilon_t)\mathbf{v} \quad (36)$$

where  $A$  is a time-invariant Leslie matrix,  $N_t$  is the size of the adult population at time  $t$ ,  $\bar{N}$  is the mean size of the adult population,  $q$  is the coefficient of the density-dependent disturbance term affecting realized fecundity,  $\epsilon_t$  is a pure random disturbance term, with mean zero, affecting realized fecundity, and  $\mathbf{v}$  is a vector with first element equal to 1 and all other elements zero, which operates on the two disturbance terms so that they only affect fecundity (in that their only contribution to the next population vector is in age class 1).

Since the expectation of both disturbance terms is zero, the expectation of the growth process itself is described by  $A$  alone. Indeed, the expected population size at any future time is governed by  $A$  alone. In other words, the vital rates in  $A$  are the rates that project the expected population. Thus we should like to know what measurements we can make that are appropriate as parameter values for  $A$ . Since the survival rates in this model are time-constant, the survival rates in the matrix  $A$  are simply the survival rates that would be observed at any time. The time-variation is in the realized fecundity, so our question now is how does the fecundity term,  $m$ , in the matrix  $A$  relate to the realized fecundities in the system.

The realized fecundity in the system,  $m_t$ , is the number of recruits to age class 1 at time  $t+1$  divided by the size of the adult population in the prior time period. That is

$$\begin{aligned} m_t &= \frac{mN_t + q(\bar{N} - N_t) + \epsilon_t}{N_t} \\ &= m + q\left(\frac{\bar{N}}{N_t} - 1\right) + \frac{\epsilon_t}{N_t} \end{aligned} \quad (37)$$

The average of this realized fecundity, which is the value we would arrive at if we were to average the

observed *per capita* recruitment over a representative history of the population, is

$$\begin{aligned} \bar{m} &= m + q\left(E\left(\frac{\bar{N}}{N_t}\right) - 1\right) + E\left(\frac{\epsilon_t}{N_t}\right) \\ &= m + q\left(\frac{\bar{N}}{\mathcal{H}(N)} - 1\right) + \frac{E(\epsilon_t)}{\mathcal{H}(N)} \\ &= m + q\left(\frac{\bar{N}}{\mathcal{H}(N)} - 1\right) \end{aligned} \quad (38)$$

where  $\mathcal{H}(N)$  is the harmonic mean of  $N_t$ .

Since the harmonic mean of  $N$  is necessarily smaller than the mean of  $N$ , namely  $\bar{N}$ , the term in the product with  $q$  is necessarily positive, and so the measured mean realized fecundity  $\bar{m}$  must be a larger value than  $m$ , the fecundity which projects the expectation of the population. That is, if we were to take the observed mean realized fecundity and use it in constructing a Leslie matrix for projecting the population, the growth rate of that Leslie matrix would overestimate the true growth rate.

Roughly, the amount of the overestimate will increase with the variance in the population's realized birth rate, and this variance will tend to decrease with the length of the reproductive span in the life history. The proof of these latter two statements is mathematically involved and will be published elsewhere.

Since it is  $m$  and not  $\bar{m}$  which correctly projects the expected growth rate, we need to rearrange our last equation to solve for  $m$  in terms of the measurable  $\bar{m}$ . In practise, unfortunately, this will not prove feasible. We see that solving for  $m$  would require that we know the history of the population size in sufficient detail to compute the harmonic mean, and we would need a detailed enough record of the recruitment rate to estimate the density-dependence coefficient  $q$ . Furthermore, when it comes to specific applications, we must bear in mind that the particular mechanism of density dependence portrayed in this mathematical model, with its linear response to total adult density with no time lag, may not be appropriate to the biology of the population in question. Therefore the formula for computing the correct  $m$  may be somewhat different in detail.

Even though there are no practical prospects for precise quantitative adjustment of an observed mean fecundity to arrive at a correct value for population projection in a random environment, we may still draw useful qualitative conclusions. In general it will be the case that the correct  $m$  is a smaller value than the observed mean realized fecundity, and the discrepancy increases with the variance in the population's birth rate and will decrease with the reproductive span in the realized life history.

This role of length of the reproductive span in stabilizing the birth rate, and thereby in allowing the actual population growth rate to be nearer that which would be conferred by the mean realized fecundity, shows that a harvest of adults will result in two levels of impact on the dynamics of a population. The harvest obviously increases the mortality rate, and so it will reduce the population size until density compensation results in a sufficiently increased birth rate to balance this new death rate (or if the new mortality rate is too high to be balanced, the population will of course collapse). The

second level of effect is that, in reducing the life expectancy of adults, the harvest reduces the effective reproductive span in the realized life history. Therefore, the harvested population will be more sensitive to environmental fluctuations which affect the birth rate; and its long-term population growth, in the face of environmental variations, will be depressed relative to the population growth which would result under the mean realized fecundity if the environment were constant. Or, to put it another way, the harvest will increase the amount by which a projection based on the mean realized fecundity overestimates the expected population growth.

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# Review of Techniques Used to Estimate the Average Age at Attainment of Sexual Maturity in Marine Mammals

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## ABSTRACT

The average age of sexual maturation (ASM) is generally used as a 'K' index to determine whether or not a population is approaching its carrying capacity. If the ASM is increasing, it is inferred that the density *per capita* of resources is increasing and that density-dependent mechanisms are operative. At least five techniques are commonly used to estimate the ASM. These techniques are mean of known-age first-time ovulators, mean deduced from age-specific ovulation rates, regression of age-specific ovulation rates versus age, graphical interpretation of age when 50% of animals have ovulated, and graphical interpretation of age at which the cumulative probability of ovulation equals the cumulative probability of not ovulating. Using hypothetical data, it is shown that different techniques produce different estimates of the ASM. The mean of known-age first-time ovulators is assumed to be the best estimator of the ASM, and other techniques are compared for bias and precision.

## INTRODUCTION

The average age at attainment of sexual maturity (ASM) refers to the average age at which females in a population ovulate for the first time. This life history parameter has been used to compare the status of marine mammal populations by assuming that a population which has a higher density will have a greater average ASM. It has been used in population models (see Eberhardt and Siniff, 1977, and Goodman, 1984) that require an estimate of the average age of first birth, which is estimated by adding the average ASM and the average duration of the first gestation period.

The average ASM can be and has been estimated in a number of different ways and from a number of different data sources. Five different estimators are in common use. They are mean age of first-time ovulators (e.g. Bengtson and Siniff, 1981), mean deduced from age-specific ovulation rates (DeMaster, 1978), regression of corpora counts versus age (e.g. Kasuya, 1972), graphical interpretation of a plot of percentage mature against age to determine the age when 50% of females have ovulated at least once (e.g. Perrin, Holts and Miller, 1977), and graphical interpretation of age at which the cumulative probability of ovulating by age  $x$  equals the cumulative probability of not ovulating at age  $x$  or older (Kasuya, 1972). The purpose of this paper is to compare the estimates of ASM values for each of the five estimators with the same hypothetical data set and to compare the variance of the estimators that utilize age-specific rates of ovulation. It is my intention to show that each estimator will produce a different estimate of the average ASM, and that comparisons made between different populations or the same population over time must be based on estimates of the ASM that are derived in the same manner. This can be a particular problem when comparing the results of one study with published results of another where the method used to estimate the average ASM may not be given.

## METHODS

### *Comparison of ASM estimators*

A hypothetical data set of age-specific ovulation rates was derived by assuming the following: annual survivorship of females is constant and equal to 0.90; no animals less than 4 years of age ovulate; 20% of 4-year-olds ovulate; 50% of 5-year-olds that did not ovulate as 4-year-olds ovulate; 70% of all 6-year-olds that did not ovulate as 5-year-olds ovulate; 90% of all 7-year-olds that did not ovulate as 6-year-olds ovulate; and all 8-year-olds that did not ovulate as 7-year-olds ovulate. It was further assumed that animals that ovulated at age  $x$  will not ovulate again until age  $x + 2$ , but at these ages all animals will ovulate independent of age. This simulates a reproductive interval of 2 years. The number of animals that ovulate for the first time at age  $x$  and the total number of ovulating animals at age  $x$ , under these assumptions, are presented in Fig. 1. The age-specific ovulation rates and number of first-time ovulators were used to estimate the average ASM for each of the five techniques.

### *Sensitivity analysis*

A sensitivity analysis was performed on the three ASM estimators that utilize age-specific ovulation rates: the mean deduced from age-specific ovulation rates, the age

	AGE IN YEARS					
	4	5	6	7	8	9
	1000	180 -ov.	162 -lact.	146 -ov.	131 -lact.	118 -ov.
		720 -no	324 -ov.	292 -lact.	262 -ov.	236 -lact.
			324 -no	204 -ov.	184 -lact.	165 -ov.
				88 -no	71 -ov.	64 -lact.
					8 -no	7 -ov.
Number Ovulate	180 (0.20)	324 (0.40)	350 (0.48)	333 (0.51)	290 (0.49)	
Number Mature	180 (0.20)	486 (0.60)	642 (0.88)	648 (0.99)	590 (1.00)	
Number Ovulate For First Time	180 (0.20)	324 (0.40)	204 (0.28)	71 (0.11)	7 (0.01)	

Fig. 1. Summary of hypothetical population of female dolphins. Annual survivorship equals 0.90, and the reproductive interval is 2 years.

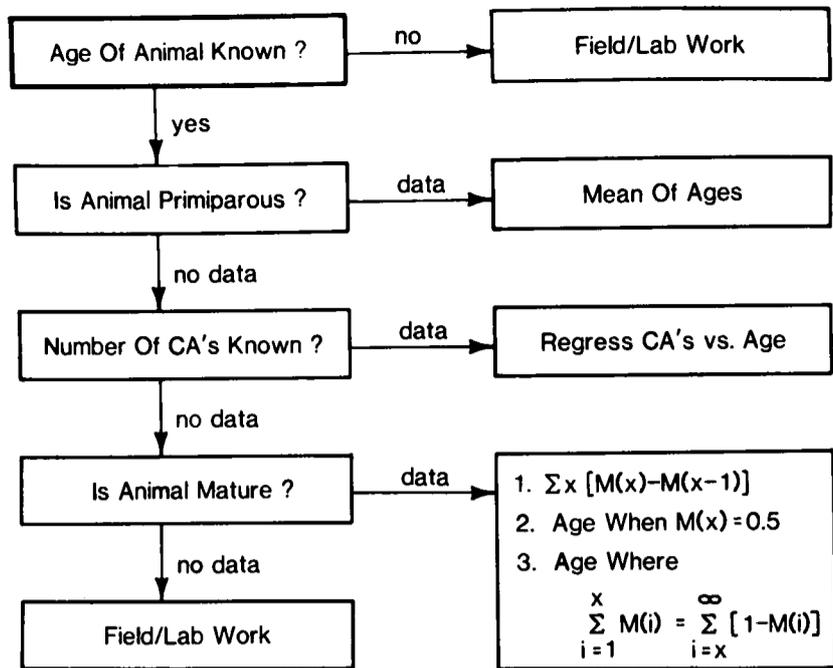


Fig. 2. Summary of which estimators for ASM are used with certain data bases.

where 50% of females are mature (i.e. they have ovulated at least once), and the age where the cumulative probability of previous ovulation equals the cumulative probability of not having ovulated. A series of age-specific ovulation rates were selected at random from a normal distribution, with means equal to the rates given in Fig. 1, and a coefficient of variance equal to 0.025. For each of the 3 estimators, 30 sets of age-specific ovulation rates were generated and estimates of the average ASM derived. This type of Monte Carlo simulation represents a situation where only the sampling variation is being compared. The biological parameters are assumed to remain constant between samples.

#### Additional consideration

Problems with obtaining precise, unbiased estimates of age were not considered in this review. It was assumed that animals that have been collected can be aged correctly. Problems in identifying corpora and questions of corpora regression and persistence were not addressed. It was assumed that all of the different estimators suffer from these problems, but future efforts should be directed at determining whether all of the estimators are equally sensitive to them. It was also assumed that the mean age of first-time ovulators is an unbiased estimate of the average of ASM. However, sample sizes of ovaries from animals that have ovulated only once are generally small, and estimates based on all ovaries sampled are more common. If counts of total corpora albicantia (CAs) in both ovaries are available, it is possible to regress number

of CAs against age. However, if only information on presence or absence of CAs is collected, then one of the three alternative estimators must be used (Fig. 2 summarizes the various analyses and data requirements). Finally, some authors have estimated the length where 50% of all females were sexually mature, and then estimated the ASM from a derived relationship between length and age (e.g. Perrin *et al.*, 1977). This estimator was not considered, as it could not be determined from the data given in Fig. 1.

## RESULTS

### Comparison of estimators

#### 1. Mean age of first-time ovulators

The mean age of first-time ovulators (AFO) is generally accepted as an unbiased estimate of the ASM. However, the sample size for this estimator is often very small, making it relatively imprecise. The mean AFO from the hypothetical population (Fig. 1) is 6.24 years (Table 1). Two advantages of this technique over the other estimators are that it is unbiased and that confidence intervals are easily constructed from the standard formula for the variance of a mean.

#### 2. Mean deduced from age-specific ovulation rates

The derivation of this estimator and its variance is given in DeMaster (1978). The mean deduced from age-specific ovulation rates (ASOR) is a positively biased estimator. This is because the estimator evenly weights all of the age classes, when older age classes clearly comprise less of the population than do younger age classes (see Table 1 for formula). Therefore, this bias is progressively worse as the annual mortality rate increases. For an annual mortality rate of 0.10, the mean of ASOR is 6.33 years (Table 1; Fig. 3). If the age structure is known, an unbiased estimate of the ASM can be made with this estimator:

$$ASM = \sum_{x=0}^{\infty} \left[ \frac{[M(x) - M(x-1)](x)f(x)}{\sum_{x=0}^{\infty} (fx)} \right]$$

where  $M(x)$  equals the proportion of  $x$ -year-old females that are mature,  $x$  is the age, and  $f(x)$  is the number of animals  $x$  years old.

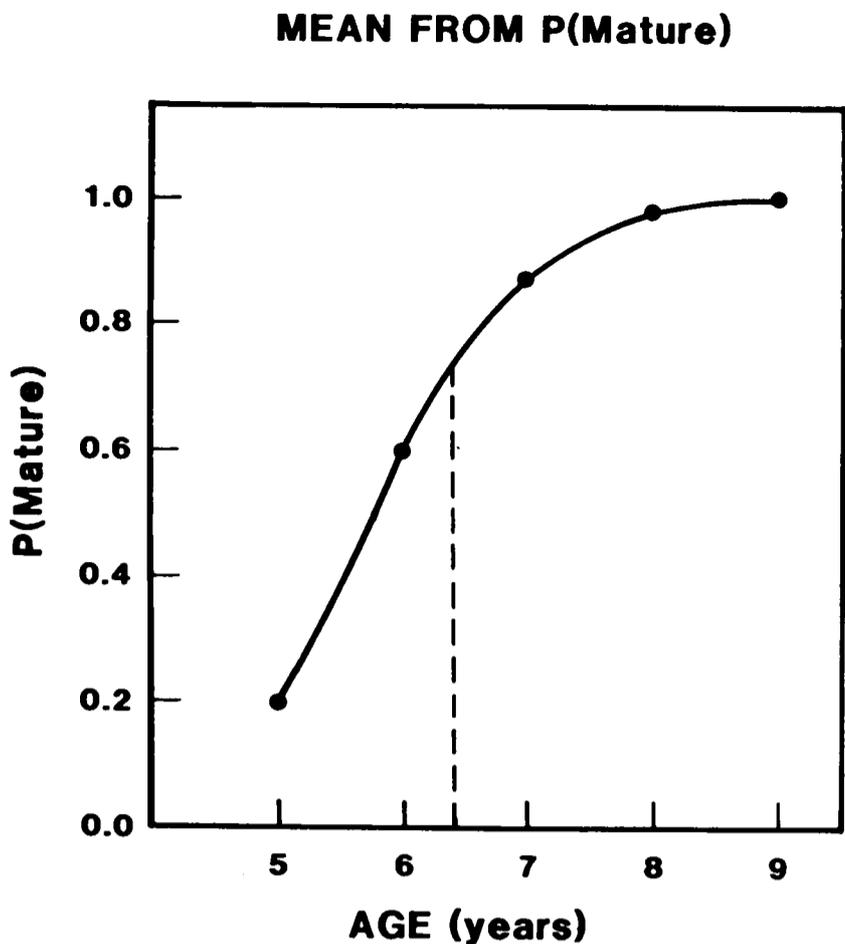
#### 3. Age where proportion mature equals 0.50

The age where 50% of the animals are mature (50% age) is a commonly used estimate of the ASM (Perrin *et al.*, 1977; Kasuya, 1976). The estimate is usually made by interpreting a plot of percent mature versus age (see Fig. 4).

Table 1

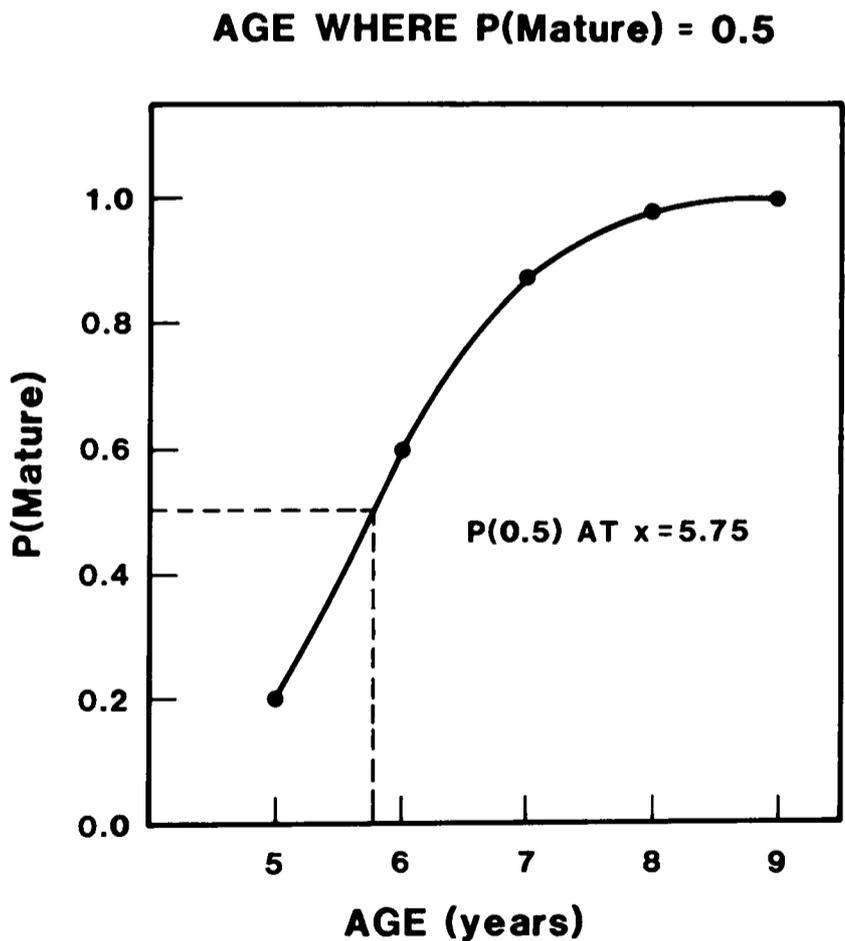
Summary of five ASM estimators. All estimates of ASM were made with the same data set (Fig. 1).  $M(x)$  is the proportion of  $x$ -year-old females that were mature, and  $x$  is the age in years. In methods 1 and 2, the summation is over all ages

1. Mean of ages:	$\frac{\Sigma (\# \text{ ovulate for the first time}) \times}{\text{total number in sample}}$	= 6.24 years
2. Mean from $P(\text{mature})$ :	$\Sigma [M(x) - M(x-1)] x$	= 6.33 years
3. Age where $P(\text{mature}) = 0.5$ :		= 5.75 years
4. Age where	$\sum_{i=1}^x M(i) = \sum_{i=x}^{\infty} [1 - M(i)]$ :	= 5.81 years
5. Regression of # CAs vs age; age where # CAs = 1.0		= 6.77 years



$$\begin{aligned}
 \text{ASM} &= \sum x [M(x) - M(x-1)] = 6.33 \\
 &= (5)(0.2) + (6)(0.4) + 7(0.28) + 8(0.11) + 9(0.01)
 \end{aligned}$$

Fig. 3. Plot of age versus percent mature (ASOR).



$$\frac{0.5 - 0.6}{0.2 - 0.6} = \frac{x - 6}{5 - 6}$$

$$x = 5.75$$

Fig. 4. Plot of age versus percent mature (50%).

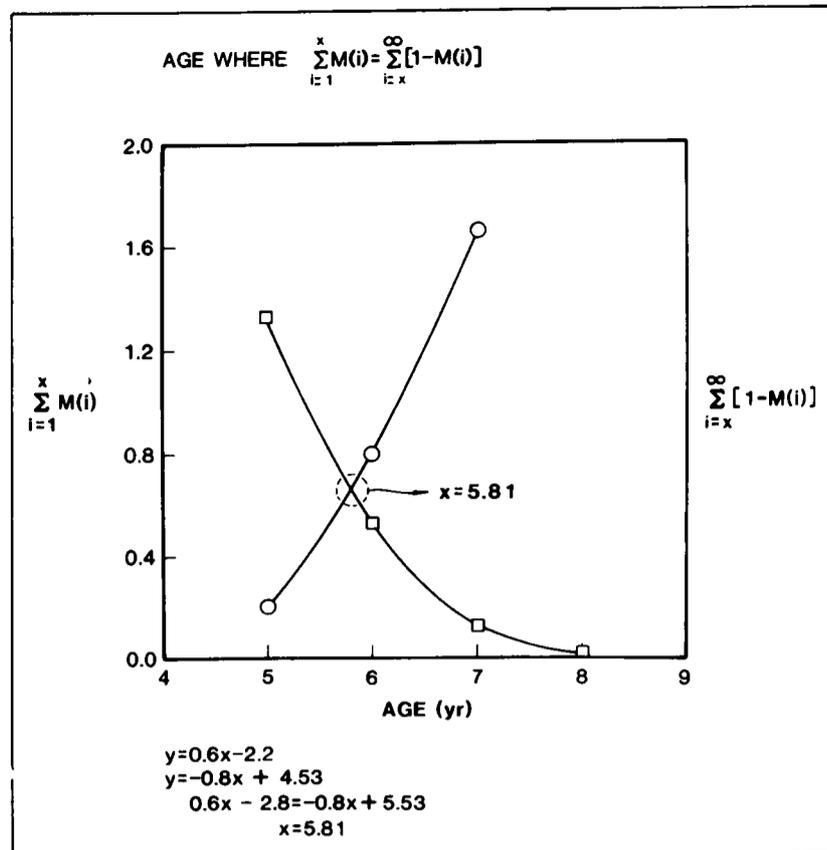


Fig. 5. Plot of terms used to estimate ASM with summation technique.

A standardized procedure for modeling the age-versus-percent-mature relationship has not been devised. If the shape of this relationship is symmetric with age, the age where 50% of animals are mature will be similar to the mean of the proportion mature. However, in general this relationship rapidly increases during the early ages and then only slowly increases to unity for the latter ages. In this case the mean AFO will generally be greater than the 50% age. In the hypothetical data set, the 50% age was approximately 5.75 years (Table 1). Variance estimates have not been developed for this estimator of ASM.

4. *Summation estimate*

The fourth ASM estimator (referred to hereafter as the summation procedure) was first described by Kasuya (1972) and subsequently used by Kasuya *et al.* (1974). The summation procedure estimates the ASM as the age where the summation of the proportion mature from birth to the ASM equals the summation of one minus the proportion mature from the ASM to the maximum age (see Table 1 for formula). Kasuya (1972) recommends this procedure over the 50% age method when sample sizes for individual age classes are small. The estimated ASM using the summation procedure and data from Fig. 1 is 5.81 years (Fig. 5). A derivation of this estimator's variance has not been developed, and, therefore, confidence intervals are generally not given. It must also be assumed in using the estimate (and the previous estimate) that a straight line adequately describes the relationship around the ASM.

5. *Regression of the number of CAs versus age*

The final estimator (referred to as the regression estimate) regresses the number of corpora albicantia against age (Fig. 6). The ASM is derived from the regression equation by estimating the age where the number of CAs is greater than zero. In using this technique it is necessary to assume that all ovulations are 'recorded' in the ovaries as

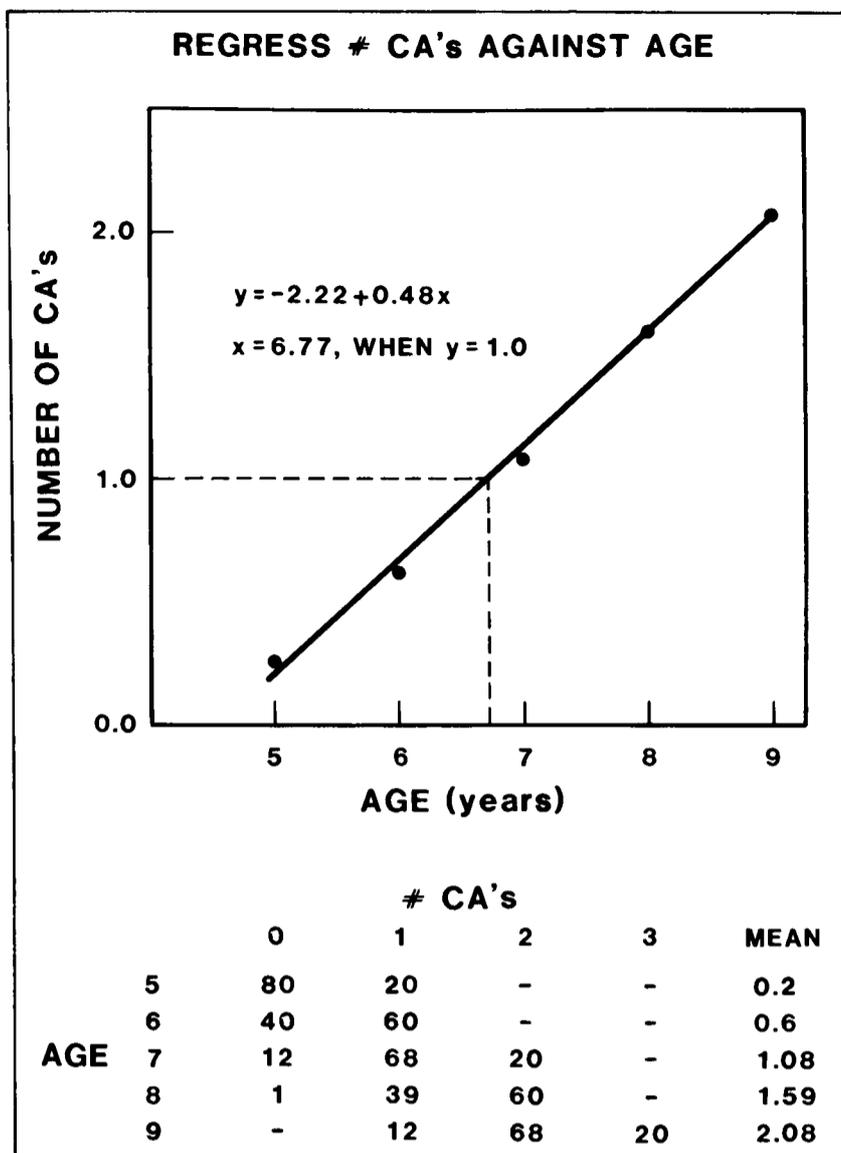


Fig. 6. Plot of number of CAs versus age.

permanent scars and that the ovulation rate is constant with age. The technique has a disadvantage in that it is positively biased whenever the reproductive interval is greater than 1 year. This is because animals with reproductive intervals greater than 1.0 often have the same number of CAs in consecutive years. This tends to make the age where the average number of CAs is equal to 1.0 greater than the average age of first-time ovulation. Also, variation in attaining maturity must be taken into account when fitting an ovulation-rate curve (see Perrin and Reilly, 1984). Using the data in Fig. 1, the regression estimate of the ASM is 6.77 years (Table 1). Confidence intervals can be derived with standard procedures for estimating the variance around the regression line, but this will provide an underestimate of the variance of the ASM.

#### Sensitivity Analysis

The results of the sensitivity analysis indicate the three techniques are equally precise (Table 2). In other words,

Table 2

Summary of three different ASM estimators, where identical data set was used to calculate the means, confidence interval, and coefficient of variance

ASM estimator	$\bar{x} \pm 2$ s.e.	C.V.
ASOR	$6.34 \pm 0.196$	0.0079
50% age	$5.75 \pm 0.164$	0.0071
Summation	$5.81 \pm 0.180$	0.0079

one estimate does not have a relatively smaller confidence interval than another. Perhaps different results would be obtained with a simulation if the coefficient of variation were larger. This should be explored in the future.

#### DISCUSSION

The ASM of a population is currently used to compare the 'status' of different populations. This assumes that the ASM is dependent on density *per capita* of resources. When used in this manner, there is a clear advantage in using those estimates that have accompanying variance estimates (AFO, ASOR, and the regression estimate). However, in those cases where the ASM is used as a discrete parameter in a population model, this advantage is no longer paramount. In such cases, one needs to consider the relative bias of each estimator. For two of the estimators, the direction of the bias will be known. That is, estimates based on ASOR and regression will usually be positively biased relative to the AFO estimator. The bias of the two graphical techniques is not consistent but depends on the form of the relationship between age and percent mature. In general, these estimators will underestimate the true mean. In making management-oriented decisions it may be necessary to consider what the expected bias is. In most cases, an overestimate of the true mean will result in a lower estimate of the replacement yield.

#### CONCLUSION

The point of this paper is not to encourage the sole use of any one technique in estimating the mean age at attainment of sexual maturity. In making statistical comparisons between populations, one seems to be limited to one of three estimators for which variances can be easily derived.

Authors should be encouraged to be consistent in their usage of ASM statistics. I recommend that the following guidelines be followed:

- (1) age-specific ovulation rates should be given,
- (2) the procedure used to calculate the ASM should be stated explicitly, and
- (3) ASMs from different population should not be compared unless the same/estimation technique was used, or comparison should be suitably qualified.

#### ACKNOWLEDGMENTS

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# Reproductive Estimates as a Source of Information on Survival Rates

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## ABSTRACT

A method of estimating the survival rates and net rates of population increase is based on estimates of the proportion of animals which are mature, the average age at attainment of sexual maturity, and the adult fecundity rate. The method is most useful for exploring the ranges of survival rates that are consistent with the estimates of these parameters. Several assumptions are necessary to obtain survival-rate estimates, including constancy of survival and fecundity rates and a stable age distribution. The method is applied to data from three dolphin populations in the eastern tropical Pacific. These data are not consistent with a positive net rate of population increase, but several possible sampling biases exist for the data and must be investigated.

## INTRODUCTION

Estimates of survival rates for natural animal populations and especially for marine mammals are difficult to obtain. Analysis of the age structure of a population is perhaps the easiest and most often used approach for obtaining survival estimates (Seber, 1973). However, it may be impossible or impractical to determine the age of a sample of individuals from a population. In contrast, it is often relatively straightforward to classify individuals according to their reproductive state. In many organisms, certain of the reproductive states are of relatively constant duration and may provide a classification of individuals into separate age groupings. Such age groupings have the potential to provide information on survival rates.

In this paper, a method is developed for estimating survival rates using the classification of animals into mature and immature classes. This method is applied to available reproductive data for dolphin populations in the eastern tropical Pacific. The method is not meant to produce precise estimates of survival but is meant to explore the range of survival rates that can be considered both biologically reasonable and consistent with the data.

## METHODS

The method requires prior estimates of three parameters and is based on four specific assumptions. The three parameters are:

- (1) the proportion of females which are mature,
- (2) the average adult female fecundity rate, and
- (3) the age at attainment of sexual maturity.

The first two parameters should be directly estimable from random samples collected for reproductive information. While estimating the age of maturation requires some aging information, it may often be a much easier quantity to estimate than the entire age structure of the population and may even be available from independent sources such as from tagged or captive animals.

The problem then becomes one of finding the sets of survival rates that are consistent with the observed values for these reproductive parameters. To answer this

problem, some assumptions about the age structure and age-specific vital rates are needed, namely:

- (1) the survival rate from birth to the age at attainment of maturity is constant,
- (2) the survival rate past the age at attainment of maturity is constant (but not necessarily equal to the juvenile rate),
- (3) the fecundity rate (i.e. the number of females born to a mature female) of mature animals is constant, and
- (4) the population is in a stable age distribution.

The fourth assumption, that of a stable age distribution, underlies any method of estimating survival rates from the age structure of a population (Seber, 1973). Some alternatives to the other three assumptions are discussed below.

The model used in this paper is based on a Leslie projection matrix modified to include a survival value in the lower right-hand corner:

$$\vec{N}(t+1) = \tilde{M}\vec{N}(t) \tag{1}$$

where

$$\tilde{M} = \begin{matrix} & \begin{matrix} 0 & 0 & \dots & \dots & \dots & 0 & F_A \\ S_1 & 0 & & & & 0 & 0 \\ 0 & S_2 & & & & \cdot & \cdot \\ \cdot & 0 & \cdot & & & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot & 0 & 0 \\ 0 & \cdot & \cdot & \cdot & \cdot & 0 & S_m & S_A \end{matrix} \end{matrix}$$

and where

$\vec{N}(t)$  = a vector of the number of females in each age class 1 to  $m$ , and the  $m+1$  element equals the number of females older than age  $m$  (i.e. the number of mature females),

$m$  = the age at attainment of maturity,

$S_A$  = the adult survival rate,

$S_i = S_j$  = a constant for  $i = 1$  to  $m$  (i.e. the juvenile survival rate), and

$F_A$  = the adult female fecundity rate.

The use of  $S_A$  in the lower right hand corner of the

matrix  $\tilde{M}$  collapses the size of the projection matrix when survival rates past a certain age are assumed constant. It is well known that a population growing according to a matrix of this form will approach a stable age distribution corresponding to the dominant eigenvector of the matrix. Thus, given the input parameters and the above matrix, any combinations of juvenile survival ( $S_j$ ) and adult survival ( $S_A$ ) rates that would yield a stable age distribution in which the proportion mature equals the observed proportion mature could be considered reasonable estimates of the survival rates. The problem of solving for values of  $S_j$  and  $S_A$  can be reduced to the following two equations (see Appendix):

$$1 = (S_j/\lambda)^m + (F_A/\lambda) + S_A/\lambda \quad (2)$$

$$R = \frac{(S_j/\lambda)^m F_A + S_A}{F_A \sum_{i=1}^{m+1} (S_j/\lambda)^{i-1} + S_A} \quad (3)$$

with symbols defined as above, and where

$\lambda$  = the largest eigenvalue of the matrix  $\tilde{M}$ , or the net rate of increase of the population, and

$R$  = the proportion of females which are mature.

Equations 2 and 3 represent two equations in three unknowns ( $S_j$ ,  $S_A$ , and  $\lambda$ ). If the value of any one of the three unknowns is specified, the other two are uniquely determined. If the assumption is made that the age distribution is stationary (i.e.  $\lambda = 1$ , Seber, 1973), then the method provides a specific set of survival estimates for a set of input parameters. This assumption usually underlies most survival-rate estimates made from age-structured data (Seber, 1973). However, if the net rate of increase is unknown and there are reasons to suspect that the population's age structure may not be stationary, it may be more informative to examine the combinations of survival rates and net rates of increase consistent with the input parameters. For the examples of dolphin populations considered in this paper, there are reasons to suspect that the population's age structure may not be stationary (Smith, 1983). Thus, solutions for the juvenile survival rate and the net rate of increase will be presented as a function of adult survival rate in order to explore biologically meaningful sets of estimates.

To illustrate this method, survival estimates are presented based on estimates of the reproductive parameters for the northern-offshore-spotted population of *Stenella attenuata* and the eastern-spinner and northern-whitebelly-spinner populations of *Stenella longirostris*. One-half the estimated pregnancy rate is used as an estimate of fecundity. The estimated proportion of mature females and the pregnancy rates are based on the pooled data base for 1973 to 1978 for each of the three stocks. (Method 1 of Henderson, Perrin and Miller, 1980). Method 2 of Henderson *et al.* has been shown to be invalid (Perrin and Reilly, 1984). The estimated ages at attainment of maturity are based on the ages estimated in Perrin, Coe and Zweifel (1976), Perrin, Holts and Miller (1977) and Perrin and Henderson (1984). The parameters used are shown in Table 1.

In considering the results, two criteria were used to determine the range of estimated survival rates consistent with the data and biological reality. The first criterion is the biological constraint that survival rates must be less than or equal to one. The second criterion is that juvenile

Table 1  
Parameters values used for estimating survival rates for the three dolphin stocks

	Northern offshore spotted	Eastern spinner	Northern whitebelly spinner
Age at attainment of maturity	8 <sup>1</sup>	5 <sup>2</sup>	6 <sup>2</sup>
Proportion mature <sup>3</sup>	0.561	0.432	0.522
Pregnancy rate <sup>3</sup>	0.376	0.339	0.356

<sup>1</sup> Rounded to the nearest year from the estimate in Perrin *et al.*, 1976.

<sup>2</sup> Rounded to the nearest year from the estimate in Perrin and Henderson, 1984.

<sup>3</sup> From Henderson *et al.*, 1980.

rates must be less than or equal to adult survival rates. While this criterion is not absolute, it is usually considered a characteristic of the survival curve for long-lived organisms (Caughley, 1966).

## RESULTS

Fig. 1 provides an example of estimates  $S_j$  and  $\lambda$  plotted as a function of adult survival rates for the northern-whitebelly-spinner population. The dotted lines corresponding to  $S_j = S_A$  and  $S_j = 1$  represent the upper bound for the survival rates corresponding to the two criteria listed in the methods section. Thus, for example, the highest estimates of juvenile and adult survival meeting both criteria in this figure is 0.81, which corresponds to a net rate of increase of 0.89. Similarly, biological limits are reached when  $S_j = 1.00$  in this figure, with corresponding values of  $S_A = 0.91$  and  $\lambda = 1.05$ . Also indicated in this figure is the line where  $\lambda = 1.00$

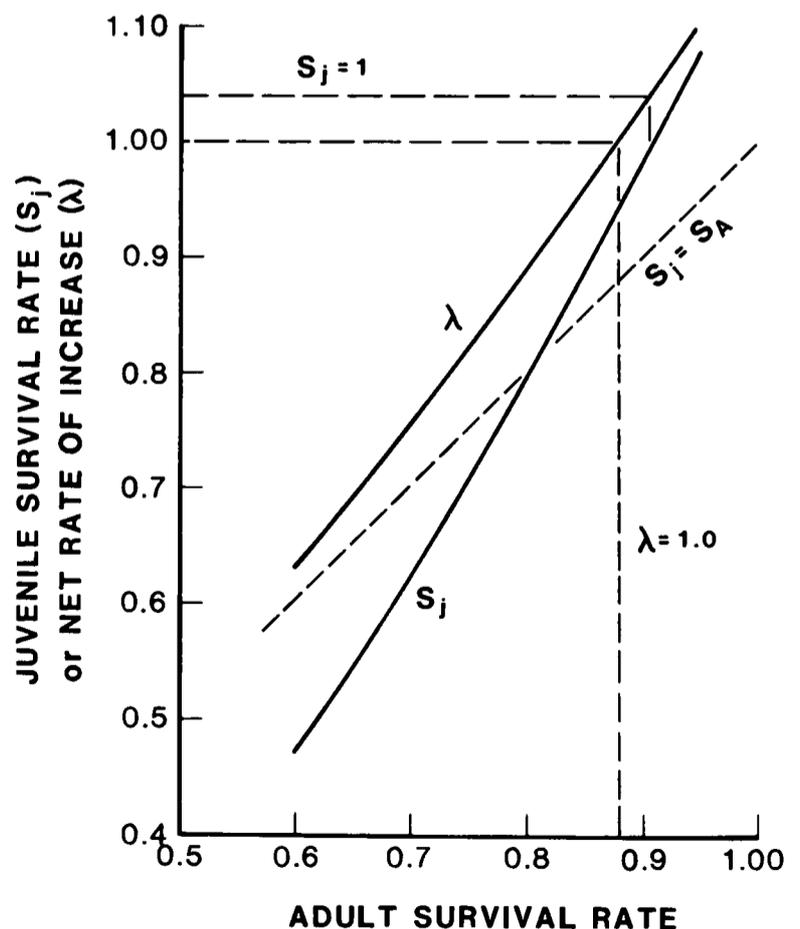


Fig. 1. Estimates of juvenile survival rate ( $S_j$ ) and net rate of increase ( $\lambda$ ) plotted as a function of adult survival rate ( $S_A$ ) for the northern-whitebelly-spinner population of *Stenella longirostris*.

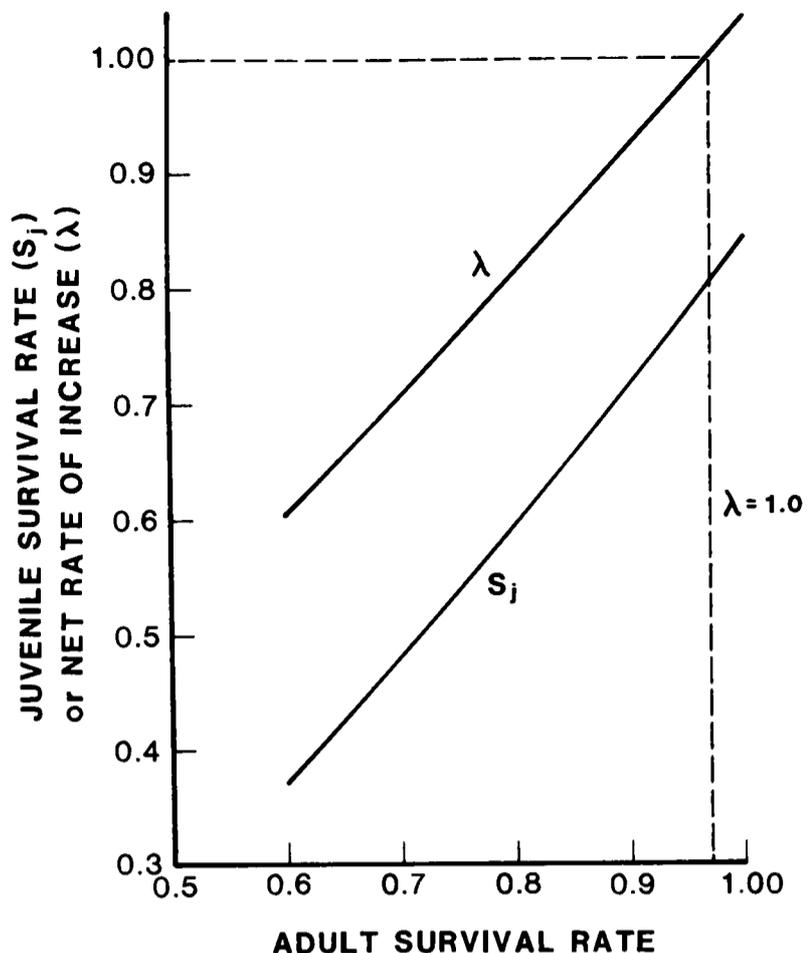


Fig. 2. Estimates of juvenile survival rate ( $S_j$ ) and net rate of increase ( $\lambda$ ) plotted as a function of adult survival rate ( $S_A$ ) for the northern-offshore-spotted population of *Stenella attenuata*.

Table 2

Estimates of juvenile survival rate ( $S_j$ ) and the net rate of increase ( $\lambda$ ) as a function of adult survival rate ( $S_A$ ) for the northern offshore spotted dolphin (*Stenella attenuata*) based on the parameter values in Table 1

$S_A$	$S_j$	$\lambda$
0.60	0.368	0.603
0.70	0.478	0.708
0.80	0.594	0.815
0.90	0.715	0.924
0.95	0.777	0.980

( $S_A = 0.88$  and  $S_j = 0.94$ ), since, from a management perspective, this may be a critical point. In Fig. 2, the results for the northern-offshore-spotted population have been plotted to illustrate a different constraint on the estimates. In this case, the estimates are constrained by biological limits on adult survival rates, with a corresponding maximum possible value for  $S_j$  being 0.84 and for  $\lambda = 1.03$ .

Results for all three populations are presented in Tables 2–4. Note, as is the case for the eastern-spinner population (Table 3), that real-valued solutions may not exist for Equations 2 and 3, since the proportion mature ( $R$ ) considered as a function of  $S_j$  for a fixed value of  $S_A$  has a minimum which can be above the observed value under consideration. While the results in this table suggest that a wide range of adult and juvenile survival rates are consistent with the observed data (except for the eastern-spinner population), none of the tabled values yield non-negative growth rates if the two criteria given in the methods section are applied. Estimated growth rates equal to or greater than one are not possible for the survival rates less than one for the observed data

Table 3

Estimates of the juvenile survival rate ( $S_j$ ) and the net rate of increase ( $\lambda$ ) as a function of adult survival rate ( $S_A$ ) for the eastern spinner dolphin (*Stenella longirostris*) based on parameter values in Table 1

$S_A$	$S_j$	$\lambda$
0.40	0.399	0.473
0.50	0.771	0.727
0.60	*	*
0.70	*	*
0.80	*	*
0.90	*	*
0.95	*	*

\* No solution for the juvenile survival rate exists that will balance this version of the matrix for the combination of values for adult survival rates, fecundity rate and age of maturity.

Table 4

Estimates of juvenile survival rate ( $S_j$ ) and the net rate of increase ( $\lambda$ ) as a function of adult survival rate ( $S_A$ ) for the northern whitebelly spinner dolphin (*Stenella longirostris*) based on the parameter values in Table 1

$S_A$	$S_j$	$\lambda$
0.60	0.469	0.630
0.70	0.620	0.755
0.80	0.790	0.888
0.90	0.980	1.031
0.95	1.083	1.107

from the eastern-spinner population. For the northern-whitebelly-spinner population, growth rates greater than one are not possible unless juvenile survival rates exceed adult survival rates. For the northern-offshore-spotted population, net growth rates greater than one require that the survival rate for adults be extremely high ( $\sim 0.97$ ), especially considering that the model makes no provision for senescence. Thus, in a population in which adult survival is constant and equal to 0.97 and the age at attainment of maturity is 8, approximately 28% of the adult population would be over age 50.

## DISCUSSION

The method presented in this paper provides a way to estimate survival rates from minimal data. Although a number of restrictive assumptions about the shape of the age-specific survival and fecundity curves are made, there are a number of ways that the matrix  $\tilde{M}$  in equation 1 could be re-parameterized and still be solvable. Such re-parameterizations can be used to explore the sensitivity of a set of estimates to these assumptions. For example, for long-lived mammals, survival rates are usually considered to be increasing from birth to the age at attainment of maturity. To explore the effect of this type of survival curve, the constant juvenile survival rate in the matrix  $\tilde{M}$  could be replaced by an increasing function, so that the survival rate at any age between birth and the age of maturity was a function of the estimated survival rate at birth and an animal's present age. In the limit, the effect of this assumption can be examined by assuming that the only difference in juvenile and adult survival rates occurs during the first year of

life. In a similar manner, the effects of assuming constant adult survival and fecundity rates can be explored, as long as the matrix contains only two unknown parameters. Thus, by considering a number of parameterizations for the projection matrix, it would be possible to refine the range of survival rates which are consistent with an observed set of data. In Polacheck (1983), a number of these different parameterizations of the projection matrix for the dolphin example were considered, and the basic results were insensitive to the different matrices.

The effect of the assumption of a stable age distribution is harder to assess. However, the method depends on the assumption of a stable age distribution only in order to compare the observed proportion mature with the proportion mature in a stable age distribution. Since the observed proportion mature is obtained as an average across a number of age classes, this method should be less sensitive to stochastic variations around a stable age distribution and sampling errors than are methods which use the entire age distribution.

The results of the application of this method to the example presented in this paper are rather disturbing, as they suggest that the only estimates of survival rates consistent with the data and with a non-declining net rate of increase are either biologically impossible or unreasonable. The difficulty in obtaining both biologically reasonable estimates of survival rate and estimates of a net rate of growth greater than one are not the same for all three populations. The spinner populations are constrained by biological limits on juvenile survival, while the northern-offshore-spotted population is constrained by limits on adult survival.

As shown in Polacheck (1983), these two different constraints have different implications for the estimates of the input parameters. When the constraints are due to biological limits on juvenile survival rates (i.e. as for the spinner populations), one or more of the input parameters must be underestimated in order to obtain higher estimates of the net rate of growth. In contrast, when the results are constrained by an upper limit on adult survival rates (i.e. as in the northern-offshore-spotted population), one or more of the input parameters must be overestimated. Because the estimates of survival and net rate of increase respond in this manner to the input parameter, increases in the estimated ages at attainment of maturity for the spinner population and decreases in the estimated fecundity rate for the northern-offshore-spotted population would have the non-intuitive effect of increasing the estimated upper bound for the net rate of increase for these populations.

The net rates of increase derived from this method are inconsistent with current evaluations of the status of these stocks (Smith, 1983). Net rates of increase used in those evaluations ranged from 1.00 to 1.06, based in part on comparisons of gross reproductive rates. Moreover, a density-dependent response in the net rate of increase is assumed, so that the most exploited stock should have the highest net rate of increase. In contrast, the estimated net rate of increase in this paper only approaches 1.00 when the survival rates approach biologically unreasonable levels. In addition, the net rates of increase tend to be in an order the reverse of that to be expected under the concept of density-dependent response. Thus, the

eastern-spinner population, which has been the most exploited, has the lowest rates, while the northern-whitebelly-spinner population, which is less exploited, tends to have the highest (Tables 2-4; and see Perrin and Henderson, 1984). If the current evaluations of the status of these stocks are correct, then the results from this method would suggest that the reproductive estimates used here are inconsistent with each other.

Before utilizing the results from this method in any specific application, the sensitivity of the estimates to both the assumptions of the methods and to the value of the input parameters needs to be considered. General conclusions about the sensitivity of this method are not possible, because the method as used here generates a range of estimates consistent with biological constraints on survival rates. The upper limits of this range are a complex, non-linear function of the input parameters. Even if this method is used to generate a single set of survival estimates by specifying the net rate of increase, the estimates will still be a non-linear function of the input parameters. For a specific set of input parameters, the sensitivity of the results can be explored by calculating estimates for a range of values consistent with possible sampling error and biases. Inclusion of such sensitivity analyses for the dolphin examples was beyond the scope of this paper. The sensitivity of the results to the values of input parameters for these dolphin populations is discussed in Polacheck (1983), where it is suggested that potential, but unknown, sampling biases (particularly in the estimates of the proportion mature) are the most likely factor to be affecting the results presented here.

In conclusion, as shown in this paper, reproductive data can be used to provide estimates for the range of survival rates and net rates of increases that are biologically reasonable and consistent. The method is not only useful for the estimates that it generates but also as a test of the consistency of a set of reproductive estimates and as a check of any independent set of estimates of survival rates and net rates of increase.

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Appendix

DERIVATION OF EQUATIONS 2 AND 3

For a stable age distribution:

$$N_i(t+1) = \lambda N_i(t) \quad (4)$$

where  $N_i(t)$  = the number of individuals of age class  $i$  alive at time  $t$  and  $\lambda$  = the net rate of increase. Also from the projection matrix  $\tilde{M}$

$$N_1(t+1) = N_{m+1}(t) \cdot F_A \quad (5)$$

$$N_i(t+1) = N_{i-1}(t) \cdot S_{i-1} \quad \text{for } 1 < i \leq m \quad (6)$$

$$N_{m+1}(t+1) = N_{m+1}(t) \cdot S_A + N_m(t) S_m. \quad (7)$$

Note that  $N_{m+1}(t)$  equals the number of adults alive at time  $t$ . Equating Equations 4 and 6 yields

$$N_i(t) = (S_{i-1}/\lambda) N_{i-1}(t). \quad (8)$$

Beginning with age class 1, repeated applications of Equation 8 yield

$$N_i(t) = (S_j/\lambda)^{i-1} N_1(t) \quad \text{for } 1 \leq i \leq m \quad (9)$$

since  $S_i = S_j$  for  $i = 1$  to  $\tilde{m}$  and  $\lambda$  is a constant. Equating the right hand sides of Equations 4 (for  $i = 1$ ) and 5 yields

$$N_1(t) = N_{m+1}(t) F_A/\lambda. \quad (10)$$

Substituting Equation 10 in Equation 9 yields

$$N_i(t) = (S_j/\lambda)^{i-1} (F_A/\lambda) N_{m+1}(t) \quad \text{for } 1 \leq i \leq m. \quad (11)$$

Substituting the right hand side of Equation 11 in Equation 7 when  $i = m$  and then equating the right hand sides of Equations 4 and 7 yields:

$$N_{m+1}(t+1) = \lambda N_{m+1}(t) = N_{m+1}(t) \cdot S_A + (S_j/\lambda)^{m-1} (F_A/\lambda) S_j N_{m+1}(t). \quad (12)$$

Division of  $\lambda N_{m+1}(t)$  and rearranging yields Equation 2. Equation 3 is derived by noting that from Equations 11 and 12, the total population size at time  $t+1$  can be expressed as

$$\sum_{k=1}^{m+1} N_k(t+1) = \sum_{i=1}^{m+1} (S_j/\lambda)^{i-1} F_A N_{m+1}(t) + S_A N_{m+1}(t) \quad (13)$$

Division of the right hand side of Equation 12 by the right hand side of Equation 13 yields Equation 3.



# Estimating the Dolphin Population Size Yielding Maximum Net Production

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ABSTRACT

A method is presented for estimating maximum net productivity level by comparing gross reproductive rates in three populations at different proportions of original size.

INTRODUCTION

The population size at which the absolute rate of change of population size is largest (maximum net productivity level or MNPL) is interesting both theoretically and in applied population assessments (Holt and Talbot, 1978; Smith and Fowler, 1981). Some general hypotheses have been developed about the relationship of MNPL and equilibrium population sizes (e.g. Gilpin and Ayala, 1976; Fowler, 1981). Fowler tested the hypotheses that density-dependent changes in vital rates, and hence MNPL, occur at a large fraction of equilibrium population size for long-lived species. He concluded that MNPL occurs at population sizes greater than one half, and likely quite near, equilibrium population size.

Few direct estimates of MNPL are available for long-lived species, and virtually none are available for cetaceans. In this paper I describe a method of estimating MNPL for dolphins in the eastern tropical Pacific Ocean, using data on the history of exploitation and the observed vital rates of different but related populations. An example is given using gross reproductive rates for three populations of spinner dolphin (*Stenella longirostris*).

MATERIALS AND METHODS

Dolphins of several species have been killed incidentally to tuna fishing in the eastern tropical Pacific tuna purse seine fishery since the late 1950s. The status of three populations of the spinner dolphin, *S. longirostris*, is described in Smith (1979; 1983). These three populations have been subjected to this incidental mortality for different lengths of time; one population, the eastern spinner dolphin, has been involved since 1959, while two other populations, the northern and southern whitebelly spinner dolphins, have been involved since approximately 1969 and 1973, respectively.

Estimates of the numbers of spinner dolphins killed in this fishery have been made as the product of the mean number of dolphins killed per net set observed aboard fishing vessels and the numbers of net sets made each year. Estimates from Smith (1979) are shown in Fig. 1 for each population. The numbers killed were very high in the 1960s and decreased markedly in the 1970s.

Estimates of the sizes of the three populations in 1979 (Table 1) were made from aerial and research-vessel dolphin-sighting survey data (Holt and Powers, 1982). Estimates of the gross reproductive rates (Table 1) of these three populations were made from data from samples of dolphins killed in the fishery (Perrin, Holts and Miller, 1977; Smith, 1979). The more heavily exploited eastern and whitebelly spinner dolphin populations have

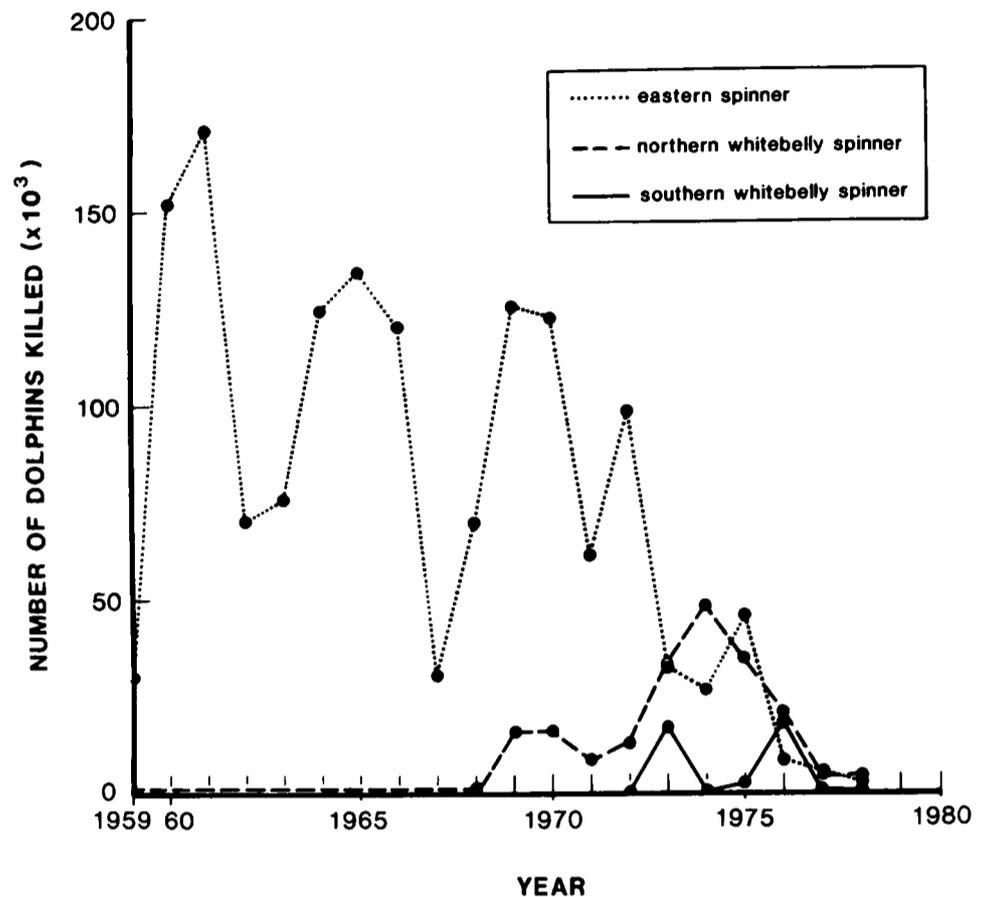


Fig. 1. Estimated numbers of spinner dolphins (*Stenella longirostris*) killed from three populations, from 1959 to 1978, incidental to yellowfin tuna purse seine fishing in the eastern tropical Pacific, from Smith (1979).

Table 1

Estimates of population size in 1979, from Holt and Powers (1982), and average reproductive rate from 1973–1978, from Smith (1979), for three populations of spinner dolphin (*Stenella longirostris*) in the eastern tropical Pacific

Spinner population	Population size (× 1,000)	Gross reproductive rate
Eastern	305	0.098
Northern whitebelly	401	0.088
Southern whitebelly	223	0.067

higher estimated reproductive rates. However, alternate methods of estimating these rates yield different results, and there is considerable uncertainty as to the appropriate estimates (Smith, 1979; Perrin and Reilly, 1984). The values used were selected to illustrate the method of estimating MNPL being described.

The estimates of dolphins killed (Fig. 1), 1979 population size (Table 1), and gross reproductive rates

(Table 1) can be used to estimate successive population sizes as

$$N_{t+1} = N_t + (\gamma - \mu)N_t - K_t = N_t(1 + \rho) - K_t, \quad (1)$$

where  $N$  = population size, in numbers;  $t$  = year;  $\gamma$  = gross reproductive rate;  $\mu$  = natural mortality rate;  $K$  = number of dolphins killed by fishery;  $\rho = \gamma - \mu$  = net recruitment rate.

In this model recruitment and natural mortality occur simultaneously, with rates applying to the whole population, not just the reproductive portion, at the beginning of the time interval. The catch is assumed to be taken after recruitment and natural mortality have occurred. This model applies only approximately to the incidental killing of dolphins in the eastern tropical Pacific in that recruitment and the incidental mortality occur simultaneously; similarly, the model does not account for age-structure changes which might affect the proportion mature. However, for this example these simplifying assumptions will suffice (Smith and Polacheck, 1979).

Solving equation 1 for the population size in previous years,

$$\hat{N}_t = \frac{N_0}{\prod_{i=1}^t (1 + \rho_i)} + \sum_{j=1}^t \frac{K_j}{\prod_{i=1}^j (1 + \rho_i)}, \quad (2)$$

where  $N_0$  is the population size in 1979,  $N_t$  denotes the to-be-estimated population size,  $t$  years earlier, and  $\rho_i$  denotes the net recruitment rate in the  $i$ th year prior to 1979. The properties of this estimate are explored in Smith and Polacheck (1979).

Values of the reproductive rate for each year can be obtained by assuming that the gross reproductive rate is a function of population size,

$$\rho(N) = \gamma(N) - \mu, \quad (3)$$

where  $\rho(N)$  = net recruitment rate as a function of population size  $N$ ,  $\gamma(N)$  = gross reproductive rate.

A suitable model for  $\gamma(N)$  is given by Allen (1976),

$$\gamma(N) = (\gamma_0 - \gamma_1) \left( 1 - \left( \frac{N}{\phi} \right)^\zeta \right) + \gamma_1, \quad (4)$$

where  $\gamma_0$  = gross reproductive rate for  $N$  near zero;  $\gamma_1$  = gross reproductive rate at equilibrium population size  $\phi$ ,  $\zeta$  = shape parameter for changes in gross reproductive rate.

The shape of this relationship is shown in Fig. 2 for several values of the shape parameter  $\zeta$ .

An expression for the net recruitment rate as a function of population size is obtained by substituting  $\gamma(N)$  from equation 4 into equation 3,

$$\rho(N) = (\gamma_0 - \gamma_1) \left( 1 - \left( \frac{N}{\phi} \right)^\zeta \right) + \gamma_1 - \mu \quad (5)$$

The net recruitment rate must be zero when  $N = \phi$ , implying that  $\gamma_1 = \mu$ . That is, the gross reproductive rate at the equilibrium population size is the same as the natural mortality rate.

An expression for historical population sizes as a function of several estimated parameters and four unknown parameters is obtained by substituting  $\rho(N)$

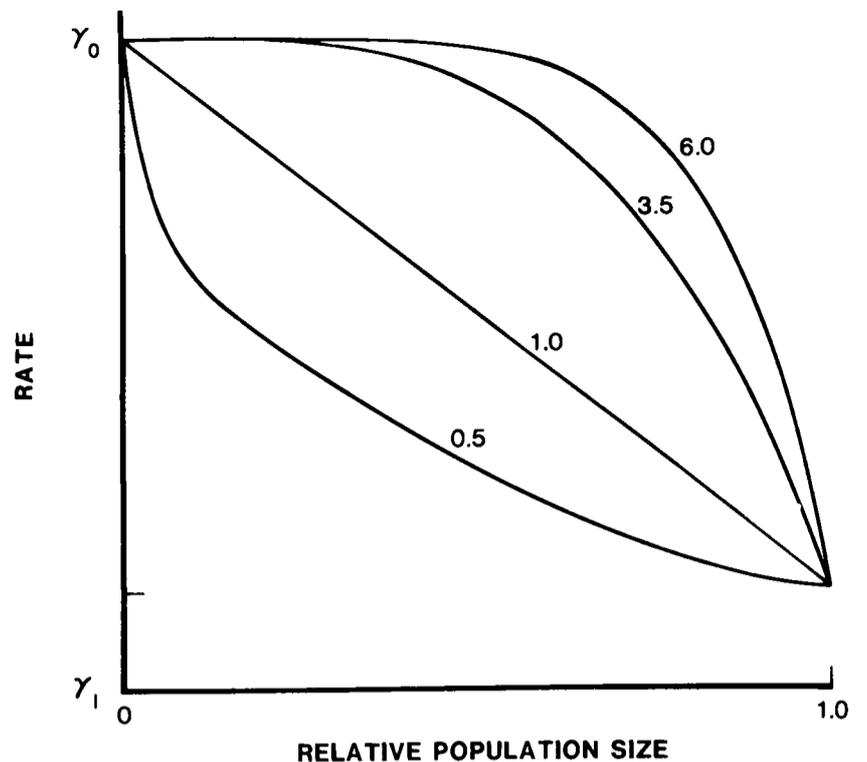


Fig. 2. The gross reproduction rate  $\gamma$  in equation 4 as a function of population size, relative to equilibrium population size ( $N/\phi$ ), for values of the shape parameter  $\zeta = 0.5, 1.0, 3.5, \text{ and } 6.0$ .

from equation 5, noting  $\gamma_1 = \mu$ , into equation 2. The unknown parameters are  $\gamma_0$ ,  $\gamma_1$ ,  $\zeta$  and  $\phi$ .

$$\hat{N}_t(\gamma_0, \gamma_1, \zeta, \phi) = \frac{N_0}{\prod_{i=1}^t \left( 1 + (\gamma_0 - \gamma_1) \left( 1 - \left( \frac{N_i}{\phi} \right)^\zeta \right) \right)} + \sum_{j=1}^t \frac{K_j}{\prod_{i=1}^j \left( 1 + (\gamma_0 - \gamma_1) \left( 1 - \left( \frac{N_i}{\phi} \right)^\zeta \right) \right)} \quad (6)$$

The equilibrium population size  $\phi$  in equation 6 can be estimated from equation 6 itself, by taking  $t$  to be the year exploitation began for each population. That is,

$$\hat{\phi} = N_t(\gamma_0, \gamma_1, \zeta, \hat{\phi}), \quad (7)$$

where  $t$  is sufficiently large, for given values of  $\gamma_0$ ,  $\gamma_1$ , and  $\zeta$ . This equation must be solved iteratively.

Values for the remaining three unknown parameters in equation 6,  $\gamma_0$ ,  $\gamma_1$ , and  $\zeta$ , can be obtained by minimizing the differences between estimates of gross reproductive rates for the three populations (Table 1) and the modeled values of gross reproductive rate from equation 4. For convenience, the sum of squares of differences can be minimized,

$$\sum_{i=1}^3 \left( \hat{G}_i - (\gamma_0 - \gamma_1) \left( 1 - \left( \frac{N_{0i}}{\hat{\phi}_i} \right)^\zeta \right) \right)^2, \quad (8)$$

where  $i (= 1, 2, 3)$  denotes the population,  $G_i$  denotes the observed gross reproductive rate for the  $i$ th population, and  $\hat{\phi}_i$  is obtained from equation 7 for each of the three populations.

Minimization of equation 8 involves evaluating the sum of squares for all possible values of  $\gamma_0$ ,  $\gamma_1$  and  $\zeta$ . For each population for each set of values of  $\gamma_0$ ,  $\gamma_1$  and  $\zeta$ , equation (7) must be solved, iteratively as noted above. Due to the complexity of the equations and the illustrative nature of the calculations, the values of  $\gamma_0$ ,  $\gamma_1$  and  $\zeta$  yielding a minimum value for equation (8) were

determined by direct examination of the sum of squares surface. Thus the solution obtained is not exact, and no variances have been calculated.

The value of  $\zeta$  which minimizes equation 8 implies a value of MNPL. This value can be determined by substituting  $\rho(N)$  from equation 5 into equation 1, and solving for the population size with maximum rate of change (Allen, 1976), yielding

$$\psi = \phi \left( \frac{1}{\zeta + 1} \right)^{\frac{1}{\zeta}} \quad (9)$$

where  $\psi$  denote the maximum net productivity level (MNPL) in numbers of animals.

### RESULTS

Using estimates of the number of dolphins killed incidentally ( $K_j$ , Fig. 1), the 1979 population sizes (Table 1) and the gross reproduction rates ( $G_i$ , Table 1), the estimated values of the gross reproductive rates at population sizes near zero and near equilibrium ( $\gamma_0$  and  $\gamma_1$ , respectively) and the estimate of the shape parameter ( $\zeta$ ) are obtained from equations 6, 7 and 8 (Table 2). The

Table 2

Estimates of parameters obtained from minimizing the sum of squares of deviations of observed and predicted gross reproductive rates in equation 8, for spinner dolphins (*Stenella longirostris*) in the eastern tropical Pacific

$\gamma_0$	$\gamma_1$	$\zeta$	$\psi/\phi$
0.098	0.048	8.0	0.76

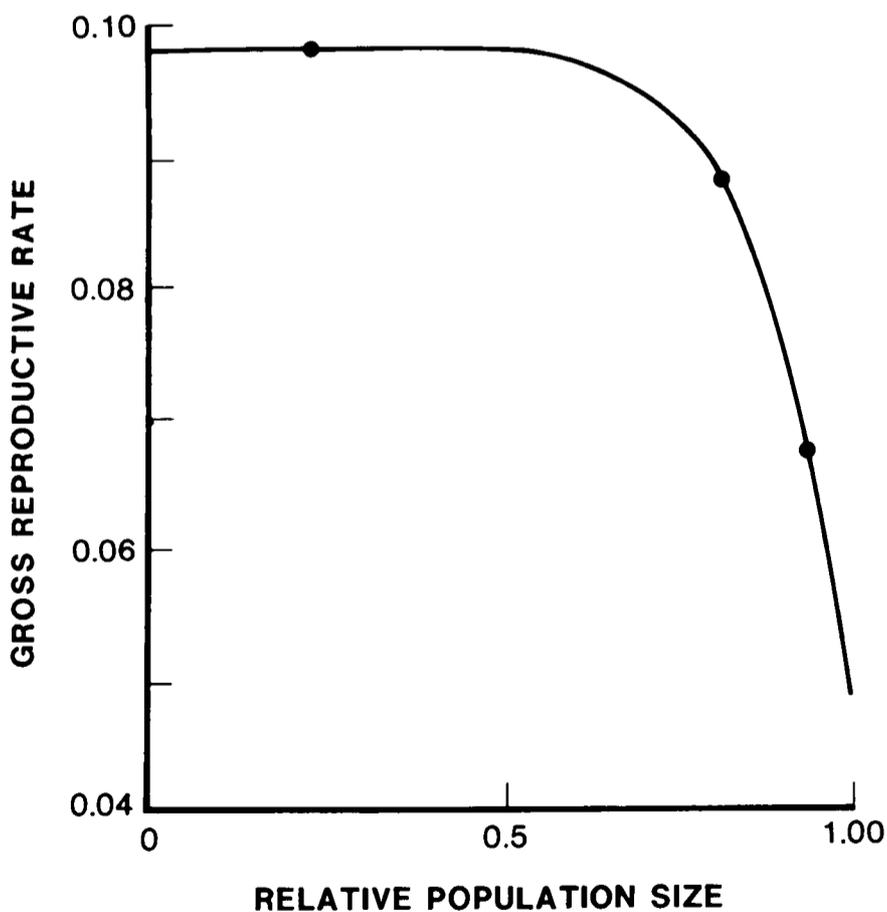


Fig. 3. Observed gross reproductive rates for three spinner dolphin populations versus estimated relative population size, and the estimated gross reproductive rate function from equation 4 obtained by minimizing equation 8.

fit of equation 4 to the observed estimates of gross reproductive rate is shown in Fig. 3. Although the deviations about the line are too small to be apparent in the graph, there is some lack of fit. The maximum net productivity level corresponding to  $\zeta = 8.0$ , as a fraction of the equilibrium population size,  $\psi/\phi$ , given in Table 2, is obtained from equation 9.

The estimated equilibrium population sizes,  $\hat{\phi}$  in equation 6, corresponding to the parameter estimates in Table 2, are 1,330, 490, and 240 thousand dolphins, for eastern spinner, northern whitebelly spinner, and southern whitebelly spinner dolphins, respectively (Table 3). The corresponding maximum net production (MNP =  $\psi\rho(\psi)$ ) are 34, 13 and 6 thousand, and are obtained from population sizes of 1,010, 370, and 180 thousand, respectively (Table 3).

Table 3

Estimates of equilibrium population size,  $\phi$ , for three spinner dolphin populations in the eastern tropical Pacific, with estimates of the maximum net productivity (MNP), and the population size producing MNP (MNPL)

Population	$\hat{\phi}$ ( $\times 1,000$ )	MNP ( $\times 1,000$ )	MNPL ( $\times 1,000$ )
Eastern	1,330	34	1,010
Northern whitebelly	490	13	370
Southern whitebelly	240	6	180

### DISCUSSION

The method of estimating MNPL which I describe has possible application to the dolphin populations in the eastern tropical Pacific. The example calculations given for spinner dolphins suggest that MNPL may occur at a relatively high fraction of equilibrium abundance. However, three uncertainties need further attention.

First, the estimates of gross reproductive rate for eastern tropical Pacific dolphin populations are crude because of possible sample biases and analytical biases owing to the methods employed (Smith, 1983; Perrin and Reilly, 1984). The present results must therefore be considered preliminary pending further investigation of the estimates of gross reproductive rate.

A second uncertainty is that only three data points for gross reproductive rate have been used in equation 8 to estimate three parameters. Additional estimates of gross reproductive rate are needed in equation 8; these could be obtained in two ways. The simplest is to assume that other dolphin species have similar reproductive and natural mortality rates at equilibrium and at near-zero population sizes, and similar MNPL values. For instance, there are two populations of spotted dolphin where data are available. A more complex approach to obtaining additional estimates of gross reproductive rate is to use the estimates for each year, rather than the single average over several years, for each population. This approach would require a more complex form for equation 8, where  $N_0$  would be replaced by the population size in the years corresponding to the available annual reproductive rate estimates. The calculations would become rather sensitive to possible time lags in density-dependent

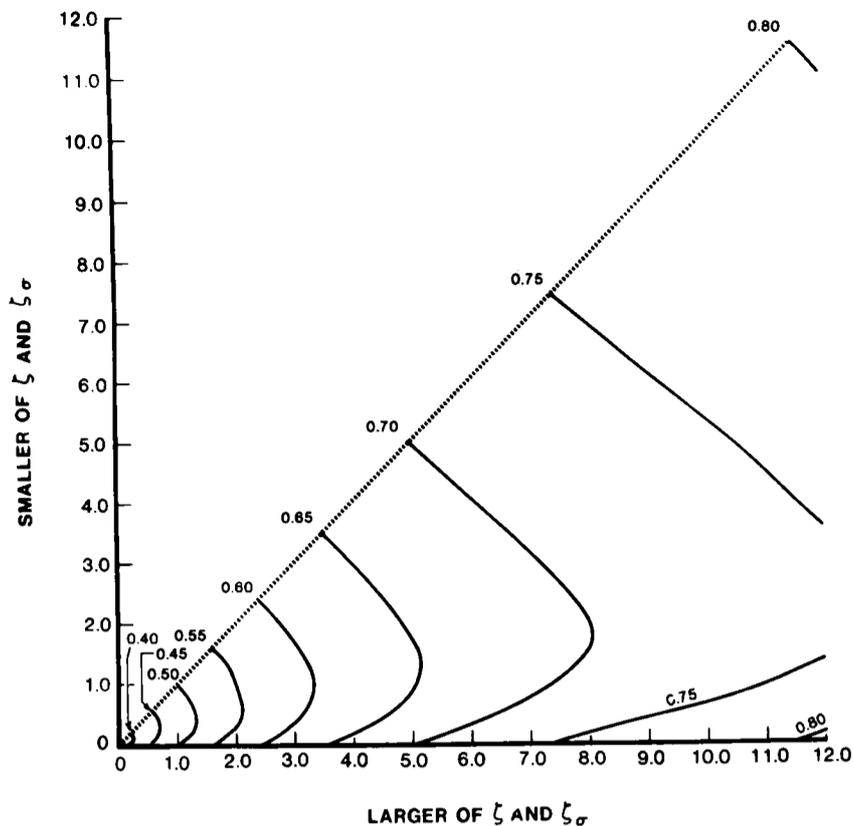


Fig. 4. Population size relative to equilibrium population size ( $N/\phi$ ) at which maximum net productivity is obtained (from equation 12) for ranges of values of both shape parameters  $\zeta$  and  $\zeta_\sigma$ .

response, but the problem of overparameterization would be minimized.

The third uncertainty in the above estimates of MNPL is that the natural mortality rate is assumed to be constant for all population sizes. This assumption can be explored by replacing  $\mu$  in equation 3 by one minus the function

$$\sigma(N) = (\sigma_0 - \sigma_1) \left(1 - \left(\frac{N}{\phi}\right)^{\zeta_\sigma}\right) + \sigma_1, \quad (10)$$

where  $\sigma_0$ ,  $\sigma_1$  and  $\zeta_\sigma$  are defined similarly to the corresponding symbols in equation 4. Thus equation 5 is replaced by

$$\rho(N) = (\gamma_0 - \gamma_1) \left(1 - \left(\frac{N}{\phi}\right)^\zeta\right) + (\sigma_0 - \sigma_1) \left(1 - \left(\frac{N}{\phi}\right)^{\zeta_\sigma}\right). \quad (11)$$

Substituting equation 11 for equation 5 in the above development yields expressions parallel to equations 6 and 8. For this model MNPL ( $\psi$ ) is obtained as the population size  $N$  which satisfies

$$\frac{\partial \rho(N)}{\partial N} = 0 = \zeta(\gamma_0 - \gamma_1) \left(\frac{N}{\phi}\right)^{\zeta-1} + \zeta_\sigma(\sigma_0 - \sigma_1) \left(\frac{N}{\phi}\right)^{\zeta_\sigma-1}. \quad (12)$$

This expression is parallel to the calculation used to obtain equation (9), but a similar closed form can not be obtained. The values of MNPL ( $\psi$ ) from equation 12, assuming  $\gamma_0 - \gamma_1 = \sigma_0 - \sigma_1$ , are given in Fig. 4, as a contour surface on  $\zeta$  and  $\zeta_\sigma$ . The results are symmetrical in these two parameters and only shown in the first half-quadrant. If  $\gamma_0 - \gamma_1 \neq \sigma_0 - \sigma_1$  this surface becomes non-symmetrical.

Values of MNPL for sections through the contour surface in Fig. 4 are shown in Fig. 5, for selected values of  $\zeta_\sigma$ . As  $\zeta$  increases along the abscissa, MNPL first decreases slightly and then increases steadily. MNPL is constrained to a narrowing range for all values of  $\zeta_\sigma$ , as  $\zeta$  increases. For instance, when  $\zeta = 8$  in Fig. 5, MNPL ranges from 0.70 to 0.76 when  $\zeta_\sigma$  ranges from 0.5 to 8.0.

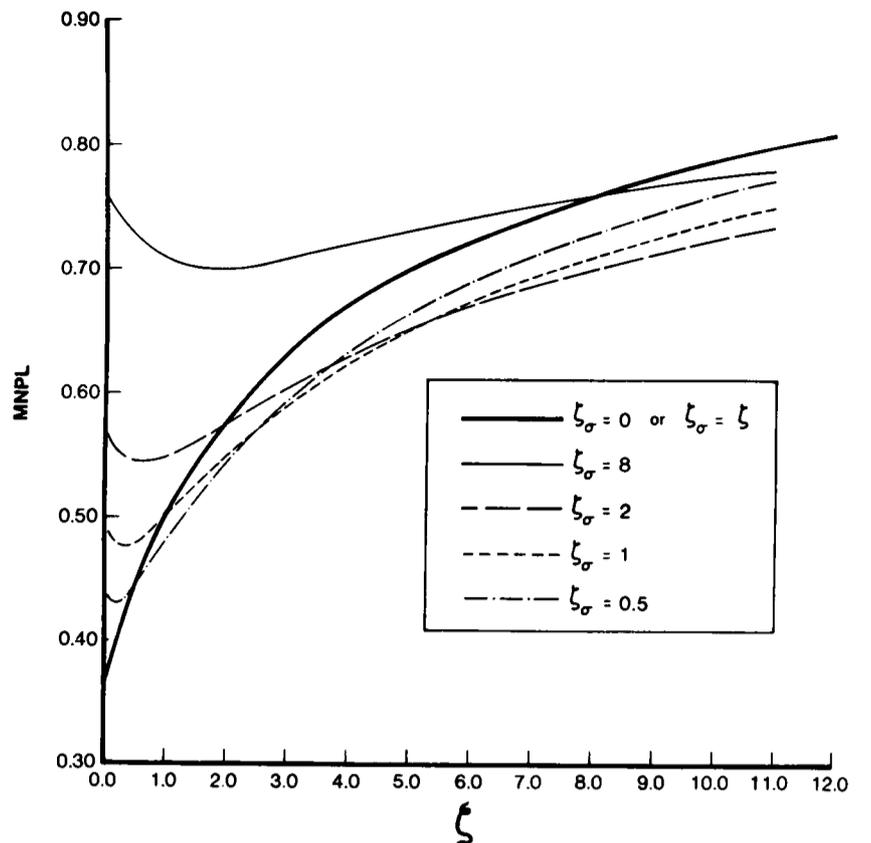


Fig. 5. Maximum net productivity levels (MNPL) versus the value of the shape parameter for changes in gross reproductive rate ( $\zeta$ ), for a series of values of the shape parameter for changes in survival rates ( $\zeta_\sigma$ ), showing the lack of sensitivity of MNPL to  $\zeta_\sigma$ , when  $\zeta$  is large.

Thus for populations with high MNP levels, the assumption that the natural mortality rate does not change with population size has relatively little effect on the MNPL estimate. Note, however, that estimates of the replacement yield are perhaps greatly affected.

The three uncertainties described suggest several directions which should be followed. Keeping these uncertainties in mind, however, the presently available data for spinner dolphins suggest a rather high value for MNPL, in agreement with Fowler (1981).

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# Reproductive Seasonality in Pelagic Dolphins (*Stenella* spp.): Implications for Measuring Rates

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## ABSTRACT

This paper examines the patterns of reproductive seasonality in two species of dolphin in the eastern tropical Pacific: *Stenella attenuata* and *S. longirostris*. These are the principal species used by tuna purse seiners in locating schools of yellowfin tuna in this area. Birthdate distributions are calculated from the lengths-at-capture of fetuses and calves killed in fishing operations, the dates of capture, and the estimated growth curves for these species. Although births were found to occur at all times of the year, distinct modes could be seen in the distributions. Geographic differences in patterns of seasonality could be distinguished on the basis of the strength of the observed modes, the number of modes, and their timing. The northern stock of *S. attenuata* has a diffuse bimodal pattern in annual reproduction with peaks in spring and autumn. The southern stock of this species has a strong unimodal pattern whose timing corresponds to the spring peak in the northern stock. The eastern spinner form of *S. longirostris* also has a single annual peak in reproduction, between March and June, with regional differences in the timing of this mode. The whitebelly spinner form of *S. longirostris* shows a bimodal pattern with peaks in spring and autumn. These seasonal patterns in reproduction can affect reproductive rate measurements by changing our concept of stock boundaries or by introducing biases due to time of sampling. If the mating season is short, this can also limit the rate at which females can be inseminated after an aborted pregnancy, calf death, or weaning.

## INTRODUCTION

This report examines the seasonal patterns of reproduction in pelagic dolphins of the eastern tropical Pacific. Four dolphin stocks are considered: the 'northern offshore' and 'southern offshore' forms of the spotted dolphin (*Stenella attenuata*) and the 'eastern' and 'northern whitebelly' forms of the spinner dolphin (*Stenella longirostris*) (see Perrin (1975) and Perrin, Sloan and Henderson (1979) for stock delineations). Stock boundaries for these species are given in Smith (1979); Figs 1, 2, and 3 show approximate ranges. A statistical method is presented for comparing distributions of birthdate, and this method is used to test geographic differences in birthdate distributions within the same species.

*S. attenuata* and *S. longirostris* are the principal species used by tuna purse-seiners in locating schools of yellowfin tuna. Historical kills of dolphins incidental to this fishery have been large, totaling several millions (Smith, 1979), which has prompted management efforts in recent years. This paper will also consider the implications of seasonal reproduction in measuring the reproductive rates of Cetacea. These implications may prove important in the management of eastern Pacific dolphin stocks.

Previous work on reproductive patterns of these dolphin stocks has shown two broad peaks in calving (one in spring and one in autumn) for spotted dolphins (Perrin, Coe and Zweifel, 1976) and a rather diffuse pattern of seasonality for eastern spinners (Perrin, Holts and Miller, 1977). Perrin *et al.* (1977) found one birth mode in late January of 1974 for eastern spinners, but noted that the timing of births appeared to vary from one area to another. Work on a different stock of *S. attenuata* off the coast of Japan indicated perhaps three peak periods of parturition (Kasuya, Miyazaki and Dawbin, 1974). Similarly Miyazaki (1977) interpreted data on a closely related species (*S. coeruleoalba*) as indicating three annual modes in births.

Of the small toothed whales, strong patterns of reproductive seasonality are most evident in the temperate and subarctic species. The common porpoise (*Phocoena phocoena*) in the North Atlantic (Fisher and Harrison, 1970), the common dolphin (*Delphinus delphis*) off California's coast (Harrison, Boice and Brownell, 1969), the white whale (*Delphinapterus leucas*) off Baffin Island (Brodie, 1971) and the white-sided dolphin (*Lagenorhynchus obliquidens*) off California (Harrison *et al.*, 1969) all show a single period of parturition during the year. Tropical species such as *S. attenuata* and *S. longirostris* and more cosmopolitan species such as *Tursiops truncatus* (Harrison and Ridgway, 1971) may have multiple breeding seasons or diffuse patterns of reproductive seasonality.

## MATERIALS AND METHODS

The data upon which this report is based were gathered between 1968 and 1978 by the National Marine Fisheries Service (NMFS) scientific technicians aboard tuna purse-seiners. The sample represents dolphins that were killed as a result of the tuna purse-seining operations. Seining for yellowfin tuna was seasonal during these years, both in its intensity and its areas of operation. Typically, the US fleet concentrated its effort near the coastline for the first several months of the year. Later in the year, fishing intensity slackened and the fleet's efforts were concentrated more offshore.

Extensive life history data were gathered by the NMFS technicians. The items of principal interest in this report were the date, lengths, and collection localities of young dolphins and fetuses that died in the purse seines.

Patterns of reproductive seasonality are most easily summarized by the frequency distribution of birthdates. Two methods were used to estimate birthdates, one from prenatal dolphins and the other from postnatal. These methods are similar to those used by Kasuya *et al.* (1974) and Perrin *et al.* (1976).

Table 1

Postnatal and fetal growth rates used in the projection of birthdate distributions. Postnatal growth parameters are as defined by Perrin *et al.* (1976)

Population	Length at birth (cm)	Postnatal growth parameters		Fetal growth rate (cm/month)	Reference
		$a$	$\alpha$		
Offshore spotted dolphin	82	0.963	1.414	8.28	Perrin <i>et al.</i> (1976)
Eastern spinner dolphin	77	0.995	1.365	8.37	Perrin <i>et al.</i> (1977)
Whitebelly spinner dolphin	77	0.950	1.290	8.37	Perrin and Henderson (1979)

The first method involves the forward projection of birthdates from fetal lengths and dates of capture. Fetal growth parameters were taken from Perrin *et al.* (1976, 1977) (Table 1). The fetal growth rate of the whitebelly spinner dolphin was assumed to be the same as its conspecific, the eastern spinner; likewise the fetal growth rate of the southern offshore spotted dolphin was taken to be the same as that of the northern offshore spotted dolphin. Only fetuses greater than 10 cm long were used, and growth rates were assumed to be constant. If gestation were significantly less than 1 year, seasonality in sampling could affect the birthdate distributions projected by this method. Since gestation is estimated to be 11.5 and 10.6 months respectively for *S. attenuata* and *S. longirostris* (Perrin *et al.*, 1976, 1977), this effect should be insignificant. No correction was made for the time of sampling.

The second method involves the back projection of the birthdates of postnatal dolphins from their lengths and dates of capture. Postnatal growth rates were taken from Perrin *et al.* (1976, 1977) and Perrin and Henderson (1979). Growth was assumed to follow the Laird/Gompertz model (Laird, 1966).

$$L(t) = L_0 \cdot \exp[(a/\alpha) \cdot (1 - \exp(-\alpha \cdot t))].$$

The values used for the parameters above are given in Table 1. These values correspond to the hypothesized 2.0, 1.5, and 1.36 dentinal growth layers in the first year respectively for spotted dolphins (Perrin *et al.*, 1976), eastern spinner dolphins (Perrin *et al.*, 1977), and whitebelly spinner dolphins (Perrin and Henderson, 1979).

The back-projection method was only applied to animals estimated to be less than 1 year old (less than 132 cm for *S. longirostris* and 138 cm for *S. attenuata*). In practice, this method is only useful for young animals, for which growth is rapid relative to individual variation in growth rate. The 1-year age interval was chosen to minimize the potential bias from seasonality in sampling.

Statistical methods used for comparing birthdate distributions are a variation of the Kolmogorov/Smirnov (K/S) one- and two-sample tests. These are non-parametric tests for goodness of fit based on cumulative distributions. Birthdate distributions are, however, circular (Fig. 4), and therefore the results of a conventional K/S test could depend on which month is taken as the beginning of the distribution. The modifications made by Kuiper (1960) and discussed by Batschelet (1965) allow the unambiguous use of these tests on circular distributions. The statistic used for the one sample test is the sum of the maximum positive and negative deviations of the observed cumulative distribu-

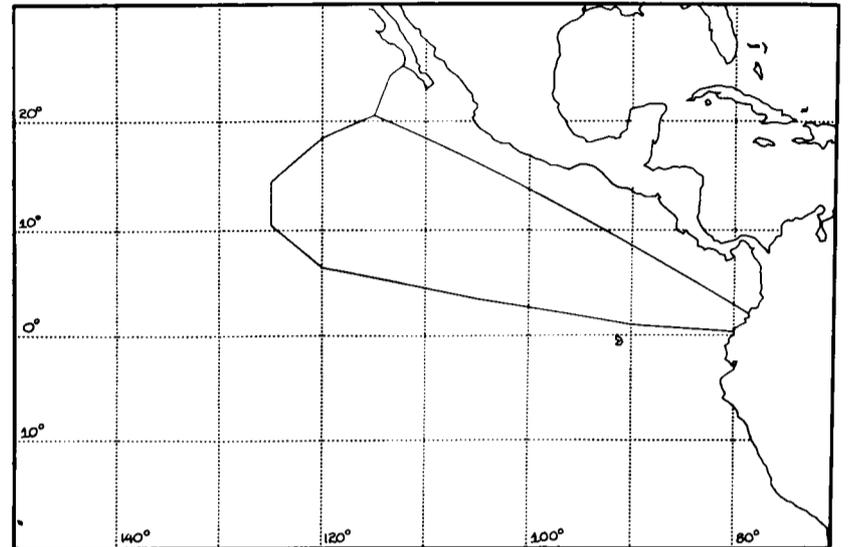


Fig. 1. Geographic distribution of eastern spinner dolphins (*Stenella longirostris*) in the eastern tropical Pacific. Inshore/offshore regions are defined by diagonal line.

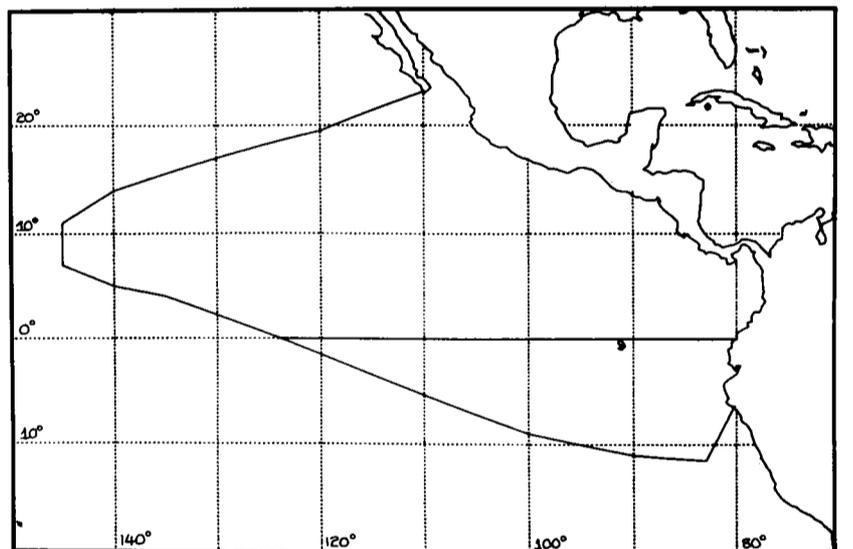


Fig. 2. Geographic distribution of offshore spotted dolphins (*Stenella attenuata*) in the eastern tropical Pacific. Northern and southern regions are defined by the equator.

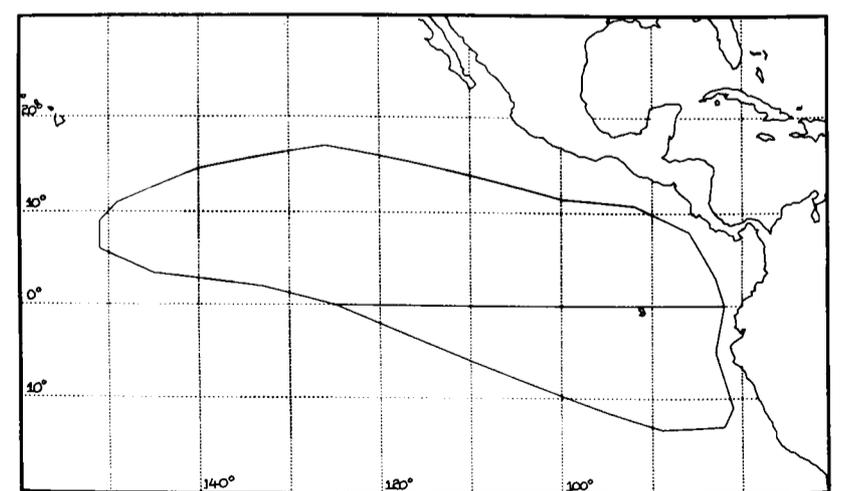


Fig. 3. Geographic distribution of whitebelly spinner dolphins (*Stenella longirostris*) in the eastern tropical Pacific. Northern and southern regions are defined by the equator.

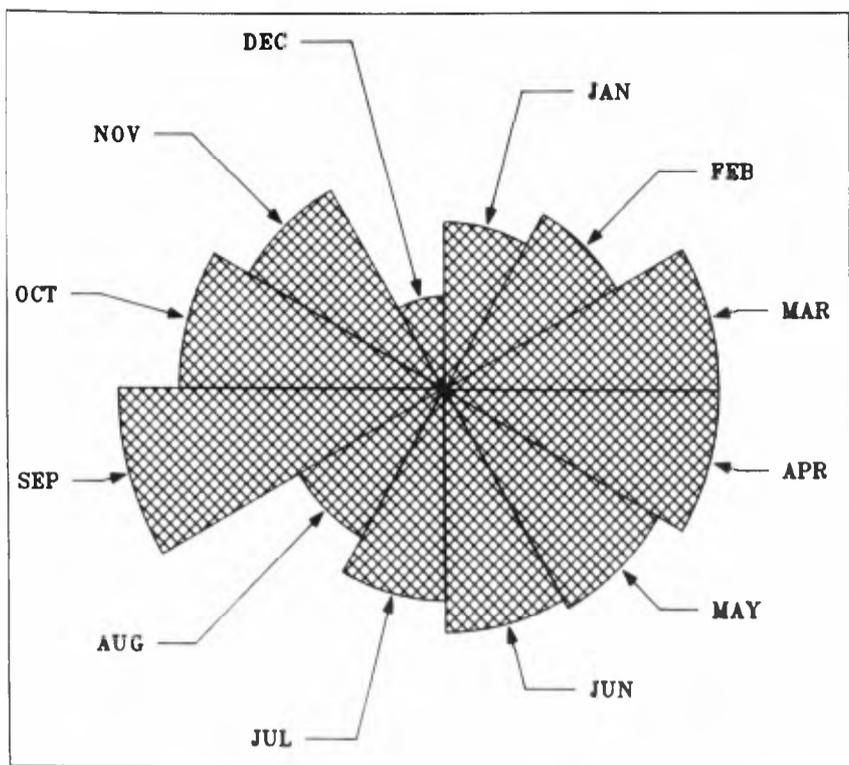
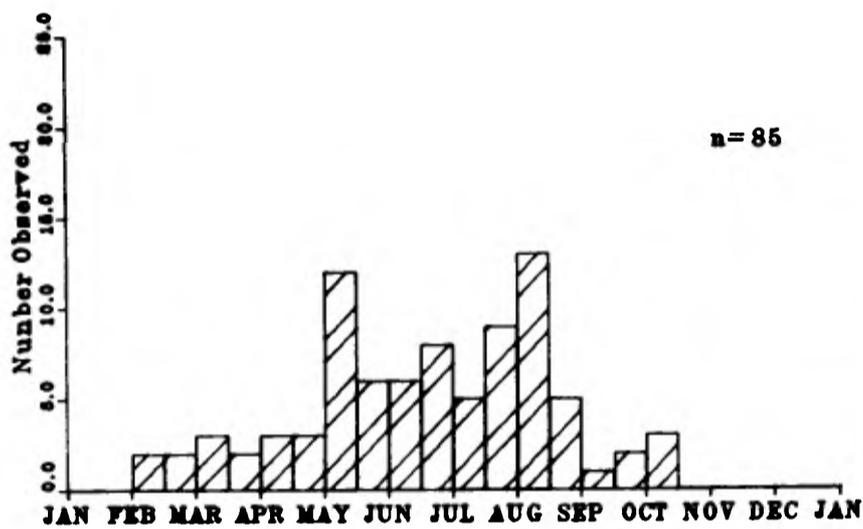


Fig. 4. Birthdate distribution of northern offshore spotted dolphins (*Stenella attenuata*) projected from lengths of fetuses. Length of each ray is proportional to the number of births expected in the given month.

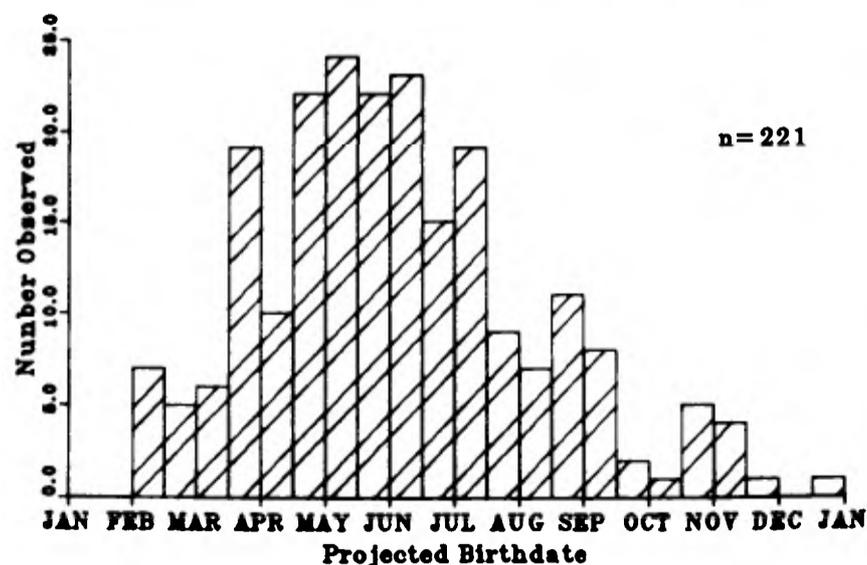
tion from the expected cumulative distribution. Similarly, the statistic for the two sample test is the sum of the maximum positive and negative deviations of one cumulative distribution from the other. The critical values for the two-sample version of this test have not been tabulated for unequal sample sizes. For this reason, statistical comparisons were made only when sample sizes were roughly equal, and in such cases, the smaller sample size was used, which makes the test conservative.

To examine geographic variability in birthdate distributions, where sample size permitted, the samples were stratified by geographical areas. Because Perrin *et al.* (1977) noted an inshore/offshore difference in seasonality for the eastern spinner dolphin, this stock was divided into inshore and offshore ranges by a line drawn roughly parallel to the coastline (Fig. 1). To facilitate statistical comparisons, the line was drawn so as to provide approximately equal sample sizes. The offshore spotted dolphins were divided into a northern and a southern stock by a line drawn along the equator (Fig. 2). In order to better understand the latitudinal variability of reproductive seasonality in this species, the sample of northern spotted dolphins was further divided into those caught between the equator and 5° N and those caught north of 5° N. Due to small sample sizes, geographical stratification of the northern whitebelly spinner range (Fig. 3) was not attempted. Also the southern whitebelly spinner was not considered due to its small sample size.

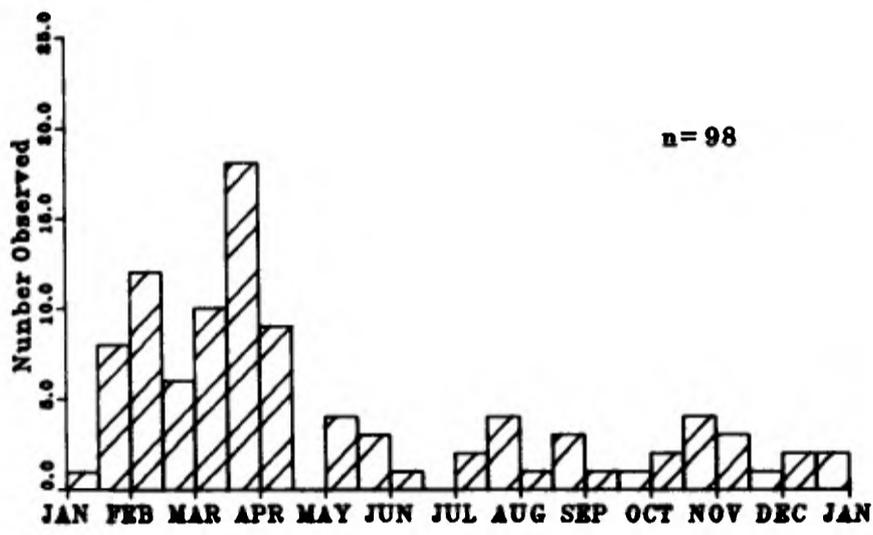
**Inshore Fetuses**



**Inshore Yearlings**



**Offshore Fetuses**



**Offshore Yearlings**

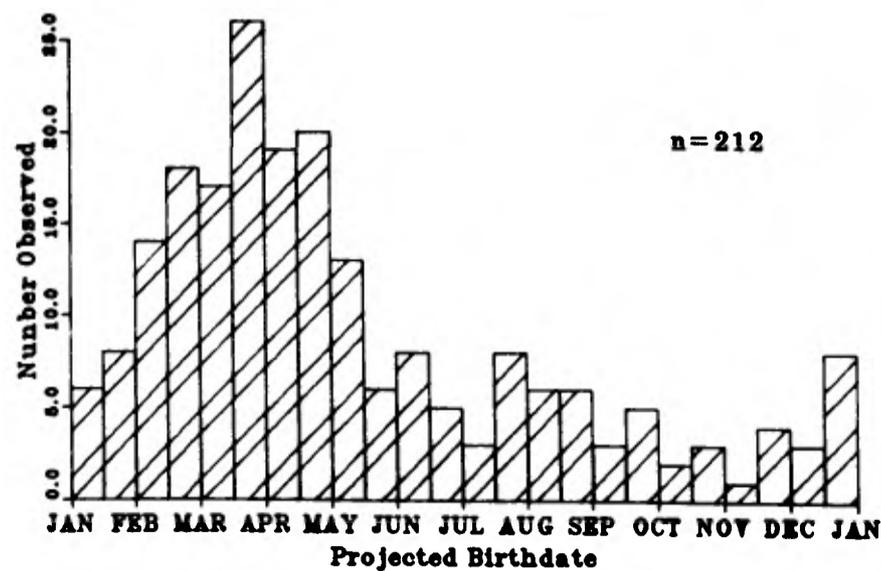


Fig. 5. Birthdate distributions of eastern spinner dolphins (*Stenella longirostris*) projected from lengths of fetuses (top) and calves (bottom). Inshore/offshore geographic stratification is as shown in Fig. 1.

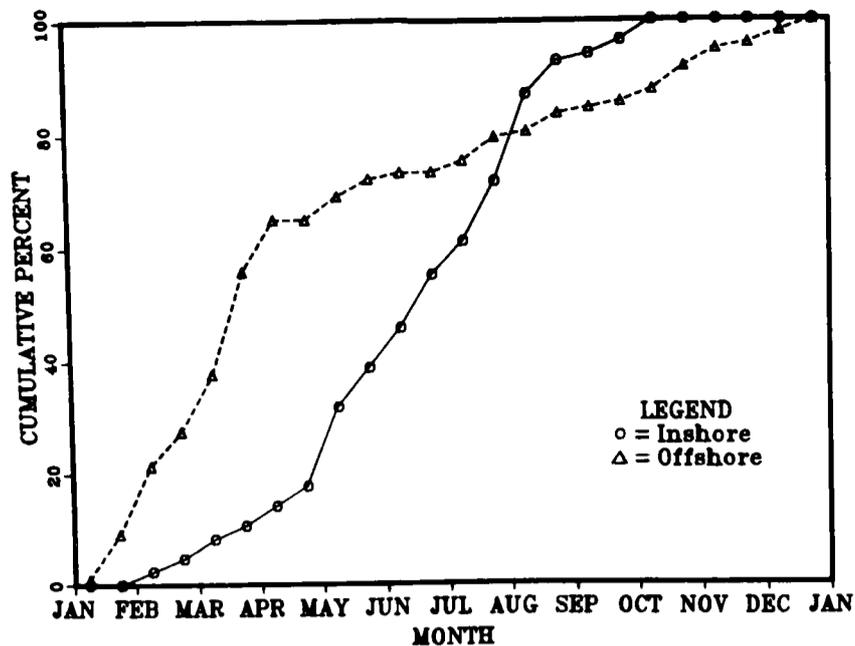


Fig. 6. Cumulative birthdate distributions of inshore and offshore groups of eastern spinner dolphins (*Stenella longirostris*) projected from lengths of fetuses. Geographic stratification is as shown in Fig. 1.

To avoid possible confounding of data for the 'offshore' and 'coastal' forms of the spotted dolphin (Perrin, 1975), only those individuals classified as belonging to the 'offshore' group and found more than 100 km from the coastline were included.

## RESULTS

### Eastern spinner dolphin

A single, strong peak can be seen in the birthdate distributions projected for the eastern spinner dolphin (Fig. 5). Although similar peaks are evident for both inshore and offshore areas, a regional difference can be noted in the timing of these peaks. For both the forward and back projection methods, the peak calving period occurs earlier in the year for the more offshore group.

The regional differences in seasonality were compared with the two sample K/S test described above (illustrated in Fig. 6 for the projection from fetal lengths). For both projection methods the differences were statistically significant ( $P < 0.01$ ). Although differential growth rates in the two regions could contribute to apparent differences in birthdate distributions, this explanation is unlikely because the forward and back projection methods corroborate each other's results. For growth rate variations to bias the result in the same way for both of the projection methods, the fetal and postnatal growth rates would have to differ in a reciprocal manner. A regional difference in reproductive seasonality is thus indicated for the eastern spinner dolphin.

### Whitebelly spinner dolphin

The birthdate distributions for the whitebelly spinner appear to be bimodal when projected from fetal lengths (Fig. 7). The modes are approximately 6 months apart. The birthdate distribution obtained from the lengths of postnatal dolphins shows no evidence of this bimodal pattern (Fig. 7). The two sample K/S test indicates that the two estimated birthdate distributions are significantly different ( $P < 0.05$ ). If a one sample K/S test is applied, the results indicate that the birthdate distribution

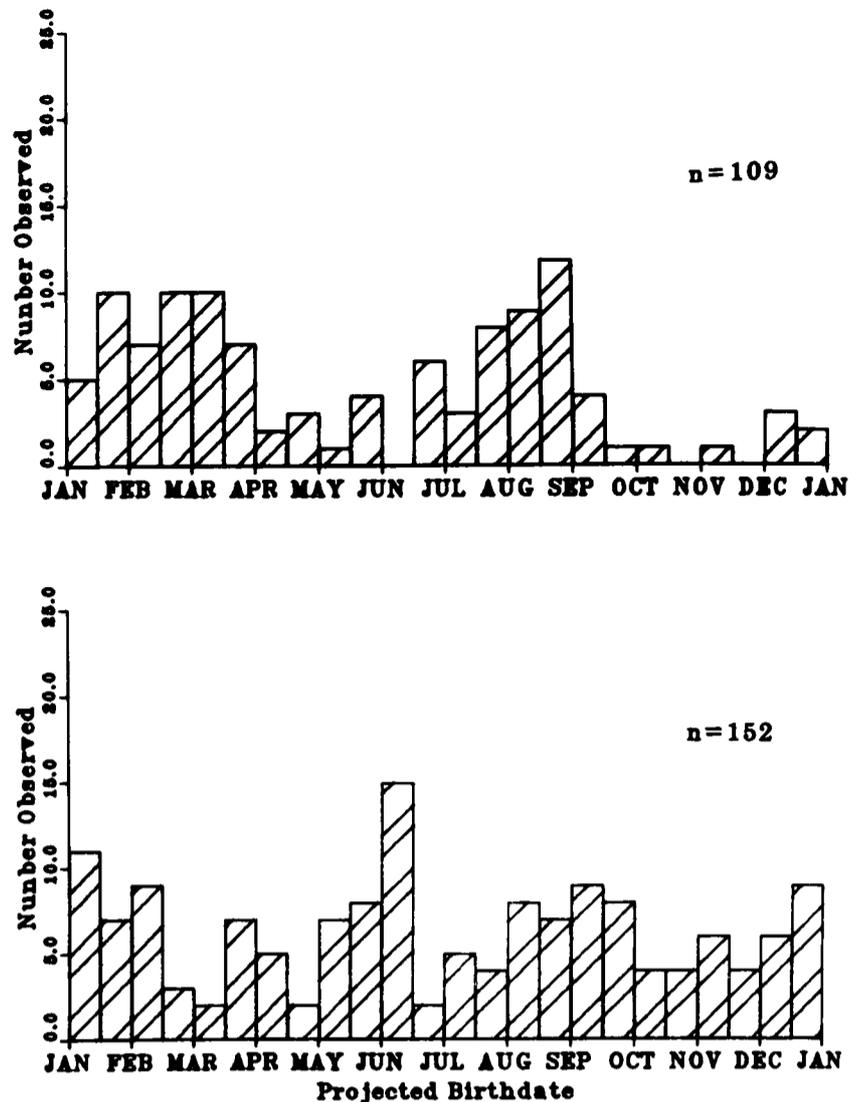


Fig. 7. Birthdate distributions of northern whitebelly spinner dolphins (*Stenella longirostris*) projected from lengths of fetuses (top) and calves (bottom). The equator was taken as the lower limit of their geographic distribution.

projected from fetal lengths is significantly different from a uniform birthdate distribution ( $P < 0.01$ ), but that projected from calf lengths is not ( $P < 0.1$ ).

### Northern offshore spotted dolphin

The birthdate distribution derived from the northern offshore spotted dolphin (Fig. 8) showed a rather even distribution of reproduction throughout the year. Using a one sample K/S test, the observed distributions can be shown to be significantly different from a uniform distribution for both methods of birthdate projection ( $P < 0.01$ , illustrated in Fig. 9 for projections from fetal lengths). Although the apparent seasonality is not strong, there is a tendency for more births to occur in spring and autumn than in other times of the year. This pattern of seasonality may not be constant from year to year. Perrin *et al.* (1976) suggested that annual changes in the season of peak reproduction might be occurring, and additional evidence for this was presented by Barlow (1979).<sup>1</sup>

### Southern offshore spotted dolphin

The distribution of birthdates from the southern stock of the offshore spotted dolphin (Fig. 8) is very different from that of the northern stock of this species. For the southern

<sup>1</sup> Barlow, J. 1979. Reproductive seasonality in pelagic dolphins of the eastern tropical Pacific. NMFS, Southwest Fisheries Center, Status of the Porpoise Stocks Workshop Doc. 26, La Jolla, California, 27-31 August 22 pp.

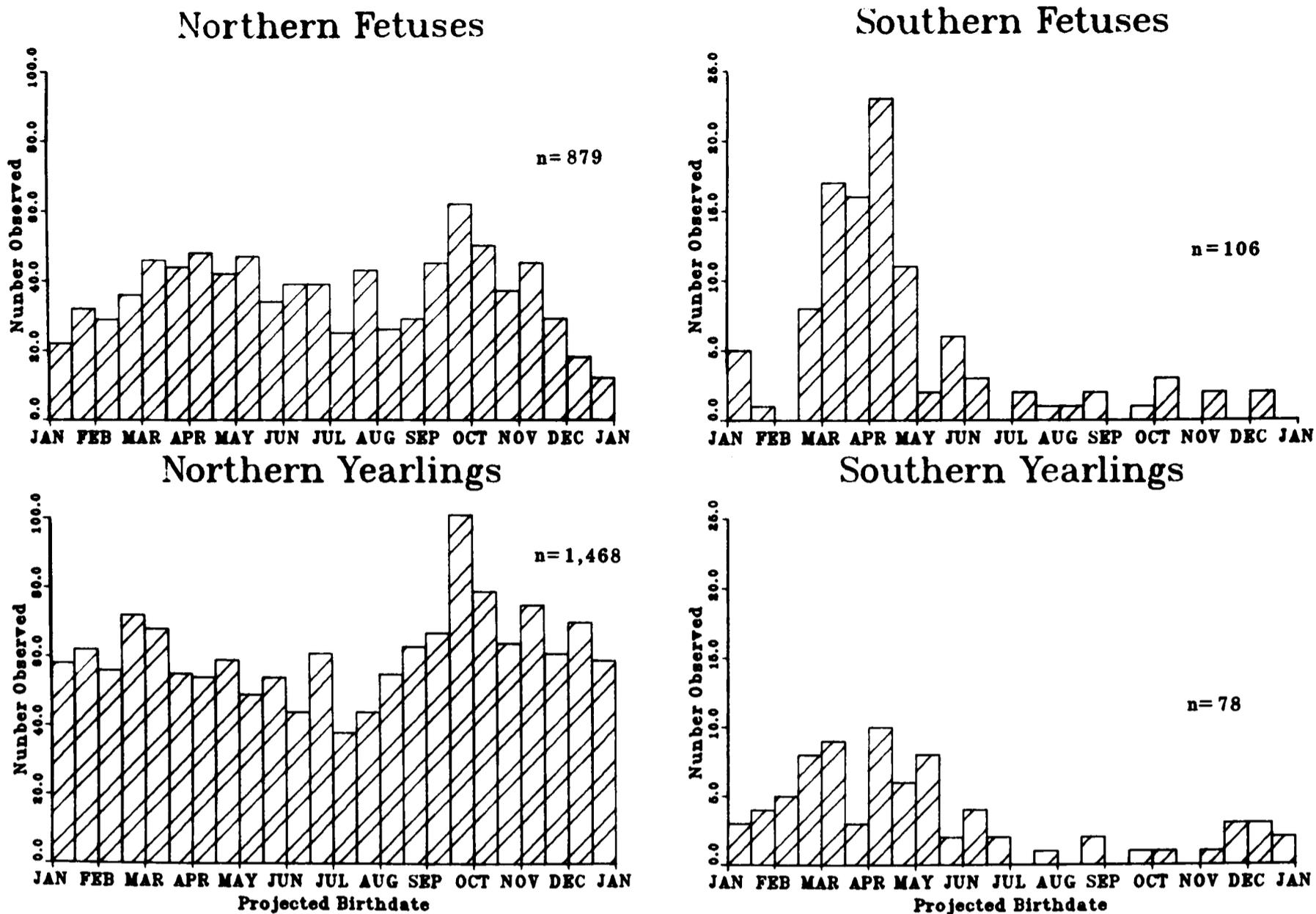


Fig. 8. Birthdate distributions of offshore spotted dolphins (*Stenella attenuata*) projected from lengths of fetuses (top) and calves (bottom). North/south geographic stratification is as shown in Fig. 2.

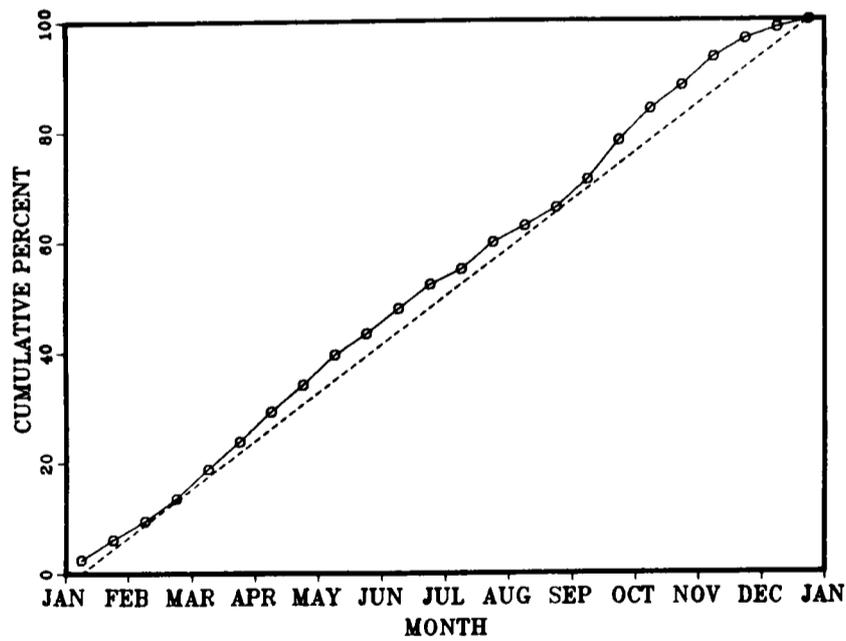


Fig. 9. Cumulative birthdate distribution of northern offshore spotted dolphins (*Stenella attenuata*) projected from lengths of fetuses. Broken line indicates expected cumulative distribution if births were uniformly distributed throughout the year.

stock, the season of parturition is quite short, with most births occurring from March through May. Indeed this group shows the strongest pattern of seasonality of any of the stocks considered here. Sample sizes for the southern population were small, so no attempt was made

to divide its range into sub-regions to examine finer geographic differences in birthdates.

Having shown distinct differences between the timing of reproduction in spotted dolphins north and south of the equator, it would be helpful to know whether these changes occur over a narrow range of latitude or whether there is a gradual change from a diffuse bimodal pattern in the north to a strong unimodal pattern in the south. The sample of northern spotted dolphins was therefore stratified into a group taken between the equator and 5° N and a group taken north of 5° N (Fig. 10). Although the sample size is small, those spotted dolphins caught between 0-5° N appear to have a diffuse pattern of seasonality but with one peak from March to June. Two sample K/S tests show this pattern to be significantly different from both that taken from south of the equator (Fig. 8) and that taken from north of 5° N (Fig. 10).

### DISCUSSION

As with other dolphin species that have been studied to date, the stocks of *Stenella attenuata* and *S. longirostris* in the eastern tropical Pacific show seasonal patterns in their reproduction. Unlike the strict seasonality of temperate and subarctic species, seasonality in these tropical dolphins is manifest as one or more calving peaks per year, with some parturition occurring throughout the

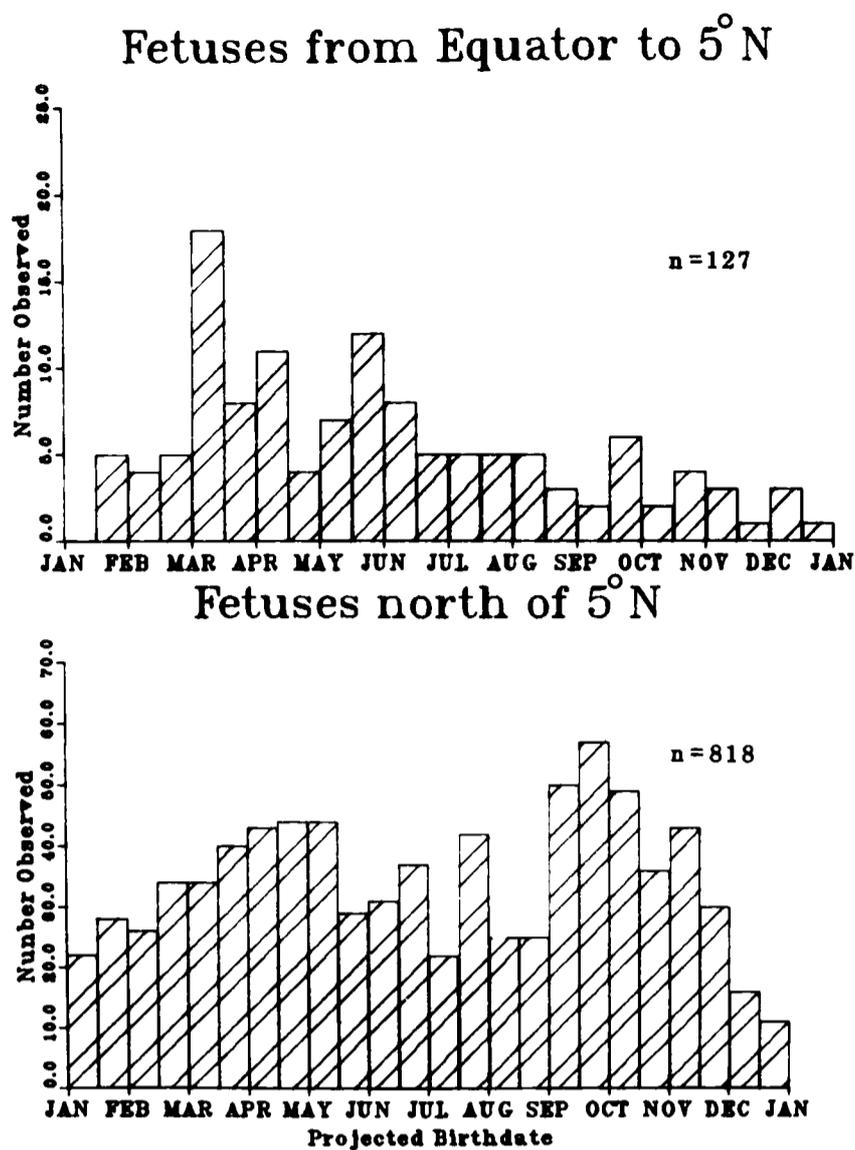


Fig. 10. Birthdate distributions projected from fetuses of northern spotted dolphins (*Stenella attenuata*) grouped by latitude at time of capture.

year. The reproductive seasonality of these species can be characterized by the strength of the observed modes, the number of modes, and their timing. Based on these criteria, there are significant differences in reproductive patterns between dolphin populations that have previously been identified based on morphological criteria, and there is evidence of significant geographic differences in seasonality within these recognized stocks.

The eastern and whitebelly stocks of *S. longirostris* were originally separated on the basis of morphology (Perrin, 1975). This distinction is corroborated by the differences noted here in reproductive seasonality. The eastern spinner (Fig. 5) has a single peak in births, and the whitebelly spinner (Fig. 7) shows at least two modes. It should be noted that the modes in both cases show a sharper definition when projected from fetus lengths. This may attest to the greater precision of the fetal birthdate projection method (despite smaller sample sizes). This would be expected if fetal growth shows less individual variability than that of postnatal animals, or if the estimated growth curves are more accurate for fetuses than for calves.

Within the eastern group, additional geographic differences in seasonality (discussed above) may indicate that a further subdivision of this species would be meaningful. Although both the inshore and offshore groups of eastern spinners show a single annual mode in parturition, this mode occurs significantly earlier in the offshore area. Distributional studies of these dolphins indicate that there are inshore and offshore population

centers for eastern spinners with a paucity of sightings in between (Fig. 5 in Au, Perryman and Perrin, 1979). These two observations suggest that the eastern spinner stock might consist of two populations. Regional differences in the timing of a reproductive cycle could be due, of course, to local differences in the seasonality of environmental factors, such as food supply. If this were the case for eastern spinners, reproductive isolation of the inshore and offshore groups would not necessarily result. Before these groups could be identified as separate stocks, further work would be required to determine the degree of isolation, perhaps by means of tagging, genetic, or morphometric studies.

The patterns of seasonality in the northern whitebelly spinner are more difficult to interpret. Although the birthdate distribution projected from fetuses shows a bimodal pattern, that projected from calf lengths shows no clear pattern at all (Fig. 7). Perrin and Henderson (1979) showed that for whitebelly spinners, variations in male testis weight were seasonal, with two modes. The peak periods of testis weight correspond well to the expected breeding seasons given the birthdate distributions taken from fetuses. As noted above, the birthdate distributions taken from fetuses tend to show better definition than those estimated from calves. For these reasons, two annual peaks in reproduction are taken to be the most likely pattern. The absence of these modes in the birthdate distributions projected from calves may be simply due to the combination of sampling error and the high degree of variance associated with this projection method. Alternatively, the difference could be due to misidentification of calves to stock in the area of overlap with the eastern spinner dolphin, or to error in estimating length at birth or postnatal growth rate for this stock. Larger sample sizes may help resolve this apparent discrepancy.

The offshore spotted dolphins were originally considered a single population (Perrin, 1975); however, more recent evidence (Perrin *et al.*, 1979) has supported the consideration of a separate population south of the equator. Evidence presented here for marked seasonal differences in reproduction supports this view. The transition from a diffuse bimodal pattern in the north to a strong unimodal pattern in the south may not be abrupt. Dolphins taken between the equator and 5° N show a single mode synchronous with that of the animals to the south, but they show a more diffuse pattern of seasonality similar to that of the northern spotted dolphins. The explanation of this gradual change is not known. If seasonality in reproduction is determined by the timing of oceanographic or trophic factors, the change could reflect a geographical change in the timing of these physical determinants. Alternatively, the area between 0° and 5° N could represent an area where two separate populations can both occur with the birthdate distribution from that area being a composite of two different distributions. A hiatus in spotted dolphin sightings has been used to determine the boundary between the northern and southern stocks; this region is just south of the equator (Perrin *et al.*, 1979). If this proves to be an accurate boundary, the latter hypothesis could be rejected.

Seasonal patterns of reproduction have been examined for the populations of *Stenella* off the coast of Japan.

Three annual periods of parturition were shown for both *S. attenuata* (Kasuya, Miyazaki and Dawbin, 1974) and *S. coeruleoalba* (Miyazaki, 1977). These estimates were based, however, on the back calculation of birthdates from animals that were up to 2 years old. Individual variation in growth would almost certainly act to obscure seasonal patterns estimated from the older animals. Using only the birthdate distributions taken from fetuses, the data indicate a single mode in the births of *S. attenuata* (Fig. 33 in Kasuya *et al.*, 1974) and an obvious bimodal pattern for *S. coeruleoalba* (Fig. 16 in Miyazaki, 1977).

The reason for the observed differences in reproductive seasonality within the genus *Stenella* are not clear. One possible explanation is that density-dependent changes occurred as a result of exploitation. The southern spotted form of *S. attenuata* has been exploited only lightly (Smith, 1979). This population shows a single strong peak in reproduction, which I will, for purpose of discussion, assume to be the 'natural state' for this genus. Given that all mating occurs at the same time each year, the calving cycle must be an integral number of years: say, for example, 3 years. As exploitation decreases population size, the calving interval might decrease to 2.5 years due to density-compensatory effects. This calving interval would not be consistent with a single annual season of births, hence a bimodal pattern might result. Such a pattern was found in *S. coeruleoalba* off the coast of Japan, in the northern spotted form of *S. attenuata*, and in the northern whitebelly form of *S. longirostris*, all of which have been exposed to moderately heavy exploitation (Kasuya, 1976; Smith, 1979). If the calving period were reduced further, say to 2 years, a single annual mode in births would again be possible. This pattern was seen in the eastern spinner form of *S. longirostris* which has been subject to very heavy exploitation (Smith, 1979). Although speculative, this explanation is consistent with the observed patterns of seasonality in this genus. These predicted patterns can be tested as accurate estimates of calving period become available for these stocks.

Regardless of their cause, the observed patterns of reproductive seasonality can affect our estimation of birth rates for these dolphins in several ways. First, reproductive seasonality, once established, can impose barriers to reproduction and hence change our concept of what constitutes a stock or population. Clearly this is of importance in the management of marine mammals.

Another aspect of seasonality of importance in management is the introduction of bias in the estimation of reproductive rates due to seasonality of sampling effort. For instance, the fraction of pregnant females in a population could be underestimated if sampling of that population were predominantly during the time between the period of peak births and that of peak conceptions. If gestation were 10 months, this time interval would be 2 months. A method for correcting this sort of sampling bias was presented by Barlow (1979). In general, if gestation is close to 1 year (as it is for most dolphins), and if reproductive peaks are somewhat diffuse (as they are for most tropical species), this bias will be small.

The final aspect of reproductive seasonality to be discussed here is a consequence of the synchrony it imposes. If births are restricted to a short season, as in

the case of the southern spotted dolphins, then the inter-birth period will necessarily be an integral number of years. This does not mean that the average calving period will be an integer since some individual variability may exist in lactation times and since not all females may become pregnant during the first breeding season after weaning. For birth rate estimates that only involve mean calving interval, synchrony need not affect the resulting estimate of birth rate. However, if the estimation of reproductive rates involve more mechanistic considerations (such as spontaneous abortions and calf mortality) the rate at which females become reinseminated becomes important. If, as was shown by Perrin and Henderson (1979), male fertility is also seasonal, a female that loses her calf might not become pregnant again until the next breeding season. This simple scenario is complicated by the fact that some males always have active sperm production and that conception can occur at any time of the year. Regardless, a model could be developed that would take such seasonal effects into consideration.

#### ACKNOWLEDGMENTS

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# Productivity and Behavior of Bowheads, *Balaena mysticetus*, and White Whales, *Delphinapterus leucas*, as Determined from Remote Sensing

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## ABSTRACT

During the NASA-supported Bering Sea Marine Mammal Experiment, remote sensing methods proved effective in gathering data on marine mammals. The walrus, *Odobenus rosmarus*, was our principal target species; data reported here were gathered serendipitously for the white whale, *Delphinapterus leucas*, and the bowhead, *Balaena mysticetus*.

We documented an expanded distribution for white whales by observations and photographs of significant numbers in *polynyas* of the summer ice front in the Beaufort and eastern Chukchi Seas and obtained an estimate of 8–13.6% gross productivity, based on a sample of 88 individuals that were measurable from photographs. For bowheads, the same technique revealed a ratio of calves (3) to adults (16) of 19%. Swimming speeds, measured from sequential photographs that contained stationary objects, were from 2 km/hr for white whales with calves to 7 km/hr for an individual in a travelling group. Bowheads swam at speeds ranging from 5 km/hr while feeding to 11 km/hr while travelling.

We also tested accuracy, precision, and sightability. These factors are associated with visual surveys. The very high variances due to these factors can be almost entirely eliminated by remote sensing methods.

Data such as these on population structure, behavior, and habitat relationships, especially if taken by methods that reduce the high variances associated with visual surveys, are essential for monitoring the status of whales in the face of extensive habitat alteration during exploitation of offshore oil and gas, as well as during continued subsistence hunting. We conclude that there is presently no more effective means to gather such data on a concurrent, synoptic level for such widely-distributed species.

## INTRODUCTION

This paper has two objectives: (1) to present data relevant to production of white whales and bowheads and (2) to illustrate the efficiency of remote sensing from relatively high-flying aircraft for acquiring such data. We emphasize biological and ecological data here; technical information is provided elsewhere.

In order to estimate the production of animal populations with reasonable accuracy, the number of individuals in the population, the age-specific productivity, and the age structure of the population should be known. Also, aspects of behavior, especially pertaining to groups containing young, and habitat, especially as related to food and feeding, are important. Yet, there remains considerable uncertainty about most whales in these respects. For example, regressions relating body size to age have not been determined for most whales; thus, even if sizes of individuals could be measured, cohort analysis is clearly not feasible. Under these circumstances, the best one can do is to estimate gross annual population productivity by detecting proportions of calves among groups. This estimate can only be converted to gross production if the total population number is known, which is highly uncertain for most species. Further, our understanding of the relationships between whales and oceanic productivity remains primitive. This is a particularly serious deficiency in view of recent concepts that the success of feeding influences recruitment (Lockyer, 1984) and that density-dependent changes occur near carrying capacity (Fowler, 1984).

Herein, we present data on population structure, behavior, and habitat obtained by remote sensing – in this case aerial photography. We also examine basic problems of sightability, accuracy, and precision that are inherent in all population assessments. Our data were obtained during our experimental research project called the Bering Sea Marine Mammal Experiment (BESMEX – Ray and Wartzok, 1974, 1980; Wartzok and Ray, 1980). We gathered data on three ‘target’ species: principally the walrus, *Odobenus rosmarus*, but also serendipitously for the white whale, *Delphinapterus leucas*, and the bowhead, *Balaena mysticetus*. It is for the latter two species only that we present data here.

Basic to determining productivity of whales are problems of population assessment. These fall into two general categories. First, sightability involves the proportion of animals visible and which can be detected. Caughley (1974) lists factors which influence sightability: the distance between the animal and the observer; characteristics of location, such as cover, background, and lighting; characteristics of the animal, such as color, size, and movement; and the observer’s eyesight, speed of travel, and fatigue. A major factor influencing sightability of cetaceans is that they spend a major proportion of their time submerged where they cannot be detected. For marine mammals, appropriate forms of sightability curves have not yet been determined, although many assessment reports address the problem to some extent. The second problem relates to the variances of the surveyed samples and the randomness of distribution of the individuals in the population. The majority of statistical theory relating to assessment has been devoted to this aspect. However, assessments rarely consider differences in accuracy and precision that vary from situation to situation and from observer to observer. Nor can sampling theory consider sightability, since major components of this must be determined

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empirically through an accumulation of natural history data. Finally, neither survey methods nor sampling theory progress much beyond population numbers to the equally important matter of population structure that is required for estimates of productivity. It is probable that for most marine mammals, segments of the population behave quite differently; females with young may associate separately and have different habitat requirements and different sightability features than do other segments of the population.

It appears that remote sensing techniques can contribute significantly towards solutions to these problems. Visual spectrum photography is the most familiar remote sensing technique. It has been previously used for studying aspects of the biology of cetaceans by Heyland (1974), Leatherwood (1979), Whitehead and Payne (1981) and Perryman, Scott and Hammond (1984) but in none of these studies were habitat and behavior also considered. Nevertheless, these investigators recognized that remote sensing – or data-gathering from a distance – adds new dimensions of synoptic coverage of animals within their habitats and has the advantage of producing ‘hard data’ suitable for repeated analyses. It is not intended to replace other methods entirely. This is true because, for the foreseeable future, ‘ground truth’ will be required.

#### METHODS

The deployment of remote sensors requires stable platforms with accurate navigation capability. In 1974 we used NASA’s Elektra NP3, a twin-engine turboprop aircraft; during 1975 and 1976 we used NASA’s four-engine jet Convair 990. Technical details on aircraft and their equipment are contained in NASA’s ‘experimenter’s handbooks’ and will be only briefly touched on here.

Both aircraft had accurate navigational capability. The NP3 carried two Zeiss aerial photographic cameras with 228.6-mm square film image and 152.4 mm focal-length lenses covering 73-degree fields of view. It also carried two Chicago KA-62 cameras with 114.3 mm square film image and 76.2 mm focal-length lenses, also providing 73-degree fields. The CV-990 carried Wild RC-8 and Chicago KS-87 cameras with 228.6 and 114.3 mm square film image sizes, respectively. The RC-8 had a 152.4 mm lens, providing a 73-degree field of view; the KS-87 camera had a 308.4 mm lens, providing a field of 21 degrees, so that a larger film image might be provided of subjects falling in the smaller field. The cameras were fitted with haze filters. We tested various sorts of films, but Kodak SO 397 was chosen as it is a visual spectrum color film. These cameras and film combinations provided resolutions approximating 40–50 line pairs per millimeter, depending on contrast and a number of other factors. We had to compensate for this relatively low resolution by flying at rather low altitudes; this was not a disadvantage as we desired to make concurrent visual observations.

On all flights, there were at least three experienced marine mammal observers, in addition to flight personnel. One was stationed in the cockpit behind the pilots, and the others on either side of the aircraft, looking through side windows forward of the wings. On the CV-990, an observer was often located in the belly, looking

downward. All verbal communications on the CV-990 could be heard by all observers by means of a communications system, and our notes were typed by a data-recorder and made available on a computer printout at flight’s end. This printout also provided data at ten-second intervals of such flight information as position, altitude, pitch, yaw, roll, and various environmental data. The aircraft usually flew at about 1,000 m at a speed of 444 km/hr on data runs. However, it occasionally descended to as low as 180 m or ascended to as high as 1,524 m.

Each aircraft had radar altimeters that were accurate to within about 2%. This, with knowledge of pitch, yaw, roll, and lens field of view allowed computations of the sizes and orientations of ground objects; calculations of sizes did not require the presence of an object of known size in the images, as does the method of Whitehead and Payne (1981).

The color transparencies were viewed on a Richards 918LW light table equipped with an Olympus SV-III binocular microscope and eyepiece with a 100-unit ocular scale, calibrated to the nearest 0.01 mm with a stage micrometer. By such means lengths and fluke spans were determined. Photographs used for measurement of swimming speed overlapped 25% between successive frames, and the intervals between pictures were 12 seconds; a stationary object such as a piece of sea ice was

Table 1  
BESMEX flight summary

Date	Area	No. of runs	Data kilometers
8 Sept. 1974	Beaufort Sea	17	193
9 Sept. 1974	Arctic Ocean	9	180
20 Sept. 1974	Beaufort Sea (Smith Bay)	14	87
20 Sept. 1974	Chukchi Sea	4	61
26 Sept. 1974	Beaufort Sea	2	13
5 Apr. 1975	Western Bering Sea (Ice edge)	18	721
6 Apr. 1975	Bering Sea	8	1,043
7 Apr. 1975	Bering Sea	14	647
8 Apr. 1975	Bering Sea	10	483
19 Aug. 1975	Chukchi Sea	6	367
23 Aug. 1975	Chukchi Sea (Barter I. and west)	19	705
24 Aug. 1975	Chukchi Sea	24	953
28 Aug. 1975	Chukchi Sea (Ice line along north coast of Alaska)	3	257
11 Oct. 1975	Chukchi Sea	—	322
17 Oct. 1975	Chukchi Sea	13	499
18 Oct. 1975	Chukchi Sea and St Lawrence Is.	—	724
22 Oct. 1975	Chukchi Sea	—	26
25 Oct. 1975	Chukchi Sea and Bristol Bay	—	547
27 Oct. 1975	Chukchi Sea	19	966
13 Apr. 1976	Bering Sea (St Lawrence Is.; Bristol Bay)	7	338
18 Apr. 1976	Bering Sea (St Lawrence Island)	9	616
19 Apr. 1976	Bering Sea (North of St Lawrence Island)	15	734
Totals:	22 flights	211 runs	10,482 km

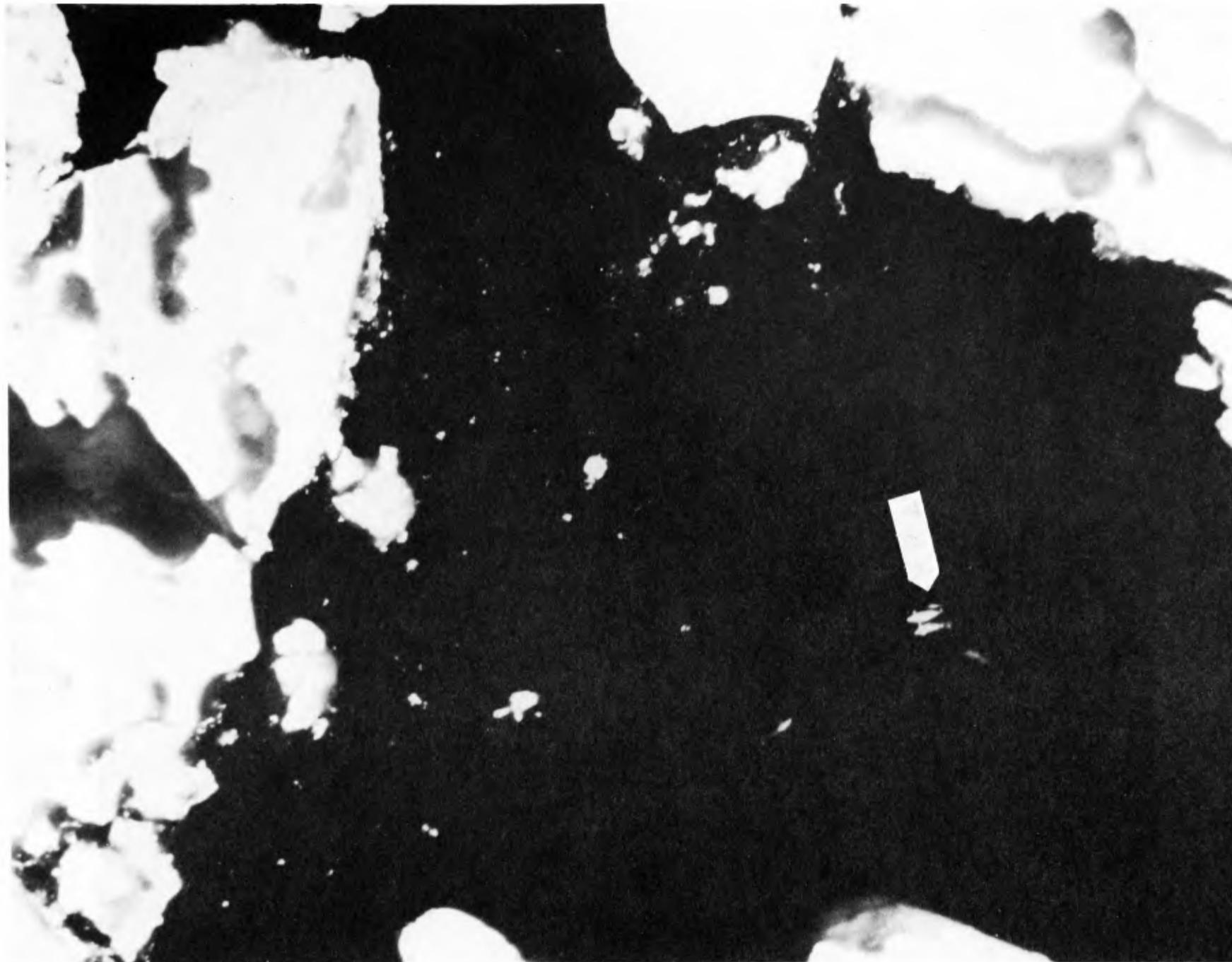


Fig. 1. An enlarged portion of a color photograph showing white whales. Note the ease with which both adults and calves can be distinguished. Taken from 354 m altitude on 8 September 1974 at 71° 38' N, 152° 35' W.

required near the whale, so that the distance travelled could be calculated.

The *polynya* (open water within the ice field) areas occupied by white whales were measured by tracing each *polynya* outline on an acetate overlay that was placed over a grid of 1.27 mm squares, and by counting the number of squares contained within the outline. These values were converted to actual areas based on altitude, roll and pitch of the aircraft, and the field of view of the camera.

To test the accuracy and precision of observers in detecting animals and estimating numbers by visual means, we conducted a test utilizing the imagery obtained on our initial remote sensing flights. Observers were divided into four categories: individuals with experience counting walruses (6); individuals with experience counting whales (8, five of which were also in the first class); pilots (4); and novices (17). Sections of the 228.6 mm square imagery were mounted in 82.6 × 108 mm slides and projected to test participants in a manner that mimicked a visual survey. The screen occupied 90° of the observers' field of view, and the image size of the animals on the screen was about the same as that of animals viewed from an aircraft at 150 m altitude. Each scene was presented for 10 sec., which is the same time an observer would have to count a group of animals

from 78° (about 0.7 km) ahead of the aircraft, until the group was directly below, flying at a speed of 260 km/hr. The intervals between slide presentations were Poisson-distributed in five-second intervals with a mean interval of 35 sec. Thus, with 10 sec. of slide presentation and a mean 35 sec. interval, the total session for the 80 slides lasted one hour; this is not nearly as long – thus, not so fatiguing – as a real flight.

## RESULTS

Table 1 gives flight data. We flew all seasons but mid-winter and sampled all subdivisions of Beringia (the Bering, Chukchi and Beaufort Seas) that comprise the ranges of the target species.

### Detection

For both species, remote sensing methods proved applicable. Both are clearly detectable against their backgrounds; both are gregarious, greatly facilitating detection. Fig. 1 shows that the white whale is quite easy to detect, due to the high contrast of its white color against the dark sea. However, individuals can be easily missed, due to similar coloration, size and shape of whales



Fig. 2. An enlarged portion of a color photograph showing bowhead whales. The whales are associated with a 'disturbance area' of suspended sediment and 'contrails,' both of which may be associated with feeding. Taken from 180 m altitude on 20 September 1974 at 71° 5' N, 154° 7' W.

to small bits of ice. For the bowhead, there is less contrast with the sea water background, as shown by Fig. 2, but this is a very large animal which frequently leaves trails of sediment in the water, presumably resulting from feeding activity or disturbance of sediment (see below). The bowhead's blows and disturbances of the water surface (splashing, etc.) are also clues to its presence. Detection of both species at the surface, therefore, offers few problems, especially as imagery can be examined at leisure.

#### Distribution and habitat

For both white whale and bowhead, we have added some visual observations to our photographic data for compiling Figs 3 and 4. We found white whales throughout Beringia. Their coastal distribution has long been documented but we have also found significant numbers along the summer ice front and a very large 'migratory swarm' in open water just south of the front. On 8 September 1974, we found white whales to be fairly

numerous in ice-front *polynyas* of the Beaufort and eastern Chukchi Seas. The habitat was a narrow strip of sea ice about 2–4 km wide containing ice-free *polynyas* well inside plumes of brash and pancake ice of the fairly well-defined ice edge. We found no animals in the rough, open water. Just north of the strip where we found whales, the *polynyas* were frozen. Thus, it appeared that there was a 'calm-warm strip' which served as habitat for the whales. We measured the sizes of *polynyas* in which we sighted whales; the mean size was 6,493 m<sup>2</sup> ( $n = 41$ ). Randomly sampled *polynyas* without white whales had a mean of 2,310 m<sup>2</sup> ( $n = 30$ ). These *polynya* sizes are significantly different ( $P < 0.01$ ). Therefore, the whales appeared to prefer the larger *polynyas*.

We estimated the number of white whales within this 'calm-warm strip' by flying a zig-zag path over the strip. We detected 88 whales on photographs covering 497 km<sup>2</sup> (0.177 whales/km<sup>2</sup>). We assumed equal mean density in the strip from 139° to 164° W in order to estimate 665 animals. This is no doubt only a portion of the animals that were actually there. Brodie (1971) assumes an

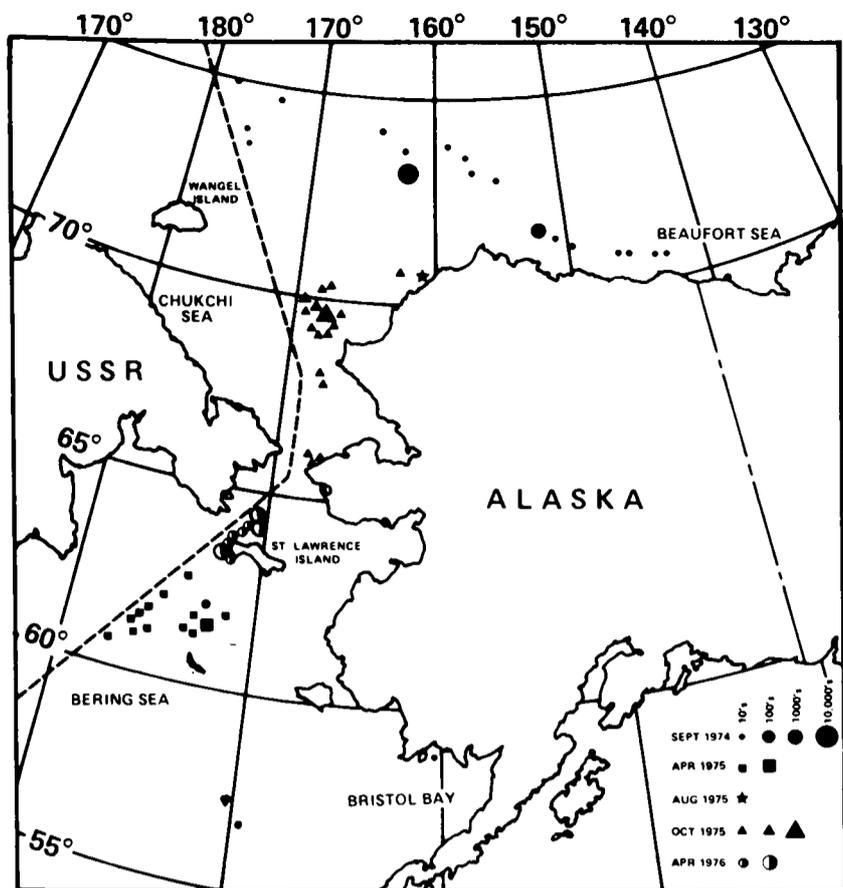


Fig. 3. White whale distribution as observed on BESMEX flights during September 1974, April 1975, August 1975, October 1975, and April 1976.

white whales may migrate from their MacKenzie River Delta summer habitat through the ice front, then they may swim south in open water in early fall ahead of the expanding pack in order to reach their winter Bering Sea habitat before extensive winter ice formation.

We found bowheads in the Beaufort Sea in September 1974 and in the northeast Chukchi Sea in August 1975. These animals were near the 20 m contour, supporting Nemoto's (1959) contention that this is a shallow-water species, at least in summer. We also found bowheads in the central Chukchi Sea in both August and October 1975, and we made an unconfirmed October 1975 sighting of a large group of over 50 animals (not shown on Fig. 4, which presents only confirmed sightings) in the Bering Sea north of St Lawrence Island. We made no aerial sightings of bowheads during winter. This species is very difficult to detect in ice; it can breathe in very small fissures and break ice of perhaps a meter's thickness. It is likely that bowheads are scattered throughout southerly Bering Sea winter ice. Observations are too few to confirm habitat preferences, although the most numbers to date have been seen in the southwest central Bering Sea (Braham, Krogman, Johnson, Marquette, Rugh, Nerini, Sonntag, Bray, Brueggeman, Dahlheim, Savage and Goebel, 1979).

**Population structure and productivity**

Of the 314 white whale images depicted on our photographs, 141 (45%) could be measured for body length, and of these, 66 (21%) for fluke span. Errors are of two sorts: (1) image measurements were accurate to  $\pm 15$  cm, as determined from replicate measurements of given animals; and (2) body lengths were biased toward underestimates due to flexure, but this source of error was minimized by deletion of images of insufficient clarity to see whether the whale was straight. A 'calf' was classified as an animal of 230 cm or less. A 'female' was classified as an animal in association with a calf or accompanied by a small whale of less than half its length. Another category was single whales, which tended to be large animals. The mean length for 12 'females' was 359 cm

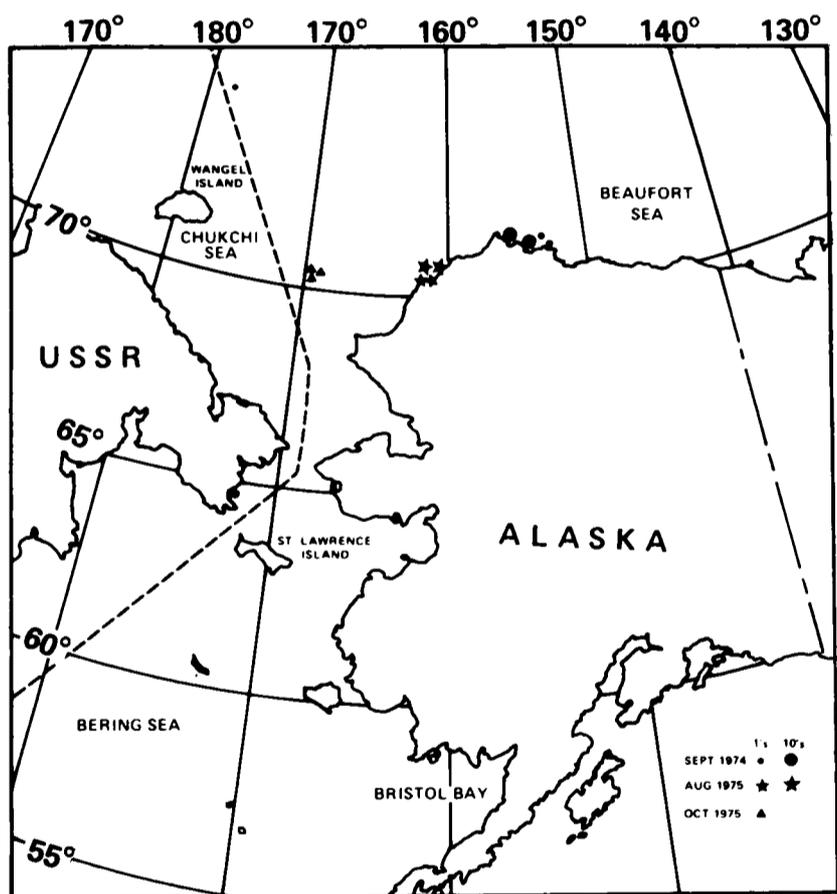


Fig. 4. Bowhead distribution as observed on BESMEX flights during September 1974, August 1975, and October 1975.

invisible (submerged) proportion of 0.29 and Sergeant (1973) assumes 0.66. Since our data cannot be used to calculate a proportion submerged, as discussed below on sightability, we have assumed a mean value of 50% submerged to estimate that about 1300 white whales might have been present; this is over one-fifth of the total Beaufort population estimated by Sergeant and Brodie (1975). The observations of a 'migratory swarm' and so many whales within a 'calm-warm strip' indicate that

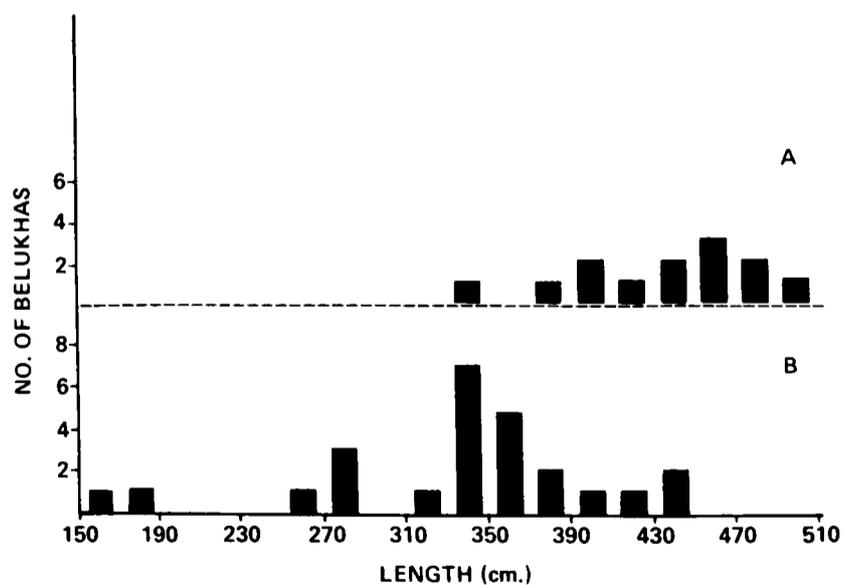


Fig. 5. Distribution of body lengths of white whales photographed on 8 September 1974. A: Animals photographed between 70° 45' to 71° 29' N lat. and 144° 6' to 151° 22' W long. B: Animals photographed between 71° 37' to 71° 45' N lat. and 152° 29' to 152° 40' W long.

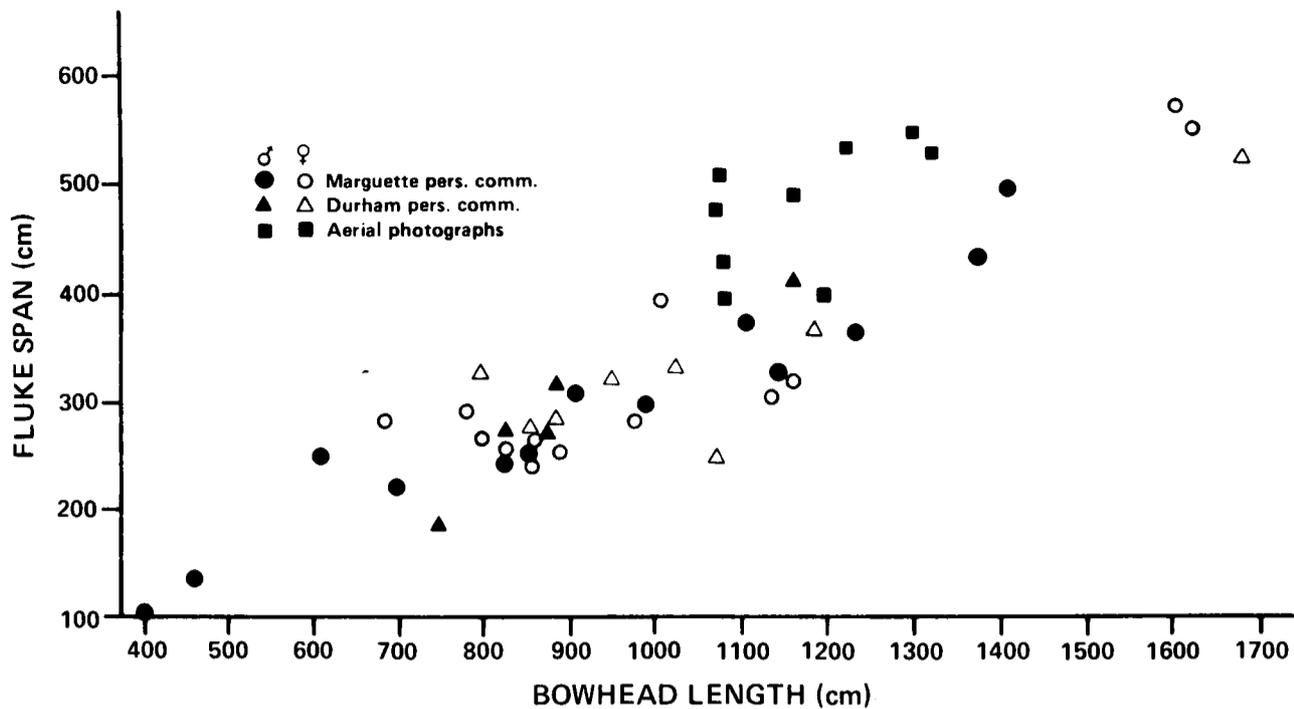


Fig. 6. Comparison of the relationship between bowhead fluke span and body length. Measurements are of animals from aerial photographs compared with harvested animals (data by personal communication: W. Marquette and F. Durham).

(s.D. = 19 cm), slightly larger than the modal maximum of 350 cm for MacKenzie Delta females of Sergeant and Brodie (1969). Eight of those females had a mean fluke span of 24.6% of body length (s.D. = 1.6%), comparable to 23.5% for St Lawrence River females (Kleinenberg, Yablokov, Bel'kovich and Tarasevich, 1964). Ten solitary individuals averaged 410 cm (s.D. = 55 cm), exactly the same as the modal maximum of 410 cm for MacKenzie Delta males (Sergeant and Brodie, 1969). Six of these had a mean fluke span of 25.4%, comparable to the 26.6% reported for males by Kleinenberg, Yablokov, Bel'kovich and Tarasevich (1964).

On 8 September 1974 we photographed 88 white whales, 27 in an easterly group (144°–151° W) and 61 in a westerly group (near 152° W). Thirty-eight of these could be accurately measured (Fig. 5). The easterly and westerly groups had quite different size compositions. Twelve, or 13.6%, of the total of 88 animals – all in the westerly group – were obviously less than half the length of neighboring whales, even though some of them could not be accurately measured. Twenty-five animals in this westerly group could be accurately measured (Fig. 5B); two, or 8%, were less than 190 cm. Although our sample sizes are small, these productivity values of 8 to 13.6% are in the general range of 11% of Sergeant (1973), 10% of Brodie (1971), and 12.1 to 17.9% of Heyland (1974). Obviously, such estimates of productivities are biased by the segment of the population sampled, as shown by differences between our easterly and westerly groups. They may also be biased by the area sampled or differences in productivity among groups or years.

We photographed a large group of bowheads in Smith Sound in September 1974. We measured only animals that were visible from well in front of the blowhole to the flukes; the whales' bodies must have been almost straight to be visible for most of their lengths in such murky water. Thirty-eight (28%) of the 138 images of whales were measurable for body length and 23 of these (17%) for fluke span. Since some flight lines recrossed the same animals, we can be positive of having photographed only 83 different animals. Of these, 21 (25%) were measurable

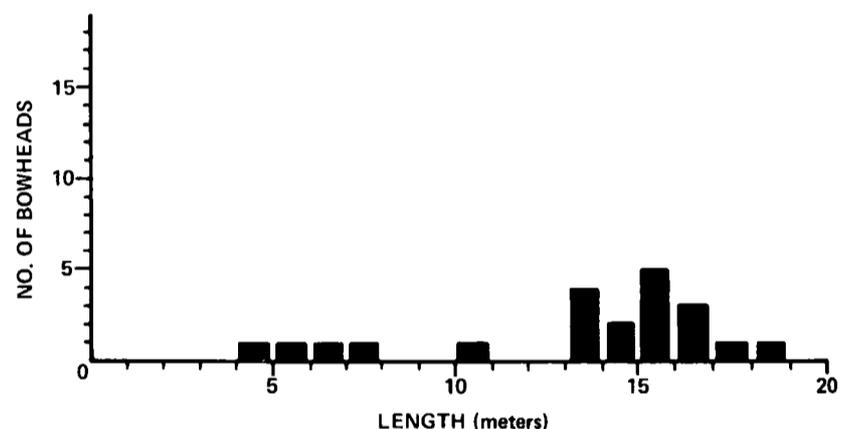


Fig. 7. Distribution of corrected body lengths of bowheads photographed on 20 September 1974.

for length and 12 (14%) for fluke span. The flukes are less subject to flexure than is the body and therefore fluke measurements are less affected by the second type of measurement errors discussed above. We used the fluke span to body length ratio as a check on our assumption that the animals measured for body length were mostly visible and reasonably straight. Any flexure of the body or any part of the whale (especially the rostrum) hidden by the turbid water would lead to an underestimate of the length and would show up as an inflated estimate of the fluke span to body length ratio. Fig. 6 shows a plot of our fluke span to body length data, compared with data obtained from harvested animals by W. Marquette and F. Durham (pers. comms). Our data points consistently fall above those from harvested animals: i.e. 41% or 1.28 times the 32% mean value from Marquette's and Durham's data. Thus, we have used 1.28 as a correction figure, although we believe the fluke span:body length ratio needs confirmation.

The corrected lengths of bowheads are given in Fig. 7. We emphasize that exact lengths are not as important as are the relative sizes of individuals, which give the proportion of calves to adults in the population. We classified the animals in Fig. 7 as 'calves' (4 to 7 m in length), 'subadults' (7 to 12 m), and 'adults' (greater than 12 m). (An 8-m whale could conceivably be either

a yearling or a calf that was born early in the year; data on growth rates do not exist to clarify this point.) The proportion of calves to adults is 0.19. If there is an equal sex ratio in the measured adults, the proportion of calves to adult females is 0.38, which is a reasonable value for a large whale which breeds triennially.

### Swimming speed, direction and interanimal distance

Speed and direction of swimming are important clues to behavior. For example, feeding is often associated with slow, deliberate, directionally random movements, whereas migration is associated with directional, more rapid movements. Table 2 gives swimming speeds of both species, with comments on observed behavior. The fastest rates for white whales were 6.1 km/hr for a diving solitary animal and 7.0 km/hr for an individual among a group of evidently travelling animals. The slowest rates were for individuals with young, 2–3 km/hr. Bowheads associated with 'disturbance areas' where they are probably feeding (Fig. 2) moved the most slowly, 5.0–6.5 km/hr. Whales not associated with such areas, thus probably travelling, moved faster at 8.6–11.2 km/hr. These data are higher than the 4.5–5.5 km/hr estimated by Ljungblad (1981) and the 7.2 km/hr reported by Hanson (1981). In fact, to state average figures can be misleading because various groups of animals travel at different speeds according to their age and behavior.

The distance to the nearest animal was measured for 66 subadult and adult bowhead whales. Fig. 8 shows the distribution of these minimum interanimal distances. Also shown are the spacings between the three animals of less than 7 m and the closest large whale. Two of these calves were less than 4 m from an adult and thus would

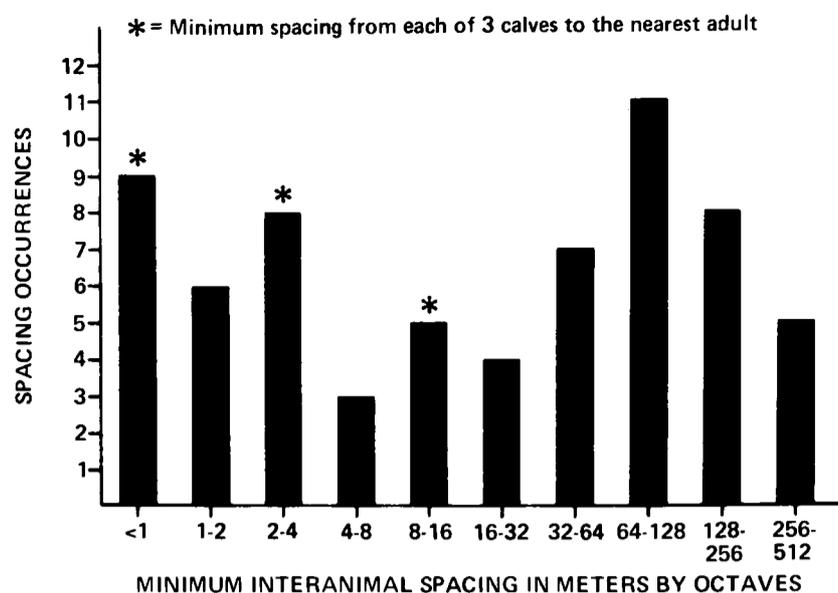


Fig. 8. Distribution of minimum interanimal distances for 66 subadult and adult bowhead whales. Asterisks show the spacing between each of the three calves and the nearest large whale.

be very difficult to detect from shipboard or ice observation platforms, especially if the calf was on the opposite side of the adult from the observer. The one calf separated 11 m from a large whale was in a group associated with a disturbance area in which the whales were probably feeding.

We determined the directional headings for 188 bowhead images (87% of the total) photographed in September. In two of the three cases where bowheads were seen in association with 'disturbance areas' the mean heading vector was not significantly different from zero (Rayleigh test; Batschelet, 1965). On the other hand, in both of the cases where bowhead groups were photographed in open water, the animals' headings were unimodal, giving a significant mean directional vector.

### 'Feeding' behavior

For the bowhead, the intensity and duration of feeding might be subject to remote sensing. We have observed 'disturbance areas' (Fig. 2), also noted by Griffiths (1981), composed at least in part of 'contrails'. Our data show that one bowhead group in Smith Sound in September 1974 containing an average (i.e. average of sightable animals during replicate flight runs) of 3.25 animals swam in a disturbance area of 8,100 m<sup>2</sup>; another group averaging 12.2 whales swam in an area of 99,300 m<sup>2</sup>; yet another of an average of 26 animals swam in an area of 65,100 m<sup>2</sup>. It has yet to be proven that feeding is all that is involved as a cause for these contrails and disturbance areas, of course, but there is a potential for investigation of feeding intensity and duration by measuring the extent of such areas and the activity and numbers of whales therein.

### Assessment variables

Two important variables are associated with visual surveys, accuracy and precision; another is common to all marine mammal surveys, sightability, in this case the proportion of animals which are at the surface where they can be detected. The latter is probably the most intractable problem; no matter what the survey design, submerged whales cannot be detected by any means

Table 2  
Swimming speeds of individual whales

Behavior/social grouping	Speed (km/hr)
<b>White whale</b>	
(1) Female with calf	2.1
(2) Subadult with female and calf in (1)	2.5
(3) Female with calf	2.6
(4) Calf with (3)	2.9
(5) Adult in same large <i>polynya</i> with (3) (4)	2.1
(6) In group with random orientation (diving – swimming over tops of each other)	2.7
(7) Solitary – after surfacing	3.1
(8) Solitary – diving	4.2
(9) Solitary – diving	5.3
(10) Solitary – diving	6.1
(11) Group of two animals in small <i>polynya</i>	4.0
(12) Solitary – in <i>polynya</i> with thin ice	4.8
(13) Adult in large <i>polynya</i> with calf	4.7
(14) Swimming in lead with other large animals	5.2
(15) Solitary	6.1
(16) In group of large animals all with about the same orientation	7.0
<b>Bowhead</b>	
(1) Moving toward a disturbance area group	11.2
(2) Moving toward a disturbance area group	10.8
(3) Open water	8.6
(4) At the edge of a disturbance area	6.5
(5) At the edge of a disturbance area	5.0
(6) At the edge of a disturbance area	5.8

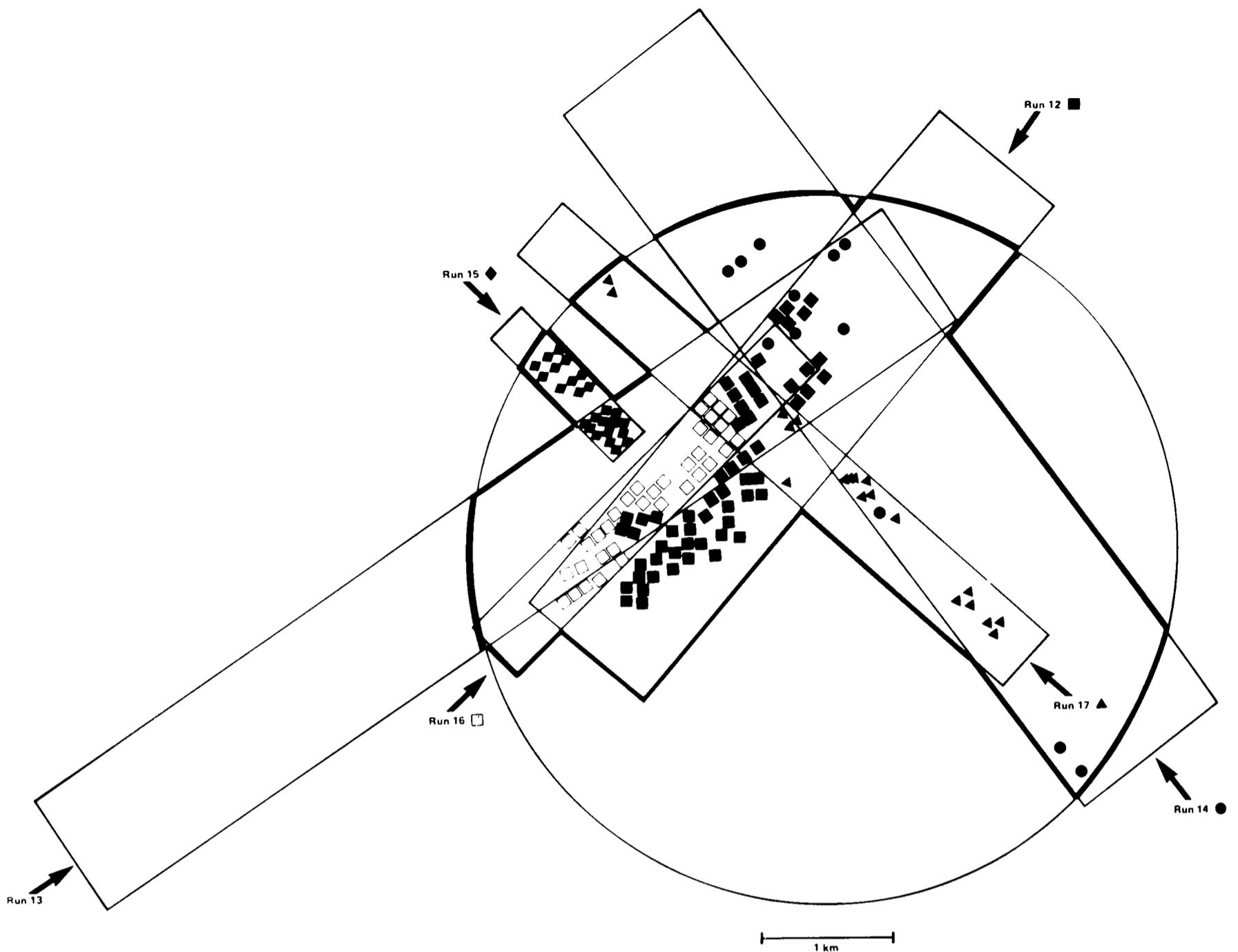


Fig. 9. Plot of six flight runs over groups of white whales. Run widths are the footprints of the aerial photographs and vary with the altitude of the aircraft. The heavy line delineates the total survey area of 11.32 km<sup>2</sup> within the 20.5 km<sup>2</sup> area of the circle. The indicator marks for each run show the locations of the animals whose direction of swimming could be determined. The total numbers of animals photographed on the runs are listed in Table 3.

unless they are at or very near the surface of clear water.

In order to measure the variation which can arise because different proportions of bowheads are submerged, we repetitively sampled groups. On 20 September 1974, we flew over two groups of whales within disturbance areas that provided markers for repetitive sampling. We flew 5 times over the first group and recorded 3, 5, 2, 3 and 0 animals consecutively; this yields a coefficient of variation of 70%. We flew over the second group four times and recorded 22, 12, 11 and 12 animals, yielding a coefficient of variation of 36%.

For white whales, we were not able to determine how much of the variation in repetitive samples could be attributed to different proportions of animals submerged, as we had no convenient marker to identify each group of whales. However, our data from repetitive sampling of a white whale concentration show that the coefficient of variation of density estimates can be greater than 160%. On 8 September 1974 we flew six runs over dispersed groups of whales within a circle covering 20.5 km<sup>2</sup>; each of the runs covered different proportions of the circle (Fig. 9). Table 3 gives the data acquired. As most runs

Table 3

Leg number	Number of white whales photographed	Area in km <sup>2</sup>	Percentage of circle of 20.5 km <sup>2</sup>	Density estimate
12	61	4.53	22%	13.5/km <sup>2</sup>
13	0	3.75	18%	0/km <sup>2</sup>
14	12	5.90	29%	2.0/km <sup>2</sup>
15	41	0.33	2%	124.2/km <sup>2</sup>
16	44	1.98	10%	22.2/km <sup>2</sup>
17	20	2.01	10%	10.0/km <sup>2</sup>
Mean density =				28.7/km <sup>2</sup> ± 47.5/km <sup>2</sup>

Total number of whales in non-overlapping areas = 80.  
Total non-overlapping survey area in circle = 11.32/km<sup>2</sup>.  
Overall density = 7.07/km<sup>2</sup>.

overlapped, some whales might have been detected more than once; therefore, in order to determine the total number of animals within the circle, we plotted all whale positions from the photographs and did not double count any animals in the areas of overlap. All runs were flown

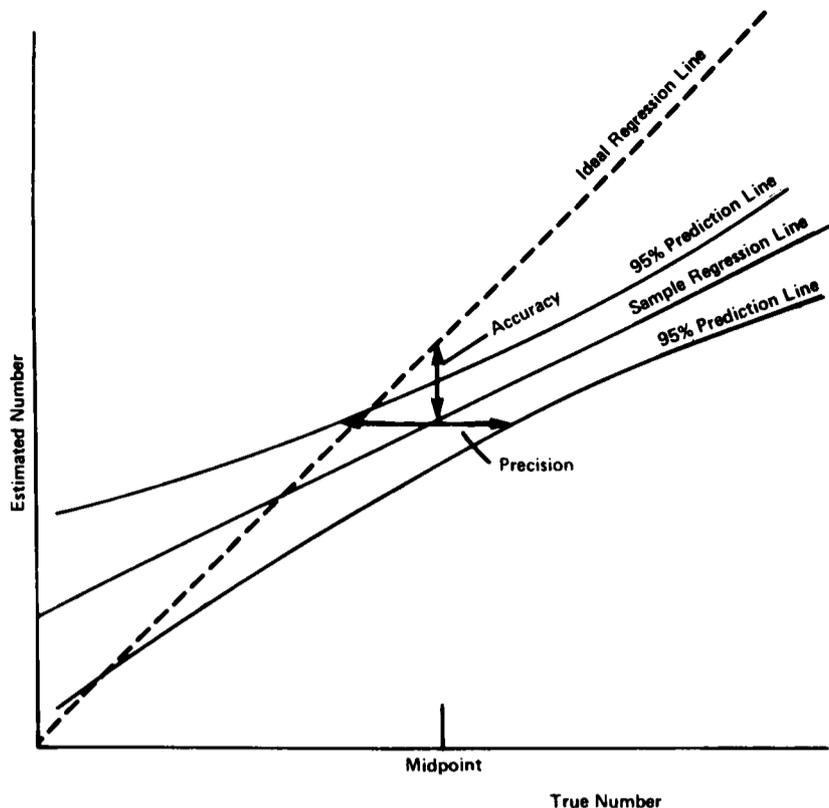


Fig. 10. A typical plot of a sample regression line as determined for each simulated-survey-flight observer viewing each species of marine mammal. In the case of the ideal regression line, the estimated number would be the same as the true number. Both the accuracy and precision were determined about the midpoint value of the true number. This is the value at which the 95% prediction lines are closest to the sample regression line.

in 20.5 min and within this short time the whales probably did not travel far, as none appeared to be moving rapidly from *polynya* to *polynya*. The result was a total count of 80 animals and a density of 7.07 animals/km<sup>2</sup> within the 11.32 km<sup>2</sup> area sampled. When each of the runs is taken separately, however, a great deal of variation is encountered. As Table 3 shows, from 0 to 61 animals were sighted on the various runs. Densities ranged from 0/km<sup>2</sup> to 124.2/km<sup>2</sup>, with a mean of  $28.7 \pm 47.5$ /km<sup>2</sup>. Unfortunately, we were unable to partition the variance between that due to sampling and that due to different proportions of animals submerged.

Contrary to problems of sightability, which can be reduced but not eliminated by replicate sampling, problems of accuracy and precision associated with visual surveys can be entirely eliminated by remote sensing methods, due to the fact that remote sensing yields 'hard-copy' data which can be examined at leisure and repeatedly. Our test of the variation involved in visual surveys utilized some of the same images from which our other data were acquired (see Methods). Each participant recorded his estimate of the number of bowheads, white whales, and walrus on each scene appearing on the screen. A regression equation was determined for each individual viewing each species. As shown in Fig. 10, if the number estimated by the observer was the same as the number of animals actually present in the scene, the regression line would have a slope of unity; a typical regression line is shown with a slope of less than unity, illustrating this observer's underestimation of animals present. Fig. 10 also illustrates accuracy and precision. Both are measured at the midpoint value in the range of the true numbers of animals presented in the different scenes of the test. The accuracy is the difference between the estimated and true number at that midpoint value.

Table 4

Accuracy and precision of individuals estimating numbers of whales

	Observers estimating		Mean percentage accuracy	Mean percentage precision
	Over	Under		
White whale: 80 scenes; midpoint value 9 animals per scene				
Experienced walrus observers	2	4	11.3	$\pm 59.7$
Experienced whale observers	2	6	14.9	$\pm 49.5$
Pilots	1	3	21.7	$\pm 28.7$
Novices	3	14	23.2	$\pm 54.9$
Bowhead: 80 scenes; midpoint value 5.5 animals per scene				
Experienced walrus observers	0	6	18.0	$\pm 7.8$
Experienced whale observers	0	8	22.2	$\pm 8.3$
Pilots	3	1	11.9	$\pm 12.9$
Novices	2	15	27.3	$\pm 45.3$

The precision is a measure of the 95% confidence interval for the true number of animals in a scene, given that the participant estimated a number equal to the midpoint value.

The results given in Table 4 show that the majority of observers underestimated the numbers of bowheads or white whales in a scene, i.e. the slope of the regression line is less than one. For the white whale, observer experience improved accuracy, but did little for precision. For the bowhead, the major difference between experienced and unexperienced observers was the increased precision of the experienced observers. Among the experienced observers, most of the individuals who were more accurate were also more precise in their estimates for both white whale and bowhead. On the other hand, there was no correlation between individual accuracy and precision for either the pilots or the novices. For no category of observers was there any correlation between the individuals who were more accurate or precise in estimating numbers of white whales and those who were more accurate or precise in estimating numbers of bowheads. Tests such as these can be used to train observers and to obtain a correction figure and a confidence interval for the estimates observers make during actual aerial censusing flights.

## DISCUSSION

Even though BESMEX was largely devoted to the walrus, we have been able to gather some important new data, all of which relate to the question of productivity for the bowhead and white whale. We have demonstrated the types of information that can be acquired by remote sensing techniques: (1) population numbers and the problems associated with estimating them, (2) population structure, (3) habitat, and (4) aspects of whale behavior. However, it must be emphasized that these data represent only a small sampling of the potential of this technology. Indeed, there is presently no more efficient way to acquire data on population ecology and behavior of sparsely distributed animals such as whales, which inhabit such large regional seas as occur within Beringia.

The study of cetaceans at sea is extraordinarily

difficult. Tillman (1980) has stated that the United States program on the bowhead is 'the most ambitious... ever devoted to a single species of large cetacean.' This program involving several agencies has led to a better understanding of distribution and population numbers and has contributed data on behavior and habitat. Still, the determination of population production is not yet close to solution, and this is critical for management. The concern expressed during the 1979 meeting of the International Whaling Commission regarding recruitment in the bowhead population stimulated intensive work toward a better determination of productivity. At this writing, the matter is still under discussion. Our small sample indicating a proportion of young relative to adults of 19% is much more encouraging than the 3 to 4% obtained by previous estimates, which may have been low for a number of reasons related to sightability and the survey methods used. There are considerable problems of detection of calves by means of visual observations from ships, ice stations, or low-flying aircraft. Calves usually stay closer to their mothers than do other whales, as our data illustrate, and conditions of light, turbidity, position on the far side of the female from the observer, and habitat, all serve to shield them from view. It should be obvious that aerial photography can help solve this aspect of sightability. However, sample sizes of photographed and measured whales must be significantly increased before anyone can take comfort in the higher productivity values reported from our study.

Productivity estimates will be improved not only by better detection of calves but also by better estimates of all segments of the population. Krogman (1980) pointed out that most survey error is 'associated with how well observers are able to count whales.' Our data for accuracy and precision indicate unacceptable variances are associated with visual methods. Remote sensing can entirely remove these variables. In their comprehensive review of marine mammal censusing methods, Eberhardt, Chapman and Gilbert (1979) concluded, as we do, that counts should be made from photographs wherever possible.

Unfortunately, group and population structure are aspects of population assessment that have been given lower priority than population enumeration. Photographs allow population structure to be determined at the same time as population enumeration. One problem in population estimation which cannot be solved with photographs is that of determining the proportion of animals submerged during a survey. A solution to this problem must await the acquisition of much more natural history data and/or development of replicate sampling techniques which can 'map' whole groups, as we have done for the white whale. Radio-tagging, or other means for following individuals – and thus, also the groups to which the tagged animal belongs – should be viewed as a companion technology which can lead the observer or remote sensing aircraft to groups of animals for repeated observation. In this way, problems of non-random patterns of distribution might also be addressed for purposes of censusing.

It should be apparent that habitat and behavioral data are no less important in the long term than the counting of whales and their calves. In fact, without such data predictions about population trends may be made only

at great risk. An obvious example concerns the habits and habitats of whales as related to areas under development for oil and gas. Sea ice conditions play a dominant role in the distribution of white whales and bowheads for much of the year. For example, the September 1974 and August 1975 distributions of bowheads were very different. This is explained by the much heavier ice conditions of 1975, which held the animals well south of their usual Beaufort Sea habitat during August. Similarly, distributions during winter must vary according to sea ice conditions. Thus, simple geographic locations of whales and their average speeds of swimming should receive less emphasis than locations relative to sea ice and the specific behavior of groups, especially those with calves. Nevertheless, habitat analysis relative to sea ice has barely been addressed by those engaged in determining the environmental impact of oil and gas leasing. Instead, the presence of any whales, young or old, within stated lease areas is stressed, without much regard to the dynamics of populations or of ice, weather, and ocean productivity that are the *raisons d'être* of habitat selection.

Remote sensing of marine animals and their habitats has recently been the subject of a conference (Botkin, Hobbs, Kelly and Pecan, 1981) that concluded, in part: 'In spite of its great potential, remote sensing remains greatly under-utilized. Its practicality has been questioned, funding limited, and communication among agencies and administrators about the utility of the available techniques sorely lacking.' One reason is the presumption that costs are excessive. Such a presumption does not bear close scrutiny. Using the best available camera systems which can provide a resolution to 5,000 m comparable to what we obtained at 1,000 m, the cost per surveyed km<sup>2</sup> is less than a quarter the cost of using conventional aircraft for visual survey.

Remote sensing is a multi-level, multi-spectral technique which can integrate a large array of data, from the level of 'ground truth' to aircraft to satellite. At the rather simple level at which we have worked, using only aircraft and photography, we have demonstrated that data on whale numbers, behavior, and habitat can be gathered at the same time and on a quantified basis. A 'picture' of whale groups at a moment in time emerges. This is in sharp contrast to the single parameter data acquisition of more conventional means. We, thus, hope to have demonstrated the essential nature of remote sensing. When such parameters as ice dynamics and ocean temperature and color (indicating chlorophyll, turbidity, etc.) are added at the regional level by satellite or aircraft, the advances in knowledge that can be acquired should be obvious.

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# The Potential Value of Electronmicroscopy to Elucidate the Function of Corpora Lutea in Small Cetaceans

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## ABSTRACT

Electronmicroscopy has been used to determine the functional status of the corpus luteum in many mammalian species. This morphological technique may help to elucidate the following in Cetacea: (1) the function and relative significance of different cell types in the corpus luteum; (2) whether changes in the capacity of cells of the corpus luteum to secrete steroids occur throughout the oestrous cycle and pregnancy; (3) whether cells retain some function after the involution of the corpus luteum.

## INTRODUCTION

Studies of the reproductive biology of totally aquatic mammals are extremely difficult. The animals are large, and highly mobile in their natural environment. Any form of restraint involves large investment in time, manpower and resources, and possibly stresses the animals, thus affecting their normal reproductive physiology. For these reasons there is little accurate information about even the major reproductive events in most species (such as seasonality, the time sequence of development and involution of the corpus luteum, and whether ovulation is spontaneous or induced). Most of what is known is based on anatomical observations of the gonads and reproductive tract. Planned physiological and endocrinological experiments using free-ranging animals would involve enormous practical difficulties and so far have not been attempted.

A major difficulty in attempting to deduce reproductive events from the morphological appearance of the reproductive organs in small cetaceans is that it has been impossible to distinguish between the cyclic corpus luteum and the corpus luteum of early pregnancy. This has meant that several important questions have remained unanswered. For example, it is not known whether there is an embryonic diapause in this mammalian group. Corpora lutea involute to form corpora albicantia, which in many species are believed to persist until death.

It is only rarely that an opportunity arises to collect ovarian material from dolphins for ultrastructural study, because samples must be fixed very soon (maximum of a few minutes) after death. The purpose of this paper is to outline a method of collecting material for electron microscopical examination, and to demonstrate the need for more exacting morphological observations of the corpus luteum to attempt to elucidate some of the aspects of reproductive biology of small cetaceans outlined above. The potential value of ultrastructural observations of the corpus luteum will be discussed in the light of previous microscopical examination of dolphin ovaries and electron microscopical studies of the corpus luteum of other mammalian species.

## FIXATION FOR ELECTRONMICROSCOPY

Rapid fixation within a few minutes of death is essential.

### (a) Perfusion

The preferred method of fixation is by perfusion of the entire organ, although this is not possible in most situations in which cetacean material is collected. Details of the method used varies among different laboratories, but the general principles are now well established and are similar. In Queensland we infuse all fluids at approximately the same rate as the flow of blood in the vessel being used, and employ the following procedure:

As soon as possible after death, preferably before intravascular clotting occurs, the organ is perfused with heparinized saline via the ovarian artery until the fluid draining from the severed ovarian vein is quite clear. In the laboratory a Harvard infusion pump is used for perfusion, although infusion by gravity pressure or with a large hypodermic syringe gives excellent results and can be done easily in the field.

The ovary is perfused then with a solution containing 1% paraformaldehyde and 1.25% glutaraldehyde in 0.067 M sodium cacodylate buffer, followed immediately by a second solution containing 4% paraformaldehyde and 5% glutaraldehyde in 0.067 M cacodylate buffer.

After adequate fixation by perfusion, the ovary is quite rigid. It is removed and immersed overnight in the second perfusion solution, then transferred to 0.1 M cacodylate buffer (pH 7.2) in which it can be stored and transported.

Subsequently in the laboratory small blocks of tissue removed from the organ (see (b) below) are postfixed in 1% osmium tetroxide in cacodylate buffer, dehydrated and embedded in Epon or Araldite.

### (b) Immersion fixation

This method is employed where perfusion is impossible or impractical. A small block of tissue to be fixed is removed as soon as possible after death, and thin slivers cut from it with a sharp razor blade or scalpel. The most important points are that the tissue should not be squashed down with the cutting instrument, and the pieces of tissue should be thin, that is 0.5 mm or less. Fixation is in 1% paraformaldehyde and 1.25%

glutaraldehyde in 0.067 M cacodylate buffer for 10 to 30 minutes, 4% paraformaldehyde and 5% glutaraldehyde for approximately 2 hours, then transfer to 0.1 M sodium cacodylate buffer at pH 7.2.

Subsequent treatment is the same as for perfusion-fixed tissue.

#### POTENTIAL VALUE OF ULTRASTRUCTURAL EXAMINATION OF CORPORA LUTEA

The gross morphology and cell structure of the corpus luteum vary among species. In Cetacea it is a large structure that protrudes from the surface of the ovary. Many descriptions of the ovaries of dolphins have been limited to accounts of the gross appearances and records of weights, and conclusions have been drawn from these observations. Benirschke, Johnson and Benirschke (1980) and Harrison, Bryden, McBrearty and Brownell (1981) have cautioned that major errors can be made using macroscopic examination only and pointed out the necessity to examine material microscopically.

The presence of a large corpus luteum with histologically fully-formed luteal cells does not confirm that the corpus luteum is physiologically active. Electron microscopy has been used to determine the functional status of the corpus luteum in other species, and examination of corpora at different stages of the estrous cycle and of pregnancy would contribute to our understanding of luteal function in dolphins. Cellular organelles such as smooth endoplasmic reticulum, lipid and secretory granules (Fig. 1) are indicators of the ability of the corpus luteum to synthesise and secrete steroid hormones (Gemmell and Stacy, 1979). The secretion of granules seems to be associated with the secretion of progesterone from the gland. When the corpus luteum of the sheep is inactive, very few if any granules are present, whereas in the actively secreting gland there seems to be a correlation between the density and secretion of granules and the levels of circulating progesterone in the plasma (Gemmell, Stacy and Thorburn, 1974, 1976).

The presence of different and apparently secretory cell types in the corpus luteum has been observed in Artiodactyla (Fig. 2) (Donaldson and Hansel, 1965; Bjersing, 1967) as well as other mammalian groups (Gemmell, 1980), and the large and small cells of the corpus luteum have been the subject of intense study recently in an attempt to define their relative functional significance (Koos and Hansel, 1981). Two cell types that are histologically distinct are particularly clearly defined in the cetacean *Pontoporia blainvillei* (Harrison and Brownell, 1971; Harrison *et al.*, 1981). An ultrastructural study of the corpus luteum of this species could make a valuable contribution to our understanding of the functional significance of these different cell types, should suitable tissue samples become available. However it is known that other cetacean species also display two secretory cell types in the corpus luteum (see Marsh and Kasuya, 1984).

The endocrinological status of the corpus luteum can be determined by assaying the steroid content of the entire organ (Lukaszewska and Hansel, 1980), but ultrastructural observation is preferable in animals as difficult to procure as dolphins. Ovaries preserved for chemical analysis must be frozen, thus rendering them unsuitable

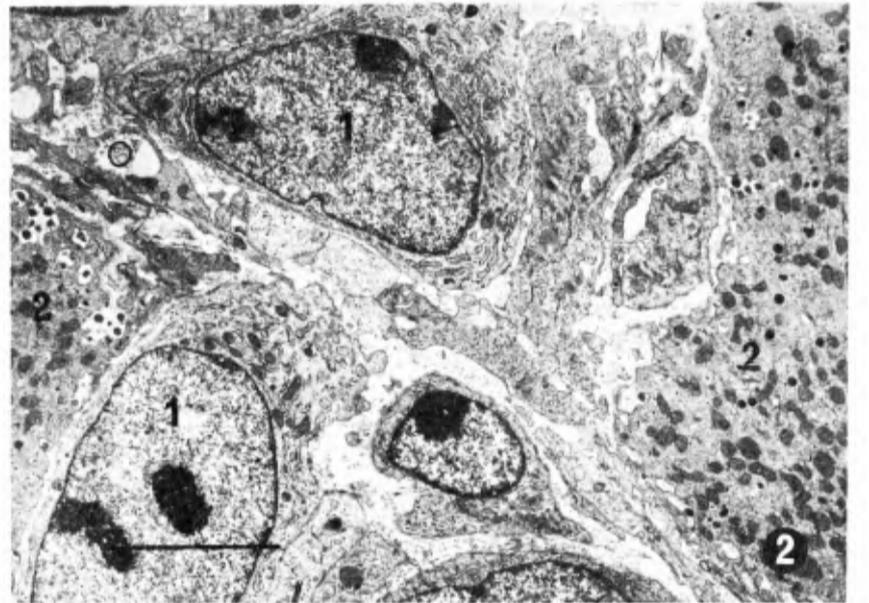
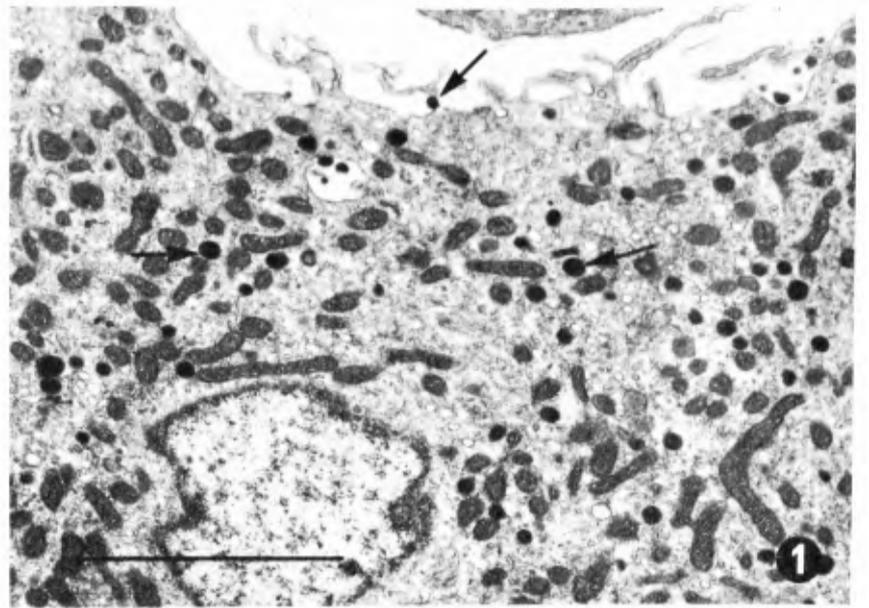


Fig. 1. Electron micrograph of a luteal cell in the corpus luteum of the sheep. The presence of granules (arrows) has been related to the secretion of progesterone. (Bar = 1.1  $\mu$ m)

Fig. 2. Different cell types, designated 1 and 2, in the corpus luteum of the sheep. The smaller cells (1) contain large amounts of granular endoplasmic reticulum and are believed to be protein-secreting cells; the larger cells (2) show characteristics of steroid-secreting cells. Note the presence of more granules in the larger cells. (Bar = 1.7  $\mu$ m)

for morphological study. Fixation by perfusion is preferable to immersion fixation, because the entire ovary is fixed and portions can be removed later if further examination of other parts is required. On the other hand, if both endocrinological and morphological data are required, then immersion fixation can be employed and the remaining tissue frozen for subsequent assay.

Comparative ultrastructural studies of the corpora albicantia may indicate why they are not absorbed, or at least why they involute very slowly. It is important to know if they show sequential ultrastructural and/or biochemical change with age, and whether they have any active function during involution. We have observed histologically intact cells in cetacean corpora albicantia, which may indicate some residual function of the bodies for a period after involution of the fully active corpus luteum.

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# Immunocytochemical Identification of Growth Hormone and Prolactin Cells in the Cetacean Pituitary

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## ABSTRACT

Prolactin- and growth hormone-producing cells were identified in the pituitaries of several cetacean species using peroxidase-anti-peroxidase immunocytochemistry. Antibodies to human and ovine pituitary hormones cross-reacted sufficiently to produce specific staining of lactotrophs and somatotrophs in the cetacean pituitaries examined. Lactotrophs were less numerous than somatotrophs and more variable in shape. Groups of somatotrophs were commonly found near capillaries and tended to contain more granules per cell than lactotrophs. The significance of the cross-reactivity with regards to future research on cetacean reproduction is discussed.

## INTRODUCTION

The anterior pituitary gland is known to secrete at least six hormones which enter the circulatory system and serve to partially regulate a variety of peripheral tissues. The pituitary is regulated, in turn, by the central nervous system through a complex of hypothalamic releasing and inhibiting factors that are secreted into its blood supply. There has been a great deal of research on pituitary structure and function of many terrestrial mammals, but relatively little is known about this gland in marine mammals. Previous anatomical investigations of the cetacean pituitary have been summarized by Arvy (1971) and Harrison (1969). These reports describe in some detail the gross anatomy of pituitaries from many cetaceans, but in his review of this work, Harrison (1969) observed that the most recent anatomical techniques have not been applied to the identification and characterization of the cell types of the cetacean pituitary. In the most detailed study of the cetacean anterior pituitary published to date, Young and Harrison (1970) investigated the ultrastructure of some common dolphin (*Delphinus delphis*) specimens in which they were able to differentiate four hormone-producing cell types. Based on granule size, cell morphology, and relative frequency, these cells were tentatively identified as lactotrophs (prolactin), somatotrophs (growth hormone), gonadotrophs (luteinizing hormone and follicle stimulating hormone), and thyrotrophs (thyroid stimulating hormone). However, they were not able to identify corticotrophs (ACTH).

The anatomical technique of immunocytochemistry is widely used in studies of mammalian pituitaries (for review see Moriarty, 1973) because of the accuracy with which the various hormone-producing cells can be differentiated. The purpose of this study was to identify growth hormone and prolactin cells in the anterior pituitaries of several cetaceans using antibodies to both ovine and human hormones. We investigated the degree to which antibodies to protein hormones from other mammalian species can cross-react with cetacean hormones in a specific manner. This cross-reaction is important since it is presently difficult to isolate cetacean

hormones in sufficient quantities to produce antibodies specifically to these hormones. Furthermore, the cross-reactivity demonstrated in this study could be the basis for the development of a heterologous radioimmunoassay that would measure circulating levels of pituitary hormones in cetaceans.

## MATERIALS AND METHODS

### (a) Histology

Pituitaries were obtained from two stranded cetaceans, an Atlantic spotted dolphin (*Stenella plagiodon*, Field # C-80-5, 197 cm) and a pygmy killer whale (*Feresa attenuata*, Field # C-80-3, 197 cm), and from a captive killer whale (*Orcinus orca*, Field # C-80-4, 700 cm) that died of a mycotic aneurysm in the right cerebral hemisphere (G. Hensley, 1981, pers. comm.). All three animals were prepuberal males as determined by testes weights and histology.

The pituitaries were removed within 12–36 hours of death, but the gland from *Orcinus* seemed to have been the best preserved.

Parts of each gland were fixed in 10% phosphate buffered formalin, dehydrated, and embedded in paraffin. Sections from these blocks were stained with hematoxylin and eosin to assess the quality of fixation. The remaining portions of each gland were cut into 1-mm<sup>3</sup> blocks, fixed for one hour in 1.5% glutaraldehyde in 0.05 M phosphate buffer (pH 7.4), washed in buffer alone, dehydrated through an ethanol series and embedded either in Epon 812 or paraffin. The paraffin blocks were sectioned at 5  $\mu$ m while the Epon-embedded material was sectioned at 1  $\mu$ m.

### (b) Immunocytochemistry

The peroxidase-antiperoxidase (PAP) immunocytochemical technique was developed by Sternberger, Hardy, Culculis and Meyer (1970), modified for electron microscopy (EM) by Moriarty and Halmi (1972), and adapted to light microscopy (LM) of epoxy-embedded tissue sections fixed for EM by Baskin, Erlandsen and Parsons (1979).

As applied to the study of pituitary tissue, this technique consists of the sequential application of three

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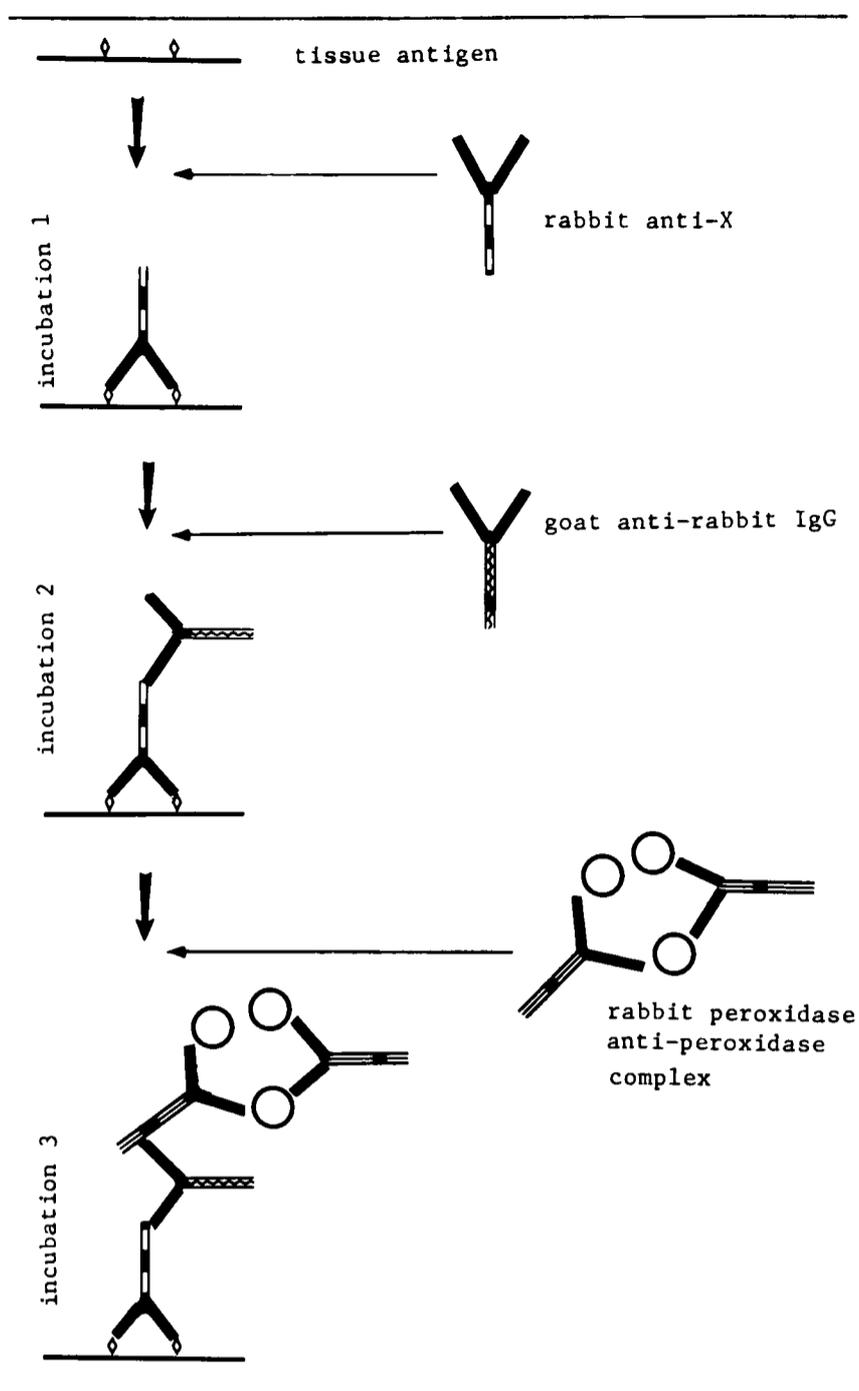


Fig. 1. Diagram of the peroxidase-antiperoxidase (PAP) technique. Incubation one, addition of primary antiserum to tissue. Incubation two, addition of goat anti-rabbit antiserum. Incubation three, addition of the soluble peroxidase-antiperoxidase complex. See text for further explanation. (After Sternberger *et al.*, 1970).

different antisera followed by a chromagen, which allows the visualization of the location of the antibody complexes on the tissue section (see Fig. 1). Since the primary antibody determines the target for the entire staining reaction, this antibody is usually specific for one hormone (or portion thereof) and therefore indicates the cells that contain that hormone. The primary antibody is produced by obtaining a highly purified sample of hormone from the species in which the investigation is to be conducted, injecting it into a different species (e.g. rabbit), and later recovering the immunoglobulin fraction from the serum of the antibody-producing species. When this antibody is applied to tissue sections, it binds to the sites that contain the hormone to which it was made.

Immunoglobulins from the antibody-producing species are used as antigens for production of the secondary antiserum in a different species (e.g. goat-anti-rabbit). The secondary antibodies will thus bind to the primary antibody. Since antibody molecules have two available binding sites, every molecule of secondary antibody bound to the primary antibody has an open site specific

for immunoglobulins from the species in which the primary antibody was produced.

The tertiary antibody is produced by injecting purified peroxidase enzyme into the same species in which the primary antibody was raised. This results in a complex of peroxidase-antiperoxidase (PAP) that will bind to the open site of the secondary antibody. Finally, the peroxidase enzyme is used to catalyze a reaction of diaminobenzadine (DAB), turning it from a clear, soluble molecule to a brown, insoluble precipitate. Since the reaction takes place at the site of PAP binding, the resulting brown deposits locate the hormone under investigation.

The following procedure was used in this study:

- (1) Epon-embedded sections of 1  $\mu$ m thickness were mounted on glass microscope slides. The Epon was then removed by application of saturated sodium hydroxide in ethanol, which was first diluted 1:1 with 100% ethanol (Baskin *et al.*, 1979).
- (2) The slides were rinsed first in 100% ethanol, and then in phosphate buffer.
- (3) Normal goat serum (1:100) was applied for 15 minutes to block non-specific binding of secondary antiserum.
- (4) The primary antibody was applied to the tissue sections and incubated for 24–48 hours in a moist chamber at 4 °C. Dilutions of 1:500 to 1:10,000 were tried for each antibody to determine optimal concentration for maximal staining with lowest background interference.
- (All following steps were at room temperature)
- (5) The slides were rinsed in phosphate buffer. The second antibody (goat-anti-rabbit) was diluted 1:200 and incubated for 30 minutes on the sections.
- (6) After a buffer rinse, the PAP complex (1:250) was incubated for 30 minutes on the tissue.
- (7) DAB (2.9 mg) was dissolved in 10 ml of 0.05 M Tris buffer (pH 7.6). With constant stirring, 8 drops of 3% hydrogen peroxide were added immediately before use. This solution was applied to the sections for 30–45 minutes until sufficient staining reaction was observed.
- (8) After rinsing in Tris buffer, the sections were either dehydrated and mounted directly, or first counterstained with hematoxylin (1–3 minutes) to allow observation of unstained cells.

The following modifications were used with paraffin embedded tissue in immunocytochemical experiments:

- (1) Tissue sections were cut at 5  $\mu$ .
- (2) The paraffin was removed by xylene and the tissue was rehydrated according to routine histological methods.
- (3) DAB incubation time was shortened to 3–5 minutes.
- (4) Hematoxylin counterstaining time was shortened to 0.5–1 minute.

All buffer wash steps were with 0.1 M phosphate buffer (pH 7.4). Human serum albumin (2.5 mg/ml) was added to 0.05 M phosphate buffer and was used as the diluent for all antisera. Diaminobenzadine was obtained from Sigma Chemical Co. (St Louis) while PAP and goat-anti-rabbit antiserum were purchased from Cappel Labs (Cochranville, Pa.). Primary antisera and purified anti-

gen were obtained from the National Pituitary Agency (NIAMDD). Specifically, the antisera used in this study were:

- (1) Human growth hormone antisera, NIAMDD-anti-hGH-1
- (2) Human prolactin antisera, NIAMDD-anti-hPRL-2
- (3) Ovine growth hormone antisera, NIAMDD-anti-oGH-2
- (4) Ovine prolactin antisera, NIAMDD-anti-oPRL-1

The following control experiments were utilized to demonstrate the specificity of the staining:

- (1) The primary and secondary antisera, PAP, and DAB were either eliminated from the protocol or replaced by normal rabbit serum in individual experiments.
- (2) Prior to application to the tissue sections, each antiserum was pre-incubated for 48 hours (at 4 °C) with increasing amounts of its antigen. If the antiserum is specific for one hormone only, then a gradual reduction of staining intensity should be observed as the antigen concentration is increased.
- (3) Each antiserum was pre-incubated with other pituitary hormones of similar structure for 48 hours prior to a set of staining experiments. In this case, no diminution of staining should be observed.

## RESULTS

Examination of hematoxylin-and-eosin-stained pituitary tissue from the three cetacean species revealed typical cords of cells comprised of acidophils, basophils, and chromophobes, and occasionally areas filled with colloid material. Aside from absolute size, there was little observable morphological variation between the three species. While the quality of fixation was best in the *Orcinus* pituitary, several blocks had to be sectioned before adequately fixed tissue was found in the *Stenella* and *Feresa* specimens.

Somatotrophs and lactotrophs were investigated using immunocytochemical techniques on both Epon and paraffin sections. However, the thinner epoxy sections provided greater resolution and were found to stain at least as well as the more traditional paraffin sections. Therefore, 1  $\mu\text{m}$  sections of Epon-embedded tissue were used in most experiments, except when background staining interfered with slide analysis, and paraffin sections were used to verify the results.

We observed positive staining for both growth hormone (GH) and prolactin (PRL) containing cells in all three species. Ovine and human antisera were equally effective in staining these cell-types. The optimal dilutions for both hormones were 1:1,000 and 1:5,000 for 24 and 48 hour incubations respectively. Both cell types were more numerous in the lateral parts of the gland than in medial sections, but GH cells were found in all sections. The small number of prolactin cells relative to other cell types is typical of prepuberal male mammals (Baker, 1975).

An Epon section from the *Orcinus* pituitary stained with anti-human PRL is shown in Fig. 2. Large, stained granules can be seen in the cytoplasm of lactotrophs surrounding a relatively clear nucleus. Background counterstained nuclei can be seen in most of the section.

Lactotrophs were far less numerous than somatotrophs and more variable in shape. At higher magnification (Fig. 3), individual granules can be seen in the cytoplasm surrounding unstained nuclei. Plasma and nuclear membranes of unstained cells are also visible.

Another section of the same tissue block stained with anti-human GH is shown in Fig. 4. These cells are far more numerous than lactotrophs, less variable in shape, and tend to occur in groups near capillaries. There are usually more granules per cell, as well. These cells have a prominent nucleus and Golgi body at the light microscopic level.

In order to demonstrate the specificity of the cross-reaction between anti-human antiserum and cetacean hormone, control experiments were conducted in which increasing quantities of antigen were pre-incubated with the antiserum at its final dilution. Anti-GH (1:1,000) was pre-incubated with 100 ng, 1  $\mu\text{g}$ , 10  $\mu\text{g}$ , and 20  $\mu\text{g}$  of human GH for 48 hours. Diminished staining was observed with increasing amounts of hormone and was totally eliminated with 20  $\mu\text{g}$ . A similar experiment was conducted using anti-PRL and identical concentrations of human PRL, with similar results (Fig. 5). The possibility of GH antibodies cross-reacting with PRL was tested by incubating 1:1,000 anti-GH with up to 30  $\mu\text{g}$  of human PRL, which resulted in no diminution of staining intensity or number of cells stained. Similar results were obtained with 20  $\mu\text{g}$  GH incubated with 1:1,000 anti-PRL. Finally, the possibility of non-specific staining by primary, secondary and tertiary antibodies was eliminated by substituting non-immune serum for each antiserum in separate experiments. This resulted in the complete elimination of staining.

## DISCUSSION

In this study, we used the PAP immunocytochemical technique to identify growth hormone and prolactin cells in the anterior pituitary glands of three cetacean species. The results clearly show that antibodies to human and ovine GH and PRL cross-react sufficiently with cetacean hormones to allow specific staining of the cells containing those hormones. To our knowledge, this is the first use of the PAP immunocytochemical technique on any cetacean tissue.

Due to the lack of ultrastructural observations on these cells, and incomplete identification of other cell types typically found in the mammalian pituitary, precise characterization of anterior pituitary cell types is not yet possible. However, based on light microscopic observations, both PRL and GH cells are similar in morphology and location to those identified in other cetaceans (Wislocki and Gieling, 1936; Young and Harrison, 1970; Arvy, 1971), in pinnipeds (Leatherland and Ronald, 1978), and in many terrestrial mammals (Moriarty, 1973; Baker, 1975).

The quality of fixation is a critical factor in the preparation of tissue for immunocytochemistry. When working with cetaceans however, one must utilize tissue from animals that have died either from natural causes, accidental catches, or from whaling operations. Even under optimal conditions, it is difficult to remove the pituitary gland from these animals in less than several hours after death. However, tissue quality at necropsy is

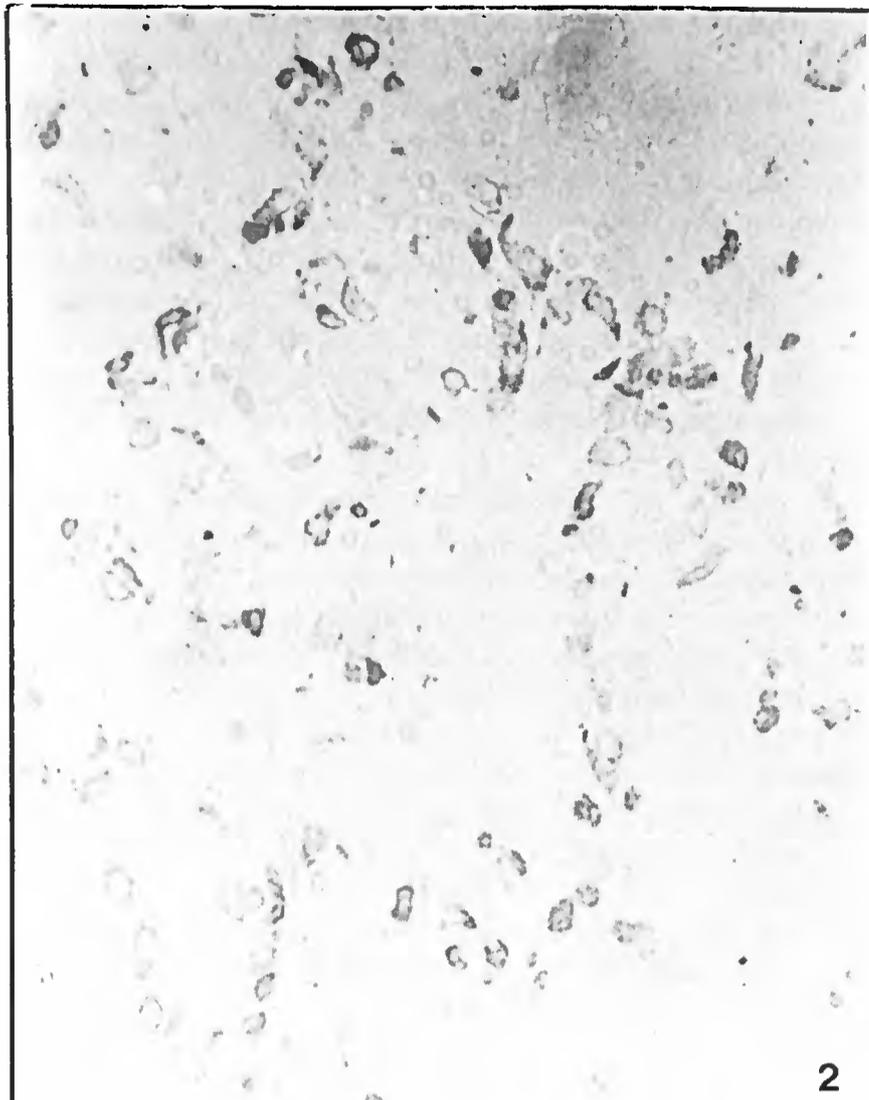


Fig. 2. Anterior pituitary section (*Orcinus orca*) stained with anti-human prolactin (1:1,000). These cells are variable in shape and granule content. (70 $\times$ ).

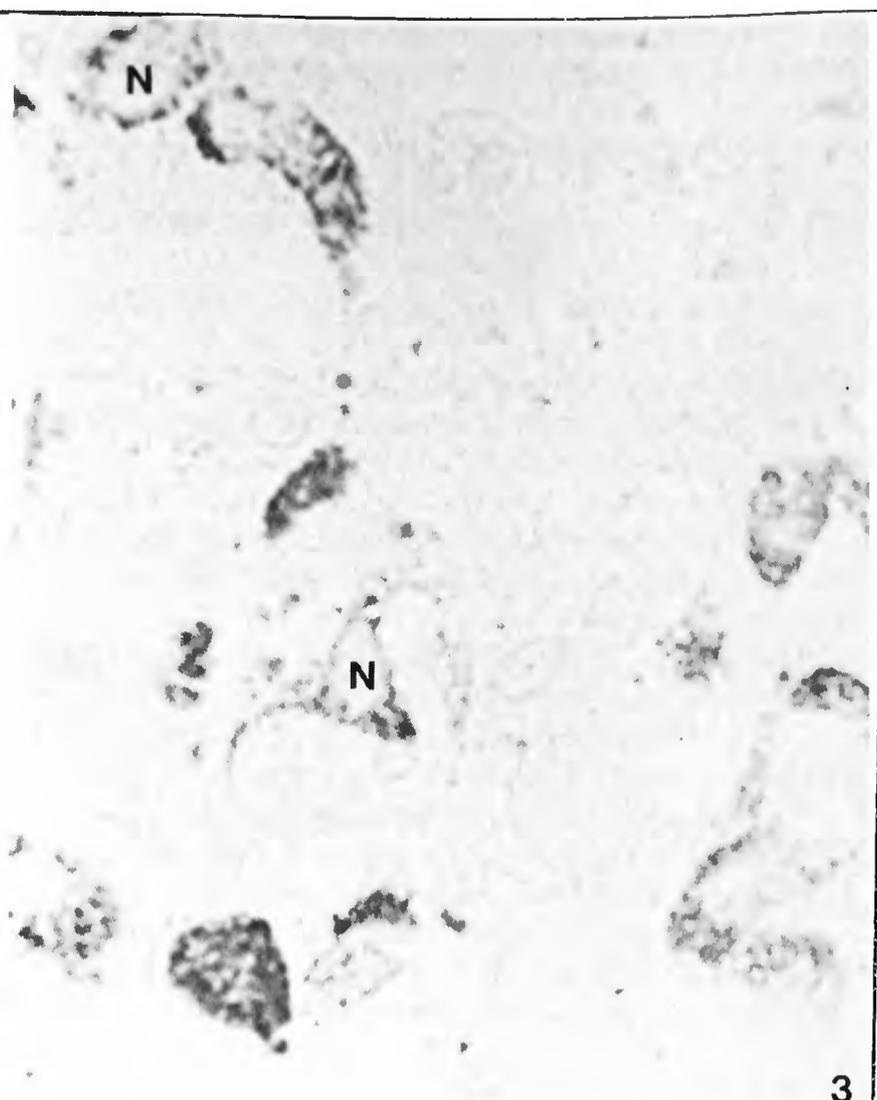


Fig. 3. High magnification of Fig. 2 showing details of cellular morphology. Nuclei (N) are surrounded with darkly staining cytoplasmic granules. Non-prolactin cells are counterstained with hematoxylin. (350 $\times$ ).

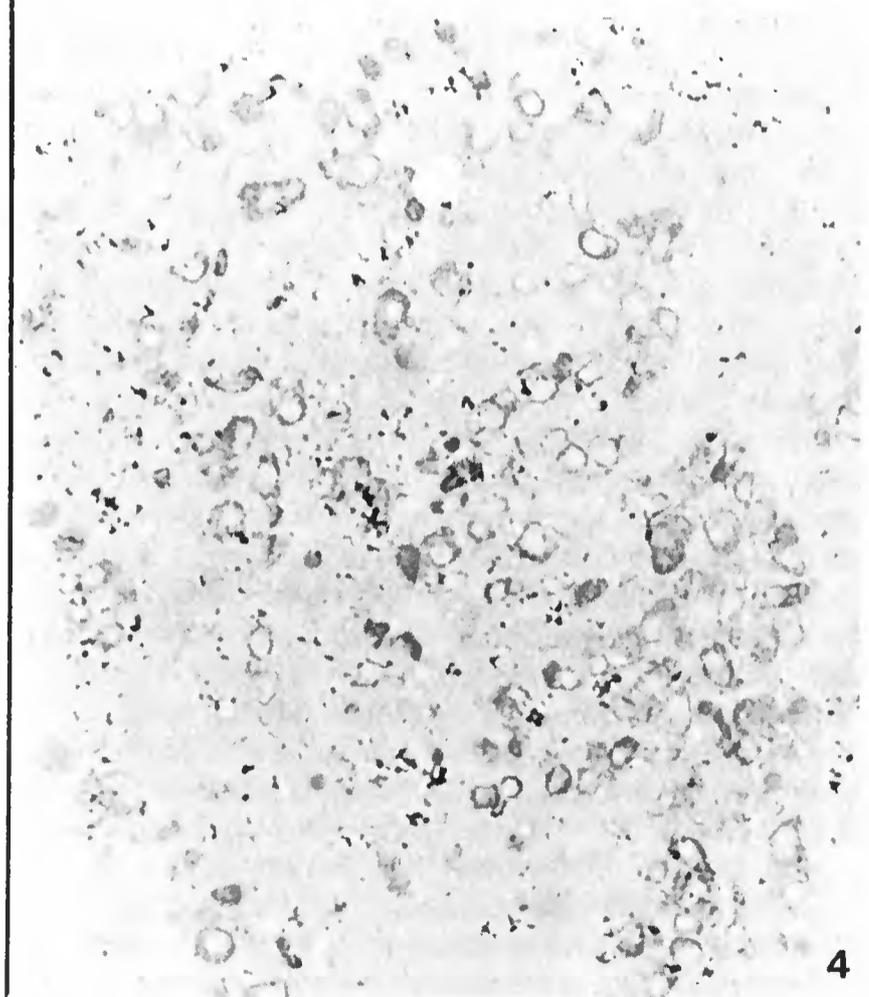


Fig. 4. Epon section from the same block as Fig. 2 stained with anti-human growth hormone (1:1,000). Cells are more regular in shape and contain more granules in their cytoplasm as compared with lactotrophs. (80 $\times$ ).

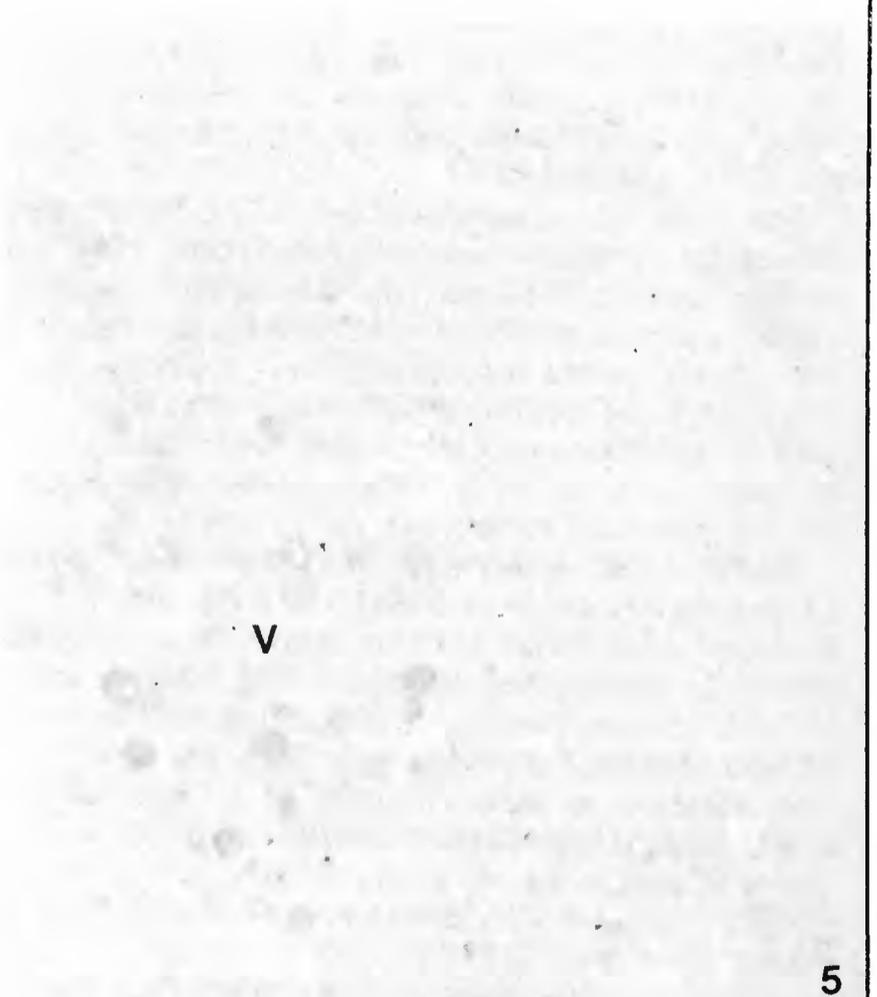


Fig. 5. Anterior pituitary section (*Orcinus orca*) stained with anti-human prolactin previously incubated for 48 hours with 20  $\mu$ g of human prolactin. No hormone producing cells were stained, indicating that the antibody is specific for cetacean prolactin. Red blood cells within a large vessel (v) exhibit non-specific staining due to endogenous peroxidase. (350 $\times$ ).

improved dramatically if the whole animal, or at least the head, is refrigerated until the pituitary can be removed. Under optimal conditions, we have obtained pituitary tissue that, when examined in the electron microscope, shows that most cells are intact, the nucleolus and chromatin are normal, and mitochondrial membranes are slightly swollen, but intact. This was approximately the condition of our *Orcinus* specimen. Although 18 hours elapsed between death and pituitary removal, the water in which this animal was kept was refrigerated and seems to have retarded autolysis. The *Feresa* specimen was beached for some time before the carcass was refrigerated, and the pituitary was not removed until about 36 hours after death. Thus, while the tissue had been refrigerated, autolysis became a significant factor due to the lengthy delay before fixation. The specimen of *Stenella* was recovered and autopsied within eight hours. However, this animal remained on a sunny beach for most of that period, which seems to have contributed significantly to the rapid autolysis. Since the quality of fixation of the *Orcinus* pituitary was found to be superior to the others, it was used more extensively in this study.

The use of antisera to hormones from one species to demonstrate location of cell types in another is not unique. For example, fish pituitaries have been examined for some time using anti-ovine, anti-bovine, and anti-human antisera (Follenius, Doerr-Schott and Dubois, 1978; Margolis-Kazan and Schrieberman, 1981). However, the techniques for quantitatively comparing the cross-reactivity of antibodies require a significant amount of purified (at least partially) hormone from the species being studied (e.g. for fish, see Follenius *et al.*, 1978). Since this is not presently available for cetaceans, we have relied on qualitative assessments of cross-reactivity between various antibodies and cetacean pituitary hormones by comparing the degree of staining at different antibody dilutions. On this basis, we found that ovine and human antisera were about equally effective in binding hormones in cetacean pituitary tissue.

Childs and Ellison (1980) discuss some of the problems and inadequacies of the PAP immunocytochemical technique. We have used iodination-grade antigen in adsorption controls and the highest working antibody dilutions without loss of staining. These steps reduce the possibility that impurities in the antiserum will be masked by impure antigen and limit the probability of non-specific staining. Another criterion for determination of antibody specificity is whether different cells are stained with different antisera in adjacent sections. In the present study, we found different cells were stained by anti-prolactin than by anti-growth hormone in adjacent sections for all three species studied. The differences in morphology of the two cell types further attests to the specificity of the staining.

Moriarty, Moriarty and Sternberger (1973) found PAP immunocytochemistry was more sensitive by several orders of magnitude than radioimmunoassay using identical antisera. With the capability to detect non-specific antibody binding or impurities in the antisera through careful controls and analysis of serial sections (Childs and Ellison, 1980), this technique affords an excellent opportunity to investigate cross-reactivity of various antisera across species lines (Margolis-Kazan and Schrieberman, 1981). This greatly facilitates development

and validation of a radioimmunoassay, since many characteristics of the antibody (specificity, avidity, etc.) can be pre-determined. Furthermore, when working with a novel species for which no homologous antibody is available, the degree of cross-reactivity (if any) of antiserum from other species can be tested directly on the tissue where the antigen is produced.

In this study we have shown that antibodies to human and ovine PRL and GH will cross-react with similar hormones in three cetacean species. The binding is shown to be specific for both lactotrophs and somatotrophs. Using these or similar antibodies, it may be possible to develop a heterologous radioimmunoassay that will measure circulating levels of hormones in cetacean blood. We are currently using immunocytochemistry to identify the remaining cell types in the cetacean pituitary. Gonadotrophs are of particular interest, since measuring luteinizing hormone and follicle-stimulating hormone would be of tremendous value for investigations of cetacean reproductive endocrinology.

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**Session III**  
**Case Studies of Populations**



# Preliminary Assessment of Annual Calf Production in the Gray Whale, *Eschrichtius robustus*, from Pt Piedras Blancas, California

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## ABSTRACT

In 1980 and 1981 a census was made of northward migrating gray whales at Pt Piedras Blancas, California to (1) monitor the migration, with special attention to the presence or absence of females with calves, and (2) attempt an assessment of annual calf production based on calf counts. Whales were counted from shore 10 hours/day, 6 days/week for 12 weeks (10 March–31 May) in 1980 and for 16 weeks (9 February–30 May) in 1981. The northward migration was observed to be bimodal, consisting of two distinct pulses of whales temporally spaced. The first pulse (Phase A, February–March), primarily whales other than females with calves, had a mean date of passage in 1981 of 1 March. Phase B (April–May) consisted primarily of females with calves and had a mean passage date of 26 April in 1981. Totals of 1,268 adult and juvenile whales and 228 calves were observed in 1980; 3,087 adult and juvenile whales and 209 calves were observed in 1981. Aerial survey flights conducted in 1981 to verify the accuracy of shore counts yielded 257 adults and juveniles and 27 calves. Estimated total populations were  $15,238 \pm 1,261$  in 1980, containing  $691 \pm 69$  calves; and  $15,640 \pm 1,227$  in 1981, of which  $768 \pm 106$  were calves. Correcting for whales missed prior to the start of the survey brought estimates to 15,725 for 1980, and 16,140 for 1981. Estimated annual calf production (after approximately three months of calf mortality) was not less than 4.7% in 1980 and 5.2% in 1981.

## INTRODUCTION

Current estimates of the total population of the eastern-Pacific stock of the gray whale, *Eschrichtius robustus*, include 15,000 at Unimak Pass, Alaska (Rugh and Braham, 1979); 15,647 near Monterey, California (Reilly, Rice and Wolman, 1983); and 18,300 off the Oregon coast (Herzing and Mate, 1981). Each of these estimates was based upon data obtained from systematic shore counts during the southward migration. Shore counts originated at Point Loma, San Diego, California (Gilmore, 1960; Rice, 1961), and were later begun near Monterey, California in 1967 (Rice and Wolman, 1971; Wolman and Rice, 1979). They continued there uninterrupted through the winter of 1979/1980 (Reilly *et al.*, 1983).

In the calving lagoons of Baja California, Mexico, boat and shore surveys have been conducted (Swartz and Jones, 1980a, 1980b; Rice and Wolman, 1979; Mate and Harvey, 1981; Bryant and Lafferty, 1980) as well as aerial surveys (Hubbs and Hubbs, 1967; Gard, 1974; Rice, Wolman, Withrow and Fleischer, 1981).

The spring northward migration has not been studied as much as either the southward migration or the calving lagoons, and certain aspects of the northward migration have remained obscure, such as the migration path followed by females with calves (also called cow/calf pairs) and the number of these pairs (Rice and Wolman, 1971; Hatler and Darling, 1974; Darling, 1977; Herzing and Mate, in press). If both calves and adults can be counted during the northward migration, annual calf production (after some initial mortality) can be determined.

In the springs of 1980 and 1981, I conducted research during the northward migration along the central California coast. This study was based at Pt Piedras Blancas, San Luis Obispo County, California ( $35^{\circ} 40' N$ ;  $121^{\circ} 17' W$ ; approximately 160 kilometers south of

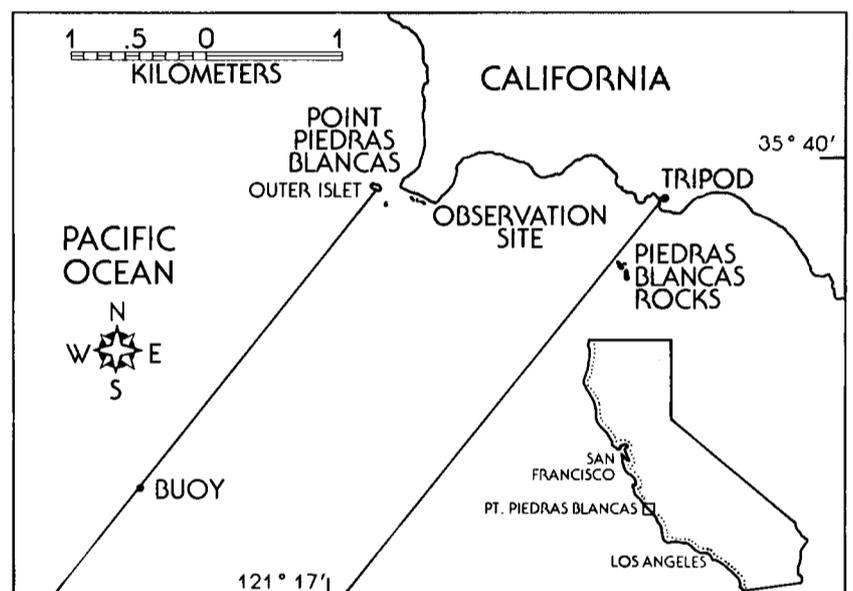


Fig. 1. Shore survey site at Pt Piedras Blancas, California showing observation zone.

Monterey and 240 kilometers north of Santa Barbara (Fig. 1).

One specific objective was to locate the migration corridor of females with calves (Poole, in press). This corridor was postulated to be farther offshore than the path used by the rest of the population (Rice and Wolman, 1971; Scammon, 1874; Townsend, 1887; Jordan, 1887; Starks, 1922). Should the migration corridor of females with calves (cow/calf pairs) be located, an attempt was to be made to assess the rate of annual calf production based on the calf counts.

## METHODS

### Shore surveys

Methods for shore-based data collection were similar to those described by Rice and Wolman (1971) and Reilly, Rice and Wolman (1980). Whales were counted from

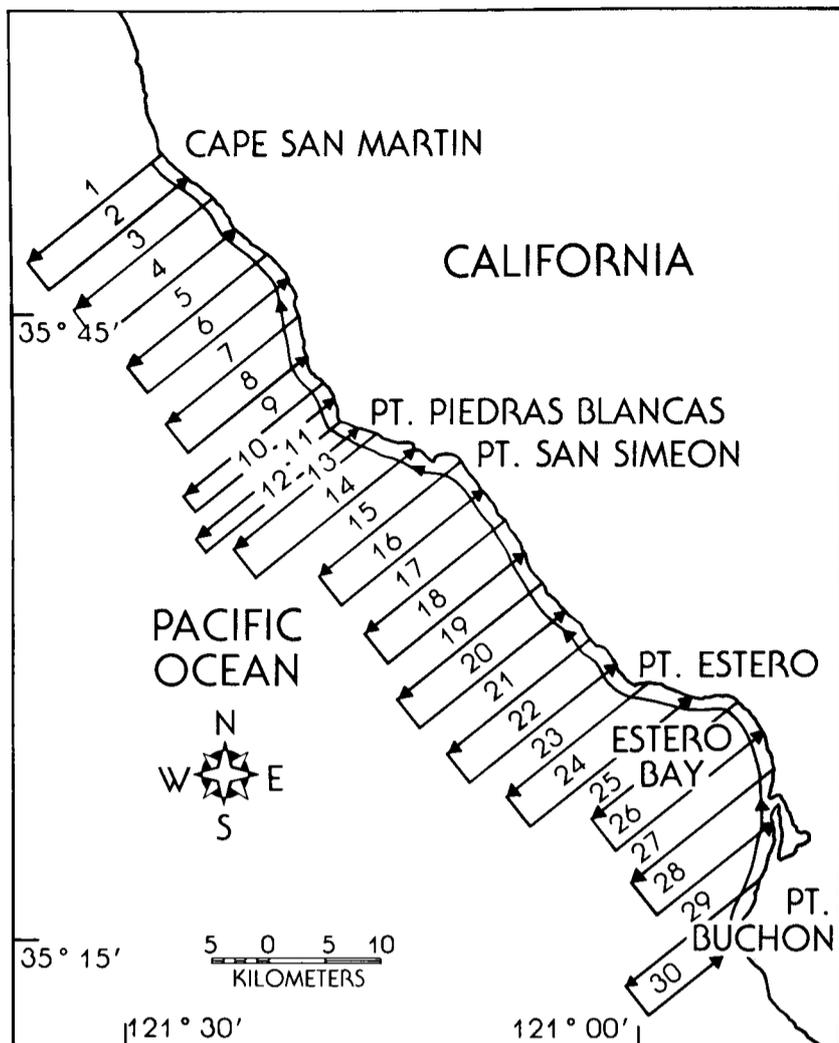


Fig. 2. Aerial survey transects from Cape San Martin to Pt Buchon.

shore 10 hours/day, 6 days/week for 12 weeks in 1980 (10 March–31 May), and for 16 weeks in 1981 (9 February–30 May). Work days consisted of two five-hour shifts (0700–1200, 1200–1700 PST) with two observers per shift. The observers monitored the movements of whales passing a 1.6-km length of coastline (Fig. 1). Boundaries of the study zone were demarcated using natural landmarks, a large tripod, and a Coast Guard buoy. Using 7×50 binoculars, a 20×–60× spotting scope, engineer's compasses, and on occasion a range-finder or surveyor's transit, the number of whales in a pod, relative positions of individuals (if determinable), and distances offshore were recorded. Individuals with distinctive scars and markings were photographed for future identification purposes. Behavior of the whales was also recorded. Wind velocity, sea state, and visibility conditions were noted at least hourly. The visibility code ranged from 1 (excellent) to 6 (terrible) and was similar to that used by Reilly *et al.* (1980; 1983).

#### Aerial surveys

Aerial survey flights were conducted in support of the shore-based observations from 3–11 March and 21–29 April, 1981. Methods for the aerial surveys were modified from those of Reilly *et al.* (1980; 1983) and Swartz and Jones (1980a). During the March flights a Cessna 172 high-wing aircraft flew at an altitude of 330 m at an average ground speed of 128 kmh<sup>-1</sup> over a series of 30 transect lines lying perpendicular to the axis of the coastline between Cape San Martin and Pt Buchon (Fig. 2). The interval between transects was 3.2 km, except at Pt Piedras Blancas, where the interval between transects was shortened to 1.6 km for five transects along 6.4 km

of coastline. All transect lines extended 16 km out to sea.

During the April flights, the scarcity of whales along the 96 km of coastline, and their proximity to shore, made the method used in March costly and unproductive. A series of transects parallel to the coastline were substituted for the perpendicular transects, except off Pt Piedras Blancas, where the five perpendicular transects 1.6 km apart were conducted in the same manner as in March, extending 16 km out to sea during the first run of the day. Any subsequent runs that same day were flown 8 km out to sea. For the parallel transects between Cape San Martin and Pt Buchon, flights were flown at 400-, 800-, and 1200-meter intervals offshore, following the contour of the coastline. This modified method proved to be cost-effective and productive during the April flights.

#### Biases

Experiments conducted by Reilly *et al.* (1980; 1983) revealed that several different types of bias affected estimates of the number of whales present in a pod or group at the Monterey station. There was a significant reduction in visibility when the weather was Code 5 (poor) or worse. There was also a consistent bias in estimating the number present in a pod even under ideal visibility conditions. Specifically, estimates of single individuals and of pods containing 4 or more whales were significantly lower than the number actually present. Estimates of pods containing 2 or 3 whales were more accurate. A correction factor was used here as calculated by Reilly *et al.*:

$$f(n_i) = n_i + b_n = \begin{matrix} n + 0.350 & n = 1 \\ n + 0 & n = 2, 3 \\ n + 0.333 & n = 4 \text{ or more} \end{matrix} \quad (1)$$

where  $f(n_i)$  is the bias correction factor for  $n_i$ ,  $n_i$  is the number of whales estimated to be in the  $i$ th pod, and  $b_n$  is the mean bias correction factor. The variance is estimated as

$$\text{var}[f(n_i)] = \begin{matrix} 0.474 & n = 1 \\ 0 & n = 2, 3 \\ 0.612 & n = 4 \text{ or more} \end{matrix} \quad (2)$$

The third area of bias investigated by Reilly *et al.* was that due to the offshore distance of the whales. A consistent bias was observed for whales passing beyond 2.4 km offshore. A correction factor  $h(k)$  was introduced for the proportion of whales missed;

$$h(k) = C_s/C_p \quad (3)$$

where  $C_s$  = the cumulative proportion of whales within 2.4 km of shore as observed from shore, and  $C_p$  = the cumulative proportion of whales within 2.4 km of shore as observed from the plane.

The variance of  $h(k)$  was estimated (assuming covariance terms = 0) as

$$\text{var}[h(k)] = [-C_p/C_s^2]^2 \text{var}[C_p] + (1/C_p)^2 \text{var}[C_s] \quad (4)$$

where

$$\text{var}[C_p] = (C_p)(1 - C_p)/n_p$$

$n_p$  = number within 2.4 km as observed from the plane

(5)

and

$$\begin{aligned} \text{var}[C_s] &= (C_s)(1 - C_s)/n_s \\ n &= \text{number within 2.4 km as} \\ &\text{observed from shore.} \end{aligned} \quad (6)$$

Presently there are no data to test for a change in migration rate at night (Rice and Wolman, 1971; Reilly *et al.*, 1980). Most previous population estimates have assumed a constant 24-hour rate; this paper does likewise. The use of radio telemetry has been demonstrated on gray whales (Mate and Harvey, 1981) and may provide data which will clarify this issue.

### Total population estimate

The total population estimates have been produced by first grouping all observations into weekly periods, Monday through Saturday, yielding 12 weeks of data in 1980 and 16 weeks in 1981. All whales observed in Code 5 or 6 visibility conditions were then removed. Only those whales observed in Code-4 conditions or better were utilized for the population estimates. Estimates were then corrected for the pod-size bias for all pods of 1 or of 4 or more individuals and summed as weekly totals. Each weekly total was then divided by the weekly total number of hours with Code 4 or better visibility, to yield an average hourly rate of whales passing Pt Piedras Blancas for that week. This hourly rate was multiplied by 168 to produce a new weekly estimate. The next step was to correct the weekly estimates for whales missed due to their distance offshore, using the correction factor  $h(k)$ . Due to the nature of the northbound migration, this correction factor was used to correct only those weeks through 21 March, as all whales observed after that time were within 2.4 km of the shore. It should be noted that the formulation of the distance correction assumes that during periods of fair or better visibility (Codes 4 or better) all pods passing within 2.4 km were sighted. The final step in producing a total population estimate was to sum the corrected weekly totals. Notation was modified from Reilly *et al.*, (1980; 1983) as follows:

The weekly estimate after pod size bias correction is

$$\hat{n}_j = [\sum_i f(n_i)/t_j] (168) \quad (7)$$

where  $n_i$  = the original estimate of the number of whales present in the  $i$ th observation,  $f(n_i)$  = the bias correction factor for  $n_i$ ,  $t_j$  = the total observational time during the  $j$ th week in Code 4 or better visibility conditions, and  $\hat{n}_j$  = the number of whales estimated for 168-hour week corrected for pod-size bias in  $n_i$ .

The variance for  $\hat{n}_j$  was estimated as

$$\text{var}[\hat{n}_j] = (168/t_j)^2 (\sum \text{var}[f(n_i)]). \quad (8)$$

The total population estimate for year  $k$  is

$$\hat{N}_k = \sum_j [(\hat{n}_j)_a h(k)] + \sum_j (\hat{n}_j)_b \quad (9)$$

where  $(\hat{n}_j)_a$  = the corrected weekly estimates through 21 March,  $(\hat{n}_j)_b$  = the corrected weekly estimates after 21 March, and  $h(k)$  = the distance-bias correction factor.

The variance for  $\hat{N}_k$  (assuming covariance terms are 0) was estimated as:

$$\text{Var}[\hat{N}_k] = \text{var}[\sum_j (\hat{n}_j)_a h(k)] + \text{var}[\sum_j (\hat{n}_j)_b] \quad (10)$$

where

$$\begin{aligned} \text{var}[(\hat{n}_j)_a \cdot h(k)] &= h(k)^2 \text{var}[\sum (\hat{n}_j)_a] \\ &+ [\sum (\hat{n}_j)_a]^2 \text{var}[h(k)] \end{aligned} \quad (11)$$

and

$$\text{var}[\sum n_j] = \sum \text{var}[n_j]. \quad (12)$$

### Estimate of number of calves

The adjusted number of calves (or cow/calf pairs) was estimated using percentages of the weekly totals. For each week in which calves were observed, all calves in Codes 5 or 6 visibility conditions were removed. The remaining number of calves was then divided by the total number of whales observed in that week during Code 4 or better conditions to yield the percentage makeup of calves per total observed. The resulting percentage was then multiplied by the corrected weekly total after adjustment for pod-size bias to yield the corrected number of calves for that particular week. Since all calves were observed within 2.4 km of the shoreline, the offshore-distance correction factor  $h(k)$  was not utilized. The final step was to sum the corrected weekly totals to yield an estimate of the total number of calves in the population passing Pt Piedras Blancas. The weekly estimate of the number of calves passing during the  $j$ th week is

$$\hat{n}_{cj} = (n_{ci}/n_i) \hat{n}_j = (p_i) \hat{n}_j \quad (13)$$

where  $p_i$  is the proportion  $n_{ci}/n_i$  and  $n_{ci}$  = the original estimate of the number of calves present in the  $i$ th observation in Code 4 or better conditions,  $n_i$  = the original estimate of the number of whales present in the  $i$ th observation in Code 4 or better conditions, and  $\hat{n}_j$  = the number of whales estimated for 168 hour week corrected for pod size bias in  $n_i$ .

The variance of  $\hat{n}_{cj}$  was estimated (assuming covariance terms = 0) as

$$\text{var}[\hat{n}_{cj}] = (n_{ci}/n_i)^2 \text{var}[\hat{n}_j] + (\hat{n}_j)^2 \text{var}[n_{ci}/n_i] \quad (14)$$

where

$$\text{var}[n_{ci}/n_i] = (1/n_i)^2 \text{var}[n_{ci}] + (n_{ci}/n_i^2)^2 \text{var}[n_i]. \quad (15)$$

The total estimate of the number of calves passing Pt Piedras Blancas is

$$\hat{N}_{ck} = \sum \hat{n}_{cj}. \quad (16)$$

The variance for  $\hat{N}_{ck}$  was estimated as

$$\text{var}[\hat{N}_{ck}] = \text{var} \sum [\hat{n}_{cj}] = \sum \text{var}[\hat{n}_{cj}]. \quad (17)$$

### Annual rate of calf production

The annual rate of calf production is defined as the number of new individuals (calves) added to the population per unit time:

$$R_k = \hat{N}_{ck}/(\hat{N}_k - \hat{N}_{ck} \Delta t) \quad (18)$$

where  $\hat{N}_{ck}$  = estimated total number of calves passing Pt Piedras Blancas,  $\hat{N}_k$  = estimated total population passing Pt Piedras Blancas, and  $\Delta t$  = one year.

The variance for  $R_k$  was estimated (assuming covariance terms = 0) as

$$\begin{aligned} \text{var}[R_k] &= (1/\hat{N}_k - \hat{N}_{ck} \Delta t)^2 \cdot \text{var}[\hat{N}_{ck}] \\ &+ [\hat{N}_{ck}/(\hat{N}_k - \hat{N}_{ck} \Delta t)^2]^2 \cdot \text{var}[\hat{N}_k - \hat{N}_{ck} \Delta t]. \end{aligned} \quad (19)$$

## RESULTS

## Raw counts

A total of 1,496 gray whales was observed during 659 data-collecting hours between 10 March and 31 May 1980; 228 were calves (Table 1). Five hundred seventy-seven (577) hours of observation were in Codes 1-4, during which 1,488 whales were seen passing the shore site; 227 were calves.

Table 1

1980 weekly raw and adjusted counts of (1) all whales except cow/calf pairs ('others'); (2) cows; and (3) calves

Week	Raw			Adjusted		
	Others	Cows	Calves	Others	Cow	Calves
3/10-3/16	390	0	0	1,815	0	0
3/17-3/23	307	0	0	1,505	0	0
3/24-3/30	146	4	4	598	16	16
3/31-4/06	69	2	2	216	6	6
4/07-4/13	38	5	5	119	16	16
4/14-4/20	25	12	12	85	49	49
4/21-4/27	24	71	71	69	204	204
4/28-5/04	23	63	63	69	188	188
5/05-5/11	8	55	55	21	160	160
5/12-5/18	8	15	15	24	47	47
5/19-5/25	2	1	1	12	5	5
5/26-6/01	0	0	0	0	0	0
Totals	1,040	228	228	4,533	691	691

Between 9 February and 30 May 1981, 3,296 northbound whales were seen during 755 hours of observation; 209 were calves. Weather conditions in 1981 were more harsh than in 1980, resulting in 638 hours of Codes 1-4 visibility conditions with 3,159 whales recorded passing Pt Piedras Blancas, of which 194 were calves (Table 2).

Table 2

1981 weekly raw and adjusted counts of (1) all whales except cow/calf pairs ('others'); (2) cows; and (3) calves

Week	Raw			Adjusted		
	Others	Cows	Calves	Others	Cows	Calves
2/09-2/15	218	0	0	942	0	0
2/16-2/22	387	0	0	1,602	0	0
2/23-3/01	704	0	0	3,297	0	0
3/02-3/08	498	0	0	2,922	0	0
3/09-3/15	395	0	0	2,165	0	0
3/16-3/22	385	0	0	1,888	0	0
3/23-3/29	145	0	0	690	0	0
3/30-4/05	84	1	1	332	5	5
4/06-4/12	6	4	4	33	23	23
4/13-4/19	20	21	21	90	81	81
4/20-4/26	13	42	42	52	164	164
4/27-5/03	9	56	56	35	185	185
5/04-5/10	9	64	64	32	211	211
5/11-5/17	4	17	17	18	79	79
5/18-5/24	1	4	4	4	20	20
5/25-5/31	0	0	0	0	0	0
Totals	2,878	209	209	14,602	768	768

## Phase A

The migration in both 1980 and 1981 contained two separate and distinct pulses that were temporally spaced and that were comprised of different subsets of the gray-whale population. I have termed these two pulses Phase A and Phase B. The first wave (Phase A) comprised whales other than females with calves. It occurred between 1 February and 1 April in 1981 and represented approximately 89% of the total population. The mean date of passage (1981) was 1 March and the median date was 3 March. Rice and Wolman (1971) found that the northward migration is segregated by age and sex, although they had no data on cow/calf pairs. They found that first to pass were recently impregnated females, then adult males, adult females, immature females, immature males, and lastly some postpartum females that had apparently lost their calves. These animals comprised Phase A.

## Phase B

The remainder of the migration (Phase B) occurred between 1 April and 25 May, comprising mainly females with calves, which migrated much closer to shore than the rest of the population (Poole, in press). The first well-supported sighting of a female with calf was on 24 March in 1980 and on 1 April in 1981. Although small whales were observed in the presence of larger whales prior to these dates, they could not be positively identified as calves and were therefore not counted as such. An animal was determined to be a calf by (1) its size (and the disparity in size between it and the accompanying whale); (2) the absence of the numerous barnacles and scars of previous barnacles found on adult whales; and (3) the 'darkness' of its pigmentation.

From 5 April 1981 until the end of the migration, an adjusted count of 1,790 whales passed Pt Piedras Blancas. Of these, 254 (14%) were not cow/calf pairs. They may have been postpartum females that had lost their calves. They were almost always in the presence of a female with calf.

The mean dates of passage for cow/calf pairs were 24 April in 1980 and 26 April in 1981. The median dates were 28 April 1980 and 30 April 1981. These dates are approximately two months later than those of Phase A. Similar temporal segregation has been observed off the Oregon coast (Herzing and Mate, 1981), and occasional observations of females with calves near shore and late in the migration have been previously reported (Morejohn, 1968; Leatherwood, 1974; Baldrige, 1974).

## Aerial surveys

During the 3-11 March 1981 flights, 225 northbound whales were observed (Poole, in press). Flights conducted along transects #9-13 yielded 119 whales. During the 21-29 April flights, 59 whales (27 cow/calf pairs, one duo, and 3 'solos') were observed between Cape San Martin and Pt Buchon.

Analysis of the aerial-survey data at Pt Piedras Blancas yielded a value for  $C_p$  (the cumulative proportion of whales passing within 2.4 km of the shoreline as observed from the plane) of 0.737 for the March flights, with a

variance of 0.0034. The April flights yielded a value for  $C_p$  of 1.0, as all whales were observed within 2.4 km.

#### Distance bias

Analysis of February and March shore data yielded a value for  $C_s$  (the cumulative proportion passing within 2.4 km as observed from shore) of 0.942, with a variance of 0.00002. Therefore the resulting value for  $h(k)$  is

$$h(k) = C_s/C_p = 0.942/0.737 = 1.28$$

$$\text{var}[h(k)] = 0.0023.$$

The value for  $C_s$  in April and May was 1.0, as all whales were within 2.4 km.

#### Total population estimate

1981. As stated previously, 3,296 whales were observed in 755 hours of observation in 1981, including 209 calves. Removing all sightings in Code 5 or 6 visibility conditions left a total of 3,159 whales in 638 hours of observation, of which 194 were calves. These data were grouped in weekly sets and used in the equations given previously to calculate the adjusted weekly counts and associated variances (Table 2).

Summing these adjusted weekly counts yielded a total population estimate:

$$\hat{N}_k = 15,640 \quad \text{var}[\hat{N}_k] = 391,648 \quad 95\% \text{ CI} = \pm 1,227$$

Therefore, the 95% confidence interval is  $15,640 \pm 1,227$ .

This estimate does not contain a correction for those whales missed prior to the start of the survey. The first sighting of northbound whales at Pt Piedras Blancas in 1981 was in the first week of February (J. Bodkin, pers. comm.). I have postulated an additional 500 whales passing prior to the survey, approximating the value of 471 whales derived from the slope of a line extended backwards from 942 whales to 0 whales in a one-week period prior to the survey. The addition of 500 whales resulted in a total population estimate of 16,140 whales passing Pt Piedras Blancas in the spring of 1981. The previous variance is not applicable here.

1980. The 1,496 whales observed during the 659 data-collecting hours were adjusted for visibility conditions, which left 1,488 whales in 577 hours of observation. These data were pooled into weekly sets and then adjusted for the various biases to yield adjusted weekly counts with associated variances (Table 1). Summing these adjusted weekly counts yielded a total of 5,922 whales, with a variance of 28,931 and a 95% CI of  $\pm 333$ . These adjusted data, however, were insufficient to provide a total population estimate for 1980, as much of Phase A had been missed. An alternative method was used.

A comparison of the adjusted counts for both years during the last eight weeks of the survey, Phase B, revealed a ratio (1981/1982) of 0.9743. This value was then used to derive a total population estimate for 1980, by utilizing the total population estimate for 1981 calculated earlier, with the assumption that  $\Sigma \hat{n}_{1980B}/\hat{N}_{1980} = \Sigma \hat{n}_{1981B}/\hat{N}_{1981}$ . The total population estimate for 1980 was therefore

$$\hat{N}_{1980} = \hat{N}_{1981} \cdot (\Sigma \hat{n}_{1980B}/\Sigma \hat{n}_{1981B}) \quad (20)$$

where  $\hat{N}_{1981}$  = adjusted total population estimate for 1981,  $\hat{n}_{1980B}$  = the sum of the adjusted counts for Phase B 1980, and  $\hat{n}_{1981B}$  = the sum of the adjusted counts for Phase B 1981.

The variance for  $\hat{N}_{1980}$  was estimated (assuming covariance terms = 0) as:

$$\text{var}[\hat{N}_{1980}] = (\Sigma \hat{n}_{1980B}/\Sigma \hat{n}_{1981B})^2 \text{var}[\hat{N}_{1981}] + (\hat{N}_{1981})^2 \text{var}[\Sigma \hat{n}_{1980B}/\Sigma \hat{n}_{1981B}] \quad (21)$$

where

$$\text{var}[\Sigma \hat{n}_{1980B}/\Sigma \hat{n}_{1981B}] = (1/\Sigma \hat{n}_{1981B})^2 \text{var}[\Sigma \hat{n}_{1980B}] + (\Sigma \hat{n}_{1980B}/\Sigma \hat{n}_{1981B}^2) \text{var}[\Sigma \hat{n}_{1981B}]. \quad (22)$$

The resulting estimate for the total population passing Pt Piedras Blancas in the spring of 1980 was

$$\hat{N}_{1980} = 15,640 \quad (\times 0.9743) = 15,238$$

$$\text{var}[\hat{N}_{1980}] = 413,864 \quad 95\% \text{ CI} = \pm 1,261.$$

Therefore, the total population estimate for 1980 with 95% CI was  $15,238 \pm 1,261$  whales. It should be noted that this estimate was produced using the 1981 estimate without correction for whales missed prior to the survey. Using the population estimate of 16,140 for 1981, the resulting estimate for 1980 is 15,725 whales. The value of 0.0257 may be construed to be the net rate of increase for the population between 1980 and 1981.

#### Estimate of number of calves

1980. A total of 228 calves was observed in 1980. After deleting those observed in Code 5 or 6 visibility conditions, 227 were left with which to produce a total estimate. Using Equation 13 these data were adjusted into weekly estimates with associated variances (Table 1, Fig. 3). These adjusted weekly estimates were then summed to yield the total number of calves:

$$\hat{N}_{c1980} = 691 \quad \text{Var}[\hat{N}_{c1980}] = 1231 \quad 95\% \text{ CI} = \pm 69$$

Therefore, the estimate for the number of calves passing Pt Piedras Blancas in the spring of 1980 is  $691 \pm 69$  calves. 1981. A total of 209 calves were observed in 1981. Deleting those observed in Code 5 or 6 visibility conditions left 194 with which to produce an estimate. Adjusted weekly estimates were calculated with variances (Table 2, Fig. 4). These in turn were summed to produce a total estimate for 1981 of:

$$\hat{N}_{c1981} = 768 \quad \text{var}[\hat{N}_{c1981}] = 2,942 \quad 95\% \text{ CI} = 106.$$

Therefore the estimate for the number of calves passing Pt Piedras Blancas in the spring of 1981 is  $768 \pm 106$  calves.

#### Annual rate of calf production

1980. Using Equation 18, the annual rate of calf production was

$$R_{1980} = 691/(15,238 - 691) = 0.0475$$

$$= 4.7\% \text{ estimated rate of annual calf production as observed at Pt Piedras Blancas after three months of mortality}$$

$$\text{var}[R_{1980}] = 0.000009 \quad 95\% \text{ CI} = 0.0059.$$

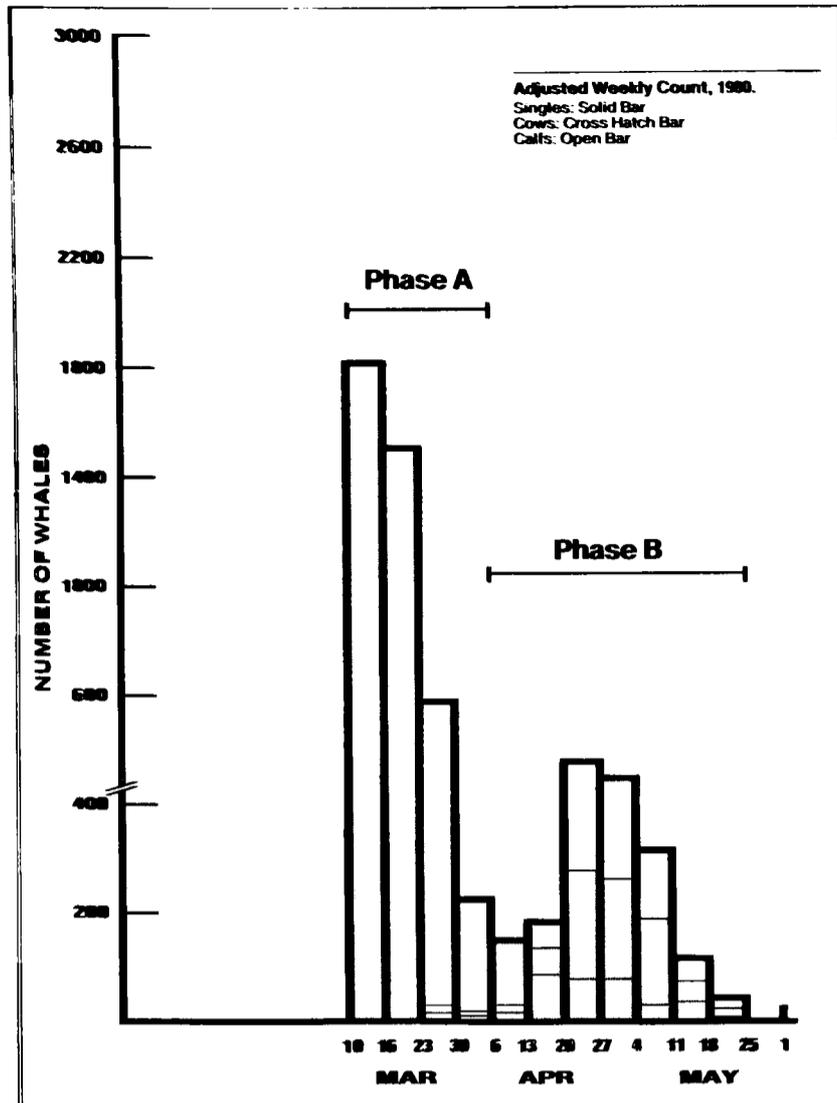


Fig. 3. Adjusted weekly counts, 1980.

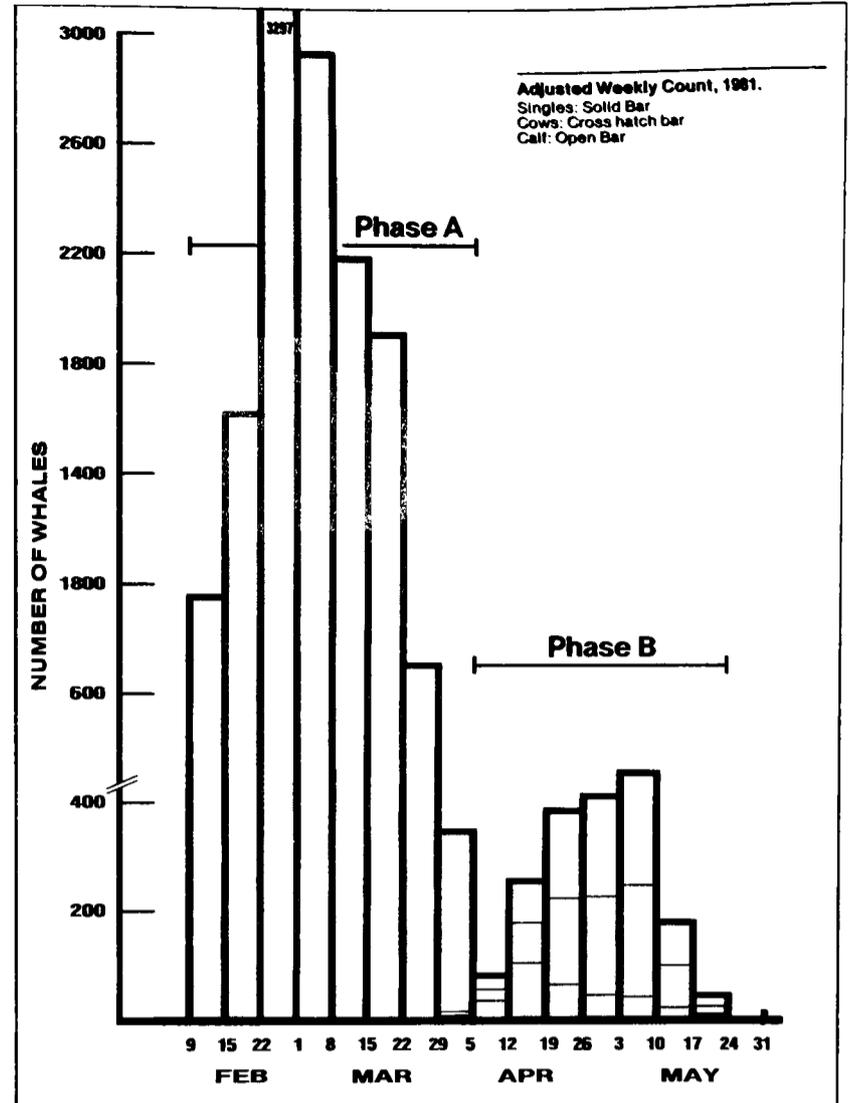


Fig. 4. Adjusted weekly counts, 1981.

Therefore, the rate of production is  $4.75\% \pm 0.59\%$ . The range is

$$(691 \pm 69) / [(15,238 \pm 1,261) - (691 \pm 69)] = 3.9-5.7\%.$$

1981. The rate of production for 1981 was

$$R_{1981} = 768 / (15,640 - 768) = 0.516$$

= 5.2% estimated annual rate of calf production as observed at Pt Piedras Blancas after three months of mortality.

$$\text{var}[R_{1981}] = 0.000018 \quad 95\% \text{ CI} = 0.0078.$$

Therefore, the rate of calf production was  $5.16\% \pm 0.78\%$ . The range is

$$(768 \pm 106) / [15,640 \pm 1,227] - (768 \pm 106) = 4.1-6.5\%.$$

It should be noted that in determining the variances for  $R_{1980}$  and  $R_{1981}$  it was assumed that covariance terms equaled zero. As an unknown but assumedly substantial amount of covariance probably exists, these estimates of variance for  $R_{1980}$  and  $R_{1981}$  are negatively biased and should be looked upon as minimum estimates.

## DISCUSSION

The population estimates presented here are reasonably close to estimates of Reilly *et al.* (1980; 1983), Reilly (1981), Rugh and Braham (1979), and Herzing and Mate (1981). Reilly's 'best estimate' for 1980 is 15,587,

obtained from an exponential regression line through 13 estimates from the Monterey shore censuses. My own estimate for 1980 is 15,238 whales; 15,725 if postulated whales missed prior to the survey are included. Reilly also stated that the annual rate of increase of the population was 2.5% (Reilly *et al.*, 1983). My own data suggest an annual increase of 2.6%, in agreement with his figures. My estimates for the number of calves (691 in 1980; 768 in 1981), however, are substantially less than might have been expected.

Rice and Wolman (1971) made an estimate of the maximum theoretical birth rate of the population in the late 1960s of no more than 0.13, based upon an equal sex ratio, an adult population of less than 0.56 of the whole, and an adult-female pregnancy rate of 0.46. Using my 1981 population estimate of 15,640, this would yield 2,033 calves. The actual birth rate may be considerably lower, however, as recent studies in the calving lagoons indicate.

Rice *et al.* (1981) counted 557 calves in Laguna Ojo de Liebre, Baja California, Mexico, which they stated may represent approximately half of the total calves produced. Swartz and Jones (1982) examined boat surveys of Guerrero Negro, Laguna Ojo de Liebre, and Laguna San Ignacio taken in 1980-1982. They arrived at an average annual gross calf production for all three lagoons combined of 865 calves, which included 46 dead ones. This represents a mortality rate of 5.3% in the lagoons. Rice *et al.* (1981) determined that these three lagoons produced 73% of all calves born. Therefore, Swartz and

Jones (1983) arrived at a total gross calf production of 1,185 calves for the entire 1982 population, with a mortality of 63 deaths before the migration, leaving a 1982 calf total of 1,122. Using a 1981 population of 15,942 (derived from Reilly *et al.*, 1983) this yields a calf total of 1,097 as the net calf production before the migration, and mortality along the route between the calving areas and Pt Piedras Blancas of

$$1 - (768/1,097) = 30\%$$

$$1 - (874-662/1,097) = 20\% - 40\% [768 \pm 106]$$

Therefore calf mortality along the migration route would be 30%, with a range of 20%–40%.

The low number of calves on the migration can be explained in at least two ways: calves were missed as they passed Pt Piedras Blancas, or they died enroute, perhaps from the stress and rigors of the migration or from attacks by predators, such as killer whales (*Orcinus orca*). In 1980 I examined a dead calf that had been attacked by killer whales. It washed ashore at Pismo Beach, approximately 85 km south of Pt Piedras Blancas. Mortality from other causes has also been documented (Brownell, 1971).

One factor to consider is that the end of Phase A is comprised of primarily smaller juveniles (Poole, in press; Rice and Wolman, 1971) along with some adult whales. As Phase A ended and Phase B began, it is probable that some calves with females were mistaken for imatures in the presence of adults. Small whales in the presence of larger whales were observed just prior to the first sightings of cow/calf pairs. But these smaller whales could not be positively identified as calves. This may not have been a major factor, however. When the first 'definite' cow/calf pairs were sighted, the size disparity between the female and calf, and between the calf and previous 'small' whales, was quite evident and very striking.

Calves can be difficult to spot. Their relatively small size and often close proximity to the female can 'hide' them from view, especially if the calf is on the opposite side of the female from the observers. Due to the nature of the migration corridor at Piedras Blancas, this too was probably not a major factor. Phase B whales most often approached the observation site head on, allowing both sides of a large whale to be observed at times. And 95% (1980) and 92% (1981) of all Phase B whales passed within 200 meters of the shoreline (Poole, in press).

In addition, few lone adult whales were observed in Phase B. Rather, adults without calves were most often observed in the presence of cow/calf pairs, traveling together as a trio. It is possible that a second calf could be overlooked in such a situation. Observations of what appeared to be a single calf with two adults may have been observations of two calves surfacing at different intervals next to the females. Again, this probably was not a major factor, due to the proximity to shore of Phase B whales and the length of time they were under observation.

However, a reasonable upper limit to the number of calves may be estimated by assuming that all adult Phase B whales had calves. In 1981 this would add 254 calves, bringing the total to 1,022, which is only 6.8% less than the total net production of 1,097 suggested by Swartz and Jones (1982) for all calving areas.

It should be noted that the last eight weeks of the

northward migration, Phase B, has the 'correct' number of females (within 6.8%); only the number of calves is significantly different. If my own Phase-B figure of 1,022 is used as the net calf production before the migration, then mortality along the migration route to Piedras Blancas was

$$1 - (768/1,022) = 25\%$$

$$1 - (874-662/1,022) = 14\% - 35\% [768 \pm 106]$$

Therefore calf mortality enroute would be 25%, with a range of 14%–35%. These data are supported by other research efforts. Herzog and Mate (in press) estimated that 534 calves were present in a total population of 11,962 whales passing within 4.8 km of Yaquina Head, Oregon in 1980. This represents an annual rate of calf production (Equation 18) of 4.7%, in agreement with my figures. Aerial surveys conducted between Pt Conception, California and the Oregon border during the northward migration (February through May) yielded rates of calf production of 6.0% in 1980, 6.3% in 1982, and 4.2% in 1983 (Tom Dohl, pers. comm.).

This suggests that either equivalent percentages of calves were missed in three very separate and distinct research efforts, or that some validity exists for these lower-than-expected calf counts. An inescapable question arises: Where are the dead calves? One would expect to find a fair number washed ashore. Records of strandings in California south of Pt Piedras Blancas do not support mortality of this level. But where would the highest degree of calf mortality during the migration occur?

Swartz and Jones (1983) suggested two critical periods for gray whale calf mortality: one at and just following birth, and a second period at the *beginning* of the northward migration. This predicts that a large proportion of calves that have died during the initial stage of the migration and washed ashore would be found along the coast of Baja California, Mexico, rather than the coast of California, USA.

Marilyn Dahlheim (pers. comm.) reported that her field assistant, Michael Symons, found numerous remains of gray whales at Miller's Landing during a recent visit to Baja California (19–28 July 1983). Forty-three whales were judged by their state of decomposition to have recently died, during the winter–spring 1982–83 season. Of these 43, 17–18 (40%) were calves. An additional 12 skulls were observed and judged to have been whales from previous seasons, as they were 'considerably eroded away'. This finding indicates that, indeed, some calves do die off the coast of Baja California and wash ashore where they would normally remain undetected.

If my estimates of total abundance of  $15,238 \pm 1,261$  (1980) and  $15,640 \pm 1,227$  (1981) whales and estimates of  $691 \pm 69$  (1980) and  $768 \pm 106$  (1981) calves are reasonably accurate, then calf mortality is greater than has been previously suspected, but the rate of increase for the population as a whole has been maintained at approximately 2.5%. If a proportionally equivalent number of calves was missed in both 1980 and 1981, the rate of increase would not be altered, but calf mortality would be less than suggested here. Clearly, more data are needed.

## CONCLUSIONS

(1) The northward migration of the California gray whale along the central California coast occurs in two distinct and separate phases which are temporally spaced and segregated by age and sex.

(2) Phase A, the migration of whales other than females with calves, occurs in February and March, and has a mean date of passage of approximately 1 March.

(3) Phase B, the migration of primarily females with calves, occurs in April and May and has a mean date of passage of 26 April, approximately two months later than Phase A.

(4) An estimated  $15,238 \pm 1,261$  whales (15,725, after correction for whales missed prior to the start of the survey) passed Pt Piedras Blancas during the northward migration in 1980. This population contained an estimated  $691 \pm 69$  calves, and had an annual rate of calf production of not less than 4.7% after approximately three or four months of mortality.

(5) An estimated  $15,640 \pm 1,227$  whales (16,140 after correction for whales missed prior to the survey) passed Pt Piedras Blancas during the northward migration in 1981. This population contained an estimated  $768 \pm 106$  calves, and had a rate of calf production of not less than 5.2% after approximately three or four months of mortality.

(6) The annual rate of increase for the population between 1980 and 1981 was 2.6%.

(7) If 1,022 calves is considered to be the net total calf production before the northward migration, then calf mortality between the calving areas in Baja California, Mexico and Pt Piedras Blancas, California in 1981 was 25%, with a range of 14–35%.

(8) Calf counts may be biased downward by at least two factors:

(a) Calves may be mistakenly identified as yearlings during the latter part of Phase A and the beginning of Phase B; and

(b) Pods containing two cow/calf pairs may be mistakenly identified as 'trios' containing two adults and a single calf.

(9) A reasonable upper limit to the number of calves passing Pt Piedras Blancas may be estimated as 1,022. A reasonable lower limit of calf mortality during the migration would then be 6.8%.

The results of this report are preliminary. However, the basic patterns and numbers of whales remained rather consistent for the two year period. Further data collection could be quite beneficial. It is recommended that an additional three years of research be undertaken to provide a larger data base from which more reliable conclusions can be drawn.

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# Reproductive Parameters of the Minke Whale, *Balaenoptera acutorostrata*, off West Greenland

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## ABSTRACT

A sample consisting of ovaries, ear plugs and tympanic bullae together with information on length of the animals and presence/absence, sex and length of foetuses from 111 female minke whales was collected on board a Norwegian whaling vessel operating off West Greenland in 1979, 1980 and 1981.

Of the 111 females, 71 (64%) were considered to be sexually mature. At least 66 of the mature animals had ovulated in the most recent ovulatory cycle, and 63 of these were pregnant, giving an apparent pregnancy rate of 0.89.

Length of foetuses ranged from 18 cm to 145 cm, with a foetal growth curve similar to that shown for Newfoundland minke whale foetuses (Sergeant, 1963). The sex was determined for 56 of the foetuses and the foetal sex ratio does not differ from 50:50. Mean length at sexual maturity was estimated at 750 cm.

## INTRODUCTION

Biological material from minke whales in West Greenland waters was collected in 1973 by Norwegian scientists, and preliminary results were presented by Christensen (1974; 1975). In 1977 and 1978, Greenland Fisheries Investigations made attempts to sample the Greenlanders' shore-based catch, but due to the opportunistic nature of this catch the results were disappointing (Anon. 1979; 1981). On the basis of this experience, arrangements were made in 1979, 1980 and 1981 (in cooperation with the Institute of Marine Research in Bergen) to have a Danish scientist on board the Norwegian small-type whaling vessel *Kato* operating off West Greenland.

This paper presents results of studies on reproduction based on the material collected on board *Kato* in 1979, 1980 and 1981.

## MATERIAL AND METHODS

The biological material consists of ovaries with information on length of animal and presence/absence, sex and length of foetus from 111 female minke whales. Both ovaries were collected from 108 animals and a single ovary from 3 animals. The ovaries from one animal (K1980/44) were excluded from the analyses as they were apparently in a pathological condition.

The ovaries were stored on board the whaling vessel and upon arrival at the laboratory preserved in 10% neutral formalin. After at least 14 days' preservation, the ovaries were trimmed, i.e. ligaments etc. were cut off, and the ovaries were weighed and sectioned at a thickness of 3–4 mm and examined macroscopically. The extracted data include the diameter of the largest follicle and the number and size of all corpora types.

## RESULTS

### Corpora lutea (CLs)

A total of 65 CLs were examined. One animal (K81/27) had a CL in both ovaries, the smallest CL apparently being in an early stage of regression. Both uterine horns

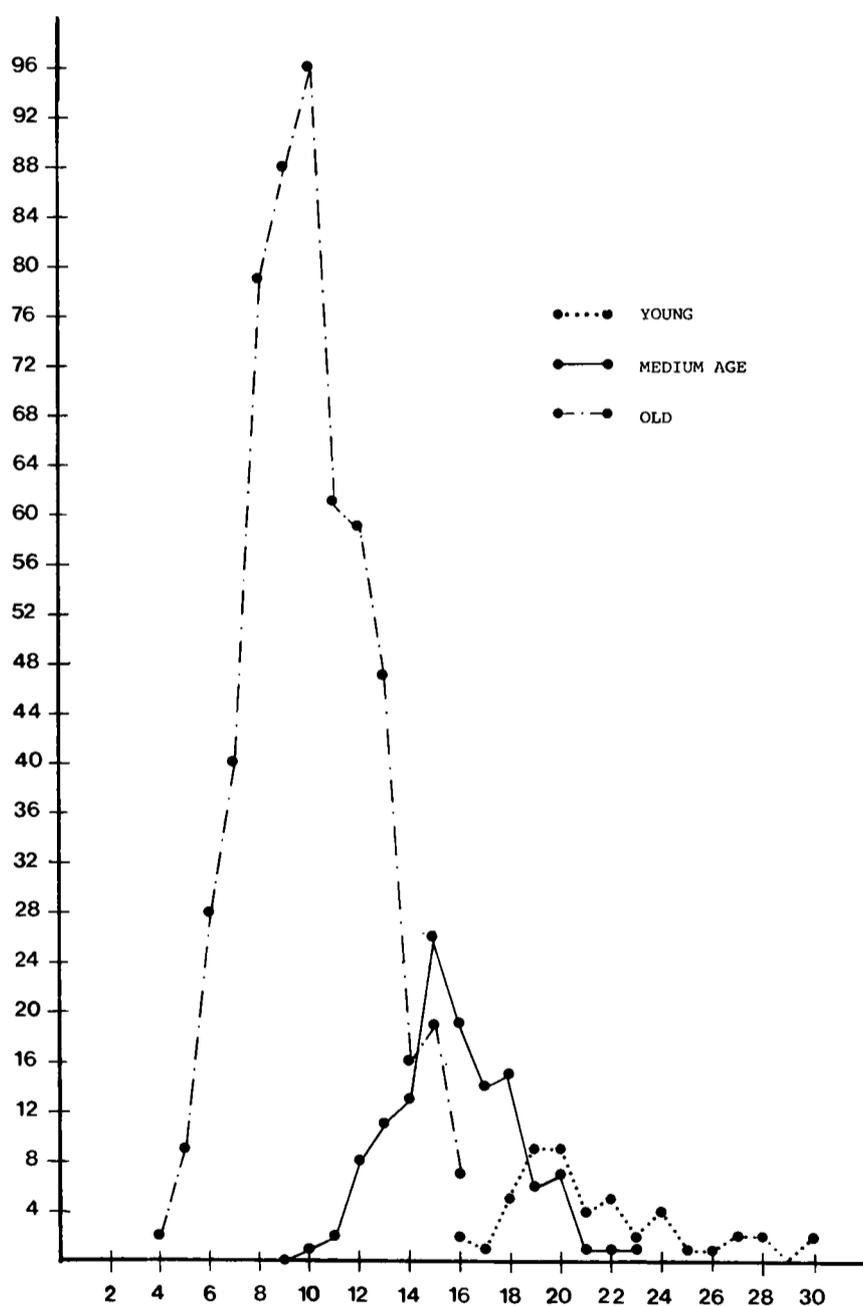


Fig. 1. Size frequency distribution of the three types of CAs, 'young', 'medium age' and 'old'. The mean diameters are 21.4, 15.8 and 10.0 mm respectively.

of this animal were dilated, but no fetus was found. 62 of the remaining CLs were found in association with a fetus, whereas the last CL was found in connection with an apparently inactive uterine cornua judging from the

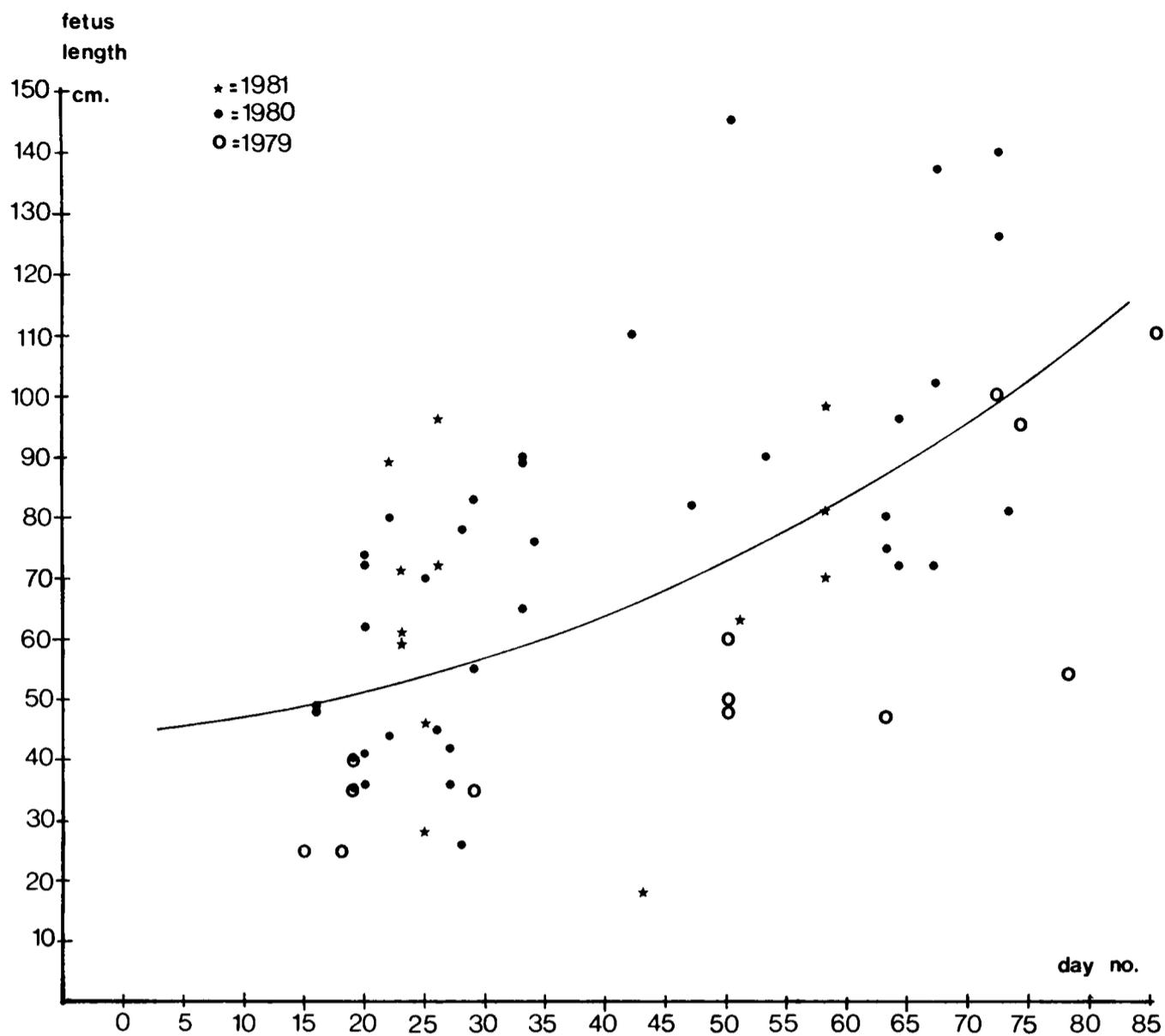


Fig. 2. Length of fetuses of minke whales caught off West Greenland, 1979, 1980 and 1981 compared with growth curve from Sergeant (1963). Day no. 0 = 12 June.

size of the cornua. A close examination of the cornua of this animal revealed no macroscopically visible fetus.

Eight (13%) of the 62 CLs of pregnancy had a central, fluid-filled cavity, 29 (47%) had a central structure of connective tissues, 21 (34%) had both, and 4 (6%) had neither. One of the two CLs without a fetus had a central structure of connective tissue without a fluid-filled cavity, whereas the other had both.

The diameter of the 62 CLs of pregnancy ranged from 43 to 68 mm with a mean of 56.6 mm (SD: 5.8 mm). There was no correlation between the size of the CL and the date of capture, nor between the size of the CL and the length of the fetus. Similarly, no correlation could be detected between the size of the CL and the total body length of the animal.

#### Corpora albicantia (CAs)

All CAs were classified by morphological characters as young, of medium age or old as described by Laws (1961).

Young CAs ranged from 16 to 30 mm in diameter (n: 49, mean: 21.4 mm, SD: 3.5 mm), medium-age CAs from 10 to 23 mm (n: 115, mean: 15.8 mm, SD: 2.4 mm), and old CAs from 4 to 16 mm (n: 528, mean: 10.0 mm, SD: 2.4 mm). Fig. 1 shows the size-frequency distribution of all CAs. There is obviously a large overlap between the size-frequency distribution of young and medium-age CAs, and between medium-age and old CAs. The largest number of CAs in a single female was 35 (1 young, 2 medium-age, and 32 old).

The mean diameter of the young CAs represents a regression to 37.8% of the mean size of the CLs of pregnancy, while the mean diameters of medium-age and old CAs represent regressions to 27.9% and 17.7%, respectively.

#### Bilateral activity of the ovary

Bilateral activity of the ovary was investigated in 25 specimens for which it was known whether the ovary with the CL was the left or the right. In 12 (48%) of these the CL was positioned on the right side. The 272 CAs found in the 25 specimens were distributed with 128 (47%) on the right side, not significantly different from parity (Chi-squared test:  $P > 0.10$ ).

Whether the equal distribution of corpora was caused by a regular alternation in ovulation between the two ovaries was investigated. Of 48 specimens with both a CL and a young CA, 31 (65%) had the young CA in the ovary opposite the CL, whereas 17 (35%) had the young CA in the same ovary as the CL.

#### Foetal development

Total body lengths of the individual foetuses in the *Kato-1979*, *Kato-1980* and *Kato-1981* samples in relation to the dates of capture are shown in Fig. 2 together with the growth curve presented in Sergeant (1963).

There is obviously a large variation in foetal length within the same time-period, probably reflecting a large variation in the individual dates of conception.

Table 1  
Length distribution of sexually immature and mature female minke whales examined off West Greenland 1979-81

	Length group (cm)															Total
	From To	550-574	575-599	600-624	625-649	650-674	675-699	700-724	725-749	750-774	775-799	800-824	825-849	850-874	875-899	
No. immature		3	3	5	3	2	9	8	5	2						40
No. mature								1	1	15	14	14	13	12	1	71
% mature		0	0	0	0	0	0	11	17	88	100	100	100	100	100	64.0

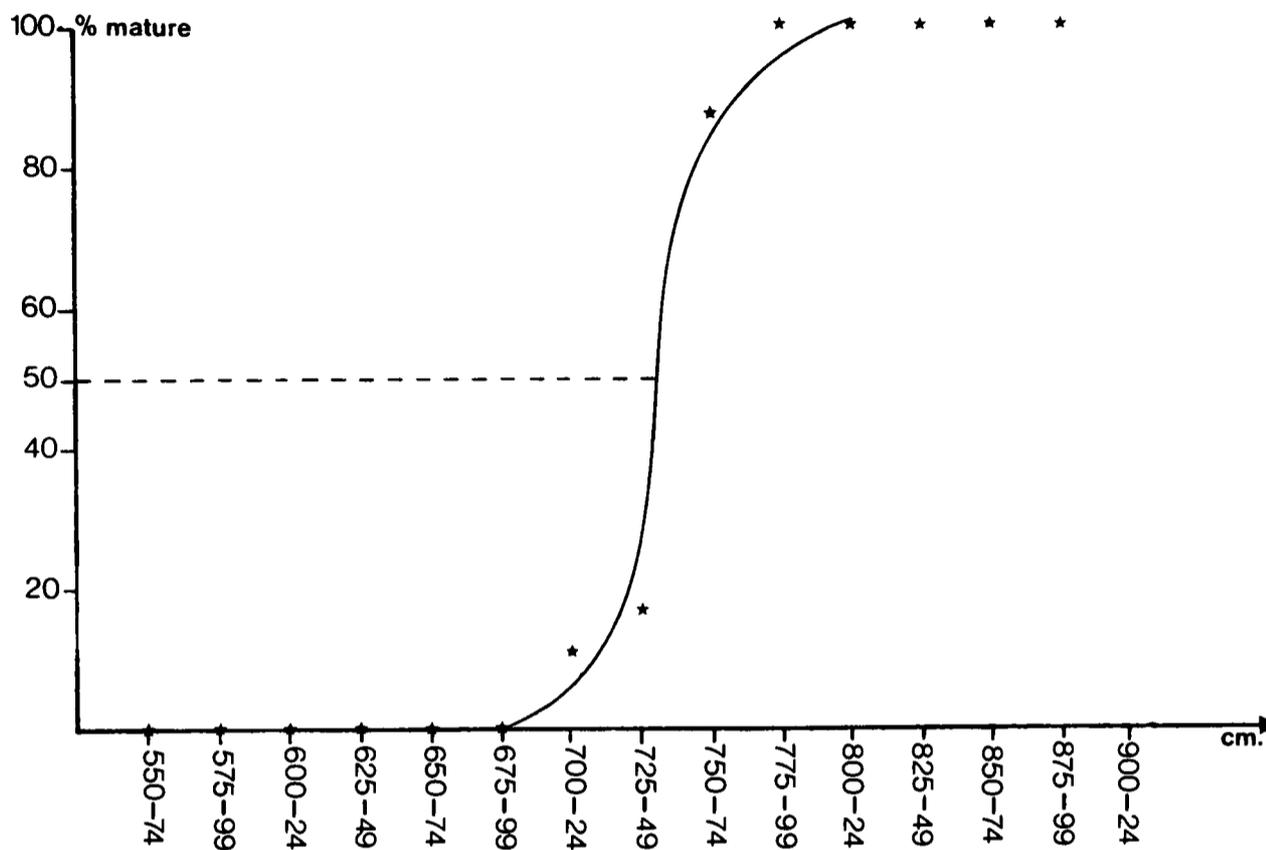


Fig. 3. The relation between body length and proportion of mature females examined off West Greenland, 1979-81. Observations are plotted at midpoints of length groups.

The foetal lengths of the 1980 and 1981 samples correspond reasonably well with Sergeant's growth curve, whereas the foetuses of the 1979 sample are generally smaller.

The sex ratio of the foetuses is estimated at 41% females on the basis of 56 foetuses of known sex. However this is not significantly different from a 50:50 ratio (Chi-square test:  $P > 0.10$ ).

**Length at sexual maturity**

Females were classified as sexually mature if they possessed a CL or one or more CAs in the ovaries. Data are available for 111 females.

The two largest immature females both had a body length of 760 cm, and the two smallest mature females had body lengths of 710 and 745 cm, with 1 and 4 CAs, respectively, in the ovaries.

Table 1 shows the number of immature and mature females in each length group, and Fig. 3 shows the percentage of sexually mature in these length groups. The length at which 50% of the females were sexually mature can be estimated from Fig. 3 to be around 750 cm (24.2 feet). The material includes 3 primiparous females with body lengths of 750, 760 and 770 cm, respectively.

**DISCUSSION**

In studies of reproductive parameters based on examination of ovaries it would be valuable to be able to distinguish CLs of ovulation from those of pregnancy.

Robins (1954) reported that the presence of a fluid-filled cavity in the CL of the humpback whale (*Megaptera novaeangliae*) indicated a CL of ovulation. Laws (1961) on the other hand showed for the Southern Hemisphere fin whale (*Balaenoptera physalus*) that a follicular cavity in the CL was not an indication of a CL of ovulation.

In the present material the 62 CLs, which are without any doubt CLs of pregnancy, exhibit all combinations of presence/absence of a follicular cavity and connective tissue formation. These features therefore cannot be used to distinguish between the two types of CLs in the West Greenland minke whale.

The two CLs without a foetus were similar to the other 62 CLs both with respect to size and appearance, and it is difficult to determine whether they are CLs of ovulation or CLs of pregnancy in an early stage. No matter how they are classified, it should be noted that the two whales have ovulated considerably later (July) than would be expected from statements in the literature concerning mating periods in other North Atlantic stocks (Jonsgård, 1951: January-May).

It should also be noted that these two whales each had a young CA, judged by the state of regression to be of the last completed sexual cycle. If the West Greenland minke whale reproduces annually, as the pregnancy rate suggests, these two newly ovulated whales should have been accompanied by suckling calves, as, in order to keep a 12-month reproductive cycle, they would have to ovulate in the middle of the 4-month lactation period. But suckling calves or lactating females have not been reported at West Greenland.

Best (1982) gives the mean diameter of 84 CLs of pregnancy from Antarctic minke whales as  $6.64 \pm 0.1$  (SE) cm (fresh material), and Lockyer (*in litt.* 18 December 1981) measured the mean size of 38 CLs from formalin-fixed minke ovaries from the Antarctic as  $6.55 \pm 0.12$  (SE) cm. The mean diameter of 62 CLs of pregnancy in the present material is somewhat lower (56.6 mm), perhaps reflecting the lower mean body size of North Atlantic minke whales.

The accumulation of CAs with age in the minke whale has been reported for the Barents Sea stock by Christensen (1981), for the Newfoundland stock by Mitchell and Kozicki (1975), and for the Antarctic minke whale by Ohsumi and Masaki (1975). It has not been possible to show directly a similar accumulation in the present analysis as none of the animals in the present material has been aged.

Laws (1961) has shown that old CAs in the fin whale shrink to about 17.6% of the diameter of the original CL, and Best (1982) gives the figure 15.7% for the Antarctic minke whale. In the present analysis, shrinkage of old CAs was to about 17.7% of the CL-size. This taken together with the symmetrical distribution of old CAs and the fact that the mean size of old CAs is considerably larger than the mean thickness of the ovary-slices suggests that it is unlikely that CAs were completely resorbed or that substantial numbers were missed during examination.

It thus seems reasonable to assume that CAs persist throughout life in minke whale ovaries, and consequently that an accumulation with age takes place.

Laws (1961) reported that there is a slight preponderance in ovulation from the right ovary in the Southern Hemisphere fin whale. The findings of the present analysis, however, supports the results presented by Ohsumi (1964), that ovulations in Mysticeti are equally frequent from both ovaries. This equal distribution of ovulations is apparently not caused by a strict alternation in ovulation between the two ovaries. Only 65% of the CLs were found in the ovary opposite the young CA.

Individual fetus lengths show a large variation within the same time-period, probably reflecting a large variation in the individual dates of conception. There is apparently also a variation from year to year, since the 1979 sample seems to be generally smaller than the 1980 and 1981 samples at the same dates. Length at sexual maturity was found by Mitchell and Kozicki (1975) to be 24.17 feet (737 cm) for the Newfoundland female minke whale, whereas the estimate presented by Christensen (1981) for the Barents Sea minke whale is 715 cm. The results of the present analysis are in agreement with the results presented by Mitchell and Kozicki (1975); the estimate is a little higher than that presented by Christensen. It should be kept in mind, however, that the methods used in the three analyses are different. The

results for the Newfoundland minke whale are based on the lengths of six first-time ovulating females, whereas the results for the Barents Sea minke whale are read from a von Bertalanffy growth curve on the basis of an estimated mean age at sexual maturity.

In his investigation of the Norwegian catch of minke whales off West Greenland in 1973, Christensen (1975) found 89.8% of the sexually mature females pregnant, whereas he found an apparent pregnancy rate of 0.944 in the Barents Sea (1981). Mitchell and Kozicki (1975) found that 85.7% of the sexually mature females were pregnant in the Newfoundland catch. The high pregnancy rate found in the present analysis is apparently in agreement with these values for other North Atlantic stocks. It is, however, not known to what extent this pregnancy rate is influenced by segregation of different reproductive classes. This kind of segregation has been reported for the Antarctic minke whale (Ohsumi and Masaki, 1975) and for the minke whale off Newfoundland (Mitchell and Kozicki, 1975).

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# Reproduction in Humpback Whales, *Megaptera novaeangliae*, in Hawaiian Waters

DEBORAH A. GLOCKNER-FERRARI<sup>1</sup> AND MARK J. FERRARI<sup>1</sup>

## ABSTRACT

In a study of living humpback whales in the waters off Maui, Hawaii, postpartum ovulation with conception was found to occur in three individual females. Seventy-six lactating females and their calves were identified through surface and underwater photographs. Seven females were photographed with calves in two or more years. Three females exhibited a one-year reproductive cycle producing two calves in two years. One of these three had a calf in three successive years. Three females, photographed in two or more years with only one calf, were found to have a two-year reproductive cycle in which postpartum ovulation with conception did not occur.

The sex of 43 calves was determined: 51.2% were males, 48.8% females. Calves were observed suckling while both stationary and travelling. The body pigmentation of the cows and calves was similar to that of humpback whales in Ryukyuan waters. Three known yearlings and a two-year-old were photographed in Hawaiian waters. Calves produced at a one-year reproductive rate were not observed in subsequent years. The survival rate of these calves has yet to be determined.

## INTRODUCTION

Much of the knowledge of the reproductive cycle of the humpback whale *Megaptera novaeangliae* has been obtained through biological examination of whales taken by the whaling industry or killed specifically for the purposes of scientific study and through analysis of data supplied by the Bureau of International Whaling Statistics (Matthews, 1937; Chittleborough, 1954, 1955, 1958, 1965; Omura, 1955; Tomilin, 1957; Nishiwaki, 1959, 1962; Dawbin, 1960; Mitchell, 1973). Matthews (1937) analyzed data on the ovaries and mammary glands of 19 humpback whales taken in the South Indian Ocean and suggested that the majority of females breed once every two years and a minority twice every three years. Through examining the ovaries and mammary glands of 390 humpback whales taken at Western Australian whaling stations, Chittleborough (1958) reported that the majority of females breed once every two years. He also found that three females were simultaneously pregnant and lactating. He reported that Norwegian observers found 8.5% of 94 females taken in Antarctic waters were simultaneously pregnant and lactating. Van Lennep and van Utrecht (1953) reported one female humpback whale in this condition. Chittleborough (1958) stated that postpartum ovulation with conception may occur commonly in humpback whales. However, obtaining no further evidence of postpartum ovulation, Chittleborough (1965) later decided that it is probably not of frequent occurrence in this species.

In a study of living humpback whales in the waters off Maui, Hawaii, we photographically identified and tracked individual females and their calves. Through resighting the females and observing how often each produced a new calf, we determined the reproductive rates of individual whales. In this paper we provide evidence for the existence of a one-year reproductive cycle in three humpback whales in which postpartum ovulation occurred with conception, discuss the sex ratio of calves, lactation, and body pigmentation, and note the presence of yearlings and immatures on the breeding grounds.

## METHODS

During January through May 1977–1981, we spent 805 hours on land and 1,079 hours on the ocean observing humpback whales in the Auau Channel off Maui, Hawaii. Through taking over 10,000 surface and underwater photographs, we identified 76 individual cows and 86 calves.

Fig. 1 shows our study area in the waters off the west coast of Maui. In 1977–79, we used a 10½' (3.2 m) inflatable boat and launched from shore to an area where we had sighted a cow and calf (Glockner and Venus, 1983). A diver with mask and snorkel entered the water to take underwater photographs while an observer remained aboard to take surface photographs. Each of the cows and calves we photographed were located within one mile of shore. We photographed one cow and calf on a second occasion four miles from shore. In 1980 and 1981, by using larger Zodiacs (17½' and 15½', respectively), we were able to cover a greater area and locate cows and calves farther from shore. 59.6% of the cows and calves we photographed were within one mile of shore. All cows and calves were photographed within the 50-fathom (91.4 m) line. Distances were visually approximated.

We catalogued each cow and calf we photographed according to the pigment pattern of its flippers, the spatial-numerical pattern of its lip grooves, the pigment pattern of the undersurface of its flukes, and the shape of its dorsal fin. We noted the sex of each whale whenever possible by examining the lateral and/or ventral side of the abdomen for the presence of a hemispherical lobe, found behind the genital slit only in females (True, 1904; Glockner, 1983).

## RESULTS

### Reproductive cycle

We have resighted 25% of the individually identified cows and calves on two or more occasions within a given year. The intervals between successive sightings ranged from 1 to 48 days (mean 13.7 days). We resighted 13 different cows at intervals ranging from one to four years. We have photographed seven of these females with newborn calves

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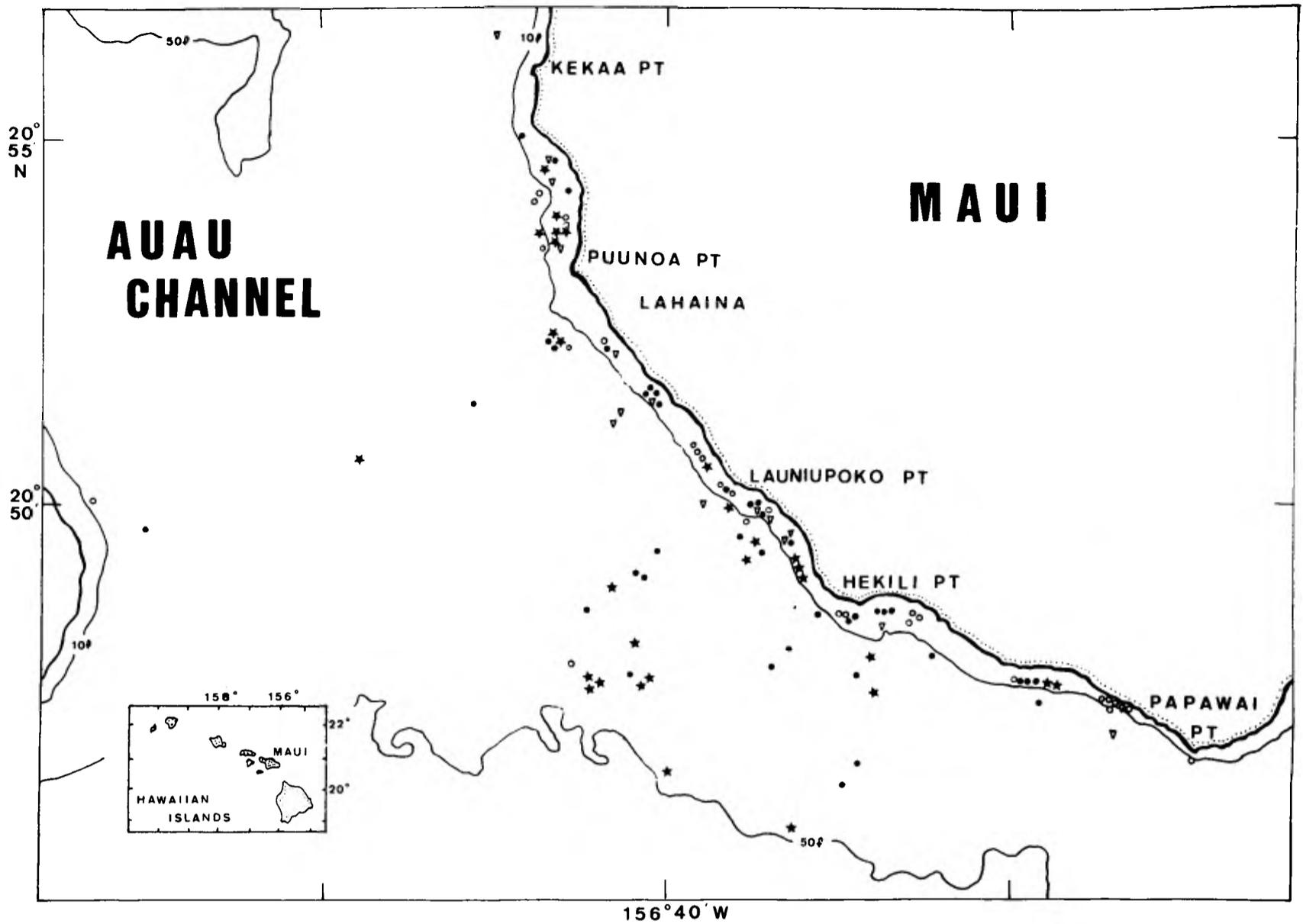


Fig. 1. Location of cows and calves photographed in the waters off the west coast of Maui, Hawaii, 1977–1981. open triangles =  $\nabla$  = 1977; closed circles =  $\bullet$  = 1978; open circles =  $\circ$  = 1979; asterisks =  $*$  = 1980; stars =  $\star$  = 1981.

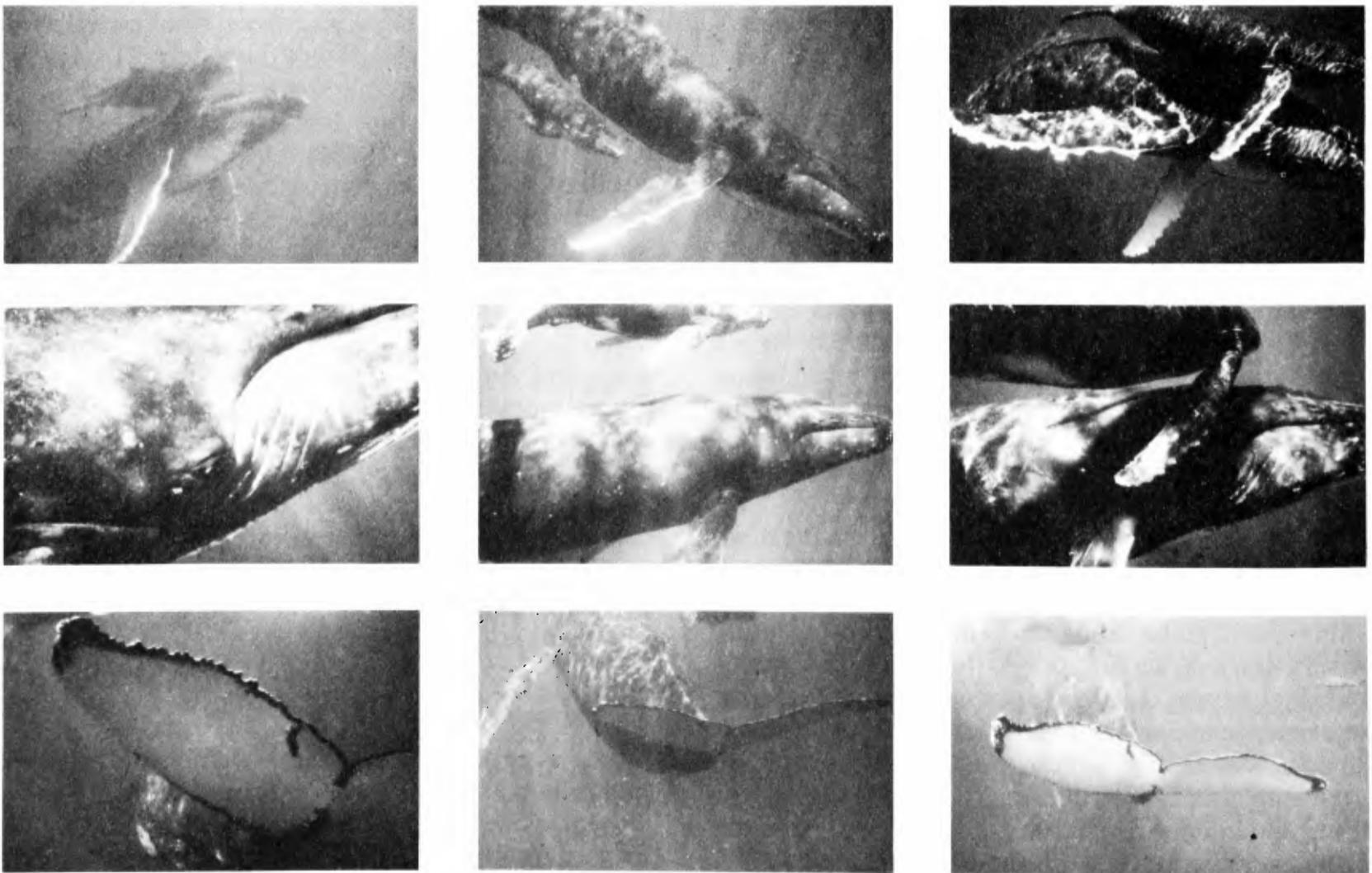


Fig. 2. Pigment pattern of flippers (top), spatial-numerical pattern of lip grooves (centre), and pigment pattern of flukes (lower) of cow 3208 photographed in 1979, 1980 and 1981 (left to right).

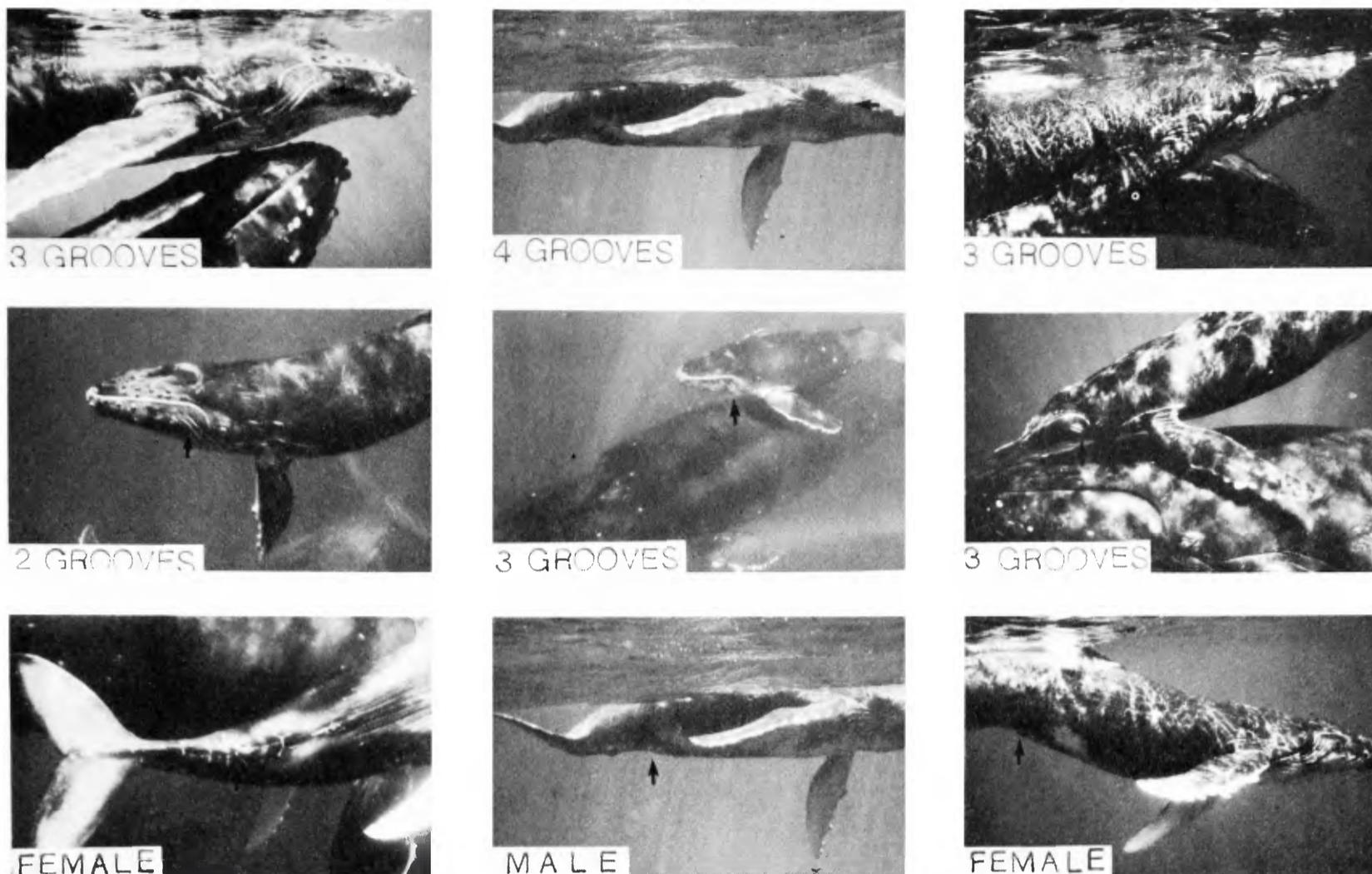


Fig. 3. Calves of cow 3208 in 1979, 1980 and 1981. The lip groove pattern and sex of each calf is shown.

in two or more years. Three females exhibited a one-year reproductive cycle, producing calves in two successive years. One of these three, cow 3208, produced calves in three successive years.

Fig. 2 depicts cow 3208 in 1979, 1980, and 1981, with a new calf each year. The cow's flippers are black with white leading edges. She has four lip grooves on her right side and three on her left. The ventral sides of her flukes are white surrounded by a black border; a small black mark extends downward from the trailing edge of the left fluke. In 1979, we photographed cow 3208 and her calf 3208C9 on 12, 13, and 24 March. On 24 March, we observed numerous black scratches covering the flukes of the cow that were not visible on 12 or 13 March. By the following year these marks had disappeared.

Fig. 3 shows the calves of cow 3208 in 1979, 1980, and 1981. Calf 3208C9 had black flippers outlined in white. It had three lip grooves on its right side and two on its left. The calf was a female. On 14 April 1980, we photographed cow 3208 with a new male calf 3208C0. This calf had four lip grooves on its right side, three on its left. Exactly one year later on 14 April 1981, in the same location and again on 17 April, we photographed cow 3208 with her third calf 3208C1, a female. The calf had three lip grooves on both its right and left sides.

Fig. 4 shows cow 1213, which we were able to photograph over a three-year period. Cow 1213 is easily identified by her white flippers, which have a distinctive black marking on the upper portion, and by the ventral side of her flukes which have two large areas of white separated by a black mid-area. On 26 April 1977, we photographed her with a female calf, 1213C7, which had black flippers. On 9 April 1980, we photographed her

Table 1

Summary of reproductive-cycle data. Females photographed in two or more years with and without a calf

Cows	1977	1978	1979	1980	1981
3208	—	—	Ca ♀	Ca ♂	Ca ♀
4201	—	—	—	Ca ♀	Ca
2210	*	Ca	—	Ca	Ca ♂
3205	—	—	Ca ♂	—	Ca ♂
2212	—	Ca ♂	—	Ca ♂	—
2203	—	Ca ♂	—	Ca	—
1213	Ca ♀	—	—	Ca ♀	—
2218	—	Ca ♀	Y ♀	—	—
2208	—	Ca	Y	—	—
1006	*	Ca	Y	—	—
1210	Ca	—	—	—	Y*
1206	Y*	—	Ca	—	—
3006	—	—	*	—	Ca ♀

Ca denotes that the female was photographed with a calf in the specified year. The sex of the calf is indicated when known.

Y denotes that the female was accompanied by her yearling.

Y\* denotes that a 'yearling-size' whale accompanied the female. It is unknown if this whale was the female's offspring.

\* denotes that the female was sighted but that neither a calf nor a yearling were present.

again with another female calf, 1213C0, which had white flippers. Cow 1213 was not observed in 1978, 1979, or 1981.

Table 1 summarizes our findings on the reproductive cycle. Three females exhibited a one-year reproductive cycle, in which postpartum ovulation with conception occurred. One of these, cow 3208, had a new calf three years in succession. Cow 4201 had a new calf two years

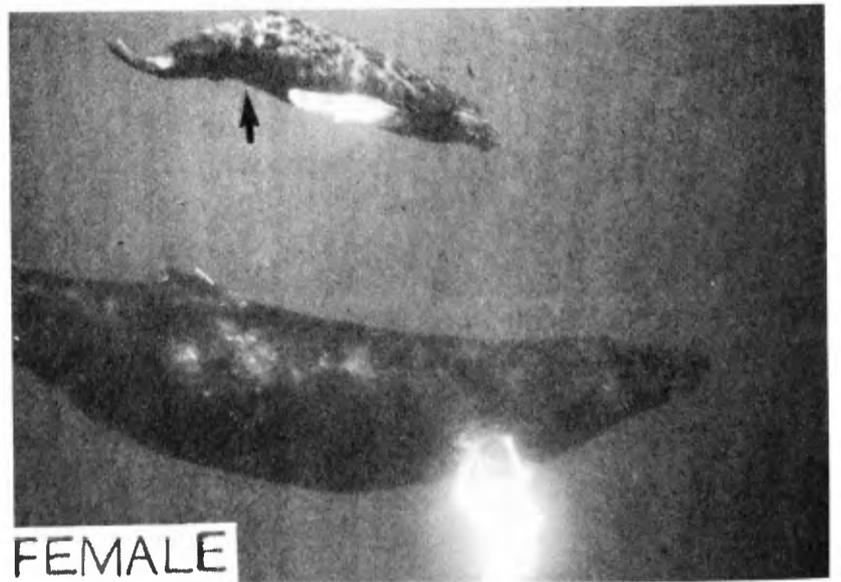
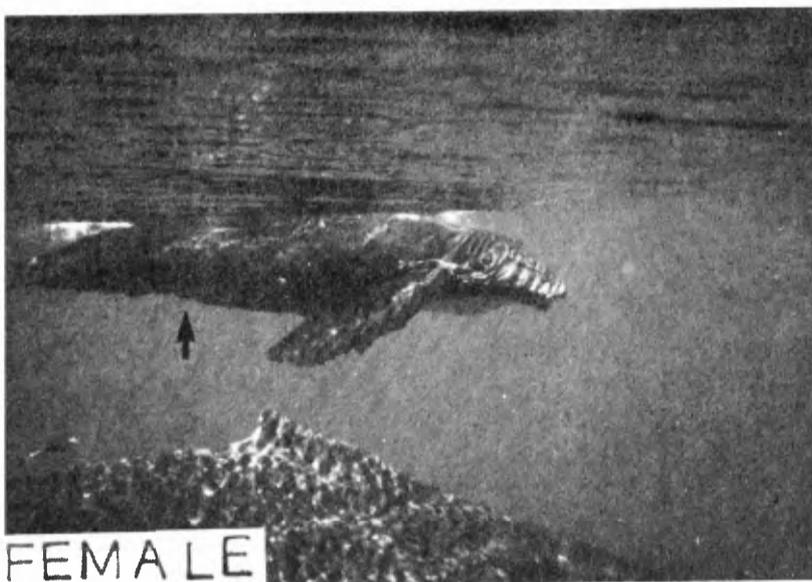
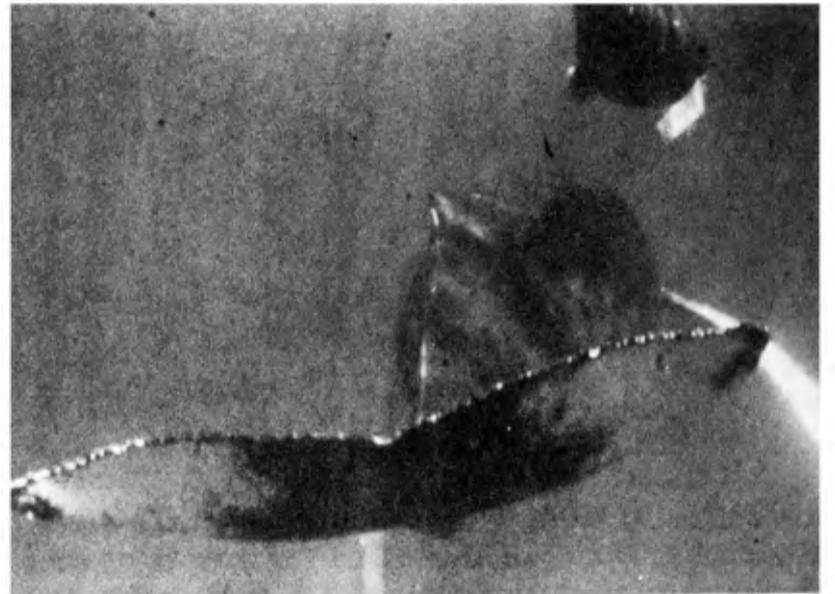
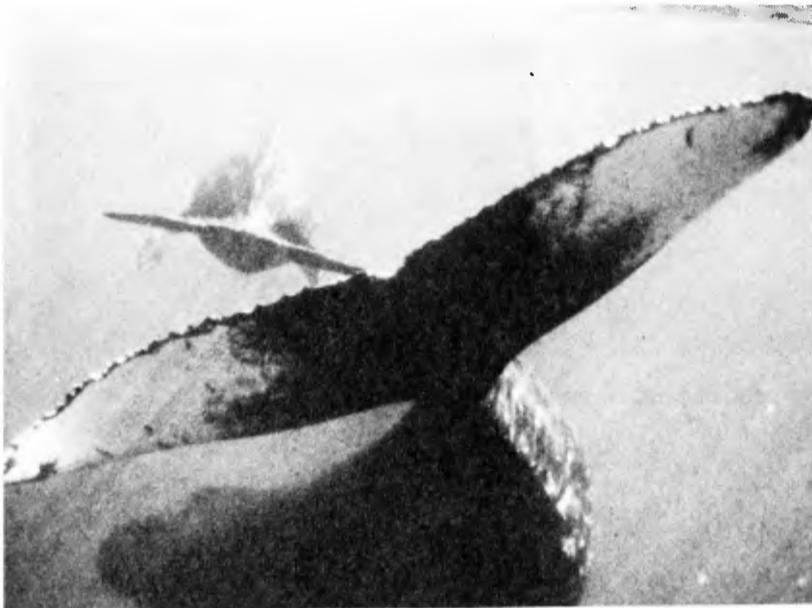
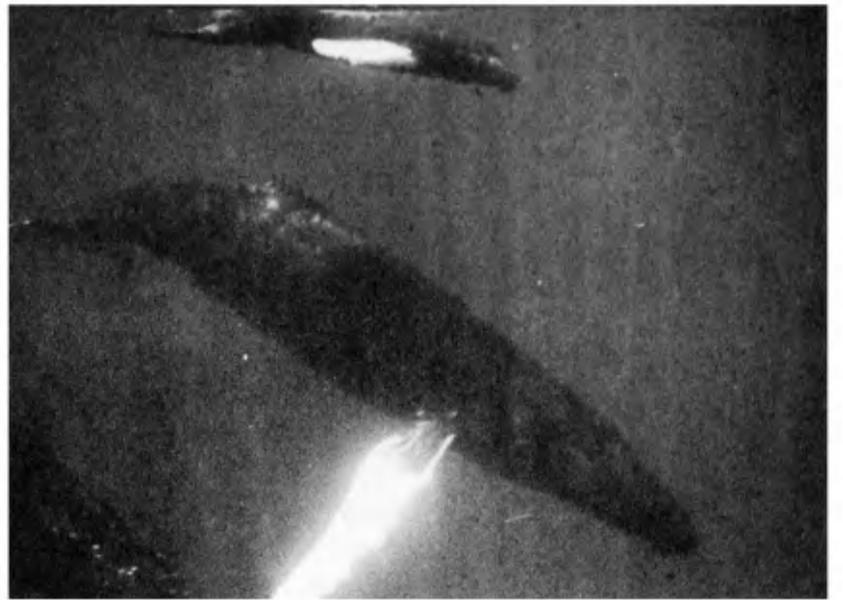
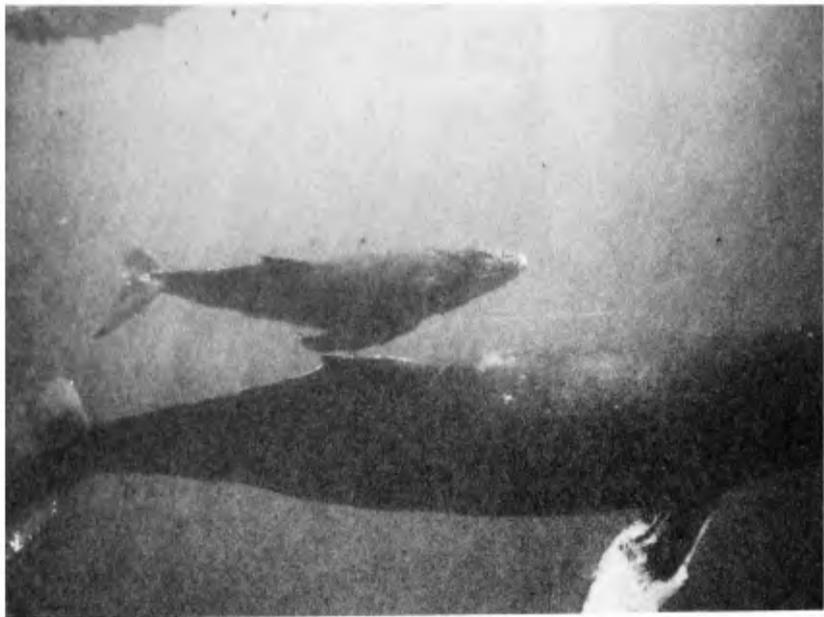


Fig. 4. Cow 1213 and her calves 1213C7 and 1213C0 in 1977 (left) and 1980 (right) respectively. The pigment pattern of the flippers (top) and flukes of the cow and the pigment pattern of the flippers (centre) and sex (lower) of each calf is indicated.

in succession. Cow 2210 had a calf in both alternate and successive years, 1978, 1980, and 1981. We did not observe cow 2210 in 1979 and thus were unable to determine if it produced a calf in this year. We observed three other cows, 3205, 2203, and 2212, with calves in alternate years. These whales are reproducing at the rate of at least one calf every two years. Again, we did not observe these whales in the intervening years. Cow 1213 produced two calves over a three-year interval.

Of the resighted females observed with one calf only,

three cows (1006, 2208 and 2218) were re-photographed with their calves as yearlings the following year. Postpartum ovulation with conception had not occurred in these females. Cow 1006 was also photographed with a group of 8 adults the year preceding parturition.

Postpartum ovulation with conception may commonly occur in female humpback whales in Hawaiian waters. Our sample size is small. From two aerial surveys Herman and Antinoja (1977) found 9.6% and 9.1% of the whales seen to be calves and suggested a low birth rate to exist.

As yet, we have not observed the calves produced at a one-year reproductive rate in subsequent years to determine if they are surviving. Chittleborough (1958) reported that the oestrous cycles of 5 out of 6 females had commenced after the loss of a calf. The survival rate of calves in Hawaiian waters must be investigated.

Chittleborough (1958) stated that an individual whale cannot continuously maintain a cycle in which postpartum ovulation occurs with conception. He suggested that a one-year reproductive cycle in which pregnancy and lactation occur simultaneously would probably be followed by a two-year cycle. More data are needed to determine the frequency of occurrence of a one-year reproductive cycle in female humpback whales in Hawaiian waters.

#### Sex ratio of calves

We determined the sex of 43 calves; 51.2% were males, 48.8% females. Glockner (1983) summarized a total of 2,128 fetuses observed by Chittleborough (1958) in Australia, Omura (1953) in the Antarctic and Matthews (1937) in South Georgia and Natal; 52.1% of the fetuses were male and 47.9% were female, a ratio not different from our result.

#### Lactation and suckling

We observed calves suckling on five occasions. Describing the mammary glands of female humpback whales, Lillie (1915) stated that there are two furrows about 1½' long, one on either side of the genital slit, each of which contains a nipple. By contraction of a compressor muscle, a stream of milk is forced into the mouth of the suckling calf. Lillie suggested that the calf holds the teat in the angle of the mouth near the eye. Scammon (1874) stated that 'a calf suckles by holding the teat between the extremity of the jaws or lips, while the mother reclines a little on one side, raising the posterior portion of her form nearly out of the water, and lying in a relaxed position'. In four of our observations, suckling occurred while the cow was lying stationary in a horizontal position at a depth of approximately 30 to 50 feet. The calf was positioned below the cow at an approximate 30° angle to the midline of her body, the tip of its mouth touching her mammary slit. In the case of calf 2210C1 we observed the calf's jaws opening and closing. After the calf stopped suckling the cow and calf slowly moved on. We observed solid fecal matter in the water but could not determine if it was produced by the cow or calf. Four days later, we observed this same cow and calf. The calf was suckling while the whales were travelling.

#### Yearlings and immatures

Yearlings can easily be distinguished from newborn calves by their length and girth. We have photographed three whales both as calves and as yearlings. We measured whale 1006C8 both as a calf and as a yearling in photographs in which the whale and its mother were perpendicular to the lens of the camera. We found the yearling had grown an additional 30% of its mother's length (Glockner and Venus, 1983). Matthews (1937) states that immatures 8–10 m in length have thicker

blubber than adults 13–14 m. Tomilin (1957) also notes that young humpbacks in Far Eastern Seas had a thicker blubber layer than the adults. We photographed whale 2218C8 both as a calf and as a yearling. As a yearling the whale appeared to be fatter than its mother.

Calf 1006C8 was photographed on 29 January 1978. The following year on 29 January 1979, we photographed this whale as a yearling still accompanying its mother (Glockner and Venus, 1983). On 9 February 1980 we photographed it as a two-year-old, accompanied by two other whales, neither of which was its mother.

#### Body pigmentation

Lillie (1915) classified New Zealand humpback whales into four main categories according to the pigmentation pattern on their flanks and belly. In type 1, the flanks and ventral side are white; in type 2, three points of black occur along the flanks; in type 3 the points of black form bands around the abdomen; in type 4, the black area covers the ventral surface except for an area below the mandible and the dorsal fin. Lillie found that the majority of New Zealand whales occurred in the intermediate categories, with a few individuals in the extreme types. Matthews (1937) found that 60% of South Georgian and South African whales occurred in the darkest category. In the North Pacific, Nishiwaki (1959) found that 92.2% of whales in Ryukyuan waters were in the darkest type-4 category, 6.4% in type 3, 1.4% in type 2. Of 162 cows and calves we have photographed in Hawaiian waters, 98.2% were in type 4, 1.2% in type 3, and 0.6% in type 2. We have photographed only one whale in the type-2 category, cow 4222 on 21 April 1981. This was the first time we observed a whale with such an extensive white area on the belly and flanks in Hawaiian waters.

Nishiwaki (1959, 1966) suggested that humpback whales in the Aleutians and the Ryukyus may be of the same origin with the recovery of six marks that confirmed the migration of whales between the two areas. The similar body pigmentation of humpback whales inhabiting Ryukyuan and Hawaiian waters may indicate that intermingling occurs between whales in the western North Pacific and Hawaii.

Pike (1953) reported 72% of British Columbia humpback whales to have flippers that were predominantly black on the dorsal surface and white on the ventral side. We previously reported 76% of the whales we photographed in Hawaiian waters had flippers with predominantly black dorsal surfaces and white undersides (Glockner and Venus, 1983). In an aerial survey, however, Herman and Antinaja (1977) reported observing predominantly black flippers on only 52% of the whales sighted in Hawaiian waters.

Darling and Jurasz (1983) confirmed the migration of humpback whales between Hawaii and Southeast Alaska by matching tail fluke identifications of seven humpback whales photographed in both areas. Photographic matches were also made of two humpbacks off the Revillagigedo Islands, Mexico and Maui, Hawaii by K. Payne and J. Darling (Payne, 1982). Recovery of marks, photographic matches of tail flukes, and findings of similar body pigmentation of humpback whales in

different areas of the North Pacific support the possibility that humpback whales throughout the North Pacific Ocean may comprise one population.

### DISCUSSION

The frequency of occurrence of postpartum ovulation with conception in humpback whales in Hawaiian waters remains to be determined; our sample size is small. Chittleborough (1958, 1965) reported that a two-year reproductive cycle resulting in one calf in two years was the most common cycle in female humpback whales taken by western Australian whaling stations. More data are needed to determine if a one-year reproductive cycle in which pregnancy and lactation occur simultaneously is common in female humpback whales in Hawaiian waters.

Frequent occurrence of a one-year reproductive rate could indicate that a population is increasing. Recruitment of new members to a population, however, is dependent not only on the reproductive rate, but also on the survival rates of calves and on the age at which the whales reach sexual maturity (Allen, 1974). Herman and Antinaja (1977) and Herman, Forestell, and Antinaja (1980) reported the percentage of calves to adults in Hawaiian waters to be less than 10%, and suggested that a low recruitment rate exists.

We have observed three known yearlings and a two-year-old in the waters off Maui, Hawaii. As yet, we have not observed any of the calves produced at a one-year reproductive rate in subsequent years to determine if they are surviving. The survival rate of the calves must be investigated. To evaluate the true significance of a one-year reproductive rate, future studies should concentrate on photographically identifying individual calves over successive years to determine if they are surviving and at what age the females produce their first offspring.

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# Reproductive Condition of Male Sperm Whales, *Physeter macrocephalus*, Taken off Nova Scotia

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## ABSTRACT

A catch of 109 male sperm whales taken ancillary to a fishery for fin and sei whales from the Blandford, Nova Scotia land station, 1964–1972, was examined. Only males were taken, due to gunner selection, segregation in the migration, or both; and most were from the edge of the continental shelf, often in the area of submarine canyons. Combined testes weight was measured from 54, and histological samples from the middle of a testis were taken from 86 animals.

There was no significant difference between the weights of left and right testes, nor any histological evidence of difference in testicular activity by month during the season of the sample (May through November).

Histological examination of testicular tubules showed that half of the tubules were mature and half were immature in a sample in which the mean body length was 1,368 cm (44.5 ft)  $\pm$  163 cm (5.0 ft). A logarithmic plot of body length against combined testes weight shows a straight line. Since most of our sample (82) was mature (95.5%), we conclude that it is from animals that had already undergone accelerated testes growth associated with the attainment of sexual maturity.

## INTRODUCTION

Large whales have been fished from eastern Canadian shores since the 1890s, with an emphasis on the mysticetes. Sperm whales (*Physeter macrocephalus*) have been taken sporadically in the Newfoundland/Labrador area since 1904, with a total of 414 taken in the first episodes or peaks in effort (Mitchell, 1974) of Canadian whaling in the northwest Atlantic, through 1963.

All of these Newfoundland/Labrador sperm whales were males, but none were sampled for testes weights or histology. The only available data are from *International Whaling Statistics* (IWS, 1930–1980), which gives only length. (The *Bureau of IWS* has on file forms which give position of catch for males.)

During the last episode of commercial whaling, 1964–1972, 119 sperm whales were taken, including 10 from Newfoundland and 109 from Nova Scotia (Mitchell, 1975). We were able to examine most (98%) of these Nova Scotia-landed animals, and since this comprises the first sample of sperm whales from the Scotian Shelf, we treat it separately from Newfoundland (and Labrador) samples. This catch was taken ancillary to a fishery for fin (*Balaenoptera physalus*) and sei (*Balaenoptera borealis*) whales pursued from the Blandford land station, south of Halifax, Nova Scotia (Mitchell, 1974).

## THE SAMPLE

The Blandford sperm whales were all taken within catcher-boat distance, up to a radius of approximately 200 miles (370 km) from the land station (cf. Mitchell, 1974, Fig. 5–1). Most were killed on the edge of the continental shelf, often in the vicinity of submarine canyons. Specifically, a few were taken on the edge at the east end of Georges Bank, and many were taken on the edge from the Northeast Channel (vicinity of the southeast end of Browns Bank) to off Sable Island.

We presume that these animals were all part of a single population because of their relatively close geographical

occurrence, repetitive seasonal occurrence, and segregation by sex. Although we attempted to collect data on pigmentation, external morphometrics and meristics from the landed sample, we have no other relevant sample with which to compare our population. Unfortunately, many sperm whales were landed at night at Blandford, and we have few photographs of pigmentation, but what we have is sufficient to show a wide variation in pattern type. Streaked, pie-bald, partially speckled and completely dark individuals were caught (Figs 1–2) showing many of the pigmentation variations (and scarring; cf. Best, 1979) for sperm whales elsewhere (e.g. Matthews, 1938; Clarke, 1956; Clarke, Aguayo and Paliza, 1968; and contained references; and see Veinger, Lagerev and Mel'nikov, 1975). However, plots of standard quantitative data (Figs 3–6) show that some body proportions (e.g. skull length versus body length, Fig. 3) and physiological features (e.g. blubber thickness versus body length, Fig. 4) show little scatter and indicate a cohesive sample. Data on physical maturity, scored as a discontinuous variable, including fusion of vertebral epiphyses versus body length (Fig. 5) and length versus age in dentinal growth layer groups (Fig. 6), do not contradict this conclusion.

Whether this Northwest Atlantic population is discrete from that fished in Denmark Strait (from Iceland) and/or elsewhere in the northeastern Atlantic is unresolved on present evidence. The only relevant information is one return from 109 tagged sperm whales in the Northwest Atlantic (Mitchell, 1975), a male tagged off the southeast end of Browns Bank in 1966 and returned as a 41-ft (12.55 m) kill on 7 August 1973 off Spain (Mitchell, 1975, Fig. 5). Although we do not necessarily believe that there is only one stock of sperm whales in the North Atlantic, this tag, comprising the only direct evidence to date, forces us to conclude that the data must be treated as if there were only one stock. (Assessments of the North Atlantic sperm whales carried out recently by the Scientific Committee of the International Whaling Commission (IWC) have been for the single stock hypothesis – e.g. Hiby and Harwood, 1981, according to



Fig. 1. a. Whale B-41-72, (10.24 m; 34 ft), pigmentation. b. c. Whale B-41-72, pigmentation. d. Whale b-3-72 (13.38 m; 44 ft), pigmentation.

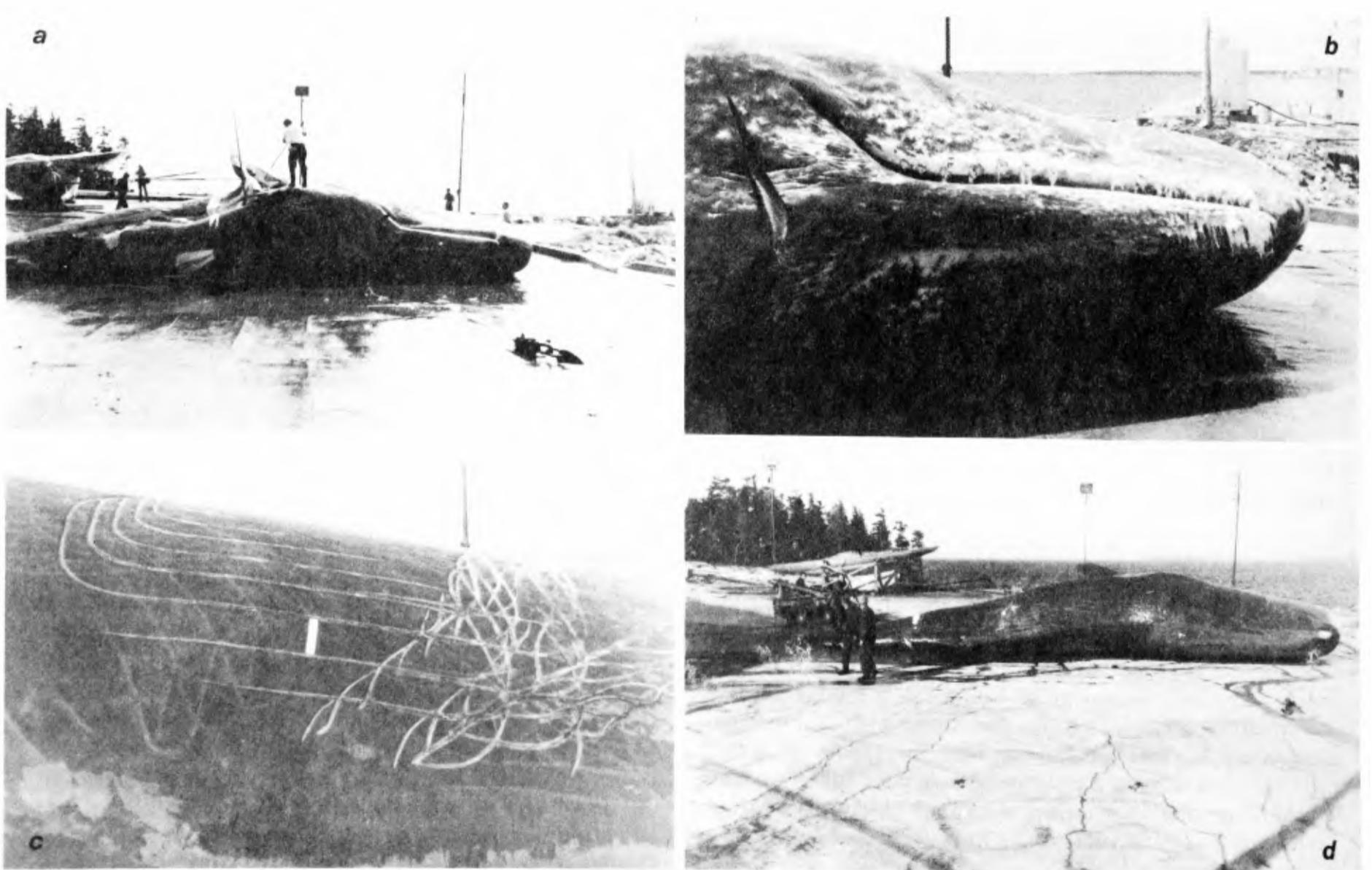


Fig. 2. a. Whale B-53-72 (15.14 m; 50 ft). b. Whale B-4-72 (13.70 m; 45 ft), head pigmentation. c. Whale B-1-72 (15.55 m; 51 ft), head. d. Whale B-1-72.

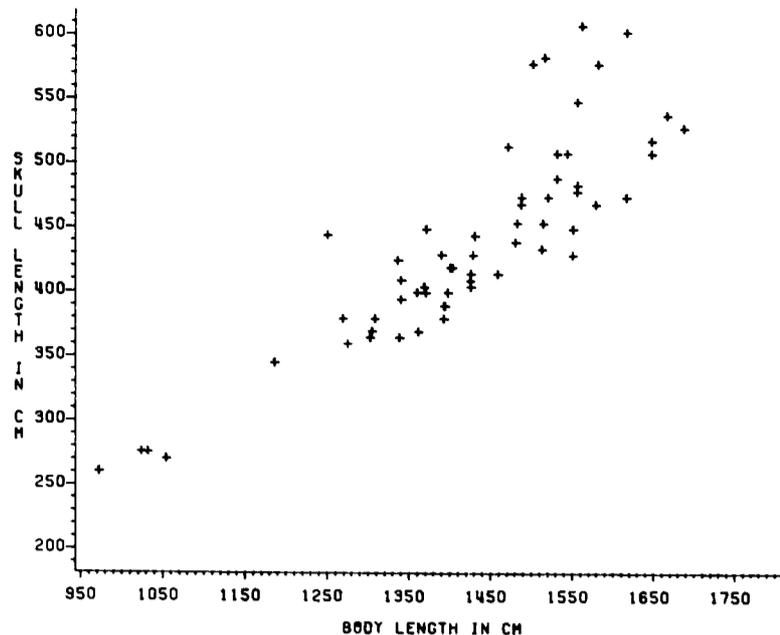


Fig. 3. Scatter diagram, skull length in cm, and abscissa body length in cm.

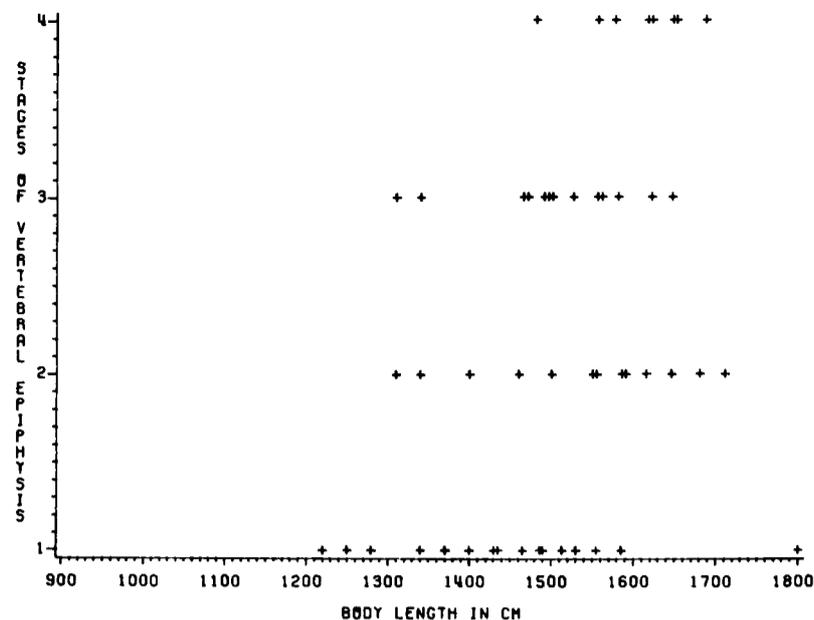


Fig. 5. Scatter diagram, ordinate stages of vertebral epiphysis, and abscissa body length in cm.

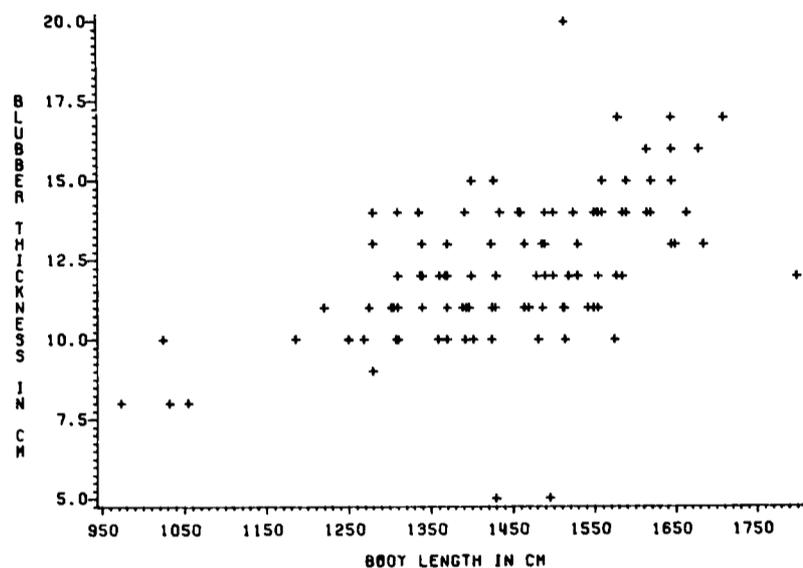


Fig. 4. Scatter diagram, ordinate blubber thickness in cm, and abscissa body length in cm.

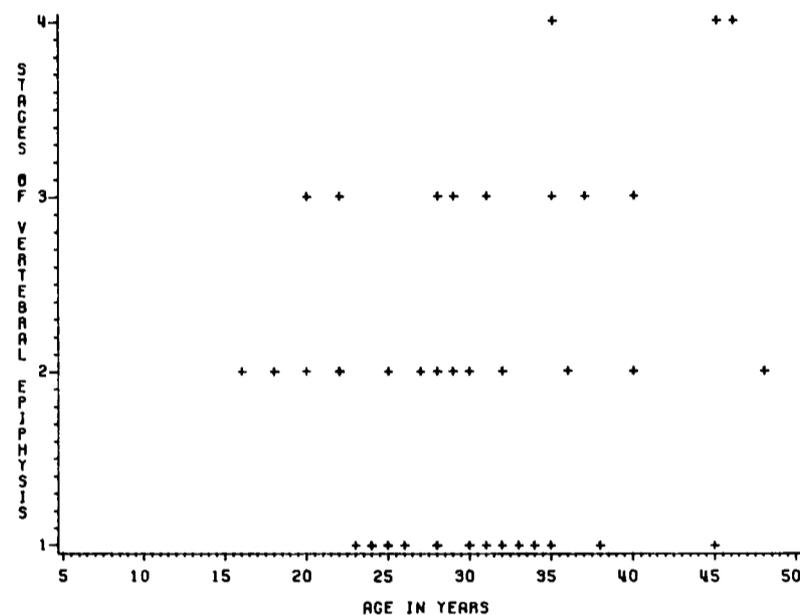


Fig. 6. Scatter diagram, ordinate stages of vertebral epiphyses, and abscissa age in dentinal Growth Layer Groups.

title, but cf. their 'catch outside Iceland' specified by six areas).

Most of our sample is comprised of sperm whales taken near the beginning and the end of the baleen whaling season (approximately mid-May to mid-November) coincident with the whaling effort for sei whales. The sei whale catch out of Blandford was consistently more to the southeast of the station, farther away, and closer to the edge of the continental shelf than the fin whale catch. The sei whale 'run' was in June and again in September. When the catcher vessels were in the vicinity of the sei whale concentration but no sei whales were sighted or caught, sperm whales were taken, hence the sporadic nature of the sperm whale fishery (Mitchell, 1975, Fig. 2).

We assume our sample is from one population. However, the actual biological population represented is in question. Based on our observations from catcher vessels and survey vessels in the northwest Atlantic, we believe that the population sampled includes large males that migrate along the continental edge of eastern North America, from off Georges Bank along the Scotian Shelf to around (or across?) the Grand Banks, and up Labrador to off Hudson Strait, then offshore into Davis Strait. We believe that the large bulls we have seen on the

West Greenland coast are from the same population. Catches of these by West Greenlanders (Kapel, 1979) have not been sampled. Mating in Azorean and other Northern Hemisphere sperm whales reportedly occurs in January through July with a peak in April-May (Clarke, 1956; Mitchell and Kozicki, 1978, and contained references); the Nova Scotian sample comprises at least 23 (22%) males over 45 ft in length caught in late May and June. These are possibly males migrating northward, departing from the 'Southern Ground' in the Northwest Atlantic (Gilmore, 1959, Figs 1-2; and cf. Clark, 1887, Sect. V, pl. 183 and Sect. V, vol. 2, pp. 8-15) after the presumed peak of mating.

Since the fishing effort for sperm whales was sporadic, coincident with that for sei and reciprocal to that for fin, the sample may not be representative or random enough to fully assess reproductive state in seasonal, polewards migrations of bulls. We do not know what portion of the migrating stream of bulls we have sampled, how fully these were sampled by the fishery, and whether the migration is annually repetitive for all large bulls.

Gunner selection may further obscure the biological usefulness of our sample in studying the composition of the migrating stream of bulls, but it might have acted to

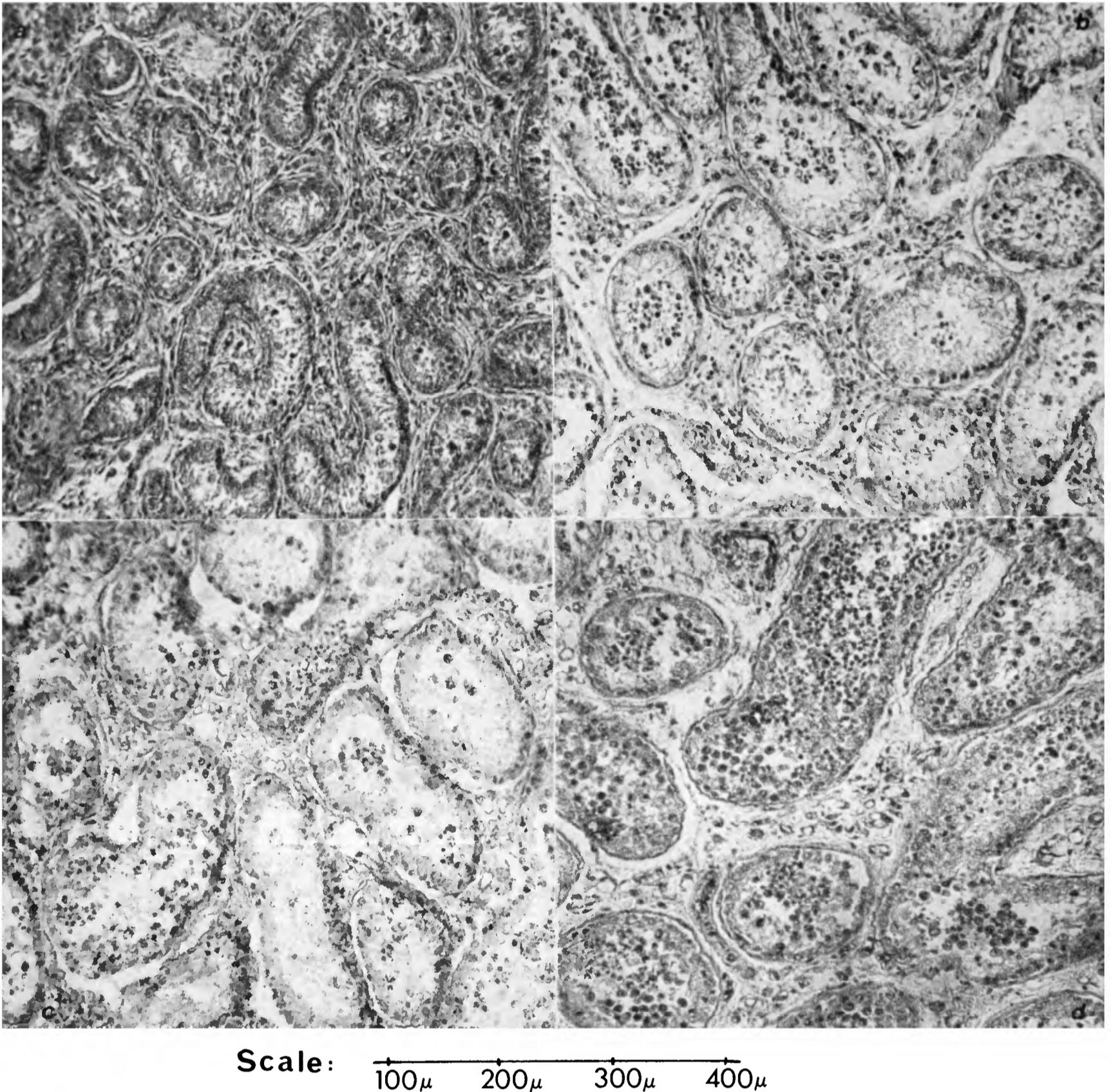


Fig. 7. A. Stage of testes development = 1, immature animal with some mature tubules present. B. Stage of testes development = 2, half immature and half mature tubules. C. Stage of testes development = 3, mostly mature tubules. D. Stage of testes development = 4, all mature tubules.

give us a narrowly defined sample (e.g. possibly the largest animals on the grounds at that time).

Our sample may be either: a sample of the largest whales from an available population of males and females, where all females fall below the minimum length being selected for; or a sample of the largest whales in an available population of males only; or a random sample of all the males present (which in this case would imply that only large males were present).

#### MATERIAL AND METHODS

##### Material

Personnel assigned to Canadian land stations sampled landed sperm whales from 1965 to 1972. At Blandford, sperm whales were sampled mainly by E. Shoubridge, D. Wood, G. Horowitz, VMK and EDM.

Because baleen whale and sperm whale products must be kept separate for commercial reasons, landed sperm carcasses were often left to the end of the day or even for days before processing, while landed baleen whales were processed within a 33-hour time limit for meat products. Thus, many of the sperms we examined were 'cooked', and the internal organs had deteriorated by the time the whale was cut open and we were able to sample them.

Both testes were removed from each whale examined, weighed to the nearest  $\frac{1}{4}$  lb (0.114 kg), and measured in three dimensions. A sample of tissue was removed from near the center of at least one testis and fixed immediately. Samples were generally preserved in alcoholic Bouin's fluid for 12–24 hours, then stored in 70% alcohol until subsequent histological preparation. Some however were preserved in 10% formalin. All samples were sent out between three months to three

years after sampling to commercial establishments for standard histological preparation and staining with haematoxylin and eosin. The slides appear to be technically well done, the stain usually uniform and the samples clearly marked. However, most of the slides are of relatively poor quality in terms of readability, clearly due to the long postmortem time before fixation. All tissue samples and slides have been retained for ultimate deposition in the Department of Mammalogy, National Museum of Canada, Ottawa. Previous work on the histology of the testes in sperm whales (e.g., Matthews, 1938; Nishiwaki and Hibiya, 1951, 1952; Nishiwaki, 1955; Nishiwaki, Hibiya and Kimura, 1956; Clarke, 1956; Nishiwaki, Hibiya and Ohsumi, 1958; Aguayo, 1963) has been referred to and evaluated by Best (1969).

### Procedure

Slides were scanned at a magnification of  $\times 125$  with a compound microscope, and selected data were recorded on edge-punch cards. Parameters used were those we devised in our own work on baleen whales, following studies on fin whales by Mackintosh and Wheeler (1929) and Laws (1961), with modifications as noted below. We selected these parameters after an examination of a small sample of slides, in order to determine stage of maturity and state of reproductive activity. Not all of the features chosen proved of equal value, and most of them are not alone definitive as to stage of sexual maturity. All are discussed below in order of descending importance (and illustrated in Figs 7–8):

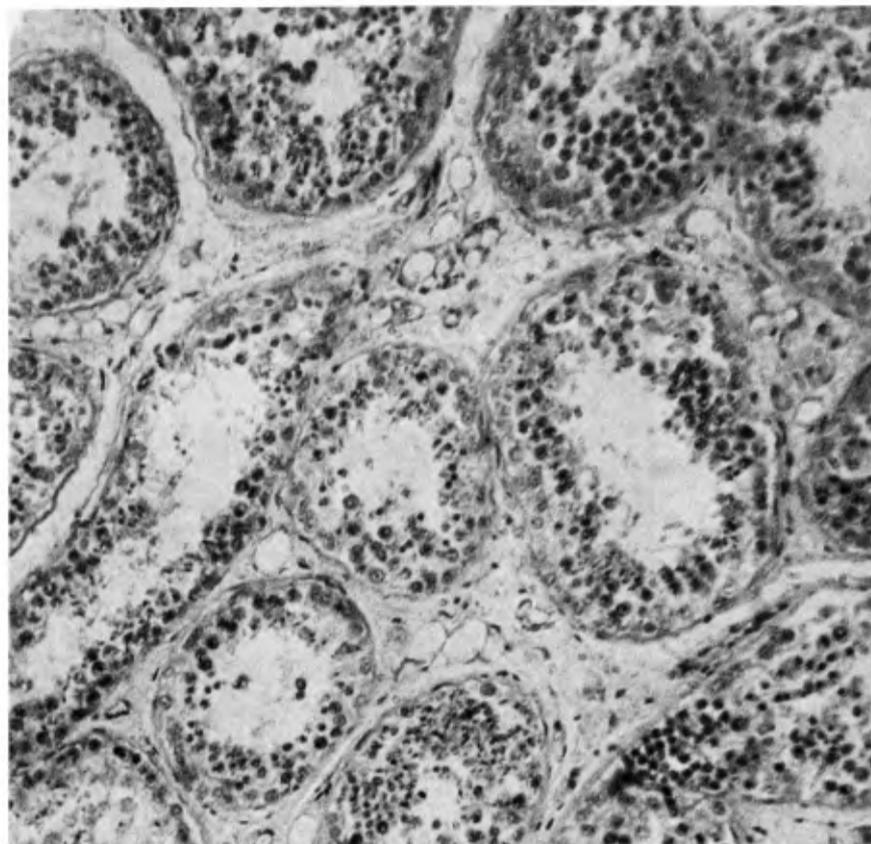
*Range of tubule sizes.* Maximum diameter of only the round tubules was measured with an ocular micrometer. The number of tubules measured was arbitrary; usually ten were measured for each sample but this was a minimum.

A problem arises when the sample is neither completely mature nor completely immature, but contains tubules of both types. In this case the average tubule diameter is not indicative of the state of activity; the maximum and minimum diameters better reflect the situation. These puberal animals comprised about 15% of the sample. Otherwise this purely numerical measurement is a useful reflection of sexual maturity. Fig. 7 presents a number of examples to illustrate these points.

*Amount of sperm present.* This is an estimation, but a more important one than 'meiotic stages in evidence' (described below) since very often cells in intermediate stages will break down with degeneration of seminiferous epithelium. The range of values we used for this character include: 'none', 'some', 'moderate', 'many'.

*Meiotic stages in evidence.* This is an estimation, done after examining a cross section of the samples. The range of value is 'none', 'some', 'moderate' or 'many'. This particular character is not as important as the amount of sperm present. As Mackintosh and Wheeler (1929) pointed out for fin whales, observation of division stages is not consistently possible in whale testes tissue preserved long after death.

*Lumen in middle of tubule.* This feature was recorded as 'yes', 'no', or 'some' (cf. Fig. 31–3 on p. 687 of Bloom and Fawcett, 1968; and our Fig. 8). There is a patent lumen, lined by Sertoli and germinal cells, in adult, active testes. In a sample preserved long after death, this lumen



Scale: 100 $\mu$  200 $\mu$  300 $\mu$  400 $\mu$

Fig. 8. Stage of testes development = 4, mature; lumen in middle of tubule open.

may be occluded by the broken down seminiferous epithelium, where the cells have sloughed off into the lumen (e.g. Fig. 7C where most tubule sections show no definite lumen). A patent lumen is not developed in immature specimens (see Fig. 7A; and Bloom and Fawcett, 1968, p. 688).

*Amount of interstitial tissue.* We originally included this feature on the basis of evidence from pinnipeds indicating that immature testes contain proportionally more interstitial tissue than do mature testes (Amoroso, Harrison, Matthews and Rowlands, 1951; Harrison, Matthews and Roberts, 1952; Laws, 1956). However, this parameter was not as predictable as we assumed it might be in whales. (For instance, we have observed that in male fin whales just maturing, there is often but not always less interstitial tissue than in mature but inactive fin whale testes – this variation was also noted by Mackintosh and Wheeler, 1929, p. 407). We used the following codes: 3 – regions of connective tissue between tubules equal to or larger than the diameter of the tubules in greatest extent; 2 – intermediate between 3 and 1; 1 – tubules closely adjacent, less than one half of a tubule diameter apart. (Figs 7A, B, C and D show connective tissue stages 3, 2 and 1, respectively.)

*Cells with dark nuclei lining the tubule.* This feature is subjective. Immature specimens show small follicular cells, with darkly staining nuclei lining the imperforate tubules. These will become Sertoli cells in the mature animals. The rest of the tubule is taken up with large primordial germ cells with lightly staining nuclei. Mature tubules are lined with primary spermatocytes. If enough of these are undergoing meiosis (and show dark nuclei) then grossly the tubules will appear to be lined with cells having dark nuclei. We used values of: 'present', 'some', or 'absent' for this parameter, but we found it the least valuable index in determining stage of maturity.

*Summary.* Because of the long postmortem time, the

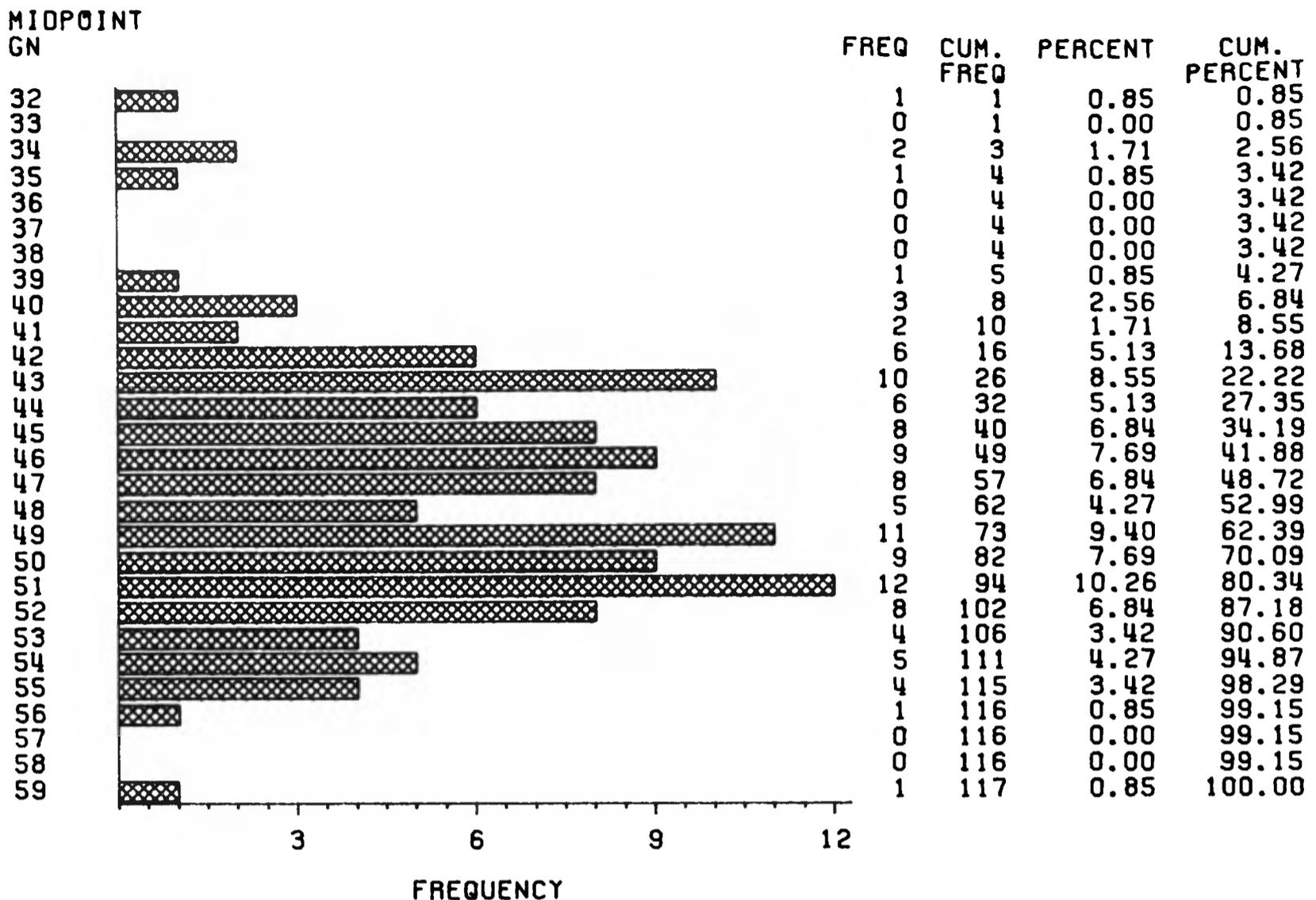


Fig. 9. Histogram of length frequencies of the Nova Scotia sperm whale catch.

seminiferous epithelium was broken down in most samples and had sloughed off into the middle of the tubule. This made detailed study of meiosis impossible. We depended largely upon mensuration of the tubule diameters and the amount of sperm present and arrived at an interpretive summary of all the above characters, scored in five stages of estimated sexual maturity: 0 – Immature animal, 1 – Some mature tubules present, 2 – Half immature, half mature tissue, 3 – Still some immature tubules present, and 4 – Mature (cf. Figs. 7A–D for examples of summary stages 1–4, respectively).

## RESULTS AND DISCUSSION

Data on maturity of testes are compared below with length, age, and other parameters. The summary parameter, 'estimated stage of the testis' (a discontinuous variable) and the character, 'average tubule diameter' (a continuous variable) are plotted separately. We found tubule diameter to be the best single histological character to judge sexual maturity, and the overall estimated stage of maturity is based heavily on it. Total testes weight is also definitive.

### Length frequency of landed catch

We have length data for 273 of the 414 pre-1964 sperm whales from the Labrador-Newfoundland fishery. (Note: BIWS forms for 1950–1951 report two 'females' in this catch but both whales were over 50 ft (15.25 m) in length.) A histogram of these data is bell-shaped, ranging

from 40 (12.20 m) to 60 (18.30 m) ft, with a mode of 55 ft (16.8 m).

The length frequency of the post-1963, Nova Scotia sample (Fig. 9) shows a similar, bell-shaped distribution, with a mean of 47.1 ft (14.4 m) (s.d. 5.0 ft (1.52 m)), a mode of 51 ft (15.5 m) and a range between 32 (9.75 m) and 59 (18.0 m) ft (the bulk of the sample occurring between 39 (9.75 m) and 56 (17.0 m) ft).

### Growth

We cut and read dentinal growth layer groups from lower, mid-row teeth of 78 (74%) whales in our sample. Most teeth were not substantially worn and gave complete counts. The resulting scatter diagram of age versus total body length (Fig. 10A) shows that aside from three younger animals, all others were over 14, with the preponderance of the sample being over 18 growth layer groups in age. Except for the three young animals, all were over 12.50 m in total body length. These data represent the right hand portion of an age-length curve. There is little pattern in a scatter diagram of combined testes weight versus age in growth layer groups (Fig. 10B), due to the biased nature of the sample.

### Comparison of left and right testes

We collected weights and volumes of both testes where possible, in order to examine this question. We also wished to determine whether we could extend the usefulness of our sample by doubling single testis weight

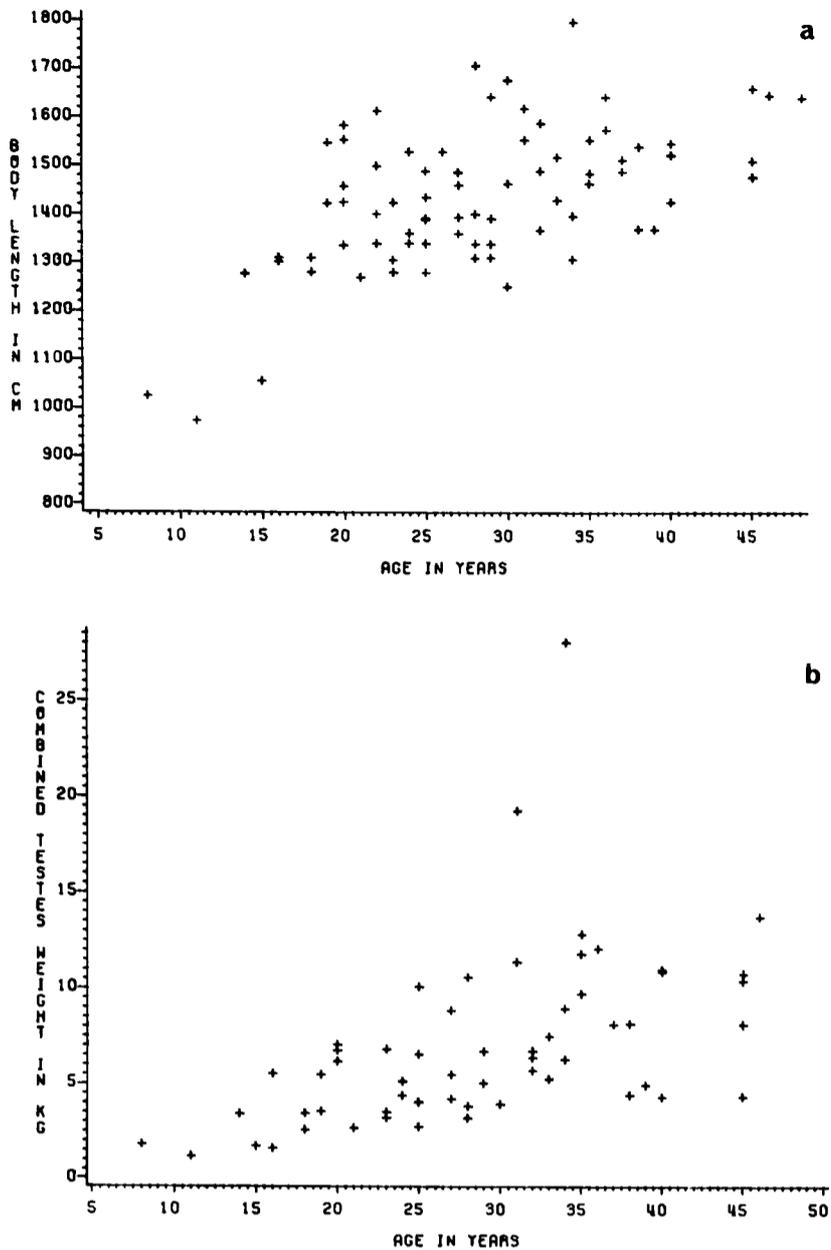


Fig. 10. A. Scatter diagram, ordinate body length in cm, and abscissa age in dentinal Growth Layer Groups. B. Scatter diagram, ordinate combined testes weight in kg, and abscissa age in dentinal Growth Layer Groups.

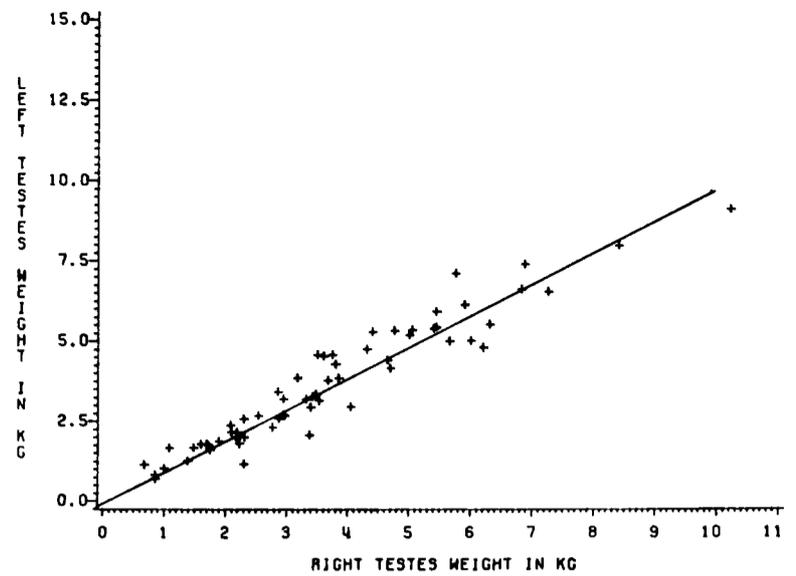


Fig. 11. Scatter diagram, ordinate left testis weight in kg, and abscissa right testis weight in kg.

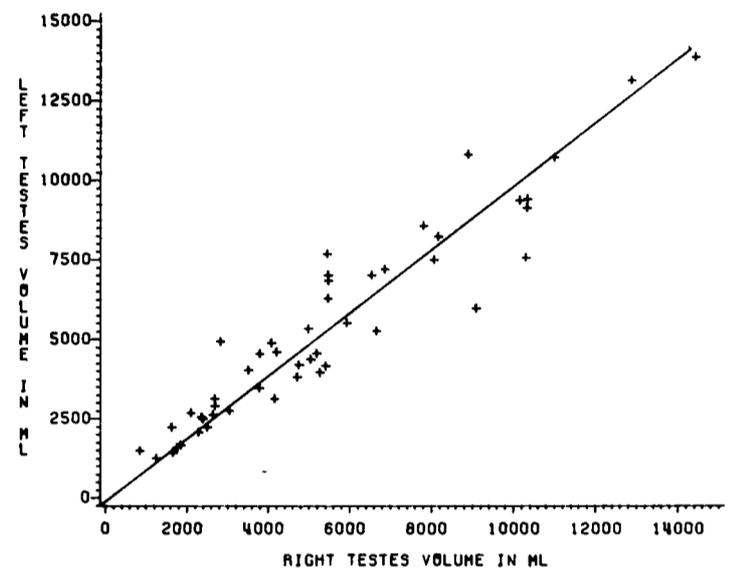


Fig. 12. Scatter diagram, ordinate left testis volume in ml, and abscissa right testis volume in ml.

to obtain a representative combined weight when only one testis had been collected.

Testes weights for 54 pairs were plotted separately (cf. Mitchell, 1975, Fig. 4), left versus right (Fig. 11). Of these, 27 rights were larger (maximum difference of 1.31 kg), while 24 lefts were larger (maximum of 1.35 kg), and left and right were equal in three cases. The mean weight of the left testis was 3.645 kg (s.d. = 1.918 kg), with a minimum weight of 0.68 kg and a maximum of 9.07. The mean weight of the right testis was 3.677 kg (s.d. = 1.972 kg), with minimum of 0.68 kg and maximum of 10.20 kg. Comparable data on the volume of right and left testes (obtained by multiplying the three dimensions) show exactly the same pattern (Fig. 12). There is no significant difference between right and left testes weight or volume in our Nova Scotia sample of sperm whales (at the 5% level). These findings are in agreement with the findings of Best (1969), and Nishiwaki and Hibiya (1951), and differ from the conclusions of Nishiwaki (1955) and Clarke (1956) regarding a disparity in size.

**Testes size relative to total body length**

Scatter diagrams of combined testes weight (Fig. 13) and combined, calculated testes volume (Fig. 14) were replotted using Best's (1969) method in order to more

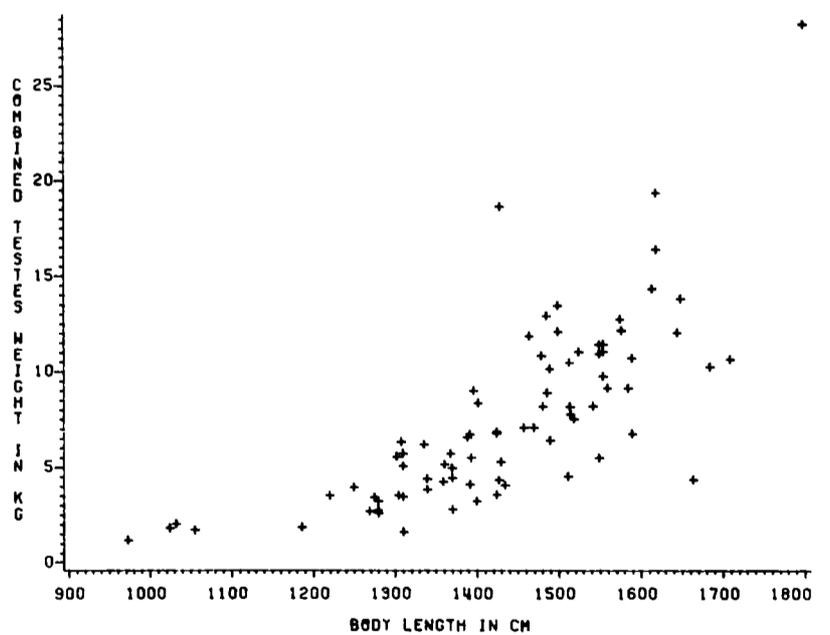


Fig. 13. Scatter diagram, ordinate combined testes weight in kg, and abscissa body length in cm.

precisely identify trends in the regression of testes size on body length. The geometric mean of combined testes weight (or volume) by 0.5-m body length classes was further smoothed by threes. With very few small animals (under 37 ft, 11.3 m), we cannot calculate the point of

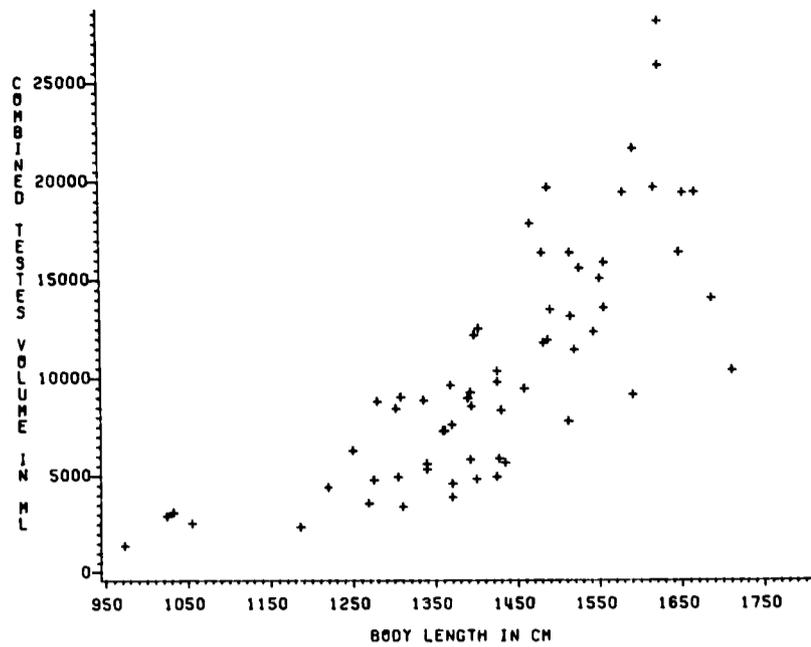


Fig. 14. Scatter diagram, ordinate combined testes volume in ml, and abscissa body length in cm.

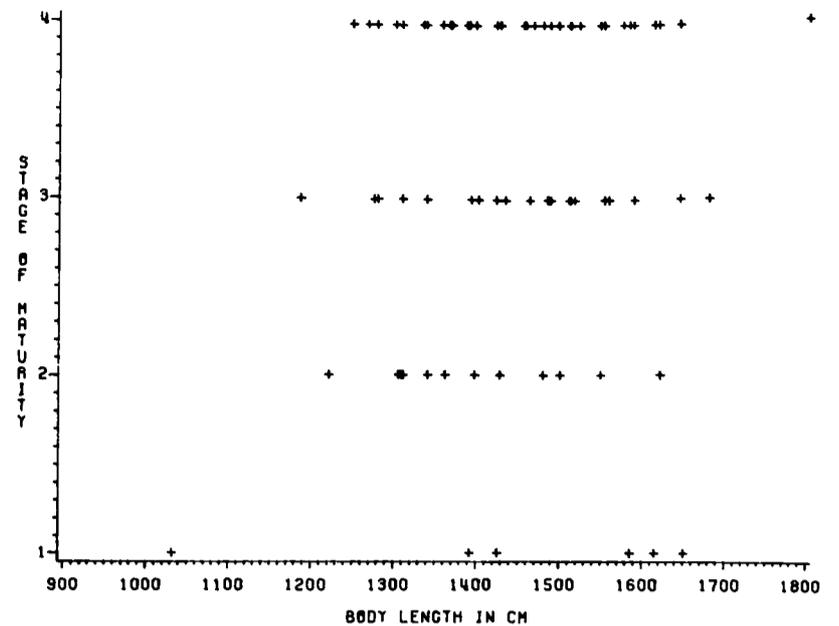


Fig. 17. Scatter diagram, ordinate stage of maturity, and abscissa body length in cm.

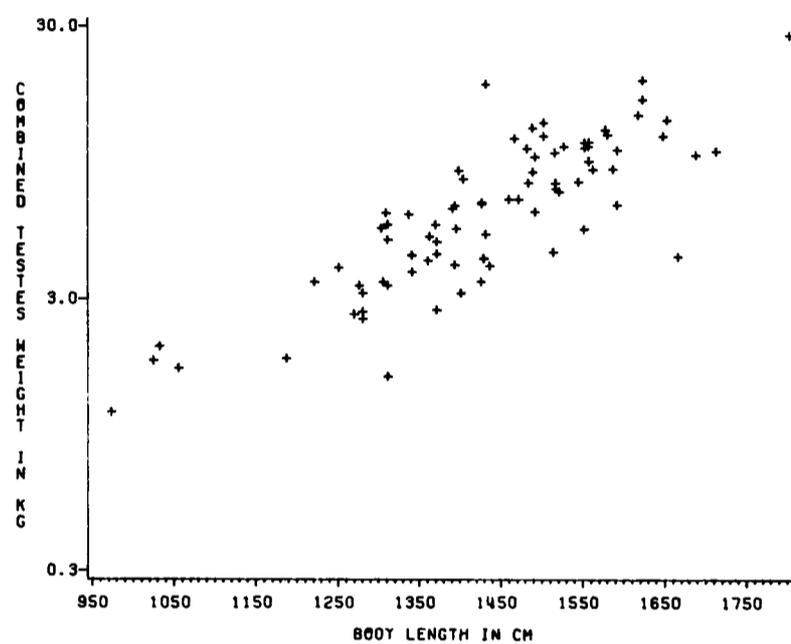


Fig. 15. Scatter diagram, ordinate combined testes weight in kg, and abscissa body length in cm.

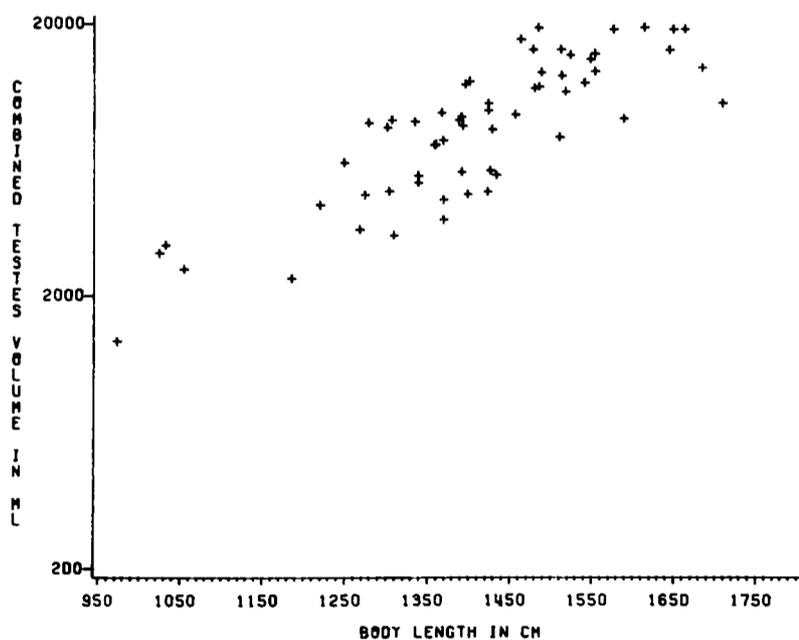


Fig. 16. Scatter diagram, ordinate combined testes volume in ml, and abscissa body length in cm.

Table 1

Seminiferous tubule diameters (in microns), tabulated by summary histological parameter, 'Estimated Stage of Sexual Maturity,' Nova Scotia sperm whales, 1964-72. Abbreviations:  $n$  = sample size; S.D. = standard deviation; Min. = minimum; Max. = maximum

	$n$	S.D.	Min.	Max.
Stage of maturity = 1				
Average min. diam.	6	32.9	50.0	120.0
Average max. diam.	6	35.1	100.0	170.0
Average diam.	6	32.1	70.0	140.0
Stage of maturity = 2				
Average min. diam.	13	13.9	90.0	140.0
Average max. diam.	13	17.4	140.0	200.0
Average diam.	13	12.1	120.0	170.0
Stage of maturity = 3				
Average min. diam.	21	14.0	60.0	130.0
Average max. diam.	21	17.7	150.0	210.0
Average diam.	21	14.3	110.0	170.0
Stage of maturity = 4				
Average min. diam.	44	17.5	60.0	140.0
Average max. diam.	44	17.5	150.0	230.0
Average diam.	44	15.4	110.0	180.0

inflexion representing the onset of sexual maturity. However, using the data of Best (1969, Figs 3A, 4A) for comparison we infer that this inflexion would lie between 40-41 ft (12.0-12.3 m) in the Nova Scotia sample (Figs 15, 16). Thus we have a sample comprised preponderantly of sexually mature bulls.

#### Evaluation of summary histological parameter, 'Estimated Stage of Sexual Maturity'

We calculated for each stage information on the average minimum, maximum and mean tubule diameter, with ancillary statistics (Table 1). Results of plotting this discontinuous variable against total body length (Fig. 17) does not show a progression of stage against body length but shows that stages 2, 3 and 4 may occur over a comparable, wide range of body lengths.

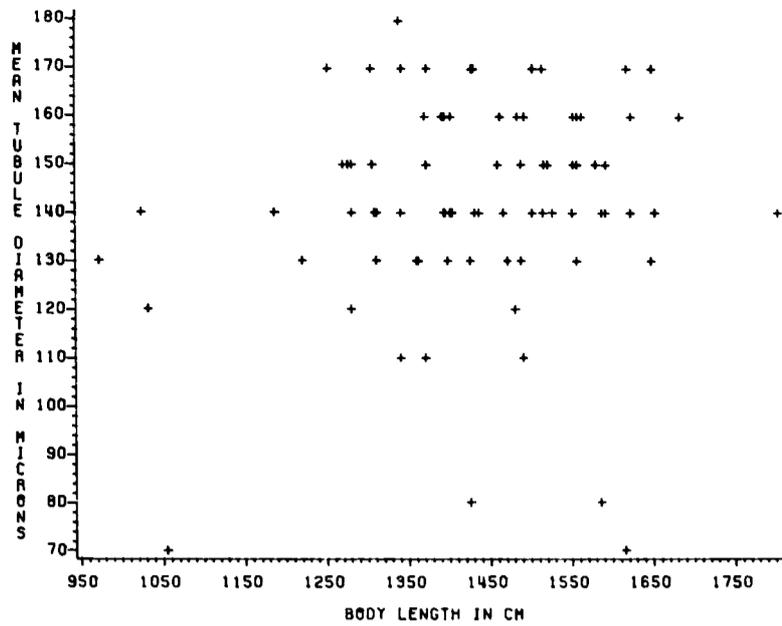


Fig. 18. Scatter diagram, ordinate mean tubule diameter in microns, and abscissa body length in cm.

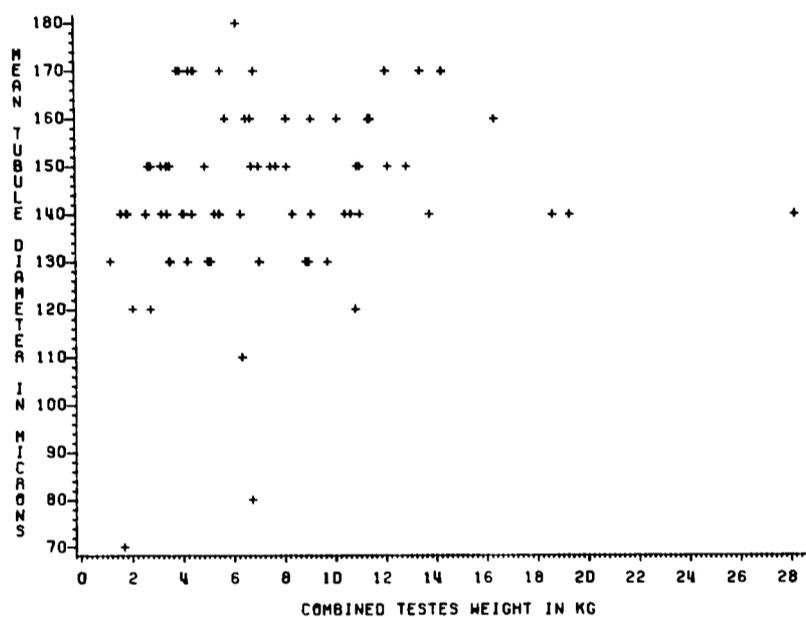


Fig. 19. Scatter diagram, ordinate mean tubule diameter in microns, and abscissa combined testes weight in kg.

**Mean tubule diameter versus total body length and combined testes weight**

A scatter diagram of these data (Fig. 18) shows a similar scatter for different diameters over a wide range of body lengths (cf. Fig. 17). Using maturity (e.g. tubule diameter and combined testes weight) in a scatter diagram (Fig. 19), we expected a tighter cluster. However, problems associated with sampling the testes (and polarity in testis maturation; Best, 1969) might account for some spread at the top of the cluster.

**Cyclical, seasonal activity**

Our sample is too small and too limited in seasonal span to allow examination of gross seasonal variation in testes activity from testis weight, seminiferous tubule diameter or abundance of spermatozoa. None of the data herein presented gives indication of such variation in e.g. testes weight indicating cyclical activity (cf. Ridgway and Green, 1967; Best, 1969).

**Length at sexual maturity**

We are unable to calculate the mean length of sexual maturity from the regression of combined testes weights on total body length (Figs 15, 16). In order to calculate this we therefore used another approach. We tabulated the summary parameter, 'Estimated Stage of Sexual Maturity,' from histological evidence, by stages (1, 2, 3+4 in Table 2) with body length data. Results show that half of the tubules were judged mature and half were judged immature in a sample in which the mean body length was 13.7 m (44.5 ft) ± 1.63 m (5.0 ft).

Our estimate (above) of the onset of sexual maturity at a length of 41 ft is likely biased due to the effect described by Best (1969) where the testis matures from the center outwards. Our samples were collected from the middle of a transverse slice, at midlength; thus the estimate should be for sexual maturity at a relatively short length. However, Best (1969) summarized findings of other workers who had sampled similarly from the exact center of the testis, with resulting lengths much lower than this. Our data may indicate differences between geographical populations.

Table 2

Body length data tabulated by summary histological parameter 'Estimated Stage of Sexual Maturity', Nova Scotia male sperm whales, 1964-72

Stage of maturity	n	Body length (cm)	s.D. (cm)	Min. (cm)	Max. (cm)
1	8	1,405	241	1,032	1,650
2	13	1,368	163	973	1,620
3+4	65	1,448	131	1,024	1,800

**SUMMARY**

A sample of 86 from a catch of 109 male sperm whales at the Blandford land station, Nova Scotia, 1964-72, was sampled. Combined testes weight (and/or calculated volume) was the best gross measure, and seminiferous tubule diameter the best histological measure of the attainment of sexual maturity. Data from combined testes weight indicates that sexual maturity is attained at a minimum of 41 ft (12.5 m); data from seminiferous tubule diameter indicates a length of 44.5 ft (13.7 m).

**ACKNOWLEDGMENTS**

We thank the technicians who collected and fixed testes samples at the whaling stations (E. Shoubridge, D. Wood and G. Horonowitsch); J. McLaren who read and scored the slides; and B. Mason and Y. Ottaviano for lab assistance. Mr Karl Karlsen of the Karlsen Shipping Co. allowed us to obtain these samples and data. The SAS statistical package at the McGill University Computer Centre was used for computer graphics, with the aid of H. Brodie. J. M. Breiwick and three reviewers gave useful criticism of the manuscript.

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# Growth and Reproduction of Killer Whales, *Orcinus orca*, in Norwegian Coastal Waters

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## ABSTRACT

Length data and reproductive material collected by coastal whalers during the period 1938–67 and 1978–81 are analysed. Female killer whales attain sexual maturity at a length of 15–16 ft (4.6–4.9 m) and an age of about 8 years, and males at about 19 ft (5.8 m) and 15 years. Mating occurs throughout the year, with a maximum in October–December. The birth rate seems to be one calf every three years. Preliminary age determinations indicate that physical maturity is attained at 20–25 years, with a life span of at least 35 years.

## INTRODUCTION

Increasing numbers of killer whales, *Orcinus orca*, sighted in Norwegian coastal waters has raised the question of interactions between whales and fisheries. Through their organizations, fishermen have expressed their concern that increasing numbers of killer whales may provide an excessive pressure on the stock of Atlanto–Scandian herring. Catches of killer whales have been small compared to the take of minke whales, *Balaenoptera acutorostrata*, and in the period 1973–77 only negligible catches (0–7 per year) were taken. In response, the Norwegian Government in 1978 permitted catches of this species outside the regular whaling season.

This expanded catch season in late autumn and early winter provided an opportunity to collect material from killer whales during a period assumed to be the peak mating and calving season.

The following report is based on an analysis of teeth and reproductive organs collected by whalers in the years 1979–80, and on biological data submitted by whalers under the compulsory reporting system during the periods 1938–67 and 1978–80.

## MATERIAL AND METHODS

For each whale caught, Norwegian whalers are required to provide data on location, sex and length (including foetuses) as well as the weight of meat and blubber. Body lengths are estimated by the whalers in English feet, while the lengths of foetuses are estimated in cm. This report is based upon analyses of records from the period 1938–67 plus the recent information provided for 173 female and 143 male killer whales caught in the Lofoten and Vesterålen areas in 1978–80.

In addition to the recorded data, teeth from 68 females and 53 males and reproductive organs from 47 females and 45 males were collected in 1979 and 1980. A reward was paid for each set of teeth and organs. For some of the whales, however, only one of the paired reproductive organs had been collected.

Ovaries were sliced in approximately 3 mm thick sections and examined macroscopically. All corpora were classified and recorded. Testes have not yet been examined. Teeth were cut in longitudinal sections, ground and then etched for 30 hours in 10% formic acid. Growth

layers were counted under a binocular dissecting microscope ( $\times 6$ ) using reflected light.

## AGE AND GROWTH

Lengths of 107 foetuses reported by whalers for the periods 1938–67 and 1978–80 are plotted against date (10-day periods) in Fig. 1. One foetus reported to be 10 ft (305 cm) long has been omitted in the figure, as there can be no doubt that a mistake was made. Two other foetuses, reported to be 250 cm and 256 cm long, are also omitted because either the lengths were overestimated or they represent extreme variants. The smallest calf in the present material was estimated at 8 ft (2.4 m). The foetus lengths show great variations within each month, and therefore it is difficult to construct a foetal growth curve. The wide ranges may partly be attributed to errors in the initial length estimates. However, our experience suggests that whalers have a fairly accurate length judgement. Foetuses smaller than 30 cm have often been overlooked, particularly in the material from 1938–67.

Assuming a constant foetal growth rate and gestation period of 12 (alternatively 15) months, the estimated months of conception for the foetuses in Fig. 1 are shown in Fig. 2.

An acid-etching of a ground bisected killer whale tooth shows clear ridges and grooves in the dentine (Fig. 3). The initial axial growth of the tooth is rapid, while the most recent increments in occluded teeth of old whales are compressed and show as very narrow ridges and grooves. For the purpose of this study, a growth-layer group (GLG) is defined as the distance from the bottom of one main groove in the etched surface to the bottom of the subsequent main groove (Perrin and Myrick, 1980). Accessory layers are sometimes numerous and can obscure the annual pattern of growth layers. However, the readability is generally good in most of the teeth. The distance between accessory layers and main layers is considerably smaller than the distance between adjacent main groups.

The cementum layer on the teeth is extremely thin, therefore no attempt has been made to utilize cementum growth layers for age determination. The growth of killer whales from the Lofoten area is illustrated in Fig. 4 by the relationship between total length and the number of dentinal GLGs. As shown in the figure there is a

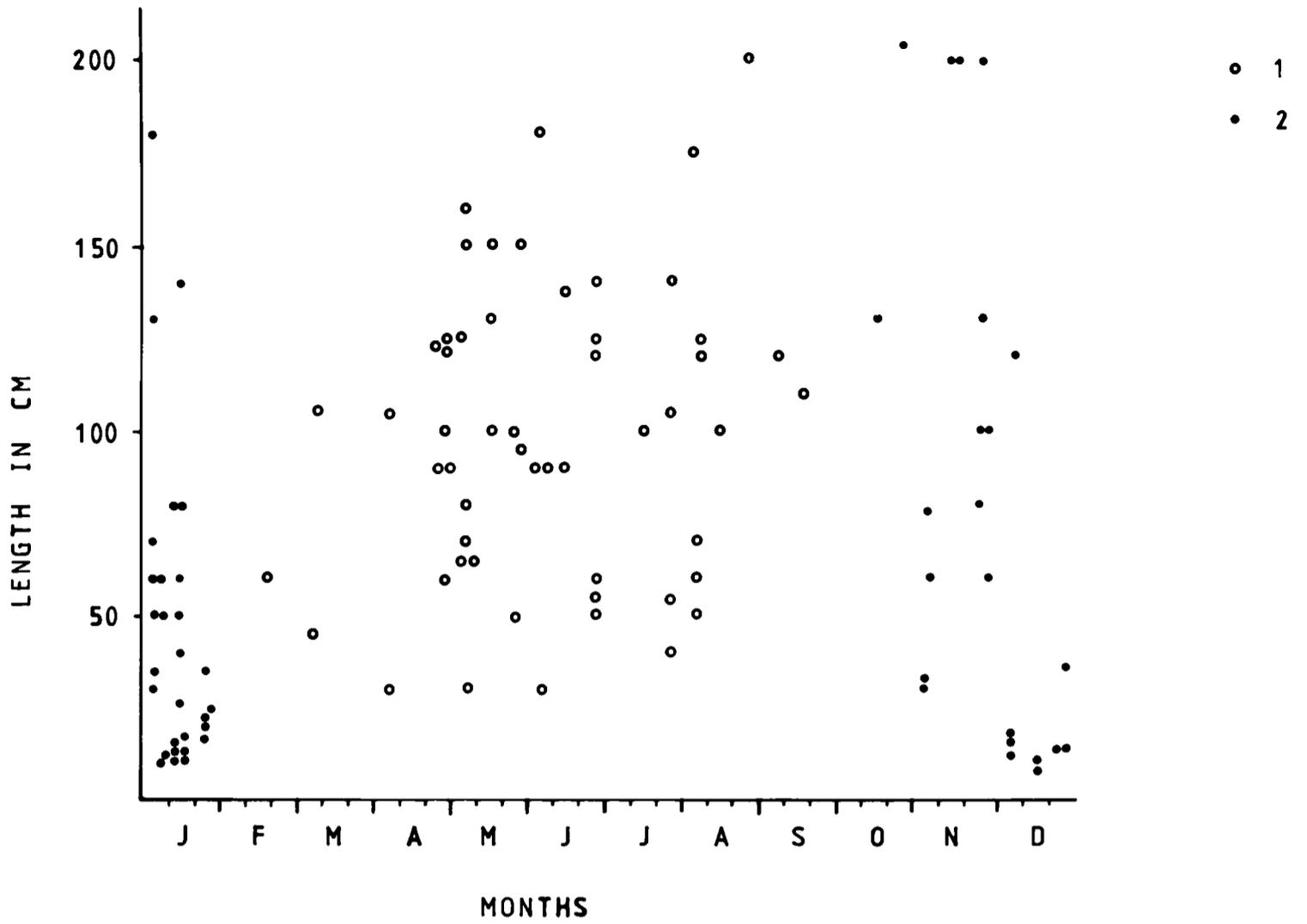


Fig. 1. Lengths of killer whale foetuses plotted against date of capture (10-day periods) as reported by Norwegian whalers in 1938-67 (1) and 1978-80 (2).

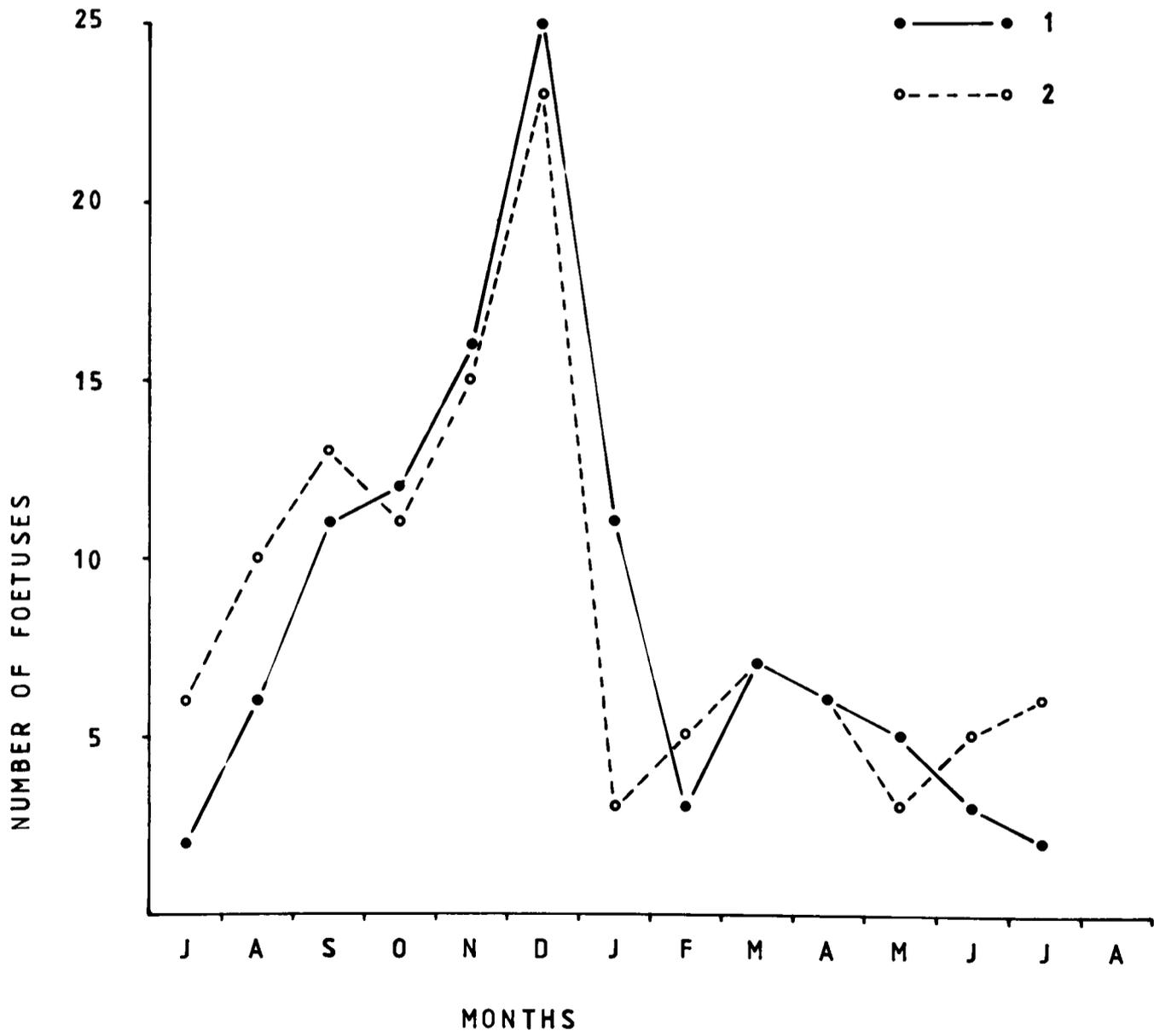


Fig. 2. Estimated month of conception for killer whale foetuses reported by Norwegian whalers in 1938-67 and 1978-80. Assumed gestation 12 months (1) and 15 months (2).



Fig. 3. Etched longitudinal section of a tooth with 29 dentine growth layers from a 21-ft (604-cm) female killer whale.

secondary acceleration in the growth of males from about 18 ft to 20 ft (550–610 cm) corresponding to between 13 and 17 GLGs.

Length distributions of catches are shown separately for each of the seasons 1978, 1979 and 1980 in Fig. 5 and pooled for all three seasons in Fig. 6. The lengths of males range from 8 ft to 24 ft (244–732 cm) and for females from 10 ft to 23 ft (305–701 cm).

**REPRODUCTION**

The length distributions of pregnant and lactating females in relation to all female killer whales taken in 1978, 1979 and 1980 are given in Table 1. The smallest pregnant whale was 15 ft (460 cm) long, and nearly half the number of 16 ft (480 cm) or longer females were either pregnant or lactating (43.4%).

Ovaries collected by whalers in 1979–1980 indicate that females smaller than 15 ft were sexually immature. Two of four 15 ft females; two of three 16 ft females; and 15

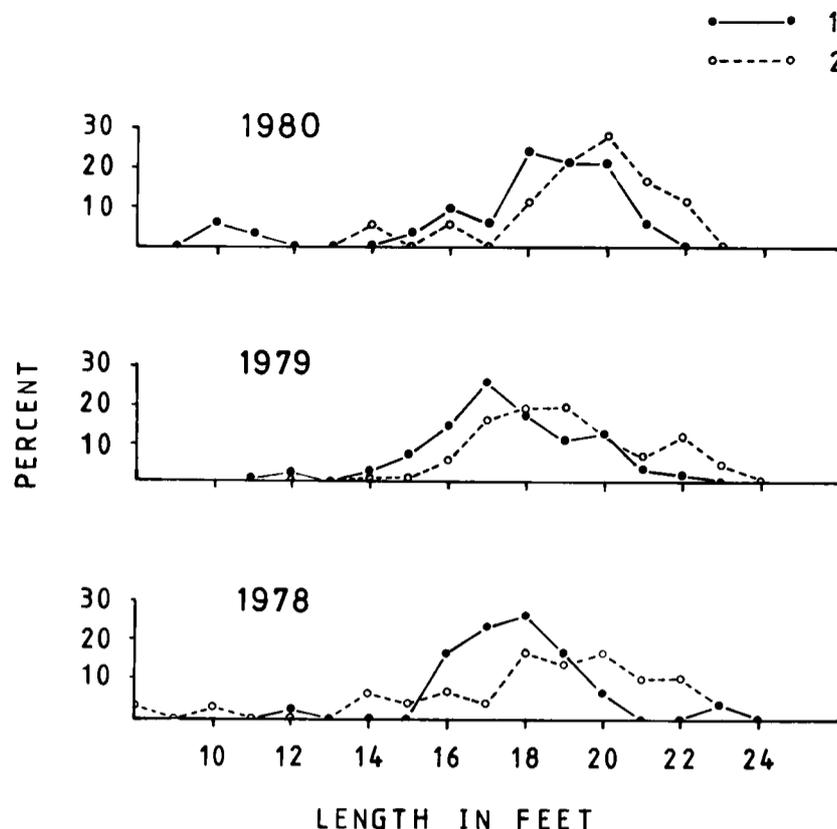


Fig. 5. Length distributions in catches of female (1) and male (2) killer whales taken by Norwegian whalers in the Lofoten area in 1978–80.

Table 1

Length distributions of pregnant and lactating females in relation to all female killer whales caught by Norwegian whalers in 1978, 1979 and 1980

Length (feet)	10–14	15	16	17	18	19	20	21	22	23	Total
No. pregnant	0	1	11	16	15	6	5	1	0	1	56
No. lactating	0	0	1	6	2	2	0	0	0	0	11
Total no.	12	9	23	37	35	26	23	5	2	1	173

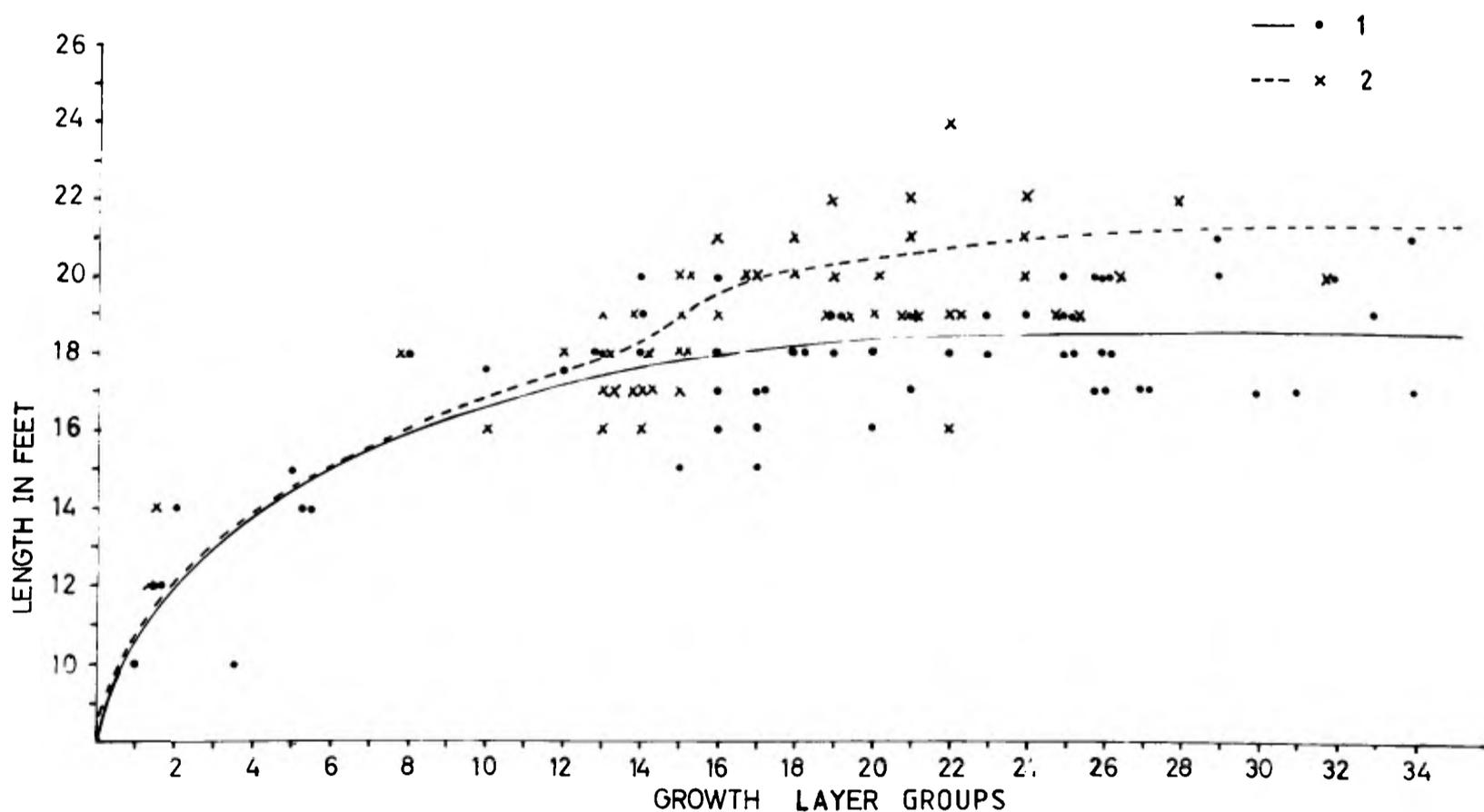


Fig. 4. Growth of killer whales from Lofoten area, fitted by eye: (1) females and (2) males.

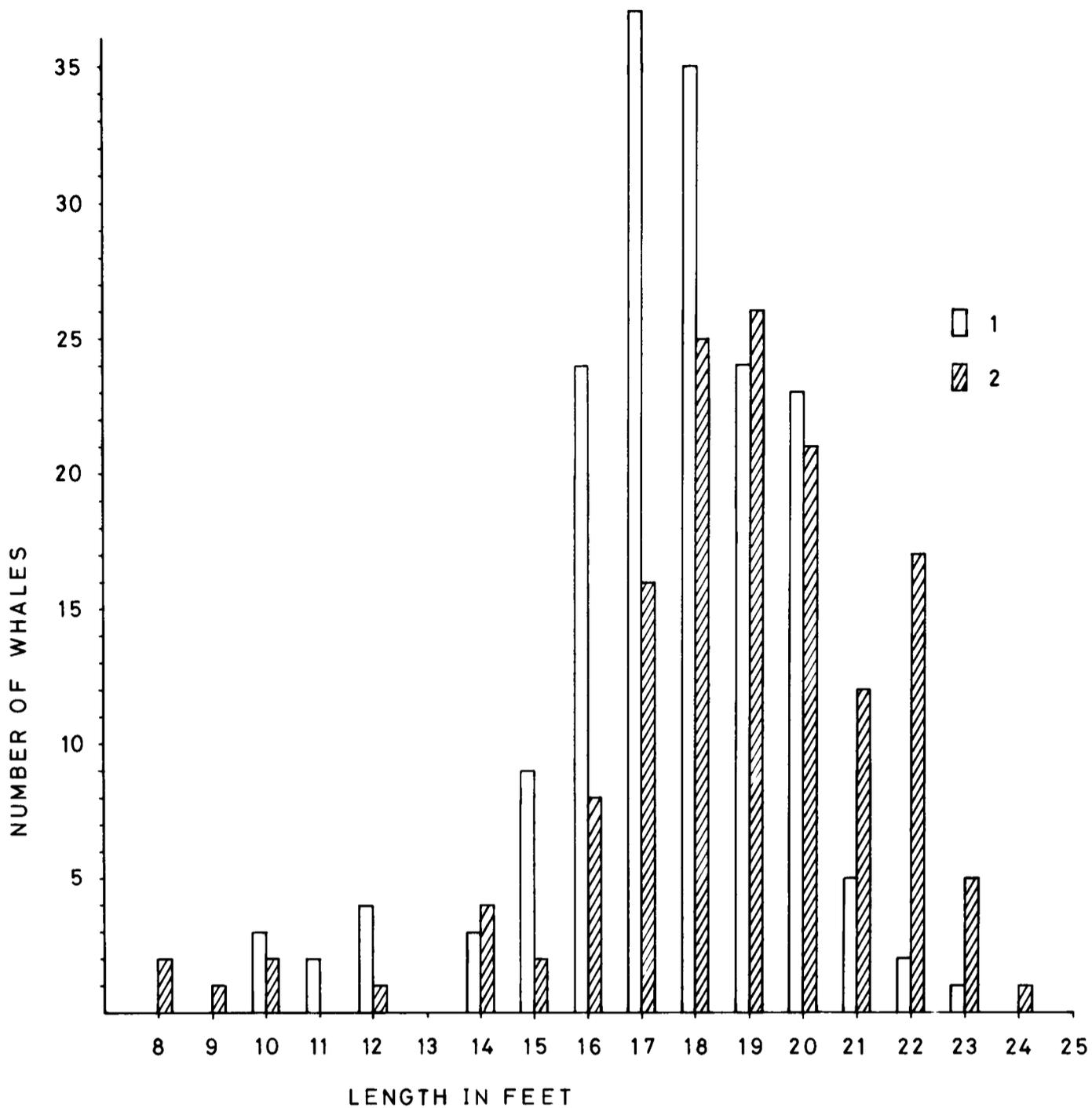


Fig. 6. Combined length distributions of female (1) and male (2) killer whales taken by Norwegian whalers in the Lofoten area in 1978-80.

Table 2

Reproductive status of mature female killer whales based on analyses of ovaries collected by Norwegian whalers in 1979-80

Length (feet)	15	16	17	18	19	20	21	Total	%
Mature	2	2	15	13	9	8	2	51	100.0
Pregnant	1	1	7	6	2	2	0	19	37.3
Lactating	0	1	5	2	2	0	0	10	19.6
Resting	1	0	3	2	3	5	1	15	29.4
Unknown	0	0	0	3	2	1	1	7	13.7

of 16 females in the 17 ft (520 cm) length group were mature. These data suggest a median length at sexual maturity of about 15 ft (460 cm) for female killer whales in Norwegian waters. In Table 2 mature females are classified from analyses of ovaries as pregnant, lactating or resting. The basic data available for individual females are listed in Table 3A and B. Excluding seven whales which could not be classified ('unknown' in Table 2, asterisks in Table 3), the pooled data for all females show 43.2% pregnant, 22.7% lactating and 34.1% resting.

When compared to the number of females classified as

pregnant from ovary analyses, the number of reported fetuses suggests that nine fetuses (47%) may have been overlooked by the whalers (Table 3A and B). Presumably these were all small fetuses.

## DISCUSSION

While the etched-tooth technique provides clearly defined dentinal growth layers, their interpretation with regard to age is provisional. The growth curves (Fig. 4) indicate that female killer whales attain a mean length of 19 ft (580 cm) and males 22 ft (670 cm). These mean lengths are approximately 3-4 ft below (90-120 cm) those reported for killer whales caught in Antarctic waters (IWC, 1981). Jonsgård and Lyshoel (1970) assumed a maximum length of 26 and 30 ft (790 and 910 cm), respectively, for females and males in the North Atlantic waters. However, this appears to be too large for those caught in Norwegian coastal waters (Figs 5 and 6). Physical maturity is attained at 20-25 years, with a maximum age of at least 35 years (Fig. 4). Bigg (1982) suggested maximum longevity of at least 48 years for killer whales off British Columbia.

Jonsgård and Lyshoel (1970) assumed that female

Table 3A

Reproductive status of mature female killer whales collected in Sept., Oct., Nov. and Dec. 1979

Date	Length of female	Length of foetus	No. of corpora		
			Gravidi-tatis	Albicans	Lactating
3/11	15	0	0	1	—
5/11	15	250	1	1	—
3/11	16	Not found	1	2	—
6/10	17	0	0	6	—
9/10	17	0	0	9	Milk
16/10	17	130	Not collected	—	—
6/10	17	Not found	1	5	—
24/10	17	0	0	13	—
29/10	17	Not found	1	5	—
3/10	17	0	0	5	Milk
3/10	17	0	0	8	Milk
3/11	17	60	1	14	—
2/11	17*	0	0	0	Milk
2/11	17	35	1	5	—
2/11	17½*	Not found	1	2	—
22/11	17½	0	Not collected	—	Milk
21/9	18	0	0	5	Milk
8/10	18	256	Not collected	—	—
8/10	18	Not found	1	3	—
29/10	18*	?	?	4	—
2/11	18	0	0	6	—
9/11	18	0	0	8	—
19/10	19	0	Not collected	—	Milk
19/10	19	0	Not collected	—	Milk
2/11	19	78	Not collected	—	—
3/11	20	0	0	7	—
5/11	20	0	0	13	—
19/12	20*	?	?	2	—

\* Incomplete data, only one ovary collected.

killer whales reach sexual maturity at a length of about 16 ft (490 cm), which is consistent with the findings in the present study of 15+ ft. The growth curve (Fig. 4) indicates that sexual maturity in females correspond to approximately eight GLGs, presumably an age of eight years.

The adolescent growth spurt which has been recorded in sexually maturing males of other toothed whales (Sergeant, 1962; Best, 1970 and others) also occurs in killer whales (Fig. 4). This accelerated growth occurs between 18 and 20 ft (550 and 610 cm), and it may be assumed that males reach sexual maturity within these lengths. This is in agreement with Jonsgård and Lyshoel (1970) and Bigg (1982), who assumed a length of 19 ft (580 cm) at sexual maturity in males, corresponding to an age of 15 years.

Ovaries in the present sample indicate that 37.3% of the mature females were pregnant (Table 2). Although it is probable that some of the seven whales in the 'unknown' group were pregnant, they are excluded from this analysis. The corrected apparent rates therefore are: 43.2% pregnant, 22.7% lactating and 34.1% resting. This would give one calf every 2.3 years for the sexually mature females. However, because the material was collected through the period when births and matings occur, individual females were taken at different stages in their reproductive cycle. Some of them clearly were in early pregnancy while others were caught towards the end of gestation; some were lactating and others were resting.

Table 3B

Sexual condition of mature female killer whales collected in January and February 1980

Date	Length of female	Length of foetus	No. of corpora		
			Gravidi-tatis	Albicans	Lactating
29/1	16	0	0	1	Milk
9/1	17	50	Not collected	—	—
16/1	17	0	0	6	—
23/1	18*	?	?	2	—
17/1	18*	40	1	0	—
9/1	18*	10	1	5	—
18/1	18	0	0	5	Milk
23/1	18	Not found	1	3	—
1/2	18	Not found	1	5	—
25/1	18*	?	?	3	—
11/1	19	0	0	6	—
21/1	19*	?	?	1	—
21/1	19	0	0	16	—
25/1	19	Not found	1	9	—
23/1	19*	?	?	2	—
31/1	19	0	0	8	—
25/1	20	0	0	7	—
21/1	20	0	0	7	—
17/1	20	0	0	10	—
15/1	20	Not found	1	8	—
23/1	20*	25	1	1	—
29/1	21*	?	?	7	—
14/1	21	0	0	6	—

\* Incomplete data, only one ovary or part of one ovary collected.

If females with large foetuses (three animals with foetuses 130 cm long or longer in Tables 3A and B) and animals reported as lactating (10 animals) are referred to the same stage of the reproductive cycle and year of mating, and females with small foetuses (7 animals) and females with a corpus luteum but no recorded foetus (9 animals) are assigned to the same phase, the apparent rates of pregnancies are: 29.6% pregnant from the previous mating season, 36.4% pregnant from the present season, and 34.1% resting. These rates give a birth interval of three years, which corresponds to the shortest interval observed by Bigg (1982) for cropped pods off Vancouver Island.

Grieg (1889) and Fraser (1938) both believed that birth and conception take place towards the end of the year, that gestation is about 12 months and that the length at birth is about 7 ft (210 cm). Jonsgård and Lyshoel (1970) arrived at the same conclusions, while Nishiwaki and Handa (1958) implied that gestation might last for more than one year, perhaps 16 months. Dahlheim (pers. comm., IWC, 1982) suggested from a pregnant female in captivity a gestation close to 15 months.

As shown in Fig. 2, most conceptions probably occur from September to January. Therefore large foetuses should have been more frequent than observed in November, December and January if gestation were 15–16 months. Segregation or particularly evasive behaviour of full-term females might explain this, and therefore no final conclusion on the length of gestation can be made from data available to this or previous studies of Norwegian killer whales.

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# Life History and Reproductive Biology of the Short-Finned Pilot Whale, *Globicephala macrorhynchus*, off the Pacific Coast of Japan

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## ABSTRACT

After a period of heavier exploitation in the 1940s, the short-finned pilot whale has been hunted at a lower rate of several hundreds per year by a small-type-whaling and drive fishery off the Pacific coast of Japan. Age data from 373 females and 170 males obtained from 27 schools which were stranded or driven during the 17-year period from 1965 cover all months except March, April, September and November. Breeding is diffusely seasonal, with a single parturition peak in July–August. A single calf is born at a mean body length of 140 cm after 14.9 months gestation and nursed for a minimum of about two years. Calves of older cows may be nursed for considerably longer than this. Females mature at 7–12 ( $\bar{x} = 9.0$ ) years, produce an average of four to five calves, and have their last calf before age 40 years, even though they may live up to 63 years. In contrast, males have a maximum longevity of only 46 years and probably continue to be capable of reproduction until death. In males, puberty begins at 7 to 17 ( $\bar{x} = 14.6$ ) years and social maturity at an average of 17 years.

The age composition suggests that the total mortality rate is lowest in the post-pubertal stage and that it increases after age 28 (male) or age 46 (female). Males have a higher total mortality rate than females at any given age. The juvenile total mortality rate is probably higher than that of post-pubertal animals. These differences in total mortality rates may reflect differences in natural mortality rates. Using an hypothetical stationary population model, we estimate that the total annual mortality rate over all age classes is 8.3% (male) and 4.5% (female). Thus there are more reproductive females than adult males. The mating system is polygynous. Males may migrate between schools after weaning. However, females probably stay in their mother's school for life, so that the breeding schools are essentially matrilineal kinship groups.

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## 1. INTRODUCTION

The genus *Globicephala* Lesson, 1828, includes two species (van Bree, 1971). The long-finned pilot whale, *G. melaena* (Traill, 1809), occurs in the higher latitudes of both hemispheres, while the short-finned pilot whale, *G. macrorhynchus* Gray, 1846, occurs in warm-temperate and tropical waters. *G. melaena edwardii* is considered to be a separate subspecies in the Southern Hemisphere (Davies, 1960). *G. macrorhynchus* also includes geographical forms (Anon. 1975; Polisini, 1980).

As *G. melaena* has not been confirmed from the North Pacific since the 12th century (Kasuya, 1975), *G. macrorhynchus* is the only extant member of the genus in this area. In the western North Pacific, *G. macrorhynchus* occurs in waters with surface temperatures above 15°–16 °C and under the influence of the Kuroshio Current and its tributaries. Thus distribution is seasonal along the Pacific coast of northern Japan and in the Sea of Japan (Kasuya, 1975). In this area, the short-finned pilot whale is thought to feed exclusively on squid, although there has not yet been a detailed study of its food habits.

Sergeant (1962a) published a study of the biology of *G. melaena* off the coast of Newfoundland. This was the first paper to detail the life history of a delphinid based on a reliable technique of age determination and was an important landmark in cetacean research. There have been several subsequent studies on the growth and reproduction of this species (e.g. Sergeant, 1962b; Cowan, 1966; Mercer, 1975).

A weakness of Sergeant's (1962a) study (which he recognized) was that because of a shortage of labour, he was forced to concentrate on collecting different data and samples at different times. This inevitably led to a lack of corroborative data from individual animals. In particular, detailed information about both age and reproductive status were generally not available. Another problem was Sergeant's inability to use cemental layer counts in the main part of his study.

Since then, there have been advances in the techniques of preparing teeth for age determination (see Perrin and

Myrick, 1980). However, up till now these techniques have not been applied to a significant sample of *Globicephala*. We report the results of a study on reproduction and life history of *G. macrorhynchus* parallel to that of Sergeant's (1962a) study of *G. melaena*. Our study is based on data of 565 females, 241 males and a few individuals of unknown sex in 27 schools caught or stranded off the Pacific coast of Japan in the 17 years since 1965. Two companion studies on *G. macrorhynchus*, one on the functional morphology of the ovaries (Marsh and Kasuya, 1984), the other on age determination and growth (Kasuya and Matsui, in press) have been reported separately.

## 2. MATERIALS AND METHODS

### 2.1. Data source

Most of the data and specimen materials were collected between 1965 and 1981 inclusive from 27 schools of *G. macrorhynchus* caught on the Pacific coast of Japan by the drive fishery at Taiji, Futo, or Arari, and from one school stranded at Choshi in the Chiba prefecture. The linear distance between the southernmost location, Taiji, and the northernmost, Choshi, is about 500 km (Fig. 1).

The quality and quantity of data and samples varied between the schools. In the early period of the study (Schools 1–6), effort was directed to the collection of materials for taxonomy, and the data obtained for the present analyses were limited and biased to adult individuals. These data have been used only for the analyses of postnatal and foetal growth. Information from four schools (Schools 8, 19, 20 and 21) examined by volunteers was usually limited to sex and body length, and thus the identification of reproductive condition was less precise. These data were also used in the analyses of foetal and neonatal growth and for some school-structure analyses. The 14 schools caught in the seven years from 1975 to 1980 and examined by Kasuya constituted the major source of data used for the study of reproduction and for the construction of the life table as well as for the analyses of growth and school structure. After most of the mathematical analyses of the present study were

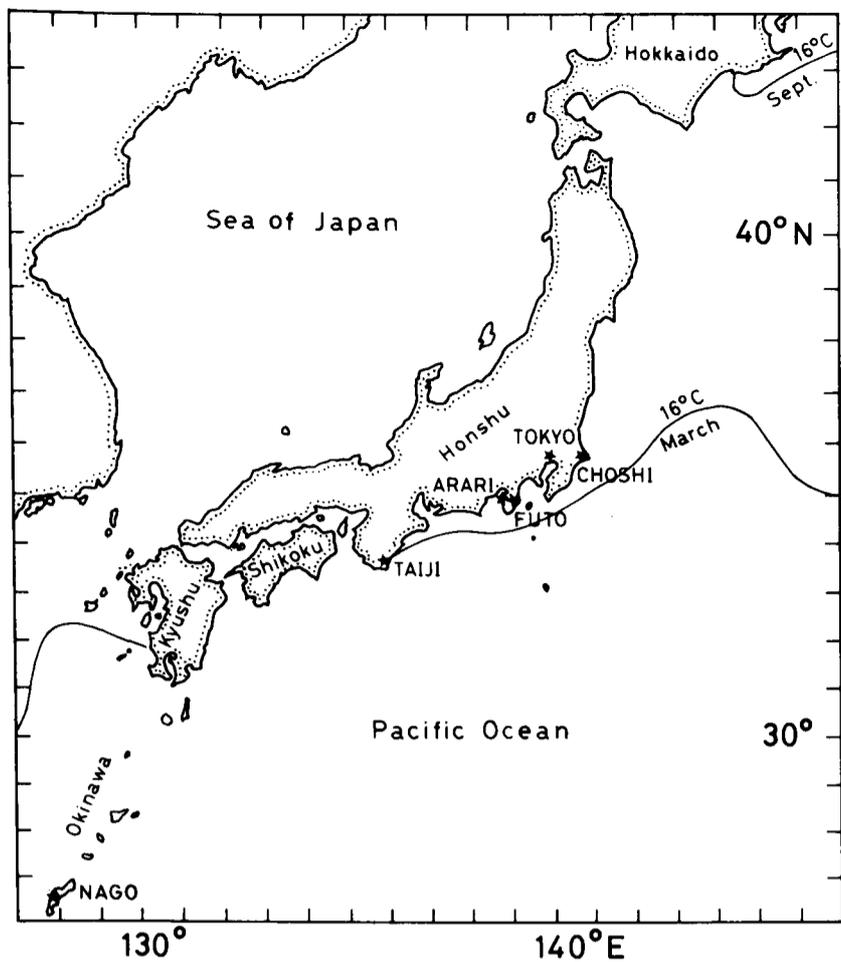


Fig. 1. Map of the waters adjacent to Japan showing the 16°C mean surface isothermal lines (Japan Oceanographic Data Center, 1978) in March and September.

completed using the data from the first 24 schools, Schools 25, 26 and 27 were examined; only adult females were aged. Data from the last three schools were not used in the main body of the study but have been included in the analysis of post-reproductive females, and where indicated in some text figures. The sex and body-length data of 19 fetuses examined between July 1976 and December 1980 and provided by Mr M. Yonekura or by Mr S. Matsui were also used.

Further details of the 27 schools are shown in Table 1. Additional information concerning the schools, which was usually collected by Kasuya from the chief of the driving team soon after the operation, is as follows:

School 1. Found 7 nautical miles NW of Arari. Six fetuses of unknown mothers were also examined. Record of female sexual condition was unsystematic.

School 2. Stranded. Large individuals were selected for skeleton and external measurements.

School 3. Large individuals were selected for skeleton and external measurements. Most of the catch was later freed.

School 4. Record of female sexual condition was unsystematic. One calf (142 cm, female) was born in captivity.

School 5. Record of female sexual condition was limited to few individuals. Two male calves (141 cm and 138 cm) were born in captivity.

School 6. No sample collected. Data for adult females probably not random.

Table 1  
Materials used in this study

School no.	Locality	Date of		No. of individuals				Used for	Examined by
		Catch	Data collection	Driven	Examined	Aged	Lost		
1	Arari	20 Oct. '65	21 Oct. '65	33	18	8	15	A	KK, SO, TK
2	Choshi	13 Dec. '66	15 Dec. '66	ca. 90	9	3	80	A	KK, SO
3	Arari	— June '67	27, 28 June '67	> 30	14	4	16	A	RLB, TK
4	Taiji	22 July '69	July-Aug. '69	31	9	2	22	A	TK
5	Taiji	27 July '69	July-Aug. '69	46	23	10	23	A	KH, TK
6	Taiji	24 Feb. '71	24 Feb. '71	24	12	0	12	A	NM
7	Taiji	17 Jan. '75	18, 19 Jan. '75	28	28	26	0	A, B, C	RLB, TK
8	Taiji	21 Jan. '75	21, 22 Jan. '75	52	52	0	0	A, C	SM
9	Taiji	24 June '75	25 June-4 Jul. '75	ca. 230	173	125	57	A, B, C	CG, NM, TK
10	Taiji	22 July '75	22-24 July '75	33	32	18	1	A, B, C	SM, TK
11	Taiji	13 Jan. '76	13-17 Jan. '76	28	26	21	2	A, B, C	TK
12	Taiji	4 Feb. '76	5, 6 Feb. '76	20	20	18	0	A, B, C	TK
13	Taiji	7 Oct. '76	8, 9 Oct. '76	38	38	38	0	A, B, C	TK
14	Futo	20 Dec. '77	21 Dec. '77	25	25	22	0	A, B, C	NM, TK
15	Futo	24 Dec. '77	25 Dec. '77	48	48	45	0	A, B, C	ST, TK
16	Taiji	20 Feb. '78	20, 21 Feb. '78	27	27	27	0	A, B, C	TK
17	Futo	4 Dec. '78	5 Dec. '78	52	52	49	0	A, B, C	EM, TK, TO
18	Futo	13 Dec. '78	13, 14 Dec. '78	28	28	28	0	A, B, C	EM, TK, TO
19	Taiji	6 Jan. '80	6 Jan. '80	26	23	0	3	A, C	SS
20	Taiji	17 Jan. '80	17, 18 Jan. '80	14	14	7	0	A, C	SS
21	Taiji	2 Feb. '80	2 Feb. '80	19	17	0	2	A, C	SM
22	Taiji	20 Feb. '80	23 Feb. '80	15	15	15	0	A, B, C	TK
23	Taiji	21 Feb. '80	24 Feb. '80	23	23	23	0	A, B, C	TK
24	Taiji	30 May '80	31 May-3 June '80	38	38	38	0	A, B, C	TK
25	Taiji	3 Oct. '81	4-6 Oct. '81	ca. 35	16	9	19		TK
26	Taiji	3 Oct. '81	4-6 Oct. '81	ca. 35	29	14			TK
27	Taiji	5 Oct. '81	6 Oct. '81	—					

A: analyses of growth and seasonality of reproduction. B: analyses of mortality and pregnancy rate. C: analyses of school and population structure. CG: Miss Camille Goebel; EM: Miss Etsuko Miyahara; KH: Dr Keiji Hirose; KK: Mr Kazuo Kureha; NM: Dr Nobuyuki Miyazaki; RLB: Dr Robert L. Brownell Jr; SM: Mr Susumu Matsui; SO: Dr Seiji Ohsumi; SS: Mr Satoshi Shiraga; ST: Dr Sho Tanaka; TK: Dr Toshio Kasuya; TO: Mr Tsuguo Otake; Arari: 34° 49' N, 138° 46' E; Choshi: 35° 43' N, 140° 52' E; Futo: 34° 54' N, 139° 09' E; Taiji: 33° 34' N, 135° 54' E.

School 7. All the members of the school were driven for four and a half hours after sighting. No other cetacean school was observed. Ages of two resting females (350 cm, 13 ovarian corpora; 352 cm, 10 corpora) were not estimated.

School 8. All members were captured and examined for body length and sex. No samples collected.

School 9. Several schools of *G. macrorhynchus* and a school of about 100 bottlenose dolphins, *Tursiops truncatus*, were found about 400 to 500 m from a school of killer whales, *Orcinus orca*. All members of the first two species are driven for 2.5 hours. Fishermen killed the larger pilot whales, and freed all the bottlenose dolphins and about 60 smaller pilot whales. The latter were probably adult females and immature individuals of both sexes. All the individuals processed (173 whales) were examined. The reproductive status of only 85 of the adult females were precisely recorded (Nos. 21–127).

School 10. Three or four schools of *G. macrorhynchus* totalling about 200 individuals were found off Taiji. One school was driven and captured. No samples were collected from nine whales killed on 22 July and examined by S. Matsui.

School 11. All members were driven into Taiji Port. After capture, one possible adult female was lost and two calves were released without examination. Several bottlenose dolphins found with the pilot whales were not captured.

School 12. One of the five or six schools of *G. macrorhynchus* was driven to Taiji together with a school of bottlenose dolphins (about 20 individuals). No individuals were lost.

School 13. Found alone, 10 to 20 nautical miles east of Taiji. All individuals were driven. Body-length measurements and collection of teeth from five individuals killed on 7 Oct. done by M. Yonekura.

School 14. Found about 30 nautical miles off the Futo Port near schools of Pacific white-sided dolphins, *Lagenorhynchus obliquidens*, and *Tursiops truncatus* only. At the entrance of the port, one adult male was lost.

School 15. Found about six nautical miles off Habu on the coast of the Ohshima Island, or about 25 nautical miles from Futo Port. One of several widely-scattered schools was driven. No whales were lost during the drive. Bottlenose dolphins were found with the whales but not driven.

School 16. Several hundred pilot whales were found. One group closest to the port was driven without loss. Bottlenose dolphins were found with the pilot whales but not driven.

School 17. Several *Globicephala* schools were found two to three nautical miles SE of Futo Port. The largest school was driven. *Tursiops* schools also present and one school driven with the pilot whales was released before arriving at the port. No whales were lost during the drive.

School 18. Several pilot whale schools were found at about four to five nautical miles off Futo Port. None was lost during the drive.

School 19. Found about five nautical miles south of Taiji (0805 hr); no other cetacean school present.

Driven into Tsuga Port near Taiji (1430 hr). Twenty-two of the 26 whales caught were examined by S. Shiraga. One adult male, a juvenile, and two individuals of unknown sex were discarded by fishermen and not examined. Only body length and sex recorded. No samples collected.

School 20. Found four to five nautical miles SE of Taiji (0800 hr), and driven into Taiji Port (0930 hr). No other cetacean school present. All individuals examined by S. Shiraga. Reproductive status not recorded for seven whales. Two live whales were sent to an aquarium.

School 21. Seventeen of the catch of 19 whales were examined by S. Matsui for body length and sex. Reproductive status was not recorded systematically. No samples collected.

School 22. Found in the morning five to six nautical miles off Taiji and driven into the nearby Tsuga Port that afternoon. All whales caught and examined. No other cetacean school found.

School 23. Found in the morning four to five nautical miles off Taiji and driven into Taiji Port that morning. All individuals captured and examined. No other cetacean school found.

School 24. Several *Globicephala* schools were found five to six nautical miles off Tawara with a school of bottlenose dolphins. One of the pilot whale schools was driven without loss to Taiji Port.

School 25. Found about five nautical miles off Taiji and driven to Taiji Port. Only 16 of about 35 whales caught were examined.

School 26. Found near school 25 and driven to Taiji Port by the other hunting team. Twenty-two of the catch of about 35 were examined.

School 27. No information, mixed with the last two or three individuals of school 26.

## 2.2. Field procedures

Flensing was usually done within a few days of the drive, but occasionally whales were kept in a netted bay for up to 16 days. The information and samples listed below were collected by Kasuya, volunteers, or both, while the fishermen were flensing. At this stage, each pilot whale was assigned a sample number which is a hyphenated combination of the school number followed by the number of the animal within the school.

### 1. Sex.

2. *Body length*. Measured to the nearest 1 cm on a straight line parallel to the long axis of the body, from the anteriormost point to the bottom of the tail fluke notch. Although the tip of the upper jaw is the anteriormost point of the body of juveniles, it lies posterior to the front end of the melon after the whale is about 240 cm long and becomes difficult to distinguish (Yonekura, Matsui and Kasuya, 1980). Thus the measurement of body length is not exactly comparable for adults and calves less than one year old.

3. *Teeth*. One to three contiguous teeth were collected from the centre of the lower tooth row with a hammer and chisel and preserved in 10% buffered formalin. The largest available teeth were selected.

4. *Mammary glands*. The presence and colour of milk

was checked by pressing and then cutting the glands. If possible, the maximum thickness of one mammary gland was measured, and a histological sample was taken and fixed in 10% buffered formalin. The presence of colostrum or other fluid in the lumen was recorded.

5. *Testes*. Both testes were collected from 51 immature and adult individuals, cut transversely at mid-length and fixed in 10% buffered formalin. Only one testis from either side was collected from the remaining 112 whales. It was fixed as above if it weighed less than 500 g. Testes exceeding 500 g were weighed at flensing after removing the epididymis. A mid-length histological sample was then collected.

6. *Epididymides*. In the case of a small testis the entire epididymis was collected and fixed as well. In fully grown individuals, a histological sample was taken opposite the testis mid-length and fixed with the testis.

7. *Ovaries*. Both ovaries were collected from all females and fixed in buffered 10% formalin. The left ovary was marked with a nick. The presence of corpora lutea, corpora albicantia and large follicles was recorded.

8. *Uteri*. If time permitted, the maximum diameter of each uterine horn was measured, with the uterus on a flat floor. Histological samples were usually collected from the larger horn and fixed in 10% formalin.

9. *Foetuses*. Sex and body length were recorded. If a corpus luteum was found and there was no large foetus in the uterus, both uterine horns were saved and opened carefully to search for a small embryo, which could be detected more easily before fixation. A foetus was often not detected in spite of the presence of a corpus luteum. If the uterine cornua were fairly similar in size, the whale was classified as recently ovulated (not pregnant). On rare occasions non-lactating females were observed with one large asymmetric uterine horn with a congested endometrium suggesting a recent abortion.

10. *Stomach contents*. Stomach contents of the juveniles were, if time permitted, examined macroscopically for solid food or milk.

### 2.3. Laboratory procedures

1. *Age determination*. This was done by Kasuya, who counted the annual growth layers in dentine or cementum in haematoxylin-stained, decalcified sections 30–40  $\mu\text{m}$  thick, as detailed in Kasuya and Matsui (in press).

The age of each individual was expressed as the number of growth layer cycles (equivalent to Growth Layer Groups – GLGs – of Perrin and Myrick (1980)). After studying the seasonal pattern of dentinal growth-layer deposition and seasonal changes in the thickness of the dentinal layer being laid down in the teeth of 270 females and 147 males which died in January, February, May, June, July, August, October and December, Kasuya and Matsui (in press) decided that dentinal growth-layer deposition was annual. For most whales in which dentine deposition was continuing (i.e. those with an open or closing pulp cavity), the counts of dentinal and cemental growth layers were very close. Kasuya and Matsui (in press) therefore concluded that cemental growth-layer deposition was also annual and used the cemental-layer count to estimate the age of individuals with teeth which had closed pulp cavities.

Kasuya and Matsui (in press) estimated the magnitude

of the errors likely to result from these methods of age determination and concluded that the 95% confidence range for the age estimates at ages 10, 20, 40 and 60 years are  $\pm 0.9$ ,  $\pm 1.8$ ,  $\pm 2.6$  and  $\pm 3.4$  years, respectively.

The ages of juveniles from which teeth for age determination were not available were estimated from their body lengths as outlined in Kasuya and Matsui (in press). Using this technique, it is possible to estimate age  $\pm$  two years for females below 280 cm (mean age about five years) or for males below 320 cm (mean age about eight years).

The age of individuals below 10 years was roughly estimated to the nearest  $\frac{1}{4}$  year by considering the thickness and nature of the first and last postnatal dentinal layers of incomplete thickness. For whales over 10 years, the age was grouped into the nearest  $n+0.5$  years ( $n = \text{integer}$ ).

2. *Testes*. Each fixed testis was weighed to 0.1 g after removal of the epididymis. A testicular smear was taken from a transverse cross-section at the mid-length, dried, stained in 0.1% toluidine blue for a few minutes, rinsed in water, and air-dried. Samples for histology were taken from the centre (position 6 in Fig. 4) of one testis at mid-length for all individuals. In some whales, additional samples were taken from the periphery near the attachment of the cauda epididymis at the testis mid-length (position 7) and from the periphery opposite the cauda epididymis (position 5). In addition, histological samples were taken from 11 sites from one testis of two whales to see if different regions of the same testis were at different stages of maturity. Haematoxylin and eosin (H–E)-stained slides were prepared from paraffin sections of all histological samples, using standard techniques.

The stained and dried testicular smears were scanned with a microscope (10–20 $\times$ ) by Kasuya. The relative density of spermatozoa was classified as follows using a field diameter of 1.82 mm (see Fig. 10 for corresponding densities in epididymal smears).

- (a) Absent
- (b) Doubtfully present: one or two spermatozoa in several fields.
- (c) Scanty: less than 10 spermatozoa per field.
- (d) Intermediate: density between scanty and copious (maximum density observed for ordinary adult testes).
- (e) Copious: abundance similar to that usually found only on an epididymal smear.

The histological slides were examined by Kasuya at a magnification of 100–400 $\times$ . By observing the entire section, which usually measured about 5 $\times$ 7 mm, the ratio of the mature and immature tubules was calculated based on 70 to 150 tubules. Usually 20 diameters of the seminiferous tubules were measured for each sample on one or two enlarged black-and-white photoprints and the arithmetic mean diameter calculated.

3. *Epididymides*. An epididymal smear was taken from a position opposite the testis mid-length, and observed by Kasuya as described for the testicular smear. A sample for histology was taken from the same location, processed, H–E stained and mounted as above.

4. *Mammary glands and endometria*. Reference histology slides were prepared from paraffin sections using standard techniques. The mammary-gland sections were stained with H–E. The sections of endometrium were

Table 2  
Catch of *G. macrorhynchus* off the Pacific coast of Japan

Year	Small-type whaling			Other fisheries, Pacific area					Total Pacific coast <sup>H</sup>
	A	B	Taiji <sup>C</sup>	Taiji <sup>D</sup>	Total Taiji <sup>E</sup>	Izu <sup>F</sup>	Okinawa <sup>G</sup>	Other areas <sup>D</sup>	
1948	725	426	38	—	—	—	—	—	—
1949	890	814	283	—	—	—	—	—	—
1950	715	668	233	—	—	224	—	—	—
1951	618	585	227	—	—	425	—	—	—
1952	335	322	131	—	—	650	—	—	—
1953	460	456	141	—	—	349	—	—	—
1954	75	80	20	—	—	31	—	—	—
1955	61	57	12	—	—	86	—	—	—
1956	297	275	141	—	—	126	—	—	—
1957	174	178	98	—	—	—	—	—	70
1958	197	—	—	—	—	—	—	—	266
1959	144	—	—	—	—	—	—	—	192
1960	168	—	—	—	—	—	243	—	560
1961	133	—	—	—	—	—	281	—	503
1962	80	—	—	—	—	—	0	—	73
1963	228	—	—	—	98	—	189	—	65
1964	217	—	—	—	146	—	318	—	145
1965	288	248	121	—	134	33*	0	—	57
1966	199	—	—	—	52	—	0	—	161
1967	237	—	—	—	68	30*	150	—	35
1968	166	121	97	—	96	—	150	—	10
1969	130	86	75	77*	77	—	500	—	10
1970	152	140	108	—	116	—	0	—	71
1971	181	140	111	24*	110	—	165	—	7
1972	91	66	60	30	91	0	170	0	6
1973	77	75	66	52	155	0	87	217	384
1974	62	76	65	94	193	0	53	23	54
1975	53	54	53	410	479	0	49	5	244
1976	11	14	14	371	369	0	36	19	830
1977	6	6	6	170	192	73*	301	0	215
1978	11	13	13	309	322	80*	0	70	129
1979	3	3	3	87	118	0	0	2	43
1980	—	1	0	605	—	0	80	0	—

A: Catch of all globicephalid species throughout Japan, from official whaling statistics. B: Catch of *G. macrorhynchus* off Pacific coast of Japan as in Table 3. C: From same source as Table 3. D: Data of Jap. Fish. Agency since 1972. E: Miyazaki, 1980b, includes both whaling and other fisheries. F: For Arari village (1950 to 1956, from Kasuya, 1976a) and for entire area (other seasons). G: Miyazaki, 1980a for 1960 to 1971 season, and J.F.A. data for 1972 to 1980. H: Statistics and Survey Div. Ministry of Agri. and Forestry, Pacific coast total, includes all kinds of 'whales'. Catch in Okinawa included since 1974.

\* Catch examined by Kasuya but not listed in other records. Underlined: Statistics used in Fig. 2.

stained both with H-E and Aldehyde-fuchsin and Haematoxylin-light-green-chromotrope 2R.

5. *Ovaries*. Ovaries were weighed and checked in the laboratory by Kasuya to confirm the reproductive condition recorded at the flensing platform. Both authors examined the ovaries of Schools 7 and 17, while Marsh examined the ovaries of Schools 9 (No. 79 to 127)-18, 20 and 21-27 as outlined in Marsh and Kasuya (1984). Marsh classified corpora into four categories: 'corpus luteum (CL)', 'young corpus albicans (CA)', 'medium CA', and 'old CA' as outlined (loc. cit.).

### 3. HISTORY OF EXPLOITATION

#### 3.1. Stock identity

The seasonal distribution of the short-finned pilot whale off the Pacific coast of Japan was analysed by Kasuya (1975) based on catch statistics (1949-52 inclusive) of the small-type whaling industry, which uses harpoon guns of 50 mm or smaller calibre and is licensed to hunt minke whales and all Odontoceti except sperm whales. He

showed that the whales migrate seasonally along the islands, expanding their range in summer up to eastern Hokkaido (*ca* 43° N) and retreating in winter to the south of the Kii Peninsula (*ca* 34° N).<sup>1</sup> Although some individuals are present throughout the year off the Kii coast, the bimodal distribution of the catch in this region suggests that the main wintering ground may be further south. Miyazaki (1980a) reported catch statistics for Nago (26° 34' N, 127° 59' E) on the west coast of Okinawa Island over the last 16 years. The catch had a

<sup>1</sup> Since completing this study, Miyazaki and Kasuya (unpublished) have observed two types of pilot whales off Ayukawa (38° 20' N) on the Pacific coast of Japan in November. This is near the northern boundary of the range of *G. macrorhynchus* at this time of year. Both types have skull features characteristic of *G. macrorhynchus* as described by van Bree (1971). The smaller type is identical to those taken off central Japan and studied in this paper. The other type is possibly a boreal form. It is from one to two metres larger, and has a more pronounced saddle mark. The forehead of the adult male is roundish rather than square as in the smaller type. The two forms may be geographical races corresponding to those reported by Polisini (1980) from the eastern North Pacific.

Table 3  
Catch of *G. macrorhynchus* by small-type whaling<sup>1</sup>

Year	Pacific Coast											
	Hokkaido <sup>2</sup>			Sanriku <sup>3</sup>			S/W Japan <sup>4</sup>			Other areas <sup>5</sup>		
	♂	♀	Total	♂	♀	Total	♂	♀	Total	♂	♀	Total
1948	0	0	0	200	121	321	69	35	104	0	0	0
1949	0	0	0	237	178	415	277	122	399	6	0	6
1950	0	0	0	126	163	289	231	130	361	3	1	4
1951	4	1	5	150	114	264	189	121	310	8	2	10
1952	3	4	7	64	56	120	118	76	194	6	3	9
1953	0	0	0	97	127	224	125	104	229	0	0	0
1954	1	0	1	25	18	43	24	12	36	0	0	0
1955	0	0	0	14	3	17	22	18	40	3	0	3
1956	53	29	82	11	8	19	99	70	169	2	1	3
1957	4	0	4	20	12	32	101	31	132	0	0	0
1965	7	7	14	76	37	113	101	10	121	0	0	0
1968	0	0	0	14	10	24	56	41	97	0	0	0
1969	0	0	0	7	4	11	53	22	75	0	0	0
1970	0	0	0	17	15	32	69	39	108	0	0	0
1971	0	0	0	15	14	29	51	60	101	5	5	10
1972	3	1	4	0	0	0	37	25	62	0	0	0
1973	5	4	9	0	0	0	37	29	66	0	0	0
1974	8	3	11	0	0	0	47	18	65	0	0	0
1975	0	0	0	1	0	1	25	28	53	0	0	0
1976	0	0	0	0	0	0	6	8	14	0	0	0
1977	0	0	0	0	0	0	3	3	6	0	0	0
1978	0	0	0	0	0	0	11	2	13	0	0	0
1979	0	0	0	0	0	0	1	2	3	0	0	0

<sup>1</sup> Compiled by Kasuya from the *Geiryō Geppo* (Monthly Report of Whaling Operation).

<sup>2</sup> 42° N–43° N.

<sup>4</sup> 31° N–35° N.

<sup>3</sup> 38° N–40° N.

<sup>5</sup> Northern Kyushu and Sea of Japan.

single peak during March to May, before the spring peak off the Kii Peninsula in May and June. This suggests that the range of the population we have studied may extend to Okinawa.

The catch statistics for this species at Taiji (33° 34' N, 135° 54' E), the only pilot whaling locality on the Kii Peninsula, indicate that the fishing season has changed in recent years (Miyazaki, 1980b). There were two peaks in the catch before 1973, one in May through July, the other in November through January (Kasuya, 1975). However, only the latter peak persisted after 1973, probably the result of changes in fishing technique and interaction with other fisheries as outlined below.

From sometime before 1965 until 1973, the pilot whale fishery was conducted year-round with a small whaling boat (*Katsumaru*) equipped with a multi-barrelled harpoon gun. Regular drives started in 1971, and by 1974 the catch of pilot whales using this technique consistently exceeded that obtained by the whaling boat (Table 2 and Fig. 2). At Taiji, the drive fishery catches delphinids of several species during period when more lucrative alternatives are not available. The hunting team(s) usually break(s) up in May for trolling or some other small-scale net fishery.

### 3.2. Catch statistics

Significant catches of *G. macrorhynchus* have been limited to Taiji and Okinawa (Table 2). Although the drive fishery at Nago (Okinawa) seems to have a long history, the available statistics are limited to those of

Miyazaki (1980a) for 1960 to 1975 and those of the Japanese Fisheries Agency for 1972 to 1980. (When both sets of data are available for a given season they are identical). The catch was sporadic and ranged from 0 to 605 individuals per year (Table 2). The drive was carried out opportunistically by small fishing boats from other fisheries (Miyazaki, 1980a).

From the early 17th century, the pilot whale was hunted at Taiji by traditional whaling teams using hand harpoons (Hashiura, 1969). The first expansion of the fishery occurred in 1903 with the successful introduction of the multi-barrelled harpoon gun, and the second in 1921 with the first use of motor vessels. The usage of motor vessels rapidly increased (Hamanaka, 1979). Hamanaka reported catch statistics for the pilot whale at Taiji from 1920 to 1931. The catch of 120 whales by 11 traditional boats in 1920 increased to 381 in 1921 with the use of motor vessels. In the 11 years from 1921 to 1931, the annual catch ranged from 144 to 708 pilot whales ( $\bar{x} = 483.6$ ). Although the fishery continued until recently, with a few years' interruption before and after 1945 (the last year of World War II), no catch statistics are available from before 1948. Table 2 summarizes the catch at Taiji since 1948. In addition to the catch statistics of the Japanese Government, Miyazaki (1980b) reported the catch of several delphinids at Taiji, including *G. macrorhynchus*, based on the records of number of viscera by species sold through the Taiji Fishery Co-operative Union from 1963 to 1979. The use of the visceral number covers carcasses which were occasionally sold through brokers and are missing from other records.

If all the statistics are correct, the sum of the columns C (whaling) and D (other fisheries) in Table 2 should be equal to the column E (Miyazaki, 1980b) of the same table. Error is inevitable in statistics, and the disagreement observed is not significant.

During the food crisis after the last war, the range of small-type whaling for pilot whales expanded from Taiji to waters off southern Kyushu ( $31^{\circ}$  N) or to those off northeastern Hokkaido ( $43^{\circ}$  N), as shown by Kasuya (1975). Table 3 lists the catch of the short-finned pilot whale (column B in Table 2) by small-type whaling compiled from the *Geiryō Geppo* (Monthly Reports of Whaling Operations) submitted by boat owners to the Fisheries Agency as well as the official statistics of 'globicephalid' whaling (column A in Table 2). In Table 2, Column A includes three globicephalid species, *Pseudorca crassidens*, *Grampus griseus*, and *Globicephala macrorhynchus*, but column B includes only pilot whales of known sex and excludes a small number (0 to 18 per year) of pilot whales of unknown sex. Although this is the main source of discrepancy between columns A and B of Table 2, there still remain some minor discrepancies which we cannot account for.

The catch of large numbers of pilot whales by this fishery lasted only from the late 1940s to the early 1950s, ceasing after the establishment of a whaling company for large cetaceans in 1951, when several small-type whaling boats were replaced with fewer larger boats licensed to catch large whales (Hamanaka, 1979). Another reason for the decline may be the intensified selection by small-type whaling boats of the more profitable minke whales, resulting from a decline in demand for dolphin meat (Kasuya, 1975). After the mid 1960s, significant catches of pilot whales by small-type whaling continued only at Taiji, because of the traditional food customs of the local people. Small-type whaling has now been almost totally displaced by the drive fishery, as discussed above.

Several Izu Peninsula villages are known to have operated a drive fishery for dolphins (Kasuya, 1976a). Arari Village caught pilot whales for an unknown part of the post-war period before 1960 (column F in Table 2). It is possible that the catch between 1948 and 1956 is under-estimated, because some other villages on the Izu coast may also have operated a drive fishery for pilot whales, but no data are available.

Fig. 2 shows the total annual catch of short-finned pilot whales off the Pacific coast of Japan, including recent records from Nago. The catch by fisheries other than whaling with harpoon guns is certainly under-estimated before 1957, because the catch of the Nago driving fishery is not included. The high catch in 1960 and 1961 resulted from the extraordinarily high catch in Shizuoka (501 individuals) and Miyagi (404 individuals) Prefectures. The former could have been caught by a drive fishery team on the Izu coast. The latter is difficult to explain, because there is no drive fishery in Miyagi Prefecture. A catch of 179 individuals is also recorded for this prefecture in 1958 (for details see Ohsumi, 1972). The high 1973 total catch is the result of the unusual catch of 217 pilot whales at Choshi in Chiba Prefecture (see column D (other area) in Table 2). These unusual catches could have been incidental or the result of a mass stranding.

We conclude that the total catch of the short-finned pilot whale off the Pacific coast of Japan may have been

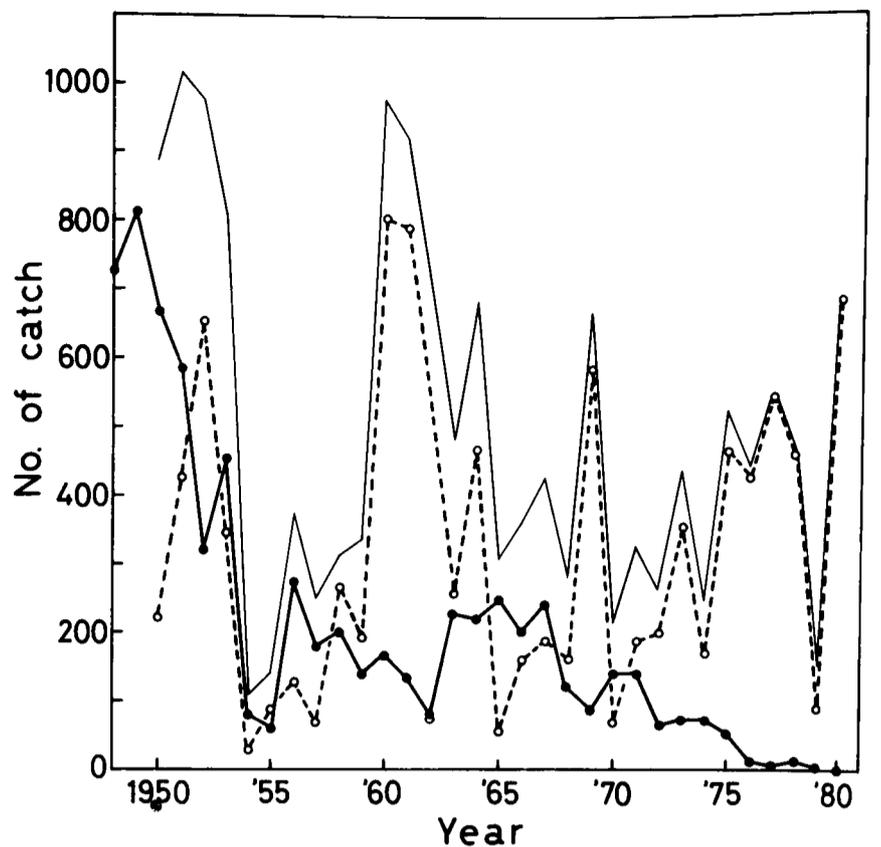


Fig. 2. Catch of *G. macrorhynchus* off the Pacific coast of Japan. The closed circles and thick solid line indicate the catch by small-type whaling (using 50-mm or smaller-caliber harpoon gun and licensed to take minke whale and toothed whales other than sperm whales). The open circles and dotted line indicate the catch by other fisheries, and the thin solid line the total. For data see Tables 2 and 3.

about one thousand individuals per year from the late 1940s to early 1950s and then declined, with a few exceptional years, to a level of 200–400 per year. The recent increase to 400–700 individuals per year results from the expansion of the drive fishery at Taiji.

#### 4. MALE SEXUAL MATURITY AND BREEDING LONGEVITY

##### 4.1. Maturity of testicular tissue

The maturity of testicular tissue was determined by examining all (70–150) seminiferous tubules in an H-E-stained histological section (approx. 5 mm × 7 mm or smaller). Tubules with spermatocytes, spermatids or spermatozoa were classified as mature. The tissue was then classified into one of the following categories (see Fig. 3):

- (1) immature: 100% immature tubules.
- (2) early-maturing: less than 50% of tubules examined mature.
- (3) late-maturing: between 50% (inclusive) and 100% of tubules examined mature.
- (4) mature: 100% mature tubules.

Although some of the tubules examined lacked one or two of the cell types of spermatocytes, spermatids and spermatozoa, there was no instance in which one or two of these three cell types were lacking in all tubules examined from a whale classified as early-maturing or later. For example, none of the testes classified as early-maturing had spermatocytes and/or spermatids only and no spermatozoa.

Different parts of the testis of the sperm whale, *Physeter macrocephalus*, (Best, 1969) and the sei whale, *Balaenoptera borealis*, (Masaki, 1976) have been shown to mature at different times. We sampled 11 sites on a

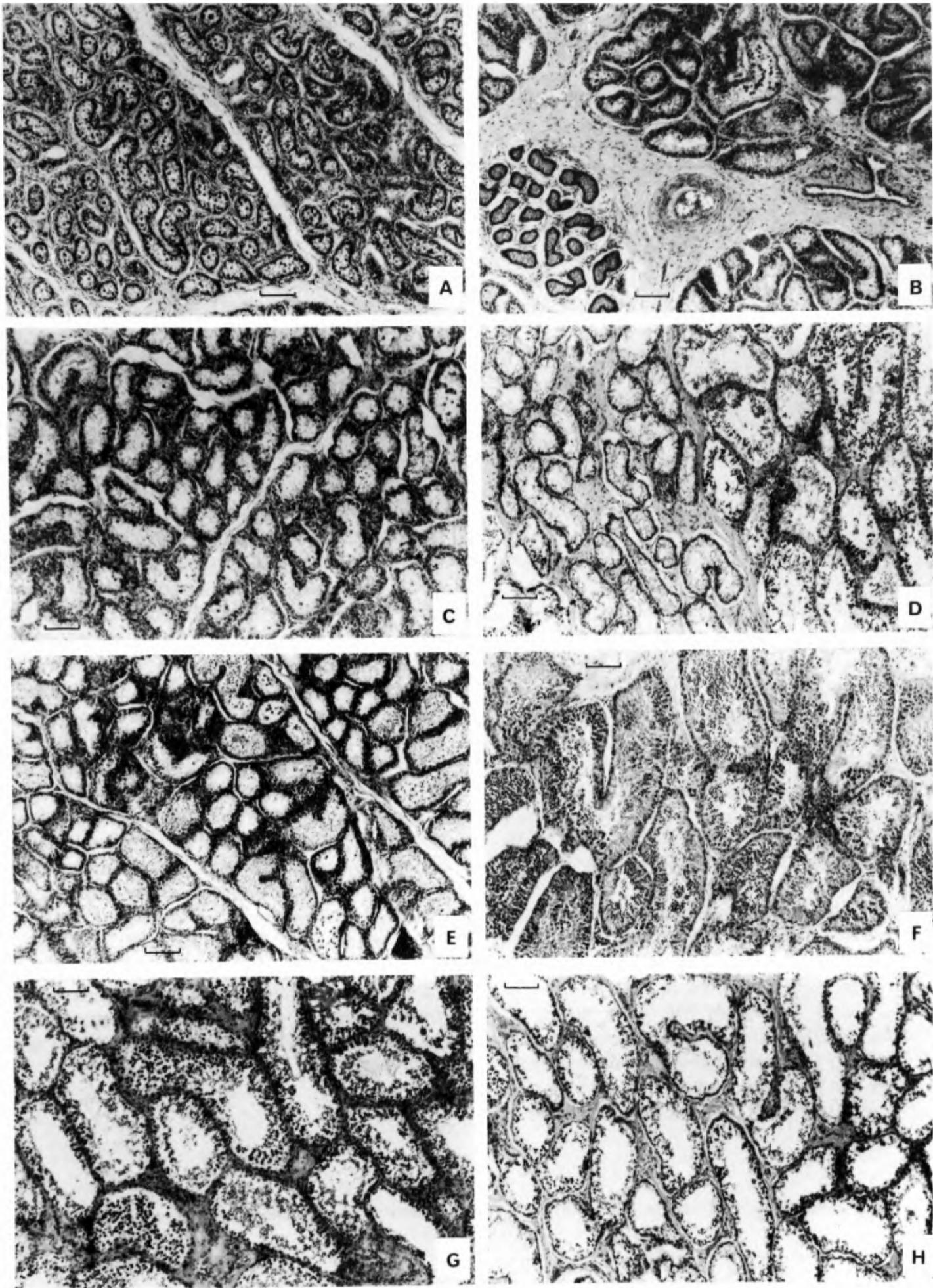


Fig. 3. Testis of *G. macrorhynchus*, haematoxylin and eosin-stained. In all photographs, the scale bar represents 0.1 mm.

- A. Immature (No. 18-34, 385 cm, 20.5 years old, weight of single testis 84.6 g). Spermatozoa were doubtfully present in testicular smear. None were seen in epididymal smear.
- B. Early-maturing (No. 15-34, 404 cm, age estimate not available, weight of single testis 122.3 g). Spermatozoa were absent from both smears.
- C. Early-maturing (No. 17-12, 390 cm, 16.5 years old, weight of single testis 154.0 g). Spermatozoa were absent from both smears (For epididymis, see Fig. 10B).
- D. Late-maturing (No. 18-42, 414 cm, 18.5 years old, weight of single testis 600 g). Spermatozoa were at 'intermediate' density in both smears.
- E. Late-maturing (No. 17-26, 420 cm, 18.5 years old, weight of single testis, 149.3 g). Spermatozoa were 'copious' in epididymis and at 'intermediate' density in testicular smear.
- F. Mature (No. 18-44, 465 cm, 20.5 years old, weight of single testis 1,000 g). Spermatozoa were 'copious' in epididymis and at 'intermediate' density in testicular smear.
- G. Mature (No. 18-36, 490 cm, 34.5 years old, weight of single testis 2,080 g). Spermatozoa were 'copious' in epididymis and at 'intermediate' density in testicular smear (For epididymis, see Fig. 10C).
- H. Mature (No. 18-39, 427 cm, 31.5 years old, weight of single testis 660 g). Spermatozoa were at 'intermediate' density in epididymis and 'scanty' in testicular smear.

Table 4

Maturity and diameter of seminiferous tubules at different positions in testis

Sample no. and position	Diameter ( $\mu\text{m}$ )		Mature tubules (%)	Maturity
	Mean	S.E.		
18-34				
1	67.4	1.30	0	immature
2	61.8	1.22	0	"
3	51.7	1.56	0	"
4	55.7	1.73	0	"
5	60.3	1.72	0	"
6	59.7	1.41	0	"
7	55.5	1.31	0	"
8	59.6	1.41	0	"
9	58.1	1.33	0	"
10	59.0	1.51	0	"
11	59.3	1.49	0	"
18-30				
1	95.7	3.01	60	late-maturing
2	96.0	2.90	59	"
3	89.0	3.28	54	"
4	95.3	2.64	66	"
5	90.2	3.23	63	"
6	81.1	3.05	65	"
7	88.4	2.44	59	"
8	84.3	3.93	55	"
9	89.8	2.06	63	"
10	93.1	3.54	46	early-maturing
11	88.2	2.46	58	late-maturing

No. 18-34: body length 385 cm, age 20.5 years, weight of a testis 94.6 g.  
 No. 18-30: body length 420 cm, age 22.5 years, weight of a testis 171.8 g.

longitudinally-sliced testis (Fig. 4) of both a maturing male (No. 18-30) and a relatively old immature male (No. 18-34) to test whether *G. macrorhynchus* testes also mature differentially. In both animals, the mean diameter and status of the seminiferous tubules did not vary much between positions (Table 4).

Similar comparisons were made between tissues taken from positions 5, 6 and 7 (Fig. 4) for seven males of intermediate testis size (53.6-1,100 g). Again no differences were detected between different positions or between contralateral testes of the same whale. Therefore we considered that it was sufficient to base our assessment

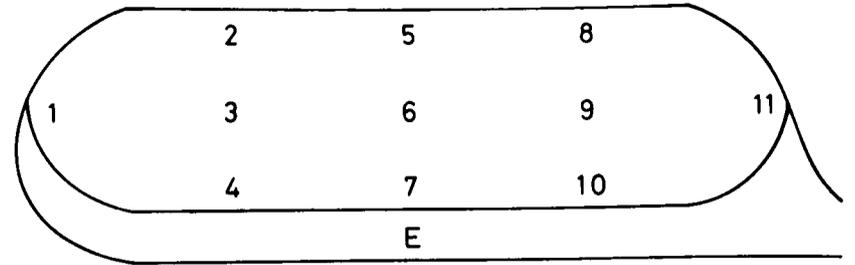


Fig. 4. Schematic diagram of a longitudinal section of a testis of *G. macrorhynchus* indicating the positions sampled. E indicates the position of the epididymal sample.

of testis maturity on one sample from position 6 (Fig. 4).

The results of these assessments of testis maturity were compared with the density of spermatozoa in the corresponding testicular and epididymal smears (Table 5). Whales with high densities of epididymal spermatozoa ('scanty' or greater (see Section 2)) exhibited similar densities on their testicular smears.

However, there are indications that there is an appreciable time lag between spermatogenesis and the appearance of sperm in the epididymis. Eleven individuals with large amounts of testicular spermatozoa had few or none in the epididymis (categories 'absent' or 'doubtfully-present', see Section 2). In contrast, only one of the 67 males studied (No. 18-41; body length 417 cm; age 21.5 years; histologically mature testis weighing 440 g) had a greater density of spermatozoa in its epididymis than in its testis. This male, which was sampled in December, may have only recently matured. Significant sperm production was often limited to the mating season (spring/summer) in such individuals (see Section 6.1).

Table 5 also shows that the testicular smears from 10 of the 50 whales with histologically-immature testes (20%) contained spermatozoa, but that only two of the 42 (4.8%) testes without spermatozoa in the smear were classified histologically as early-maturing. These contradictions indicate that about 20% of testes classified as immature may possibly belong to the early-maturing stage. The chance of misclassification should be much lower using the smear method because the smear was taken from a larger cross-section than was the histological block.

Table 5

Correspondence between three measures of male sexual maturity (histological maturity of testis and abundance of spermatozoa in testicular and epididymal smears)

Abundance of spermatozoa	Number of males in each category																		
	T/H	Im	EM	LM	M	$\Sigma$	E/H	Im	EM	LM	M	$\Sigma$	E/T	(a)	(b)	(c)	(d)	(e)	$\Sigma$
Absent	(a)	40	2	—	—	42	(a)	47	4	2	—	53	(a)	44	9	3	—	—	56
Doubtfully-present	(b)	8	3	—	1	12	(b)	3	5	2	1	11	(b)	1	2	8	—	—	11
Scanty	(c)	2	6	6	23	37	(c)	—	2	2	10	14	(c)	—	—	11	4	—	15
Intermediate	(d)	—	—	3	42	45	(d)	—	—	1	18	19	(d)	—	1	8	8	2	19
Copious	(e)	—	—	—	3	3	(e)	—	—	2	40	42	(e)	—	—	7	35	1	43
$\Sigma$		50	11	9	69	139	$\Sigma$	50	11	9	69	139	$\Sigma$	45	12	37	47	3	144

H: Histological maturity; Im: immature; EM: early-maturing; LM: late-maturing; M: mature.

T: Density of spermatozoa in testicular smear.

E: Density of spermatozoa in epididymal smear.

For details of the scale used in measuring the abundance of spermatozoa in smears see Section 2.

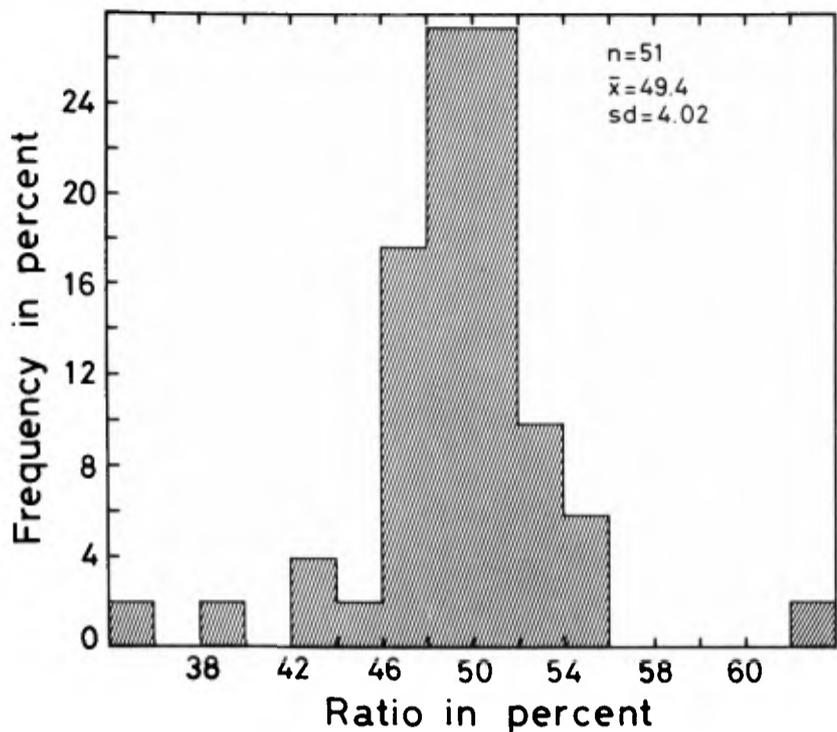


Fig. 5. Weight of the left testis expressed as the percentage of the combined weight of the testes in *G. macrorhynchus*.

4.2. Weight of testis

*Contralateral comparison.* The weights of the right and left testes were compared for 51 individuals ranging from immature to fully mature (Fig. 5). The weight of the left testis ranged between 34 and 66% of the combined testis weight ( $\bar{x} = 49.4\%$ ;  $SD = 4.02\%$ ). The testis of one side was not consistently heavier than that on the other. Thus the use of only one testis probably did not cause significant bias, although it may have caused apparently greater individual variation than would have the use of combined weights. Accordingly, we have usually used the arithmetic mean when the weights of both testes were

available; otherwise the weight of one testis from either side was used.

*Increase in testis weight.* Fig. 6 shows the relationships between single testis weight and body length and between testis weight and age. Testis weight (log scale) increased linearly from about 15 to 100 g (about sevenfold) as body length increased from 220 to 380 cm. After this, testis weight increased to about 700 g (also about sevenfold) while the body length increased only about 50 cm. Testis weight then increased at a rate intermediate between the above two rates (Fig. 6) until the whale reached a body length of about 500 cm (larger than the 95% confidence range for the asymptotic length ( $473.5 \text{ cm} \pm 9.1 \text{ cm}$ ) (Kasuya and Matsui, in press)). This result suggests that for fully-grown males, those of large body size tend to have heavier testes than do smaller animals.

The relationship between testis weight and age shows a similar pattern (Fig. 6). Testis weight increased linearly from about 20 g at two years to about 100 g at 14 years of age, i.e. an annual increase of about 14%. Testis growth was most rapid between 14 and 17 years of age, with an increase from 100 g to about 700 g, an annual increase of about 90%. This was followed by a relatively slow increase until an age of about 25 years. After this age, testis weight varied from 700 to 3,000 g, a much wider range than the 1,700 to 3,000 g range in testis weight of males which have ceased growing.

As shown in Fig. 6, greatest growth occurred mostly in the early and late-maturing stages. This rapid weight increase may indicate puberty. Although our sample was small and seasonally limited and individual variations are expected, we estimate the weight of a testis at the four stages to be approximately as follows (also see Table 6):

Immature	≤ 100 g
Early-maturing	100 g–170 g
Late-maturing	170 g–400 g
Mature	≥ 400 g

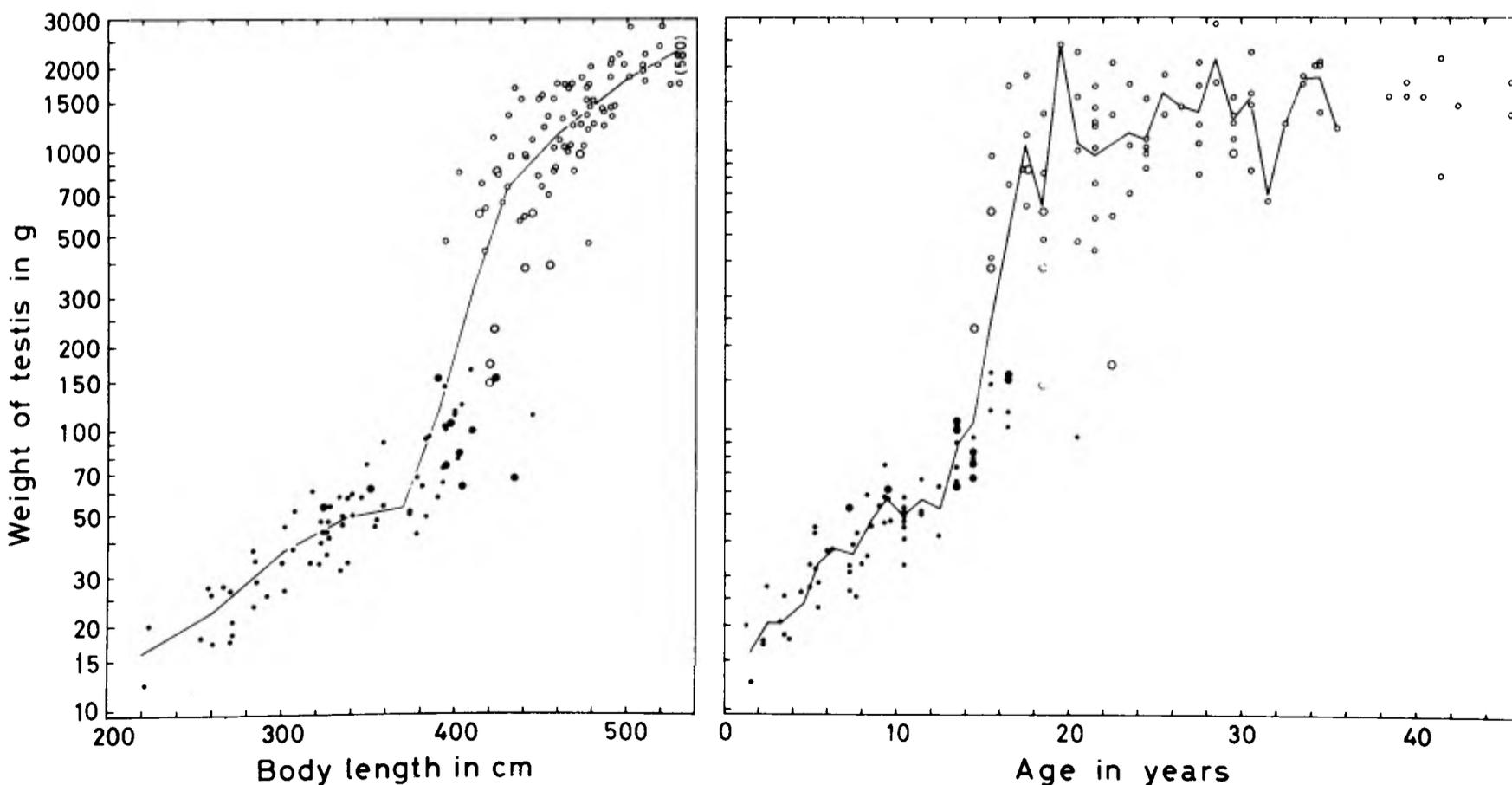


Fig. 6. Scatter-plot of weight of testis against body length (left) and age (right) in *G. macrorhynchus*. Small closed circle: 'immature' stage; large closed circle: 'early-maturing' stage; large open circle: 'late-maturing' stage; small open circle: 'mature' stage. The lines connect the arithmetic means of the testis weights for each body length (or age) class.

Table 6

Relationship between testis weight, histological maturity of testis, and spermatozoan density in epididymal smear<sup>1</sup>

Range of testis weights (g)	Number of whales in each category				Σ
	Immature	Early-maturing	Late-maturing	Mature	
0-25	8a	—	—	—	8
25-50	26a	—	—	—	26
50-75	12a, 2b	1a, 3b	—	—	18
75-100	4a	1b, 1c	—	—	6
100-125	3a, 1b	2a, 1b	—	—	7
125-150	1a	—	1e	—	2
150-175	1a	1a, 1c	1a	—	4
175-200	—	—	—	—	0
200-225	—	—	—	—	0
225-250	—	—	1a	—	1
—	—	—	—	—	—
375-400	—	—	1b, 1c	—	2
400-425	—	—	—	1d	1
425-450	—	—	—	1d	1
450-475	—	—	—	1c	1
475-500	—	—	—	1d	1
—	—	—	—	—	—
550-575	—	—	—	1d	1
575-600	—	—	—	1e	1
600-625	—	—	1b, 1d	—	2
625-650	—	—	—	1e	1
650-675	—	—	—	1d	1
675-700	—	—	—	—	0
700-750	—	—	—	1c	1
750-800	—	—	—	1d, 1e	2
800-850	—	—	—	1d, 1e	2
850-900	—	—	1c	1c, 1d, 1e	4
900-950	—	—	—	—	0
950-1,000	—	—	1e	2e	3
≥ 1,000	—	—	—	50	50

<sup>1</sup> Spermatozoan density index in smear: a, absent; b, doubtfully present; c, scanty; d, intermediate; e, copious. For a description of each category see Section 2.

**Diameter of seminiferous tubules.** Seminiferous tubule diameter increased as the testis matured as shown in Table 7 and Fig. 7. In the immature and early-maturing stages, this increase was very slight compared to the corresponding changes in testis weight (Fig. 8). A rapid increase in tubule diameter was observed between the ages of 15 and 21 years (Fig. 7), when many testes were

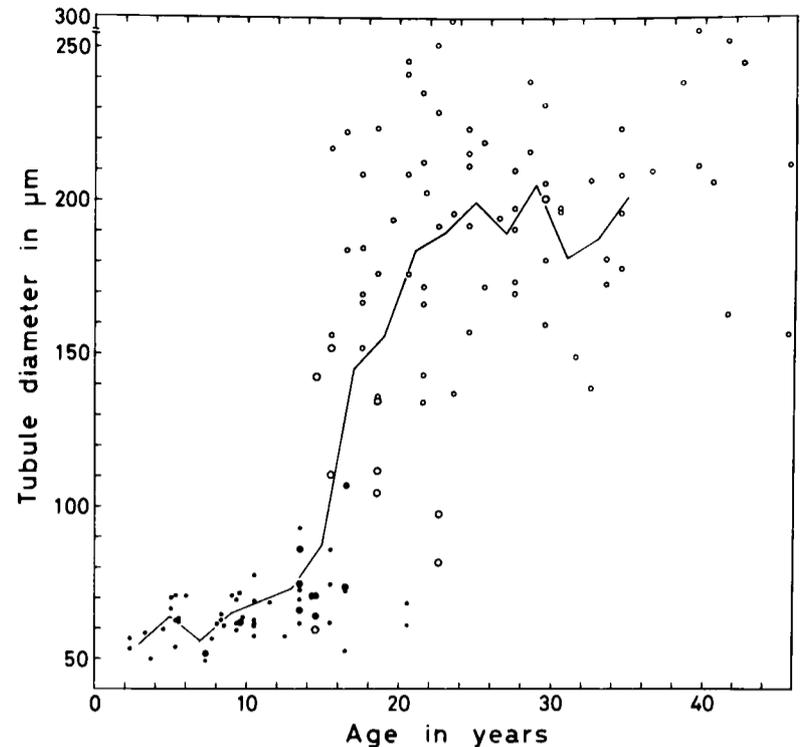


Fig. 7. Scatter-plot of diameter of seminiferous tubule against age in *G. macrorhynchus*. All of the dot symbols are as in Fig. 6. (Small closed circle: 'immature' stage; large closed circle: 'early-maturing' stage; large open circle: 'late-maturing' stage; small open circle: 'mature' stage.) Line connects mean diameters of each age class.

classified as late-maturing, suggesting that a rapid increase in tubule diameter is a feature of this stage. The wide individual variation in tubule diameter and testis histology (Fig. 3) observed in adult testes could reflect a seasonal or aseasonal reproductive cycle, but we had insufficient data to study this in detail.

Fig. 8 shows the relationship between tubule diameter and testis weight plotted on logarithmic scales. The immature and early-maturing testes formed one group; the late-maturing and mature testes another. The relationships (see Fig. 8) are described by the following least-squares equations:

$$\log Y = 0.1441 \cdot \log X + 36.5452$$

$$(X < 80, r = 0.49) \quad (\text{Equation 4.1})$$

$$\log Y = 0.3828 \cdot \log X + 12.7160$$

$$(X > 80, r = 0.93) \quad (\text{Equation 4.2})$$

where  $X$  indicates the single testis weight in  $g$  and  $Y$  the mean seminiferous tubule diameter in  $\mu m$ . Comparison

Table 7

Age (years) and diameter of seminiferous tubules ( $\mu m$ ) of *G. macrorhynchus* at each stage of male sexual maturity

Age range	Diameter of seminiferous tubules at each stage							
	Immature		Early-maturing		Late-maturing		Mature	
	Range	Mean	Range	Mean	Range	Mean	Range	Mean
2-5	49.8-59.9	56.0	—	—	—	—	—	—
5-10	49.0-70.6	62.8	51.4-61.8	56.6	—	—	—	—
10-15	57.1-74.0	67.9	59.2-85.7	69.8	142.0	142.0	—	—
15-20	52.2-85.5	69.1	73.0-106.9	89.9	104.2-166.6	130.8	135.6-223.6	184.9
20-25	60.1	60.1	—	—	96.9	96.9	133.4-298.1	201.9
25-30	—	—	—	—	200.8	200.8	159.0-239.7	197.1
30-35	—	—	—	—	—	—	148.9-223.5	188.7
35-40	—	—	—	—	—	—	209.4-278.2	234.3
40-46	—	—	—	—	—	—	156.4-263.5	207.2
Overall figures	49.0-85.5	64.2	51.4-106.9	71.2	96.9-200.8	136.1	133.4-298.1	198.8

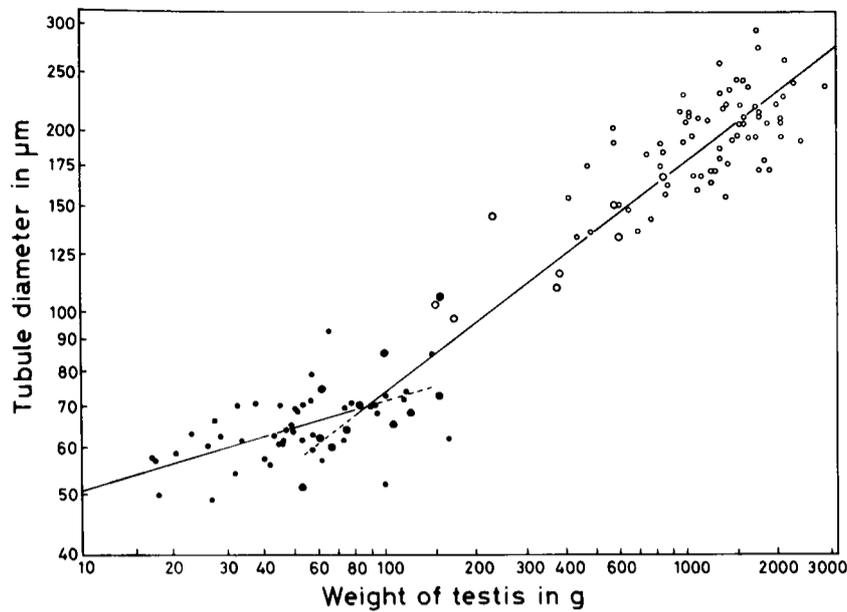


Fig. 8. Relationship between diameter ( $Y$  in  $\mu\text{m}$ ) of seminiferous tubule and weight ( $X$  in g) of testis in *G. macrorhynchus* plotted on a double logarithmic scale. All of the dot symbols are as in Fig. 6. (Small closed circle: 'immature' stage; large closed circle: 'early-maturing' stage; large open circle: 'late-maturing' stage; small open circle: 'mature' stage.) Lines are least-square regressions of  $\log Y$  and  $\log X$  calculated separately for  $X < 80$  (Equation 4.1) and  $X > 80$  (Equation 4.2).

of the above correlation coefficients suggests that the increase in tubule diameter made a limited contribution to the testis weight increase in the immature and early-maturing stages, while in the late-maturing and mature stages most of the weight increase was accounted for by the expansion in tubule diameter. For a testis weighing more than about 1,500 g, tubule diameter and weight were no longer correlated (Fig. 8), supporting our earlier evidence that very high testis weight tends to correlate with large body size.

#### 4.3. Growth and sperm-density changes in the epididymis

It is difficult to define when an individual male becomes sexually mature, i.e. physiologically capable of breeding, on the basis of the epididymal smear alone. Spermatozoa were absent from the epididymal smears of many males less than 17 years old (Fig. 9), and males whose smears were classified as 'sperm doubtfully present' (Fig. 10) were (with one exception) between 9 and 19 years old. Animals with 'scanty' epididymal sperm were all 14 years old or older, those with 'intermediate' amounts of epididymal sperm were all 15 years old or older, and those with copious amounts of epididymal sperm (see Fig. 10 for details) were all 15 years old or older (see Fig. 9). Although the first two stages were limited to the younger ages and seemed to be correlated with maturity as classified on the basis of testis histology, the latter three epididymal-smear stages correlate with neither age ( $\geq 15$  years) nor the histological stages of 'late-maturing' and 'mature' (Table 5 and Fig. 9). Therefore, we consider that these last three stages of epididymal sperm density represent individual or seasonal variation within mature males rather than growth stages, i.e. many of the males with 'scanty' or more epididymal sperm were reproductively mature.

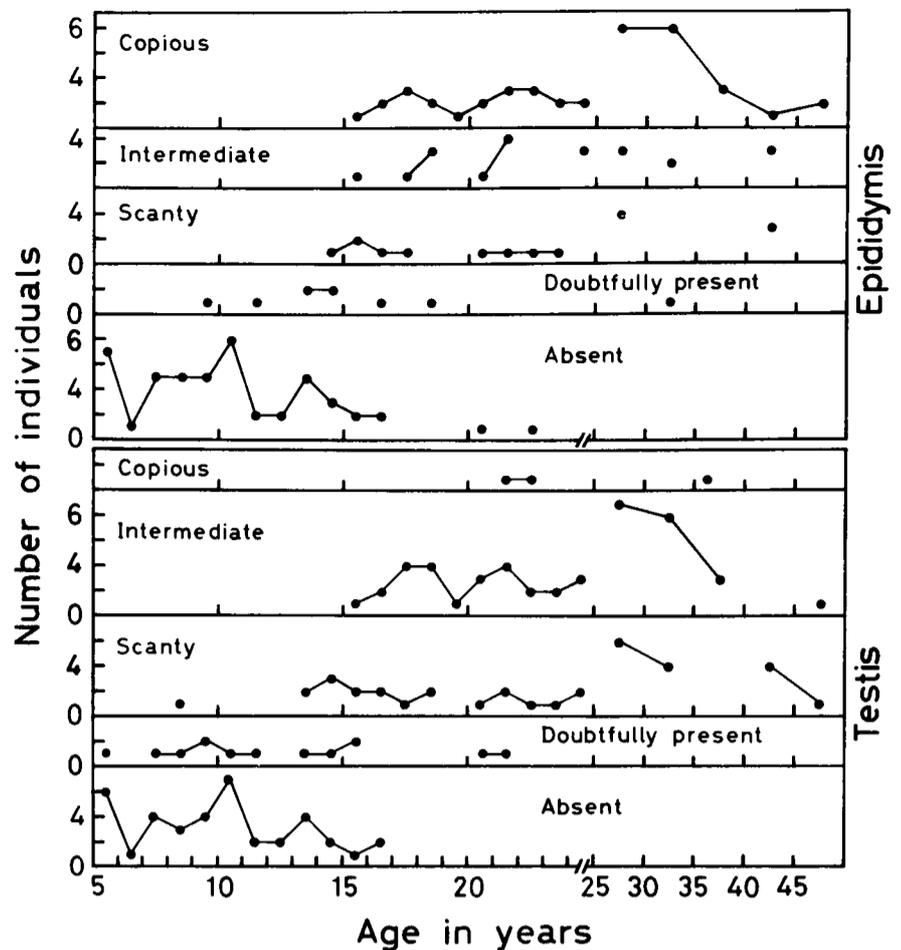


Fig. 9. Relationship between age and density of spermatozoa in epididymal (top set) and testicular smears (bottom set) in *G. macrorhynchus*.

#### 4.4. Maturity, age and body length

Fig. 11 summarizes the relationship between testis maturity, age and body length. The immature and early-maturing stages were difficult to separate, as were the late-maturing and mature stages. However, immature and early-maturing individuals were distinct from late-maturing and mature whales. The boundary between these two major groupings was more closely related to body length than age, i.e., there was a tendency for males of large body size to mature younger.

For each stage of male sexual maturity (early-maturing, late-maturing, and mature), the percentage of individuals at or beyond this stage was plotted against both body length and age. The resultant linear regressions follow:

##### Maturity on body length ( $X$ , cm)

$$\text{Early-maturing and later} = 2.985X - 1,147.2 \\ (380 < X < 420, r = 0.94) \quad (\text{Equation 4.3})$$

$$\text{Late-maturing and mature} = 4.375X - 1,759.8 \\ (400 < X < 430, r = 0.90) \quad (\text{Equation 4.4})$$

$$\text{Mature} = 2.274X - 909.9 \\ (400 < X < 440, r = 0.83) \quad (\text{Equation 4.5})$$

##### Maturity on age ( $X$ , year)

$$\text{Early-maturing and later} = 16.206X - 186.6 \\ (13 < X < 18, r = 0.91) \quad (\text{Equation 4.6})$$

$$\text{Late-maturing and mature} = 21.660X - 293.2 \\ (14 < X < 18, r = 0.87) \quad (\text{Equation 4.7})$$

$$\text{Mature} = 16.691X - 233.6 \\ (14 < X < 20, r = 0.88) \quad (\text{Equation 4.8})$$

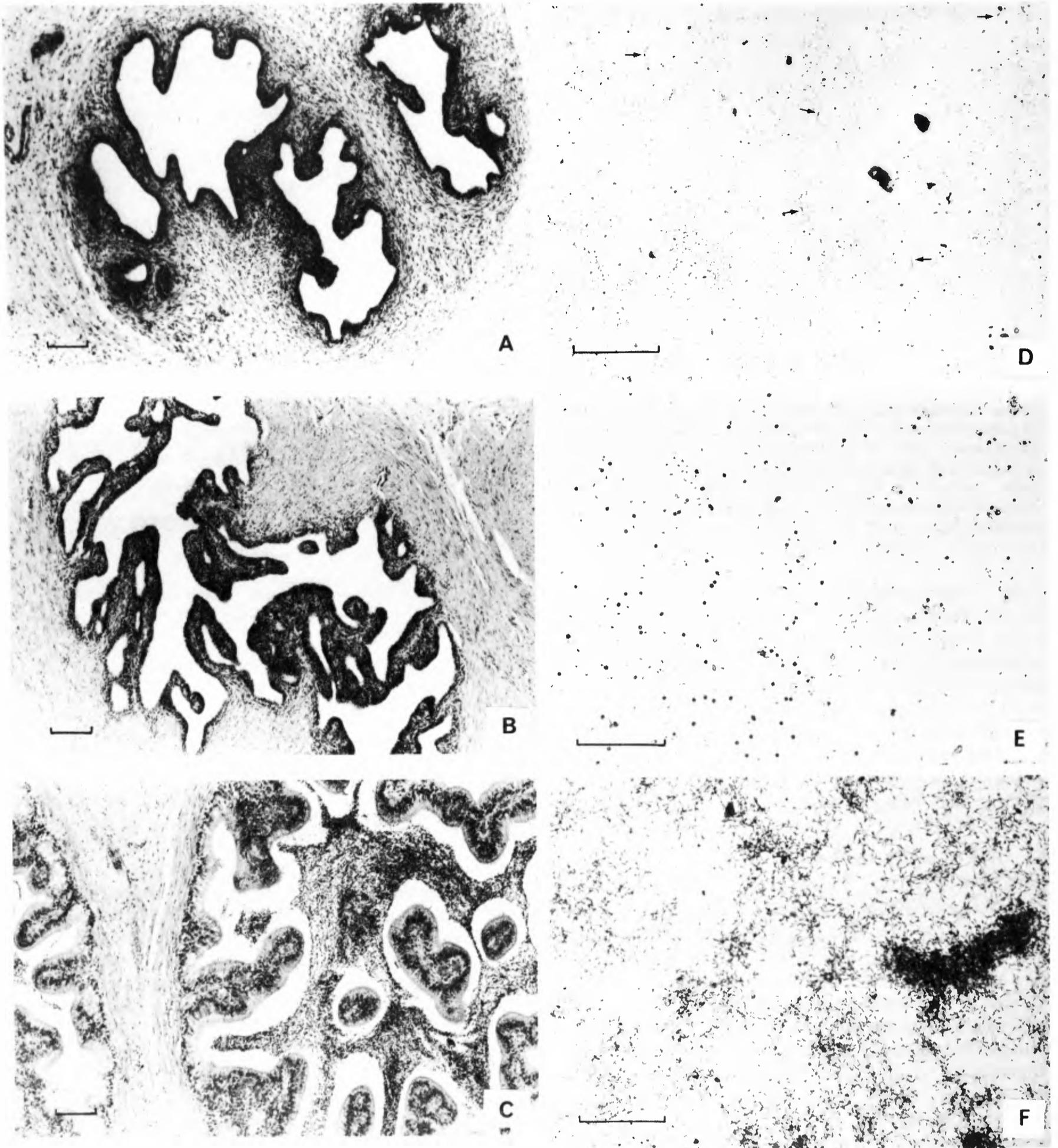


Fig. 10. Epididymis of *G. macrorhynchus*. In all photographs the scale bar represent 0.1 mm.

- A. Epididymis of an immature male (No. 15-9, 341 cm, 10.5 years old, weight of single testis 50.0 g). Spermatozoa were absent from both the epididymal and testicular smears. Haematoxylin and eosin-stained.
- B. Epididymis of a male at the early-maturing stage (No. 17-12, 390 cm, 16.5 years old, weight of single testis 154.0 g). Spermatozoa were absent from both the epididymal and testicular smears. Haematoxylin and eosin-stained. (For testis, see Fig. 3C).
- C. Epididymis of a mature male (No. 18-36, 490 cm, 34.5 years old, weight of single testis 2,080 g). Spermatozoa were 'copious' in the epididymal smear and at 'intermediate' density in the testicular smear. Haematoxylin and eosin-stained. (For testis, see Fig. 3G).
- D. Epididymal smear at the upper limit of the 'scanty' spermatozoan density stage. Each spermatozoon is indicated by an arrow.
- E. Epididymal smear at the 'intermediate' spermatozoan density stage.
- F. Epididymal smear at the 'copious' spermatozoan density stage.

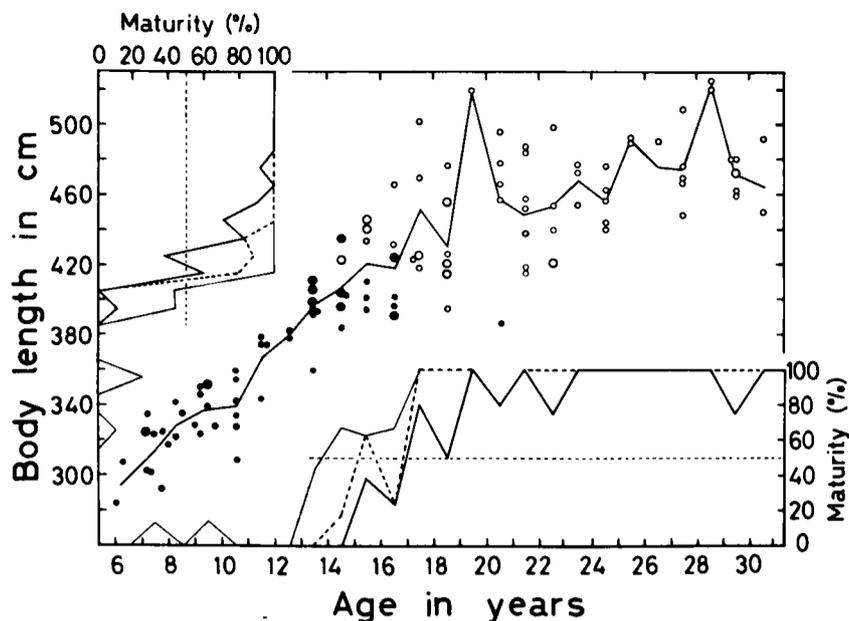


Fig. 11. Relationships between sexual maturity, body length and age in males of *G. macrorhynchus*. In the relationship between body length and age (centre), the dot symbols are as in Fig. 6. (Small closed circle: 'immature'; large closed circle: 'early-maturing'; large open circle: 'late-maturing'; and small open circle: 'mature'.) The line joins the mean body lengths in each age class. The symbols in the age-maturity (bottom) and body length-maturity (upper left) relationships are: thick solid line: 'mature'; dotted line: 'late-maturing' plus 'mature'; thin solid line: 'early-maturing' plus 'late-maturing' plus 'mature'. Individuals over 31 years are, as well as those below 31 years, included in the maturity-body length relationship.

Table 8

Range of data and mean (50% point on the linear regression\*) at the attainment of each stage of sexual maturity in male of *G. macrorhynchus*

	Body length (cm)			Age (years)		
	Min.	Mean	Max.	Min.	Mean	Max.
Immature	—	—	409	—	—	20.5
Early-maturing	324	401.1	434	7.25	14.6	16.5
Late-maturing	414	413.7	455	14.5	15.8	29.5
Mature	394	422.1	525	15.5	17.0	45.5

\* Equations 4.3 through 4.8 in text.

The body length and age at which 50% of individuals were at (or beyond) each stage, calculated from these regressions, are listed in Table 8. These values have been used in the latter sections of this study as the mean age (or body length) at the attainment of each stage.

#### 4.5. Discussion

The epididymal smear is suitable for detecting the presence of spermatozoa (see Section 4.1). However, we consider that the density of sperm in an epididymal smear may not be a reliable index of the actual density of epididymal sperm. A further problem is that epididymal sperm density fluctuated seasonally in maturing individuals (see Section 6.1). Therefore we decided to use testis histology as the basis for recognizing male sexual maturity. We consider that males classified as 'late-maturing' or 'mature' were probably functionally mature. Thus functional maturity is attained at a mean age of 15.8 years, a mean body length of about 414 cm (Table 8) and a mean single-testis weight of 170 g (see Section 4.2).

As the body weight (Kasuya and Matsui, in press) and testis weight of males of *G. macrorhynchus* both continued to increase after the age of functional maturity until about age 25 years, we consider that it is likely that males do not mate successfully until several years after they are 'functionally mature'. Of course, this will be difficult to confirm even by behavioural observations (see Section 10).

Sergeant (1962a) used histology to study the maturity of the testis and epididymis of a limited number of samples of *G. melaena*. In both *G. melaena* and *G. macrorhynchus*, the tubule diameter was less than 80  $\mu\text{m}$  in immature individuals and about 200  $\mu\text{m}$  in fully-grown males. In *G. melaena*, dividing spermatocytes were first observed in a 75 g testis, and spermatids or spermatozoa were first observed in a testis weighing 573 g. However, in *G. macrorhynchus*, spermatocytes, spermatids and spermatozoa were all observed in every testis classified as early-maturing or later, and the smallest single testis in this category weighed about 50 g (Table 6). We suspect that these apparent 'species' differences may be due to the different techniques of preparation and examination.

Sergeant (1962a) considered that in *G. melaena*, sexual maturity occurred at a testis weight of 500–1,000 g and at ages between 11 and 16 years. According to his analysis, these corresponded to the stage of rapid testis-weight increase and to a seminiferous tubule diameter of 80–150  $\mu\text{m}$ . Since both these phenomena occur in early-maturing and late-maturing individuals in *G. macrorhynchus*, we consider that Sergeant's criterion of sexual maturity in *G. melaena* corresponds to what we define as functional maturity in *G. macrorhynchus*. Thus according to Sergeant's criteria in the populations studied, males of *G. macrorhynchus* mature at 14–23 years, significantly later than in *G. melaena* (11–16 years).

## 5. FEMALE SEXUAL MATURITY AND BREEDING LONGEVITY

### 5.1. Puberty

Fig. 12 shows the diameters of the largest Graafian follicle in the ovaries of immature, pregnant, lactating and resting females (the last defined as sexually-mature females neither pregnant nor lactating).

The maximum follicle size in immature individuals was bimodally distributed. The larger mode (eight individuals) ranged from 4 to 8 mm, and the smaller mode (30 females) ranged below 4 mm, including follicles below measurable diameter (< 1.0 mm). Females younger than two years usually did not develop measurable follicles, an exception being a 0.25-year (190 cm in body length) female with one 1.0-mm follicle. Although some immature females had follicles more than 4 mm in diameter at ages over 2 years, individuals with no measurable follicles were still common up to the age of six years (about one year earlier than the age of the youngest mature females, estimated below).

The maximum follicle size in sexually-mature females varied with their reproductive status. In pregnant females, the follicles were least developed. The upper range was similar to that of immature individuals, but the boundary of the two modes lay between 1 and 2 mm. The size of follicles in lactating females showed a diffuse

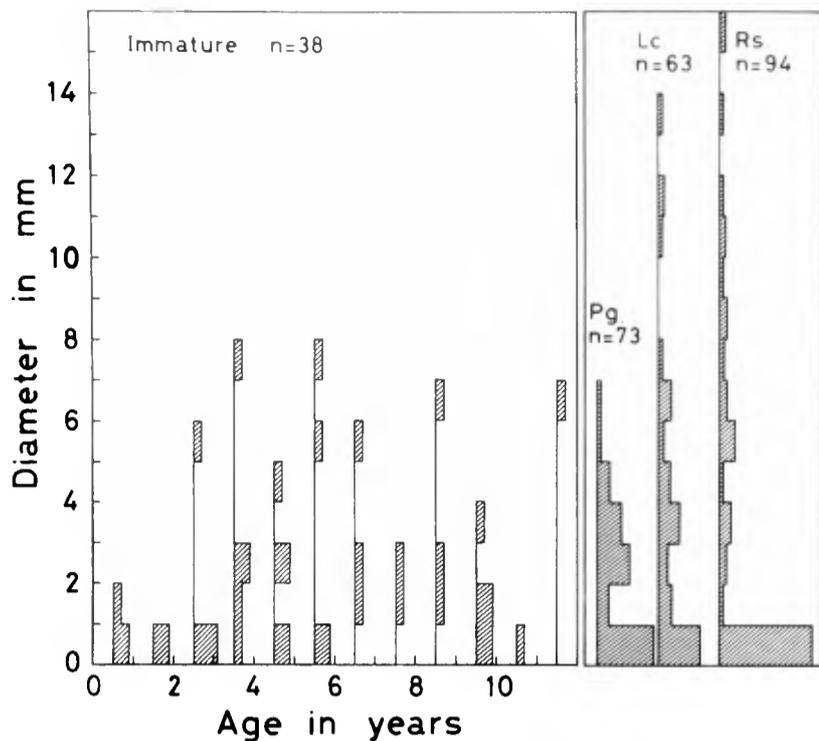


Fig. 12. Diameters of the largest Graafian follicles in the ovaries of immature, pregnant (Pg), lactating (Lc), and resting (Rs) females in *G. macrorhynchus*.

trimodal distribution. The smallest group included follicles below 3 mm (females without measurable follicles included), the intermediate mode range from 3 to 8 mm, and the largest group included a small number of follicles of 10 to 14 mm. The distribution of follicle diameters in resting females was similar to that of lactating females; however, the last two modes were continuous and the upper range of the largest group was slightly greater. Therefore we suspect that the diameter of follicles at rupture is close to the range of the largest-follicle group, i.e. 10–15 mm, and that the growth of follicles in mature ovaries is often suppressed at one of the first two stages, i.e. below 8 mm. The growth of follicles between the three stages, when it happens, is probably rapid.

The development of follicles to macroscopic size usually occurred in immature females at ages greater than two years, and further development appeared to follow the pattern of mature females. Although follicle size in some immature females varied seasonally from below 4 mm (outside the season) to 8 mm (during the mating season) (Marsh and Kasuya, 1984), further growth seemed to be suppressed for several years, probably until seven years or later, when the first ovulation occurred in some females. These data suggest that the length of time during which follicle growth is suppressed is flexible and that it may contribute to the change of age at attainment of sexual maturity of females of *G. macrorhynchus* brought on by a change in the environment or social structure.

## 5.2. Age at attainment of sexual maturity

We define sexually mature females as those which have ovulated at least once. As the corpus luteum formed after ovulation degenerates into a corpus albicans, which we believe persists for life in *G. macrorhynchus* (Marsh and Kasuya, 1984), the presence of one or more corpora was used as a direct indication of sexual maturity.

The relationship between age and sexual maturity is

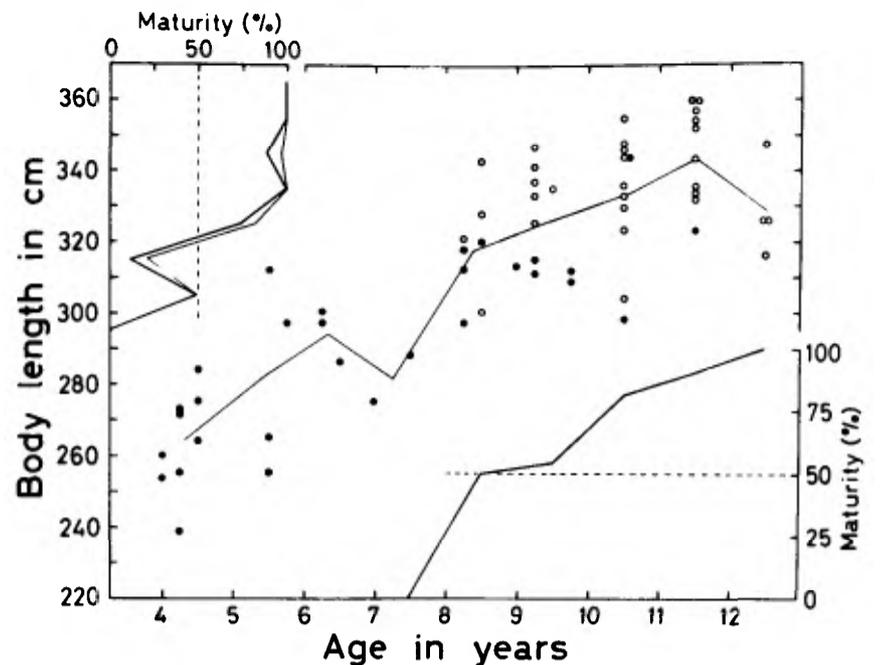


Fig. 13. Relationship between sexual maturity, body length and age in female *G. macrorhynchus*. In the body length – age relationship (centre), open circles indicate mature and closed circles immature animals, and the line connects the mean body length for each year class. In the maturity-body length relationship (upper left), the thick line includes only individuals less than 13 years old; thin line includes individuals over 13 years of age as well. The age-maturity relationship is shown at the lower left.

Table 9

Age at the most recent conception estimated for pregnant females less than 10 years old

Sample no.	Age at death (years)	No. of corpora	Foetal length (cm)	Pregnancy <sup>1</sup>		Age at conception (years)
				(days)	(years)	
7-17	8.25	1	90.0	306	0.84	7.4
26-9	8.25	1	40.5	160	0.44	7.8
17-2	8.5	1	66.5	237	0.65	7.9
9-122	8.5	4	3.0	50 <sup>2</sup>	0.14	8.4
24-25	9.25	1	132.0	430	1.18	8.1
14-15	9.25	3	100.0	336	0.92	8.3

<sup>1</sup> Length of pregnancy (days) =  $(452 \cdot 0.91 \cdot (\text{foetal length}) / 139.5) + (452 \cdot 0.09)$ .

<sup>2</sup> Probable overestimate.

shown in Fig. 13. The youngest sexually mature female and the oldest immature female appeared at 8.25 and 11.5 years of age, respectively. A better estimate of the age at first ovulation was obtained from six pregnant females based on age at death, foetal body length and the mean foetal growth curve (Fig. 16, Table 9). Four of these females had only one corpus luteum, indicating that their first ovulation occurred between 7.4 and 8.1 years. Thus we conclude that the first ovulation occurs in *G. macrorhynchus* between the ages of 7.0 and 12.0 years.

Fig. 13 shows that 50% of females become sexually mature by 8.5 or 9.5 years. The least-squares regression between age ( $X$ , years) and proportion of mature females ( $Y$ , %) weighted by sample size, is as follows;

$$Y = 20.6111X - 135.81 \\ (7 < X < 11, r = 0.93). \quad (\text{Equation 5.1})$$

when  $Y = 50$ ,  $X = 9.0$ . Accordingly, we have used 9.0 years as the mean age at the onset of female sexual maturity in *G. macrorhynchus*.

### 5.3. Body length at sexual maturity

The body lengths of the smallest sexually mature female and the largest immature female were 300 cm and 344 cm, respectively. The thin solid line in the upper left-hand corner of Fig. 13 shows the relationship between body length and the proportion of sexually mature females for 182 individuals ranging from 290 to 359 cm in body length. Our sample in the 290 to 310 cm range was very small. The least-squares regression between body length ( $X$ , cm) and the proportion of sexually mature females ( $Y$ , %) weighted by sample size is

$$Y = 2.5570X - 756.89$$

( $290 < X < 340$ ,  $r = 0.93$ ) (Equation 5.2)

and when  $Y = 50$  (%),  $X = 315.6$  (cm).

Thus we tentatively consider 316 cm as the mean body length at the onset of sexual maturity. An improved estimate will require more data. The body length on the mean growth curve (Kasuya and Matsui, in press) at 9.0 years of age (the mean age at the onset of sexual maturity) is about 320 cm, which is slightly larger than in the above estimation. This kind of discrepancy can occur when the growth rate declines soon after the attainment of sexual maturity, as observed in several small odontocetes (Kasuya, 1976a; Kasuya and Brownell, 1979).

### 5.4. Breeding longevity

The oldest pregnant female, which had a foetus 20 cm long, was aged at 34.5 years and was lactating. Assuming a normal termination of pregnancy, parturition would have been expected when the mother was about 35.5 years old (for method of estimation, see equation at the bottom of Table 9). Another indication of parturition at the same age came from a female (No. 9-116) that was observed to give birth in the harbour and was identified by a large nick on the dorsal fin. The next day this whale was killed, and very recent parturition was confirmed (lactating, uterine widths 16.0 cm (left) and 10.5 cm (right)). The next oldest pregnant females (four individuals) were 32.5 years old.

The oldest female with a corpus luteum of 'ovulation' was aged 39.5 years (No. 11-24, resting). The next oldest females with a corpus luteum of 'ovulation' were aged 38.5-years old (No. 9-3, resting) and 37.5-years old (Nos 7-26 and 24-9, resting; No. 10-15, lactating). Although the frequency of ovulations, the proportion of ovulations followed by conception, and possibly the proportion of conceptions ending at normal parturition rapidly decrease with increasing age of females (Marsh and Kasuya, 1984), there is still a possibility of parturition for whales in the 36.5- to 39.5-year classes.

Marsh and Kasuya (1984) tentatively identified post-reproductive females based on ovarian anatomy and age-related changes in fecundity (for further details, see Section 8). According to their criteria the youngest post-reproductive female appeared at age 29.5 years; the proportion increasing with increasing age, i.e. 8.5% at ages from 28 to 32 years, 19.6% at 32 to 36 years, 33.3% at 36 to 40 years, and 100% thereafter. We consider that these criteria probably underestimate the number of females less than 40 years old that have ceased to bear calves (see Section 8), and as such, are probably a more

reliable index of the minimum age of post-reproductive females (i.e. 29.5 years) than of the mean or maximum ages at which females become post-reproductive.

We conclude that females of *G. macrorhynchus* cease to bear calves when aged between 29.5 and 39.5 years inclusive. As sexual maturity occurs at 7.5 to 11.5 years, followed by first parturition between about 8.5 and 12.5 years inclusive, we estimate breeding longevity to be from about 17 to 31 years, with a probable mean of about 24 years.

### 5.5. Discussion

Sergeant (1962a) reported that the long-finned pilot whale in the western North Atlantic attained sexual maturity at 6-7 years (female) or at about 12 years (male). The corresponding figures for *G. macrorhynchus* are 9 and 16 years, respectively. Thus in both species the males mature about 6-7 years later than do the females. This delay is undoubtedly related to much larger male body size and possible polygynous breeding behaviour (see Section 10).

Even though *G. melaena* is larger than *G. macrorhynchus*, it attains sexual maturity several years earlier in both sexes. The cause of this difference is unknown. Our sample was taken from a stock subject to continuous fishing pressure at a relatively low level. In contrast, Sergeant's collection of samples from *G. melaena* was started in 1951 and continued during a period of heavy exploitation. However, the level of previous exploitation seems to have been low. In spite of these uncertainties, we consider that the earlier maturation and higher pregnancy rate in *G. melaena* (see Section 8) are parallel changes expected for a mammal population that lives in a better environment, and suggest that the observed difference in age at sexual maturity between the two *Globicephala* species may reflect differences in the history of exploitation or food availability.

For discussion of the incidence of post-reproductive females see Sections 8 and 10, and Marsh and Kasuya (1984 and in press).

## 6. SEASONALITY OF REPRODUCTION (INCLUDING FOETAL GROWTH AND NEONATAL LENGTH)

### 6.1. Male

Seasonal changes in male reproductive activity were investigated by studying testis weights, diameters of seminiferous tubules, and the density of spermatozoa in testicular and epididymal smears.

*Weight of testis.* Seasonal changes in single-testis weight are shown in Fig. 14. No significant seasonal fluctuation was detected in the mean weights of immature testes or maturing testes (early and late-maturing males combined). Because of the small sample sizes, the mean weight of histologically-mature testes was comparable only between February, May/June/July, and December. When the mean weights were compared between these three seasons, the value in May/June/July was slightly higher than that in December; the difference being just significant ( $T$ -test,  $P = 0.05$ ). Although this apparent increase in testicular activity coincided with the breeding season estimated from the seasonality of the female

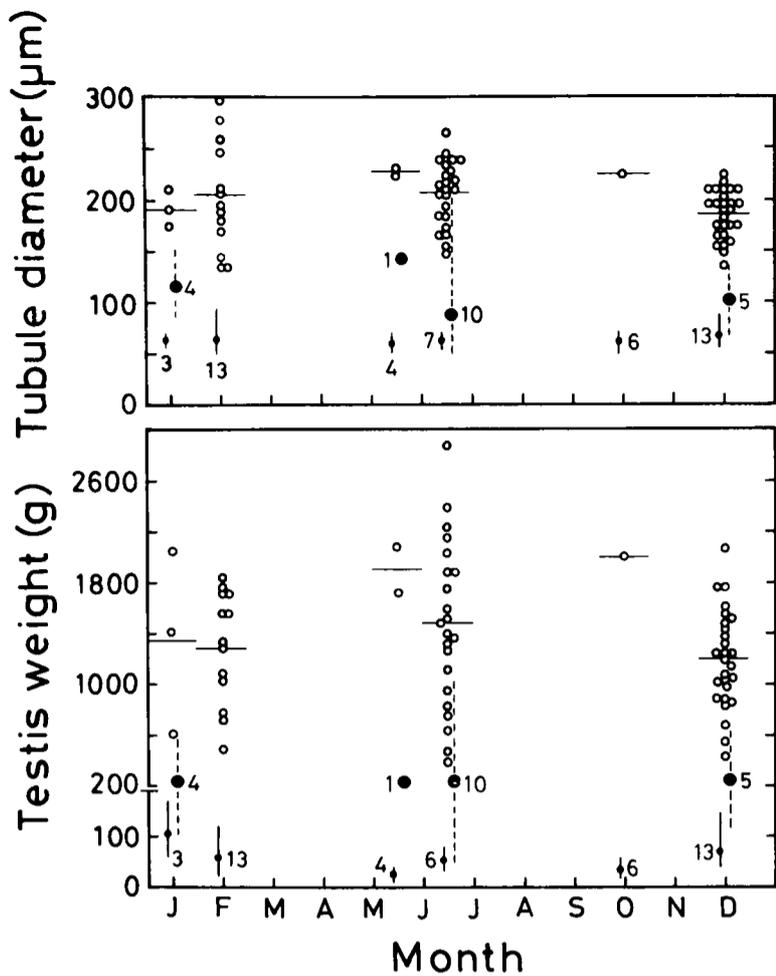


Fig. 14. Seasonal fluctuation of single-testis weight and diameter of seminiferous tubules. The open circles and bars indicate the individual and mean values for adult males respectively, the dotted lines and large closed circles the range and mean of the early and late-maturing males; and the solid lines and small closed circles the ranges and means of immature males in various seasons. The numerals indicate the sample size. Maturity was determined histologically. Data from 13 schools (nos 9 through 18, and 22 through 24).

reproductive organs, this may be a sampling artefact. The sample from May/June/July included 20 histologically-mature males from School 9, two from School 2 and two from School 24. School 9 contained adult males of large body size (Fig. 28). There was a positive correlation between body length and testis weight in mature males (Fig. 6). In order to examine the confounding effect of body size on the seasonal differences in mean testis weight, the testis weights in the months May to July were grouped by body length and compared with those in December (Table 10). The seasonal distribution of the heavier testis was variable between the body-length groups. The difference in mean testis weight was not significant for any of the body-length ranges ( $T$ -test,  $P > 0.05$ ), and no seasonal fluctuation was detected. However, as the sample size is limited, we cannot conclude from this analysis that there is no seasonal change in the testis weight of adult pilot whales.

**Seminiferous-tubule diameter.** The mean seminiferous-tubule diameters of whales in various reproductive categories and body length classes are shown in Fig. 14 and Table 10, respectively. There was no significant seasonal difference in mean tubule diameter for either immature or maturing (early and late-maturing individuals combined) males ( $T$ -test,  $P > 0.05$ ).

However, when the mean-tubule diameters of histologically-mature males in February, May/June/July and December were compared, a significant difference was found between May/June/July and December ( $T$ -test,  $P < 0.01$ ), the mean tubule diameter being larger by about

Table 10

Comparison of single-testis weight and seminiferous-tubule diameter between whales examined in December and those examined in May–July

Range of body lengths (cm)	December			May–July		
	<i>N</i>	Mean	S.D.	<i>N</i>	Mean	S.D.
	Testis weight (g)					
400–419	4	310.3	251.3	3	256.6	319.1
420–439	7	758.4	545.7	7	590.6	430.3
440–459	7	1,065.7	275.3	3	611.0	445.0
460–479	10	1,295.0	284.4	6	1,140.0	454.9
480–499	4	1,560.0	360.4	9	1,702.2	390.3
500–519				7	2,112.8	413.6
520–539				2	2,325.0	799.0
	Tubule diameter ( $\mu\text{m}$ )					
400–419	4	101.7	37.3	3	98.9	45.7
420–439	7	156.6	44.4	7	144.3	58.1
440–459	7	182.2	20.4			
460–479	10	194.9	22.0	6	208.4	26.2
480–499	4	189.7	12.1	8	224.7	27.1
500–519				5	211.5	16.3
520–539				2	227.9	16.6

22  $\mu\text{m}$  in May/June/July. When seasonal comparisons were made within body-length groups (Table 10) the tubule diameter of males more than 460 cm long in May/June/July also appeared to be consistently greater than in December, although the difference was statistically

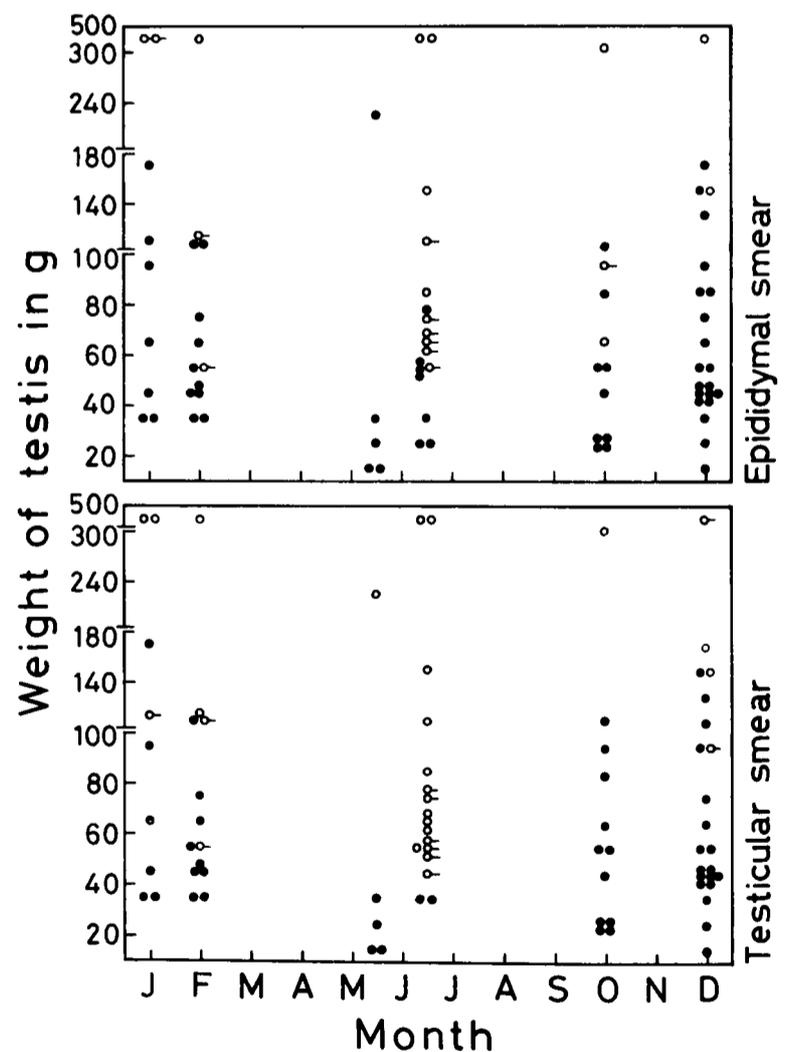


Fig. 15. Seasonal change in testes weight and density of spermatozoa in testicular (bottom) and epididymal (top) smears. Closed circles indicate individuals without spermatozoa, open circles with bars sperm 'doubtfully-present', and open circles without bars a higher sperm density. Only juvenile testes weighing less than 500 g (single testis) in 17 schools (nos 7, 9 through 18, and 22 through 27) are included.

Table 11

Seasonality of spermatozoan density in epididymal and testicular smears of males exceeding 600 g in single-testis weight

Month School no.	Number of whales						$\Sigma$
	Jan. 7, 11	Feb. 12, 16, 22, 23	May/June 24	June/July 9, 10	Oct. 13	Dec. 14, 15, 17, 18	
<i>Testicular smear</i>							
Absent	0	0	0	0	0	0	0
Doubtfully present	0	0	0	0	0	0	0
Scanty	1	5	0	5	0	10	21
Intermediate	4	6	2	17	1	15	45
Copious	0	1	0	0	0	1	2
<i>Epididymal smear</i>							
Absent	0	0	0	0	0	0	0
Doubtfully present	1	0	0	0	0	1	2
Scanty	1	4	0	4	0	2	11
Intermediate	0	4	0	2	0	9	15
Copious	3	4	2	16	1	14	40

significant only between length groups from 480 to 499 cm ( $T$ -test,  $0.02 < P < 0.05$ ).

*Density of spermatozoa in the smear.* Fig. 15 shows the seasonal change in the relationship between the density of spermatozoa in epididymal (top) and testicular (bottom) smears for juveniles with a single-testis weight of less than 500 g. In May/June/July, spermatozoa were detected in the smears of all the testes exceeding 40 g. This threshold increased in December/January to between 90 and 160 g. The corresponding figures in October and in February were presumably intermediate between these two seasons. The epididymal smears showed the same seasonality, although the threshold level was slightly higher (testis weight 50 to 80 g in May/June/July and 140 to 180 g in December/January). This difference was expected, because further increase in testicular weight may take place from the stage of first spermiogenesis to the stage when the spermatozoa are transported to the epididymis. The density of spermatozoa found in the testis or epididymis of these juveniles was usually at the level of 'doubtfully present' and occasionally 'scanty' (Table 6), much lower than in adult males (below).

Table 11 shows the seasonal fluctuation in the density of spermatozoa of individuals with a single-testis weight of more than 600 g i.e. the approximate minimum testicular weight of fully-grown individuals (Fig. 6). There were 65 histologically-mature males and three late-maturing males with testicular weights in this category. With the exception of two epididymal smears, all samples had a sperm density of 'scanty' or greater. No seasonal difference was detected in these limited data.

*Conclusion.* The most definite indication of seasonal changes in the male reproductive tract is found in the threshold weights of testes producing spermatozoa. This threshold weight was low in summer and high in December/January. We consider that the reproductive activity indicated by this change probably starts in February, attains a peak in early summer, and gradually decreases towards October. This cycle is identical with the frequency of conceptions analysed below. The threshold testis weight at which sperm are produced increases from 40 to 100 g within about six months. However, it takes five years (from the ages of seven to 12 years) for the mean

testis weight to increase a corresponding amount (Fig. 6). This result and the absence of seasonal fluctuation in immature testis weights suggest that the seasonal change in threshold weight is not due to an increase in testis weight *per se* but reflects the seasonally-limited spermiogenesis of juveniles. The limited amounts of sperm thus produced suggest that these juveniles are probably not reproductively successful in the mating season.

We have no clear evidence for a seasonal cycle in the adult testis, although the wide variation in the testicular histology of mature males (Fig. 3) suggests that at least some individuals may exhibit fluctuations in reproductive activity. However, there is only a slight increase in seminiferous-tubule diameter in the mating season, and testis weights and testicular and epididymal sperm densities show no seasonality. We consider that a substantial proportion of the adult male population of *G. macrorhynchus* is probably capable of successful reproduction throughout the year.

## 6.2. Female

*Neonatal body length.* Table 12 shows the body-length frequency of 36 foetuses over 109 cm and 11 calves below 170 cm. The latter have been classified into neonates and older calves. The neonates included individuals with no neonatal line in their dentine and consequently no identifiable postnatal dentine. We do not consider these individuals to be stillbirths, because they had a healed or healing umbilicus and an erect dorsal fin. The largest foetus was 146 cm in males and 144 cm in females, and the smallest postnatal individual was 136 cm (males) and 142 cm (females). We have excluded one postnatal female of 117 cm from the following analyses, because it probably represented a premature birth. No difference between the sexes in neonatal length was detected in the somewhat scanty material presently available.

The body lengths of the five neonates were 136 cm (♂), 138 cm (♂), 141 cm (♂), 142 cm (♂) and 142 cm (♀). The mean (139.8 cm) is an estimate of the mean body length at birth. We consider that any growth between the birth and death of these neonates is probably insignificant.

Another estimate of the neonatal length was obtained from the proportion of postnatal individuals in each

Table 12  
Estimation of neonatal body length

Range of body lengths (cm)	110	120	130	140	150	160	Σ
	to 119	to 129	to 139	to 149	to 159	to 169	
Number of whales in each category							
<b>Males</b>							
Prenatal	4	5	6	5	0	0	20
Postnatal, 0 years	0	0	2	2	0	0	4
Postnatal, older	0	0	0	0	1	0	1
<b>Females</b>							
Prenatal	3	4	8	1	0	0	16
Postnatal, 0 years	1	0	0	1	0	0	2
Postnatal, older	0	0	0	0	1	3	4
<b>Males plus females</b>							
Prenatal	7	9	14	6	0	0	36
Postnatal, 0 years	1	0	2	3	0	0	6
Postnatal, older	0	0	0	0	2	3	5
<b>Corrected frequency*</b>							
Postnatal	—	9	14	6	0	—	29
Postnatal, <i>n</i>	—	0	8.3	12.4	8.3	—	29
Postnatal, %	—	0	37.2	67.4	100.0	—	—

\* Corrected for under-representation of young calves relative to pregnant females (see Section 8).

length group (Table 12). The method required a correction for the abundance of foetuses and postnatal calves in the sample. As shown in Table 12, 29 full-term foetuses but only seven calves between 120 and 159 cm long have been measured. Three reasons for this discrepancy are suggested: (1) not all small calves caught were measured, (2) many of the data were obtained in May to July, before the parturition peak in August, and (3) there was probably segregation of schools with lactating cows accompanied by small calves (see Section 8). Reasons (1) and (2) certainly apply to School 9, which was processed in June and July and had many full-term foetuses. A correction was made to equalize the number of foetuses and calves in the body-length range 120–159 cm (Table 12). The relationship between body length ( $X$ , cm) and the corrected proportion of postnatal calves ( $Y$ , %) is shown by the following least-squares regression.

$$Y = 3.302X - 409.479 \quad (r = 0.999)$$

(Equation 6.1)

The mean body length at birth 139.2 cm was calculated from the equation as the length corresponding to  $Y = 50\%$ . This value is close to the above estimate (139.8 cm). The mean of the two estimates, 139.5 cm, is used below as the mean body length at birth.

**Foetal growth.** Fig. 16 shows the seasonal change in body length frequency of 132 foetuses and 39 postnatal individuals below 210 cm. Although the distribution is diffuse, the data collected between May and August inclusive showed relatively high frequencies at body lengths from 120 to 150 cm (near-term foetuses and newborn calves) and below 20 cm (recently conceived smaller embryos). The frequency distribution of foetal lengths in the period October to February was also diffuse, but the values tended to be intermediate between the two size groups of foetuses in early summer. The foetal lengths also showed a gradual increase from October

Table 13  
Monthly change in mean body length of hypothetical cohorts of foetuses and newborn calves of *G. macrorhynchus*

Month	Mean date <sup>1</sup>	Length range (cm)	<i>N</i>	Mean (cm)	S.D.
J./July	2 July	0–55	18	14.61 <sup>2</sup>	18.83
August	15 Aug.	0–75	4	39.25 <sup>2</sup>	36.55
October	13 Oct.	5–70	9	35.61	20.91
November	17 Nov.	5–85	4	48.62	31.20
December	16 Dec.	0–120	28	56.18	31.13
January	15 Jan.	15–115	17	70.97	29.38
February	14 Feb.	30–140	12	88.87	27.96
May/J.	1 June	70–145	7	120.28	27.01
J./July	2 July	65–170	32	123.79	22.61
August	15 Aug.	100–165	10	137.50	17.08
October	13 Oct.	140–195	3	171.33	25.71

<sup>1</sup> Mean date of data collection.

<sup>2</sup> Not used in Equation 6.2.

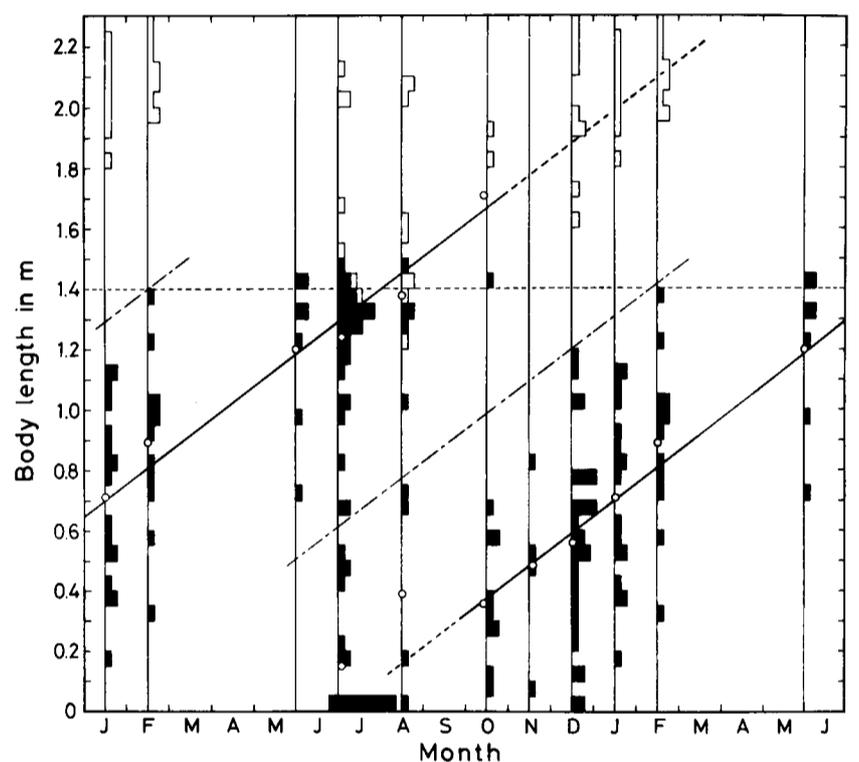


Fig. 16. Body length frequencies of foetuses (black) and neonates (white). Each open circle indicates a monthly mean of the hypothetical cohort and each thick solid line the least-squares equation fitted to the means weighted by sample size (Equation 6.2). The dotted lines are extrapolations beyond the range of the data. The dashed lines separate the two cohorts. The horizontal dotted line indicates the mean body length at birth. All data collected before July 1981 have been included.

to February. This suggests that gestation in *G. macrorhynchus* lasts more than one year, as indicated for the allied species *G. melana* (Sergeant, 1962a), and that the seasonal changes in the foetal length-frequency distribution reflect foetal growth.

The monthly body lengths of foetuses and newborn calves were divided somewhat arbitrarily into two cohorts as shown by the dashed lines in Fig. 16, and their mean body lengths were calculated (Table 13). Of the 11 means listed in Table 13, nine (excluding the smallest two) increased linearly from one October to the next. However, the mean body lengths of the smaller foetuses for both June/July and August were situated slightly above the values expected from the trend in later months. We suggest two explanations for this result:

1. the samples were taken in the mating peak and were therefore biased by an over-representation of relatively larger foetuses conceived earlier in the season;

2. errors were caused by small sample size.

The first reason accounts for the large mean value of the June/July data. Both reasons probably contribute to the August value.

The least-squares regression equation fitted to the nine means weighted by sample size (the smallest two means are excluded) is

$$Y = 0.3398X - 60.1 \quad (r = 0.99)$$

(Equation 6.2)

where  $Y$  indicates body length in cm and  $X$  the number of days from the first of January. (Fitting individual data gives a similar equation,  $Y = (0.3386 \pm 0.0425)X - 60.1$   $r = 0.82$ , (95% confidence limits of the regression coefficient are also included)). Solving Equation 6.2 gives 11 August (day 588) as the date when  $Y = 139.5$  cm (mean body length at birth) and 26 June (day 177) as the date when  $Y = 0$ . The time between the two dates is 411 days.

Hugget and Widdas (1951) suggested that foetal growth (expressed in terms of body weight) is curvilinear soon after conception and linear thereafter. They also suggested that the time from conception to the day when the extended linear-growth line cuts the axis of time ( $t_0$ ) is a function of the total gestation time, being about 10% of gestation periods lasting more than 400 days. Laws (1959) established a similar pattern for the growth of cetaceans expressed in terms of body length. He indicated that  $t_0$  of the body-length growth curve is about 90% of the corresponding value based on body weight. As we estimate the length of gestation in *G. macrorhynchus* to exceed 400 days, then  $t_0$  of the body-length growth curve will be  $0.1 \times 0.9 = 0.09$  of the total gestation time. The mean length of gestation of *G. macrorhynchus* is thus estimated as follows;

$$(588 - 177)/(1 - 0.1 \times 0.9) = 452 \text{ days or } 14.9 \text{ months}$$

(assuming 30.4 days per month)

(Equation 6.3)

The mean date of conception is thus 17 May. The 95% confidence interval for the gestation period is between 402 and 512 days.

Perrin, Holts and Miller (1977) obtained the following relationship for Delphinidae,

$$\log Y = 0.4586 \log X + 0.1659$$

(Equation 6.4)

where  $Y$  is the length of gestation in months, and  $X$  the length at birth in cm. Using this equation and 139.5 cm as the neonatal length of *G. macrorhynchus* (see above) gives a gestation length of 14.1 months, which is close to the 14.9 months estimated above.

Kasuya (1977) suggested the following relationship for delphinids;

$$Y = 0.001462X + 0.1622, \text{ (Equation 6.5)}$$

where  $Y$  indicates the daily foetal growth rate (cm) during the linear part of the growth, and  $X$  the neonatal length. The neonatal body length of *G. macrorhynchus* and the above equation suggest a foetal growth rate of 0.37 cm/day, which is similar to the growth rate of

Table 14

Mean date of parturition calculated from the body-length frequencies of foetuses and juveniles below one year of age

Length class	N	Mean date of parturition <sup>1</sup>	S.D.
Foetus < 10 cm	16	25th Aug.	70.5
Foetus 10–20 cm	7	9th Oct.	87.9
Foetus and calves, 21–155 cm	117	25th July	70.1
Total < 156 cm	140	2nd Aug.	73.3
Calves ≤ 213 cm (♀)	15	26th June	83.8
Calves ≤ 216 cm (♂)	13	5th July	83.5
Total calves	28	1st July	82.2

<sup>1</sup> Parturition season defined as 1 February to 31 January (see Section 6.2).

0.34 cm/day estimated above from the seasonal change in foetal body length.

*Parturition season based on foetal lengths.* The seasonal frequency of parturition was calculated from the mean foetal growth curve and the body-length frequencies of foetuses and newborn calves below 155 cm. The date of parturition was calculated for this purpose as the date when the foetus or calf is estimated to have passed the mean neonatal body length of 139.5 cm. The single linear growth curve obtained above (Equation 6.2) was fitted over the entire foetal size range, although it is probably strictly applicable only to foetuses more than 10 cm or 15 cm long. Because growth in the early embryonic stage is probably not linear and because our data were seasonally biased (we lack data for the months March, April and September), our estimated frequency distribution of parturition dates was subject to different biases for extrapolations based on different foetal lengths. We examined this problem by comparing the parturition seasons calculated separately for the three foetal-length groupings of under 10 cm, 10 to 20 cm and over 20 cm. The results are shown in Table 14 and Fig. 17. Although there were some differences in the mean parturition dates, all suggested that calving mainly occurs between May and November.

Ignoring these inaccuracies and combining the frequencies of the three foetal groups, we obtained the monthly distribution of births in Fig. 17. The distribution was unimodal, with a single peak in August, and reached a minimum in January. As breeding is annual, the estimated mean date of parturition will be affected by the arbitrarily chosen dates at which the annual breeding cycle is assumed to begin and end. We selected 1 February to 31 January, because this choice minimizes the variance of the dates of birth in comparison with the two other alternatives, i.e. from 1 January to 31 December or from 1 March to 28 February. The mean date of birth thus obtained was 2 August. This was not significantly different from our other estimates, e.g. 25 July estimated from the length frequency of the larger foetuses and newborn calves (Table 14) or 11 August estimated from the mean foetal growth curve and the mean neonatal length (see above). Although we have no special reason for concluding that 2 August is the best estimate, we have tentatively elected to use it below in our analysis of the seasonal change in apparent pregnancy rate.

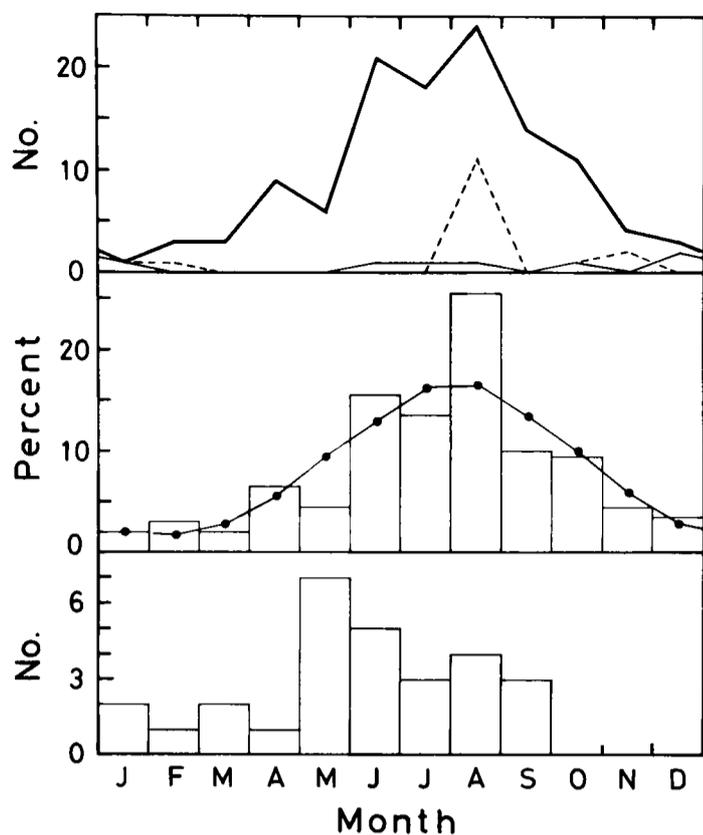


Fig. 17. Top: Estimated frequency of parturition calculated from the body lengths of foetuses and neonates between 20 and 155 cm long (thick solid line), those based on foetuses 10 to 20 cm inclusive (thin solid line), and those based on foetuses below 10 cm (dotted line). Middle: Sum of all the above parturition dates (histogram) and the normal distribution fitted to these data (closed circles and solid line). Bottom: Frequency histogram of the estimated dates of birth of neonates below one year of age calculated from the body length-age key.

*Parturition season based on the lengths of calves.* As discussed in Section 8, we consider that there is a significant segregation between pregnant females and lactating females accompanied by suckling calves. Consequently it is interesting to examine whether the parturition season estimated from calf lengths coincides with the above results based on foetal lengths. Fig. 17 shows the dates of birth of 28 calves below 214 cm (females) or below 217 cm (males) estimated using the body length - age key developed by Kasuya and Matsui (in press). The upper bounds of the lengths (213 and

216 cm respectively) corresponded to an age of about 1 year. The dates of birth were distributed from January to September, with relatively high frequency in the later part of this range. If the sample size and the over-simplifications inherent in our calculations are taken into consideration, the pattern of birth dates calculated by this method does not seem to be significantly different from that estimated from the foetal length data.

*Seasonal change of apparent pregnancy rate.* The above analyses indicate that gestation lasts more than one year and that breeding is seasonally unimodal, although some conceptions may occur in any month. This means that (1) the pregnant females in a sample may have resulted from more than one mating season (2) the proportion of pregnant females in the sample of adult females may be greater than the annual pregnancy rate (ratio of the number of females which conceive in a certain year to the total adult females in a population) and (3) the proportion of pregnant females may fluctuate seasonally as a function of the timing of parturition and conception. These problems are analysed below.

A normal distribution fitted to the predicted dates of parturition of 140 foetuses and newborn calves, assuming a mean of 2 August and a standard deviation of 73.3 days (Fig. 17), had a high chi-squared goodness-of-fit probability ( $0.7 < P < 0.8$ ) and was therefore used to compute seasonal fluctuation in the apparent pregnancy rate. The monthly probability (relative frequency) of parturition was calculated from this distribution (Table 15). Then the normal distribution was moved forward 452 days to obtain the monthly relative frequency of conceptions (Table 15). The relative frequency of pregnancies for a cohort in a given month is the difference between the relative frequency of births and the cumulative relative frequency of conceptions for that cohort at that time. For example, let us trace the history of an imaginary cohort. The first conceptions occur in November. The relative frequency of pregnant females steadily increases until the mating season is completed in the following October. Parturition starts in the second February and the number of females in that cohort which are pregnant steadily falls until the next December. Thus

Table 15

Seasonal frequency of conceptions, births and pregnancies (see also Fig. 17)

Month	Conception frequency	Birth frequency	Frequency of pregnancies			Correction factor for pregnancy rate <sup>2</sup>
			Cohort A	Cohort B	Cohort C	
November	0.017	0.059	0.017	1.000	0.050	1.067
December	0.026	0.031	0.043	1.000	0.019	1.062
January	0.054	0.019	0.097	1.000	—	1.097
February	0.081	0.017	0.178	0.983	—	1.161
March	0.131	0.028	0.309	0.955	—	1.264
April	0.155	0.055	0.464	0.900	—	1.364
May	0.166	0.096	0.630	0.804	—	1.434
June	0.141	0.132	0.771	0.672	—	1.443
July	0.107	0.162	0.878	0.510	—	1.388
August	0.066	0.165	0.944	0.345	—	1.289
September	0.033	0.136	0.977	0.209	—	1.186
October	0.023	0.100	1.000	0.109	—	1.109
Total	1.000	1.000	—	—	—	—

<sup>1</sup> All events are assumed to occur in the middle day of the month.

<sup>2</sup> Required to compensate for the seasonal change in the apparent pregnancy rate due to the 14.9-month gestation period and seasonality of breeding.

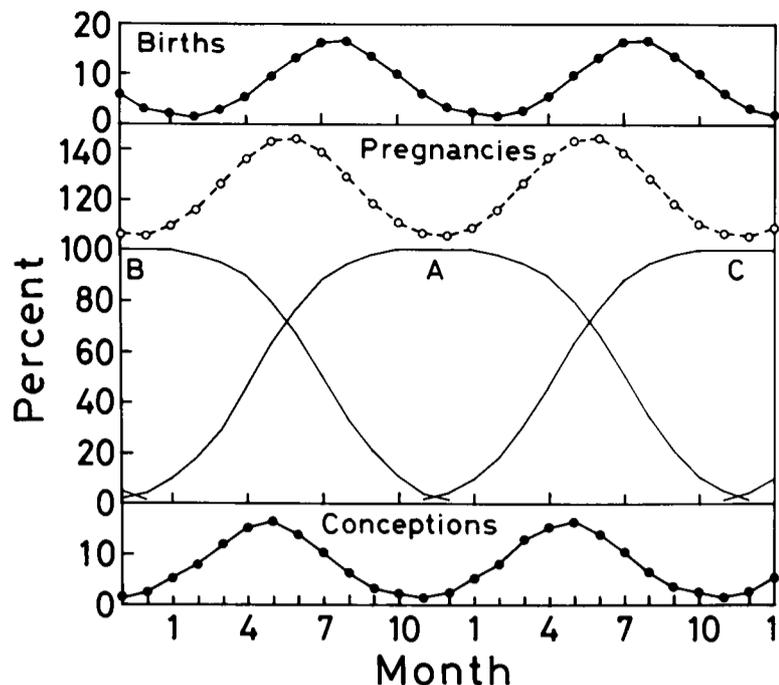


Fig. 18. Hypothetical seasonal frequencies of conception (bottom) and birth (top). Middle indicates frequencies of pregnancies for cohorts of three successive years (A, B and C), and the seasonal change of pregnant females (sum of the cohorts) expressed by open circles and dotted line.

it take two years and two months to complete this cycle. However, as the population is continually cycling, the pregnant females in the population in any one month represents two or three mating seasons (cohorts A, B and C in Table 15 and Fig. 18). Accordingly, the monthly abundance of pregnant females in a population (apparent pregnancy rate) is obtained by totalling the three cohorts for each month. The apparent pregnancy rate in June is thus 1.443 times higher than the annual pregnancy rate, whereas the corresponding figure for November is only 1.067 times the annual pregnancy rate. These figures can be used to estimate the annual pregnancy rate based on seasonally biased samples.

Table 16 compares the apparent pregnancy for each month estimated from samples and those estimated above. The two sets of figures show no correlation ( $r = 0.35$ ), and the regression coefficient is not significantly different from zero ( $T$ -test,  $0.5 < P < 0.7$ ). We consider that this is caused by the small sample size and the wide variation between schools in the proportion of pregnant females.

**Conclusion.** We conclude that breeding in this population is diffusely seasonal, with a single peak of

conception in April/May and of parturition in July/August. Gestation on the average lasts for 452 days. These figures suggest that the proportion of adult females which are pregnant fluctuates seasonally, ranging from about 107% (December) to about 144% (June) of the annual pregnancy rate, even though this pattern was not confirmed by the seasonal changes in pregnancy rate observed in our sample. However, the seasonal pattern of female reproduction reported here does coincide with the seasonal change in the abundance of nonpregnant females having a corpus luteum of 'ovulation' and with the seasonal change in the diameter of Graafian follicles in immature and lactating females as discussed by Marsh and Kasuya (1984).

## 7. LACTATION AND WEANING

### 7.1. Identification of lactation

The lactating female was identified visually by pressing the mammary gland externally and then cutting the gland with a knife. Colostrum was distinguished from ordinary milk. When a dense or thin brownish fluid was found in the lumen of the gland, it was recorded, but not as milk. The substance identified as milk in the present study had a texture like cow's milk and a colour varying from creamy white to a distinct green. The intensity of the green tinge is not dependent on the apparent quantity of milk present in the mammary gland or on the length of time between death and necropsy. Processing and subsequent biological examination of these whales were usually carried out within one hour of death, or rarely after 10–15 hours after death by drowning. The time between the drive and the slaughter does not seem to influence milk colour, because the proportion of lactating females secreting green milk in individuals processed the day after the drive did not differ from that for animals kept alive for more than one week (School 9). However, there is an indication that the occurrence of green milk is a seasonal phenomenon. The proportion of lactating whales secreting milk with some green tinge was high from February to October (Table 17). We suspect that the occurrence of green milk may depend on diet.

### 7.2. Analyses

We estimated the length of lactation by four different methods, (1) direct observation of stomach contents, (2)

Table 16  
Seasonal variation in the reproductive status of all adult females sampled

Month	School no.	No. of adult females				$\Sigma$	CP <sup>1</sup>	APR <sup>2</sup>
		Preg.	P. and L.	Lact.	Rest.			
January	7, 11	5	0	5	13	23	1.097	0.217
February	12, 16, 22, 23	5	0	17	22	44	1.161	0.091
May/June	24	7	0	8	8	23	1.439	0.304
June/July	9, 10	40	1	19	39	99	1.416	0.414
October	13	7	0	8	7	22	1.109	0.318
December	14, 15, 17, 18	26	0	17	29	72	1.062	0.361
$\Sigma$	14 schools	90	1	74	118	283	—	0.322

<sup>1</sup> Correction factor for the overlap of pregnancies of animals from different cohorts (see Fig. 17 and Table 15).

<sup>2</sup> Apparent pregnancy rate, (P. + P. and L.)/Total adult females.

Abbreviations: preg.: pregnant; P. and L.: simultaneously pregnant and lactating; lact.: lactating; rest.: resting.

Table 17

Seasonality of females secreting green milk in *G. macrorhynchus*

Month	School no.	No. lact. females	Green milk (%)
January	7, 11	5	20.0
February	12, 16, 23	17	76.5
June/July	9, 10	17	82.5
October	13, 25, 26, 27	16	68.8
December	14, 15, 17, 18	17	0.0
$\Sigma$	—	72	54.2

Abbreviation: lact. = lactating.

comparison of the number of lactating females and the age of the corresponding number of juveniles caught at the same time, (3) computing the age difference between the greatest age at which a female was estimated to give birth and the age of all lactating females older than this, and (4) the ratio of the numbers of lactating females and pregnant females. As method (4) involves estimation of the number of pregnant females, we will consider it separately in Section 8. The results and deficiencies of the first three methods are discussed below.

*Method 1. Age at which calf starts taking solid food*

This is based on the direct evidence of the presence of solid food and/or milk in the stomach. Since the visual detection of a small amount of milk mixed with solid food is difficult, this method gives reliable information on the timing of the start of taking solid food rather than on the completion of weaning. All available data are shown in Table 18 together with corresponding observations on tooth eruption.

Eruption of the upper teeth started at between 0.25 and 0.75 year of age (body length of about 160 to 207 cm). Although eruption of the lower teeth tended to start after that of the upper teeth, the difference in timing was small. By the age of 0.75 years (body length of about 211 cm), all individuals had some erupted teeth in both jaws.

The stomach contents of eight small calves were examined. The smallest, 180 cm in body length and 0.5 year old, contained the remains of solid food, but no milk was detected. The oldest individual identified with milk in its stomach was 272 cm long and 2.75-years old. (Squid beaks were also present.) Records of two unidentified older suckling calves were obtained from School 14. We found two stomachs containing milk and squid remains in a pile of viscera from 23 individuals of this school processed on the same day. The other nine stomachs contained squid remains only. Although the suckling

Table 18

Information on tooth eruption and weaning in *G. macrorhynchus*

Sample no.	Body length (cm)	Sex	Age <sup>1</sup> (years)	Tooth eruption status	Stomach contents <sup>3</sup>
9-177	136	M	0 (0)	Not erupted	—
5-6B	138	M	0 (0)	Not erupted	—
5-4B	141	M	0 (0)	Not erupted	—
4-7A	142	F	— (0)	Not erupted	—
9-119	142	M	0 (0)	Not erupted	—
1-15	154	M	0.13 (0.11)	Not erupted	—
17-46	163	F	0.25 (0.18)	Several in up. and one in lower jaws	—
10-18	167	F	— (0.22)	Not erupted	—
15-1	170	F	0.50 (0.26)	One in each rami of upper jaw, none in lower jaw	—
7-20	180	F	0.50 (0.38)		Shrimps and squid beaks
13-19	182	M	0.25 (0.40)	Not erupted	—
13-20	190	F	0.25 (0.50)	Few in upper jaw, none in lower jaw	—
12-20	197	F	— (0.59)	Erupted in both jaws	Squid beaks (II)
12-19	207	M	0.75 (0.75)	Only upper teeth erupted	Squid beaks (II)
15-35	211	F	0.75 (0.91)	Erupted in both jaws	—
16-26	235	M	2.10 (1.70)	Erupted in both jaws	—
16-27	258	M	3.50 (2.75)	Erupted in both jaws	—
24-27	263	F	3.25 (3.9)	Erupted in both jaws	Squid beaks (I)
24-26	271	M	2.25 (4.0)	Erupted in both jaws	Squid beaks (I)
24-28	272	F	2.75 (4.5)	Erupted in both jaws	Milk (I) and squid beaks (II)
14-? <sup>2</sup>	≥ 258	—	≥ 2.5	—	Milk and squid beaks (I)
14-? <sup>2</sup>	≥ 258	—	≥ 3.0	—	Milk and squid beaks (I)

<sup>1</sup> Ages estimated from body length given in parentheses.<sup>2</sup> The stomachs from eleven whales over 258 cm and over 2.5 years were examined (see Section 7.2, Method 1). Individual whales not identified.<sup>3</sup> Numeral indicates stomach compartment.

individuals were not identified, the youngest individual in the school was 2.5 years old and the second youngest 3.0 years. (Both had body lengths of 258 cm.) These data indicate that calves of *G. macrorhynchus* start taking solid food at between 0.5 and 1.0 year of age, the time when the teeth start to erupt, and that some calves continue to take both solid food and milk until the age of at least 3.0 years. Sergeant (1962a) estimated that *G. melaena* starts taking solid food at a similar age, 6–9 months.

#### Method 2. Age at which weaning is completed

This method is based on the comparison of the number of lactating females and the age composition of juveniles in a school, making the following assumptions: (1) *Each lactating female is nursing one calf at the time of her death.* If a female adopts a calf after the loss or weaning of her own, this will not cause error in estimating of the length of *suckling*. However, in this case, the calculated length of *lactation* will not be correct, the direction of bias depending on the age difference between the adopted and natural offspring. (The possibility of communal nursing will be discussed later.) (2) *There is no suckling calf older than any weaned calf in the same school.* This assumption may not be correct. The age of weaning is probably influenced by (a) individual variation in the behaviour of the cow or calf and by (b) the age of the cow. Although this assumption may underestimate individual variation in weaning age, it should not cause a large bias in the mean age. (3) *Both mother and calf are caught together without the loss of either during the drive.* A calf may not be able to swim as fast as its mother and may be lost if the driving is done too fast. This will cause an over-estimation in the age at weaning. However, a school of *G. macrorhynchus* which is being driven is usually small for the three to five driving boats involved, and the extent of the school can be seen from all boats, decreasing the chance of losing individuals. Although only schools which (in the fishermen's opinion) included the whole group were used in the following analysis, the possibility of loss has to be carefully examined when we compare these results with those obtained by other methods.

Results of the analysis using this method are shown in Fig. 19. The weaning status of two calves in school 10 could not be determined, because the sex and growth stage of one individual were unknown. Similarly, it is possible to say only that there were at least six suckling calves in school 12, because the reproductive status of three adult females was not known. These assumptions, applied to School 23, suggested that the oldest suckling individual was a 12.5-years old pregnant female. We find this conclusion difficult to accept without further evidence, even though lactating Steller's sea lions (*Eumetopias jubatus*) are known to suckle occasionally from another lactating female (Pitcher and Calkins, 1981). Accordingly, we have added a rider to our second assumption, i.e. that sexually-mature individuals shall be assumed to be completely weaned. If this rider is applied, a 15.5-year-old histologically-immature male in School 23 is classified as suckling instead of the 12.5-year-old pregnant female, and a 13.5-year-old immature male in School 12 is classified as suckling instead of a 11.5-year-old pregnant female. (However, the age of the oldest suckling calf in School 12 is not changed by this process). Our cumulative analysis of 12 schools is summarized at the

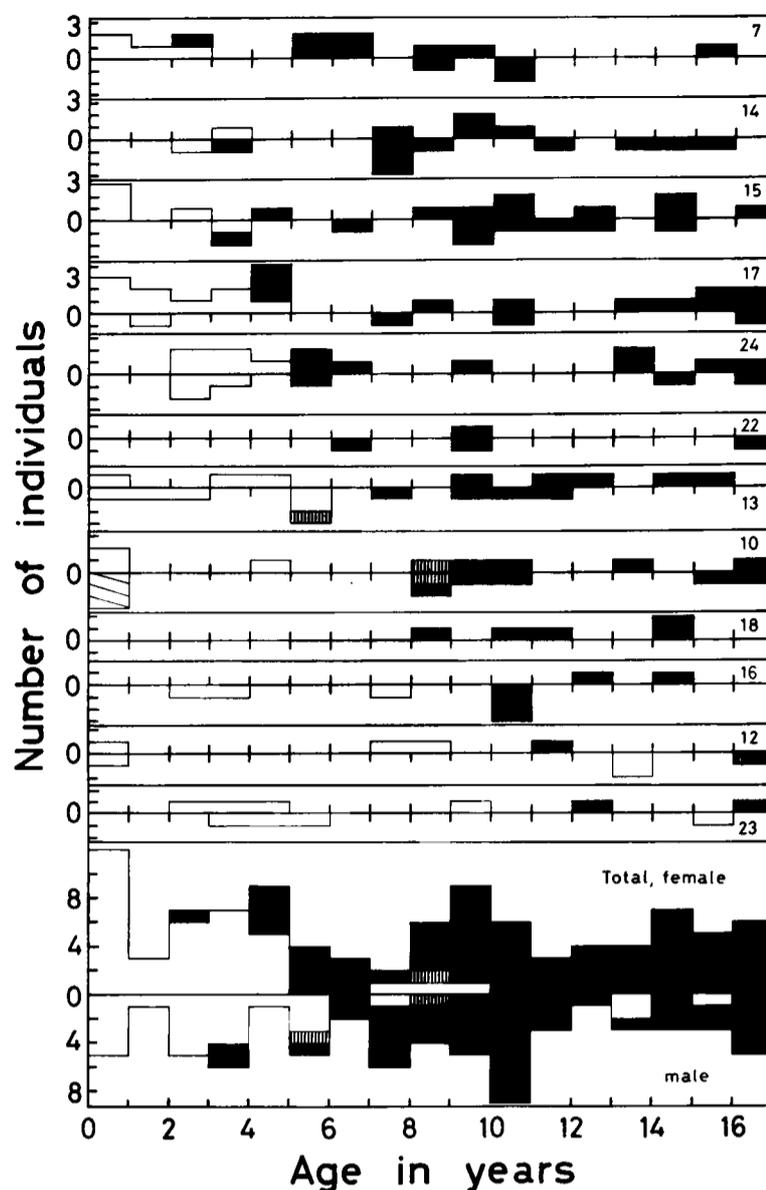


Fig. 19. Estimation of weaning age: the number of lactating females and the ages of juveniles in each school are compared. The number of the school is indicated on the right. The frequency histogram of the age distribution of females in each school is situated on top of the line; that for males is on the bottom. Code. White: presumed suckling calf; black: presumed weaned individual; vertical stripe: uncertain; diagonal stripe: sex unknown. For full data concerning these schools see Table 36 and Fig. 27.

bottom of Fig. 19. The youngest weaned calf appeared at 2.0 years, but suckling calves were abundant until the age of 6.0 years. The four calves apparently suckling when between seven and 10 years of age were from three different schools. Accordingly, we conclude (without any direct evidence) that some precocious calves complete weaning by the age of 2.0 years, but that a few calves continue to suckle until the age of 10 years.

The three immature males, from two schools, classified as suckling at the ages of 13.5 and 15.5 years were unexpected. The alternative explanation that smaller calves were lost during the drive necessitates assuming the loss of two suckling calves out of the six initially present in School 12 and one calf out of the eight in School 23. The sea state at the time of these captures did not differ from the usual calm conditions needed for driving. We consider that our conclusion that some calves suckle for up to 13 to 15 years is probably valid, especially as it is supported by the result of our third method of estimating the length of lactation (see below). Using the chemical identification of lactose in stomach contents, Best (1979) verified that some male sperm whale calves may suckle until they are 13 years old.

We examined the linear relationship between the mean

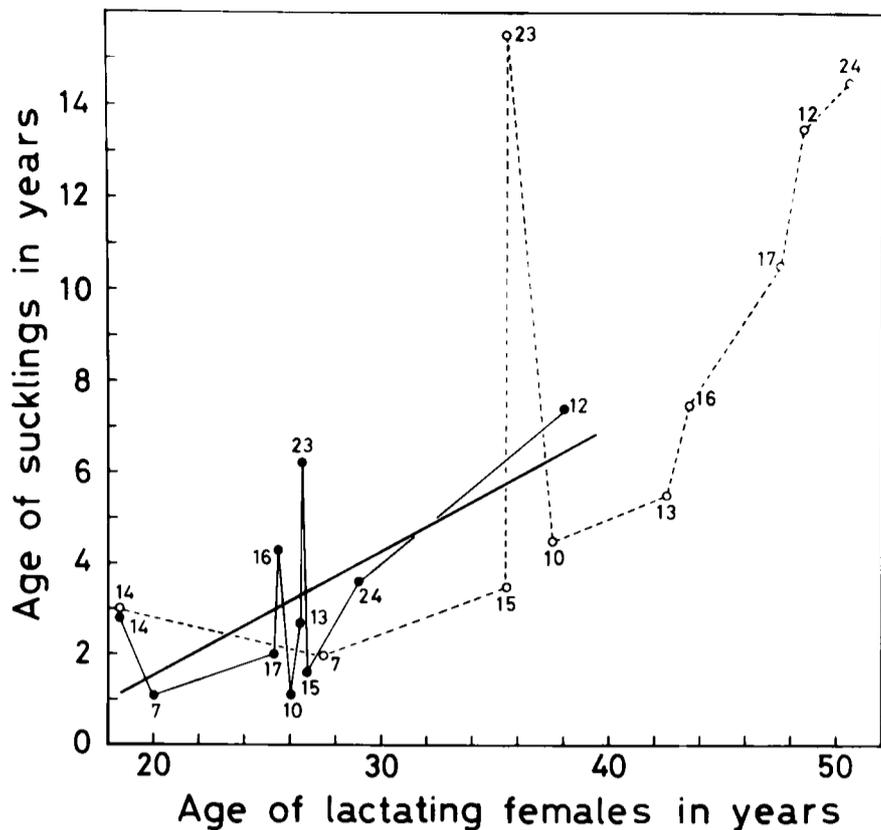


Fig. 20. Mean age of lactating females plotted against that of the probable suckling calves in the same school obtained by the second method (matching numbers of lactating cows and calves, Section 7.2) (closed circles and solid line). The age of the oldest suckling calves estimated either by the second method or third method (age of lactating cow older than oldest pregnant female, Section 7.2) has also been plotted against the age of oldest lactating cow in the school (open circles and dotted line). The thick solid line is the linear relationships between the mean age of the lactating females in a school and the mean age of the calves in the same school (Equation 7.1). Numerals indicate school number.

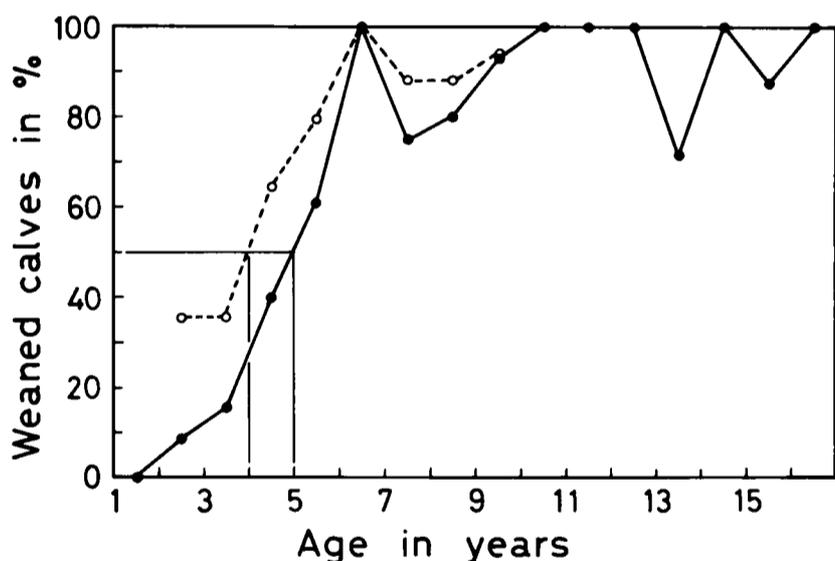


Fig. 21. Estimation of age at completion of weaning. The estimated proportion of weaned individuals in the total number of immature whales plotted against calf age. The closed circles and solid line indicate the figures calculated from Fig. 19, and the open circles and dotted line the corresponding figures assuming that weaned calves segregate.

age of the lactating females in each school ( $X$ , years) and the mean age of the calves in the same school ( $Y$ , years) which we classified as suckling using the assumptions outlined above. The relationship is expressed by the equation,

$$Y = 0.273X - 3.89, \\ r = 0.67 \text{ (Fig. 20)} \quad \text{(Equation 7.1)}$$

The regression coefficient is significantly different from 0 ( $0.02 < P < 0.05$ ).

For each school, the age of the oldest suckling calf estimated by this method or by the third method (see below) was also plotted against the age of the oldest lactating female (Fig. 20). There are indications that older suckling calves were caught together with older lactating females, suggesting that older females may nurse their calves longer than do younger cows.

The analysis of calf age and the proportion of weaned calves in Fig. 21 is based on data in Fig. 19 and two alternative assumptions: (1) all the weaned calves remain in the mother's school, (2) there is no calf mortality below the age of 10 years, the differences between the observed frequencies of 0 to 1.0-year-old (17 individuals) and of other age groups over 2.0 years (see Fig. 19) being caused by segregation of the weaned calves. The former assumption gives 5.0 years as the age at which 50% of the calves have completed weaning and the latter an age of 4.0 years. The former assumption also suggests that weaning usually occurs between the ages of 3.5 and 5.5 years; and the second method at ages between 2.5 and 4.5 years.

We anticipate that there could be two kinds of segregation between weaned and suckling calves. (1) The segregation of *schools* which contain high numbers of either weaned or suckling calves. This case is not considered here, because we are analysing only mother-calf pairs in each school, but it is considered below (see Section 8). (2) In addition, it is possible that weaned calves segregate from their mother's school. Although such segregation is considered to occur in the western North Pacific populations of spotted (*Stenella attenuata*) and striped dolphins (*S. coeruleoalba*) (Kasuya, 1972; in press; Kasuya, Miyazaki and Dawbin, 1974; Miyazaki and Nishiwaki, 1978) and in the sperm whale (Best, 1979), there is no evidence for this behaviour in the long-finned pilot whale (Sergeant, 1962a) or in the killer whale pods which are under regular observation off Vancouver island (Bigg, 1982; Balcomb, Boran and Heimlich, 1982). The similarity between the breeding behaviour and school structure of short-finned pilot whales and killer whales suggests that weaned calves may not segregate in *G. macrorhynchus* to the same degree as in spotted and striped dolphins. We therefore suggest that weaning usually occurs between 3.5 and 5.5 years of age.

### Method 3. Lactation in old females

This method is based on the age difference between the estimated age of last parturition and the ages of older lactating females. A defect of this method is the uncertainty that surrounds the ages of last parturition and the cessation of the subsequent lactation on a population basis. As outlined in Section 5, although the oldest age at parturition indicated by the pregnant females in our sample was 35.5 years, the age of the oldest females with a corpus luteum of 'ovulation' was 39.5 years. This suggests that conception followed by parturition and lactation may occasionally occur in animals up to 40 years old. On the other hand, many females probably cease to bear calves between the ages of 29.5 and 35.5 years (Marsh and Kasuya, 1984). However, we decided to use this method because: (1) a larger sample may find older pregnant females, but it may also find older lactating females, causing only a limited change in the result, and (2) the length of lactation

Table 19  
Length of lactation after oldest estimated parturition

Sample no.	Age (years)	Female			Length of lactation after age 35.5 (years)	Maximum age and sex of sucklings in the school		Female Estimated age at last parturition <sup>3</sup>
		Number of corpora				Calculated using		
		'CLO'	Medium CA	Old CA		Method 2 <sup>1</sup>	Revised Method 2 <sup>2</sup>	
24-14	50.5	—	—	7	15	4.0 (♀)	14.5 (♂)	36
12-3	48.5	—	ovaries pathological	—	13	≥ 13.5 (♂)	—	35
17-41	47.5	—	—	7	12	4.25 (♀)	10.5 (♂)	37
9-47	45.5	—	—	—	10	—	—	—
12-11	43.5	—	—	10	8	≥ 13.5 (♂)	—	30
16-19	43.5	—	—	16	8	7.5 (♂)	—	36
12-12	42.5	—	1	10	7	8.25 (♀)	—	34
13-10	42.5	—	2	11	7	5.5 (♂)	—	37
9-25	41.5	—	—	—	6	—	—	—
13-31	40.5	—	—	13	5	5.5 (♂)	—	35
10-15	37.5	1	1	4	2	4.5-8.5	—	—
12-7	36.5	—	1	8	1	7.0 (♀)	—	29
Mean	43.4				7.83			34.3

<sup>1</sup> Based on the comparison of the number of lactating females and the age composition of juveniles in the school assuming that suckling calves are always younger than weaned calves.

<sup>2</sup> Based on revised assumption that suckling calves are not always younger than weaned calves (see Section 7.2, Method 2).

<sup>3</sup> Female's age minus age of suggested suckling calf.

Abbreviations: 'CLO': corpus luteum of 'ovulation'; CA: corpus albicans. See Marsh and Kasuya (1984) for descriptions of medium and old CA. No young CAs were observed.

estimated by this method is not affected by the segregation of calves or by a sampling bias in estimating the pregnancy rate.

Assuming that each of the 12 'old' lactating females (Table 19) had its last calf at 35.5 years, we have estimated the length of the last lactation of each female as the difference between its age and 35.5 years. The 95% confidence interval of each of these estimates is between  $\pm 2$  and 2.5 years. (The coefficient of variation of each age reading is about 2%; see Kasuya and Matsui (in press).) Table 19 compares each of these 10 estimates of the length of the last lactation with the age of the oldest suckling calf in the same schools (estimated by Method 2 above). In six instances there was good agreement between the two methods. Two of the individuals for which there was a discrepancy were respectively 37.5 years old (No. 10-15) and 35.5 years old (No. 12-7). The discrepancy is eliminated if we assume that they had been nursing calves born when they were about 30 years old (Fig. 19).

Results for whale No. 24-14 (50.4 years old) were anomalous, as the oldest suckling calf estimated by Method 2 (above) was aged four years. This suggests that either (1) our identification of the 'oldest suckling calf' in this school was incorrect, i.e. the assumption that suckling calves are always younger than weaned calves in the same school is invalid, or (2) No. 24-14 was nursing a foster calf. We have no evidence pertinent to the second hypothesis. If we accept the first alternative, Fig. 19 suggests that a 14.5 year old male might have been suckling instead of one of the eight calves less than five years old. (The three females in the school between nine and 14 years old were pregnant.) The testis of this male was at the late-maturing stage (weight of testis was 230 g and 60% of the tubules were mature), and no

spermatozoa were detected in its epididymis. Thus this male had not yet matured. If this male was indeed the calf of No. 24-14, this female would have last given birth at 36 years of age.

Results for whale No. 17-41 (47.5 years) were similarly anomalous (Fig. 19). In School 17 the oldest suckling calf identified by Method 2 (above) was only 4.25 years old, while two females between the ages of 8 and 11 years were pregnant. However, if the 10.5 year old immature male was the calf of No. 17-41, this whale would have last given birth when 37 years old.

### 7.3. Discussion

Milk as a major source of nutrition may be essential for odontocetes for only the first few months of life. In aquaria, bottlenose dolphins have been variously observed to start taking solid food at 3.5 months (Tavolga, 1966), 205 days (6.7 months) and 195 days (6.4 months) (Nakajima, Takahashi, Ogura and Sawaura, 1963) or 9 months (Tavolga and Essapian, 1957), and *Neophocaena phocaenoides* at eight months (T. Kataoka, pers. com. 1982). Although suckling was considered to be infrequent by the time a *T. truncatus* calf was between 12 and 16 months old, the mother's mammary gland was still active at the time of her death when the calf was 2.5 years old (Nakajima, 1963). We suggest that the minimum requirement for suckling as a *nutritional* source may be about a year, by which time a calf may have also gained the minimum skills required for independence, e.g. *T. truncatus* calves do not establish the frequency modulation and stereotypy of their whistles (characteristics common to all adult bottlenose dolphins) until they are about a year old (Caldwell and Caldwell, 1979). Weaning

is usually completed by eighteen months, but the mother-calf bond is retained for more than two years if the mother is not pregnant (Tavolga, 1966).

Brodie (1969) observed that four species of odontocetes, i.e. sperm whale, white whale (*Delphinapterus leucas*), long-finned pilot whale and bottlenose dolphin, had prolonged nursing periods (of about two years) compared to those of mysticetes. He postulated that lengthy lactations were related to training period required by these animals with their complex social structure. The nursing period of the common porpoise (*Phocoena phocoena*) has been estimated at eight months (Mohl-Hansen, 1954) and that of *Pontoporia blainvillei* at less than nine months (Kasuya and Brownell, 1979). A nursing period of about one year was estimated for eastern tropical Pacific *Stenella attenuata* (Perrin, Coe and Zweifel, 1976) and *S. longirostris* (Perrin *et al.*, 1977). In the western North Pacific, a lactation period of about two years was estimated for *S. attenuata*. For the more heavily exploited *S. coeruleoalba*, Kasuya (in press) has demonstrated a decrease in the lactation period from 2.64 years in 1955 to 1.59 years in 1977. Both the lactating and resting periods are considered to increase with age in these populations of *Stenella* species. A wide individual variation of up to five years in the length of the nursing period was suggested for *S. attenuata* by Kasuya, Miyazaki and Dawbin (1974). These results suggest the potential both for a relatively extended lactation period and for considerable flexibility in lactation length in accordance with the physiological or social requirements of the population. Although the mean lactation length for the sperm whale is believed to be about two years (Ohsumi, 1965; Best, 1968), there are indications of large individual variation extending up to 7.5 years for female calves and up to 13 years for male calves (Best, Canham and MacLeod, 1984). Longer suckling may serve to maintain the cow-calf bond while the calf improves its communicational ability under the protective and perhaps educational care of its mother (Brodie, 1969).

Of the three methods used in this study to estimate length of *lactation* or *weaning age*, the analysis of stomach contents (Method 1) provides firm data on the start of taking of solid food (0.5 year) and verification of suckling up to 3.0 years.

School analysis (Method 2) is based on an unconfirmed assumption that each calf suckles from its own mother. Although this is generally accepted for most mammals, a captive *Neophocaena phocaenoides* calf has been observed to occasionally suckle from a non-lactating adult female while it was suckling from its own mother. Also in captivity, another orphan calf of the same species was adopted by a lactating female soon after the abortion of her own near-term foetus (T. Kataoka, pers. comm. 1982). This behaviour was not observed on all possible occasions in the aquarium and might be due to crowded conditions. However, communal nursing has been reported in several species of wild land mammals (see Gubernick, 1981 for details). The third method of analysis (*lactation length* in old females) is not affected by communal nursing.

Our results using these three methods were in good agreement. The result of the fourth method (mean lactation length and its increase with age of cow, see Section 8) were similar to those produced by the second

method. We consider this indicates that communal nursing is uncommon in *G. macrorhynchus* and that the extended lactation period of the older females will be attributable, in most cases, to the suckling of their own calves. The last calf of a female seems to be sometimes nursed for a very long time, possibly up to 13 or 15 years.

The rapid increase in mean lactation length after 24 years of age is partially related to the lengthy lactation by some post-reproductive females, as discussed in Section 8. An increase in mean nursing period with increasing maternal age has been observed in four stocks of *Stenella* (see above) as well as *G. macrorhynchus*. The occasional long nursing periods suggested for *G. macrorhynchus* are similar to those reported for the sperm whale (Best *et al.*, 1984). Although we are not certain whether the maximum duration of suckling in *G. macrorhynchus* is longer for male than female calves (as in the sperm whale), we suggest that this result is highly probable, because both species exhibit a parallel marked difference in the age of sexual maturation of males and females (Best, 1970).

Once lactation is established, it will be maintained by the stimulus of regular suckling. However, there are at least two requirements for this. (1) The calf has to maintain a close relationship with its mother, and (2) the mother has to continue to allow the calf to suckle. Although suckling may inhibit the onset of estrus it clearly does not always prevent estrus or subsequent conception in *G. macrorhynchus*, since three simultaneously pregnant and lactating females were observed in our sample. As we have no information on the effect of the behaviour of the mother at estrus on her interaction with her calf, we do not know whether this tends to terminate suckling behaviour. However, by analogy with other mammals, lactation will almost certainly be terminated towards the end of pregnancy at the latest. In domestic cows, *Bos taurus*, for example, pregnancy has no measurable effect on milk production before the fifth or sixth month, but by eight months, production usually falls rapidly. It is, however, well known that barren cows can lactate for extended period (Lascalles and Lee, 1978). Similarly, in the case of post-reproductive females of *G. macrorhynchus*, lactation will not be interrupted by estrus or pregnancy and can continue as long as the suckling stimulus is maintained. A similar situation can occur in human societies. Lee (1980) reported that it is not uncommon for women in the !Kung tribe (an African hunter-gatherer community) to undergo menopause while still nursing.

We thus consider that the extended suckling of the last calf of post-reproductive females is the *result* of the long mother-calf bond and stable school structure, not the *cause* of that bond. A large proportion of calves are certainly weaned at a younger age, and most post-reproductive females are not lactating. The reasons for stable long-lasting school structure in *G. macrorhynchus* are considered separately below (see Section 10).

We further suggest that this extended period of maternal care is likely to be much more common in some species of odontocetes than others. We do not expect spotted and striped dolphins to have such an extended suckling period as *G. macrorhynchus*. Not only does sexual maturity occur earlier in both sexes (7-10 years) of these species, but most of the weaned juveniles

segregate from the breeding schools until puberty (Kasuya, 1972; Miyazaki, 1977; Miyazaki and Nishiwaki, 1978; Kasuya, in press). In contrast, sperm whales do not segregate into bachelor schools until after puberty at 10–13 years (Best, 1970; 1979). Thus even male sperm whales have the opportunity to suckle for many years, as observed by Best (1979).

## 8. REPRODUCTIVE CYCLE

### 8.1. Outline of reproductive cycle

We have classified adult female of *G. macrohynchus* as pregnant, lactating (defined above), pregnant and simultaneously lactating, or resting. The resting category comprises all adult females which were neither pregnant nor lactating, including the post-reproductive 'resting' females identified by Marsh and Kasuya (1984). Lactation and pregnancy usually do not overlap. Only three females (Nos. 26–8 (12.5 years), 25–38 (13.5 years) and 10–12 (34.5 years)) were simultaneously pregnant and lactating, compared with 94 pregnant, 81 lactating and 129 resting females (Schools 25, 26 and 27 included). As shown in Table 20, some of the lactating and resting females had an ovarian corpus luteum even though their uteri showed no indication of recent parturition or abortion. These females are considered to have ovulated shortly before death.

Fig. 22 compares the width of the uterine horn between females of different reproductive status. The horn width was below 3 cm in immature females. In most lactating females, the uterine width ranged from 2 to 4 cm (with no obvious contralateral size differences). However, some exceptionally large uteri of lactating females (who presumably had recently given birth) measured over 20 cm. The uteri of resting (but not recently ovulated) females exhibited slight contralateral size differences, and the upper range of widths was about 7 cm above that of most of the lactating females. This suggests that some of the resting females were killed at about the time of estrus and had slightly distended uteri as a result. The two uterine horns of one whale (No. 25–1, 28.5 years old), one of the two pregnant females in Fig. 22, measured 4.5 and 6.0 cm. Although the larger horn contained an embryonic membrane about 10 cm long, it was pathological and presumably represented a degenerating pre-implantation stage of pregnancy (see Benirschke and Marsh, 1984).

The uteri of recently ovulated, non-pregnant females were intermediate in width between those of resting females and females in early pregnancy. This suggests that the ova shed by these females were either (1) not fertilized, (2) aborted before implantation, or (3) at the pre-implantation stage. In view of the high number of ovulations per reproductive cycle (see Table 23) and the significant increase in the proportion of females having a corpus luteum of 'ovulation' at ages between 20 and 40 years (when the pregnancy rate was declining (Marsh and Kasuya, 1984)), we expect that many of these corpora had resulted from infertile ovulations. As pointed out by Benirschke, Johnson and Benirschke (1980) and confirmed by the large size of the membranes found in whale (No. 25–1) above, a small embryo in a relatively large embryonic membrane is unlikely to be missed.

Although our estimates of the length of the lactating

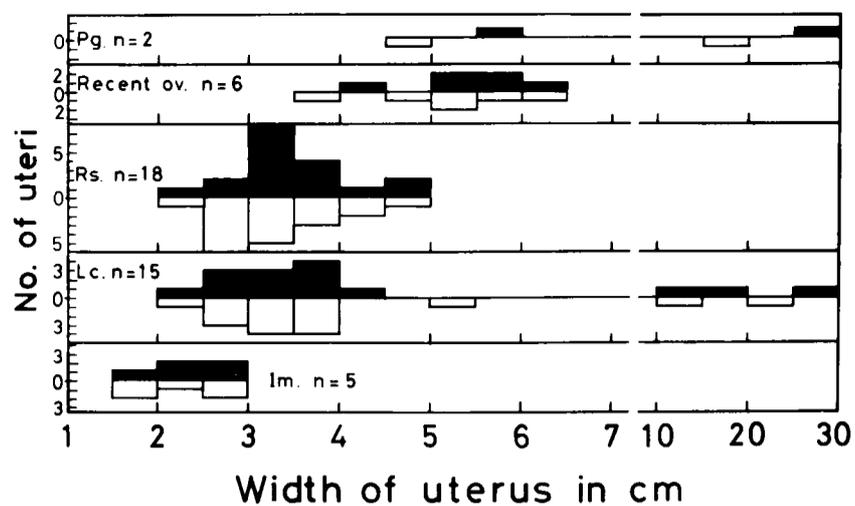


Fig. 22. The width of the uterus of pregnant (top), recently-ovulated/non-pregnant (2nd), resting (3rd), lactating (fourth), and immature females (bottom). Black squares indicate the larger horns, and white squares the smaller.

and resting periods based on a gestation period of 452 days are likely to be over-estimates, we used these values in this section because we do not know when pregnancy first becomes macroscopically visible. We presume that the length of invisible pregnancy will be less than 45 days ( $= t_0$ , estimated in Section 6). Thus the error produced by using 452 days as the length of visible pregnancy should be less than 10%.

Another error in the calving cycle estimation in Sections 8.2 and 8.3 comes from ignoring pre- and post-natal mortality and undetectable early pregnancies in the correction for overrepresented pregnant females. We do not know the resultant effect of these factors, although it is expected that they will act in opposite ways, i.e. the first will cause overestimation and the second, underestimation of pregnant females.

All the estimates below are correct to only one or at most two decimal places. However, the subsequent calculations were made on the unrounded estimates to avoid rounding-off errors. Unrounded figures have been given to aid the reader who wishes to check the calculations.

### 8.2. Mean reproductive cycle

The annual pregnancy rate and mean length of the reproductive cycle are estimated from the proportion of mature females that are pregnant, by assuming (1) that the length of each reproductive stage is proportional to the relative frequency of adult females at that stage in the sample, and (2) that the gestation period is 452 days. This method is affected by two types of biases: (1) seasonal biases in both sample collection and reproductive status, (2) the school-specific bias, i.e. the fact that the proportion of females at each reproductive stage in a school may not be representative of the proportions in the population.

If both biases are neglected, the annual pregnancy rate (APR) can be calculated from the following equation:

$$\text{APR} = \frac{P_m + PL_m}{S_m} \cdot \frac{365}{452} \quad (\text{Equation 8.1})$$

where  $P_m$  indicates the number of pregnant (but not lactating) females,  $PL_m$  the number of females pregnant and simultaneously lactating, and  $S_m$  the total number of

Table 20

Reproductive status and apparent pregnancy rate of adult females in various age classes: Schools 7, 9 through 18, 22, 23 and 24

Age class (years)	Number of whales at each reproductive stage			A.P.R. (%)
	Preg.	Lact.	Rest.	
6-9	3	0	1	75.0
9-12	12	3	5 (2)	60.0
12-15	13	3 (1)	3	68.4
15-18	9	9	3	38.1
18-21	14	6	6 (4)	53.8
21-24	14	9 (2)	5 (3)	50.0
24-27	6	9	7	27.3
27-30	7	4 (1)	8 (3)	36.8
30-33	7	4	5 (2)	43.8
33-36	1*	10 (1)	6 (1)	5.9
36-39	0	2 (1)	17 (5)	0
39-42	0	2	8	0
42-45	0	4	14	0
45-48	0	2	13	0
48-51	0	2	2	0
51-54	0	0	3	0
54-57	0	0	4	0
57-60	0	0	1	0
60-63	0	0	2	0
< 36	86	57 (5)	49 (15)	44.8
N/A	5	5	5	33.3
Total	91	74 (6)	118 (20)	32.2

\* Pregnant and simultaneously lactating.

Non-pregnant females with a corpus luteum of 'recent ovulation' are given in brackets.

Abbreviations: Preg.: pregnant; Lact.: lactating; Rest.: resting; A.P.R.: apparent pregnancy rate; N/A: age estimate not available.

adult females whose reproductive status was determined. Using this Equation 8.1 and the data for 283 adult females in 14 schools (Table 20), the annual pregnancy rate not corrected for other biases is given as

$$\frac{90 + 1}{283} \cdot \frac{365}{452} = 0.2597$$

However, if the sample is seasonally biased, it is better to estimate the annual pregnancy rate as follows;

$$APR = \frac{\sum ((P_m + PL_m)/C_m)}{\sum S_m} \quad (\text{Equation 8.2})$$

where  $m$  indicates month and  $C_m$  the proportion of mature females that are pregnant in each month (last column of Table 15). The other abbreviations are as in the first equation. The same data and this equation give the corresponding value as

$$\frac{72.77}{283} = 0.2571$$

The figures obtained by the two methods are similar. This may be partially because (1) the present sample covered nearly all seasons of the year and (2) the between-school variation in the apparent pregnancy rate was almost large enough to mask the seasonal change. We used the first method to calculate the annual pregnancy rate below, solely because of the simplicity of calculation. In view of the apparent unimportance of the correction for seasonality, we have ignored the seasonal bias in the number of lactating females, because we expect the

seasonality of weaning to be more diffuse than that of mating or parturition.

A school-specific bias is indicated by Table 21, which shows that the number of calves below the age of 452 days (equivalent to the length of gestation) was only 20 individuals, in contrast to the estimate of 60.7 pregnant (plus pregnant and simultaneously lactating) females in the sample (adjusted to include females of unknown status, see Table 21). This difference seems unreasonable even assuming a high neonatal mortality rate and the inaccuracies discussed in Section 6.2. The number of calves of suckling size (not necessarily below the age 452 days) missing in this comparison is only two, in School 11 (see Fig. 28). Among several hypotheses tested, the assumption that pregnant females were over-represented relative to the other two reproductive stages of adult females was the only hypothesis that did not contradict the other biological results obtained in this study.\*

For this reason, our analysis of the reproductive cycle is based on this assumption. The other hypotheses tested and rejected are detailed below (Section 8.4).

The data from School 9 are initially excluded from the following analyses because females below 15 years of age are under-represented in our sample from this school (see Section 9.4). However, they are included in the final calculation with appropriate corrections (see Section 8.3).

If pre- and post-natal mortality is ignored,  $P + PL$  should equal the number of calves below the age of 452 days, which is 20.

$$PL = 1 \therefore P = 19.0$$

$$PL + L = 1 + 63.5$$

$$R = 84.8$$

where  $P$  = No. pregnant,  $PL$  = No. pregnant and simultaneously lactating,  $L$  = No. lactating,  $R$  = No. resting (All figures have been adjusted to include adults of unknown reproductive status in Table 21). The mean length of each reproductive stage in years is calculated from

$$\frac{X}{P + PL} \cdot \frac{452}{365} \quad (\text{Equation 8.3})$$

where  $X$  indicates the number of females at the reproductive stage being considered (see Table 21).

The mean calving interval for all adult females (10.42 years (excluding School 9) or 10.13 years (with School 9)) is the sum of the length of each stage. Inclusion of School 9 does not affect the length of the resting period but shortens the mean lactation length (sum of periods of

\* Footnote: After completing the present analysis, Kasuya examined 178 short-finned pilot whales caught in six drives at Taiji. The reproductive status of the adult females was as follows:

School	Date	Preg.	PL	Lact.	Rest.	Total	Missing
25	Oct. '81	2	1	0	6	9	1 or 2
26+27	Oct. '81	1	1	7	4	13	10% (26)
27	Oct. '81	—	—	—	—	—	80% (27)
28	Jan. '82	2	0	6	4	12	0
29	Oct. '82	4	1	10	7	22	3
30	Oct. '82	9	0	13	6	28	0
Total		18	3	36	27	84	—

The number of lactating females in these schools was about twice that of pregnant females, close to the value estimated in this study and suggesting that segregation of schools based on female reproductive status may be more apparent in the summer, e.g. School 9, than in the fall/winter.

Table 21

Estimates of mean reproductive cycle with and without corrections for sample bias and including and excluding School 9

	No. of adult females of all ages						No. of calves <sup>2</sup>
	Preg.	P. and L.	Lact.	Rest.	Unknown	Total	
<i>13 schools<sup>1</sup> (excluding School 9)</i>							
No. of whales at each stage	59	1	61	81	7	209	20
No. extrapolated to include whales of unknown reproductive status	59.7	1.0	63.5	84.8	0	209	20
% at each stage	28.5	0.5	30.4	40.6	0	100	—
With correction for sample bias							
No. of whales	19.0	1.0	63.5	84.8	0	168.3	—
%	11.3	0.6	37.7	50.4	0	100	—
Estimated length of stage (years)	1.18	0.06	3.93	5.25	0	10.42	—
<i>14 schools (including School 9)</i>							
With correction for sample bias (all adult females)							
Estimated length of stage (years)	1.19	0.05	3.43	5.46	—	10.13	—
With correction for sample bias (excluding post-reproductive females)							
Estimated length of stage (years)	1.20	0.04	2.86	2.78	—	6.88	—

<sup>1</sup> Schools 7, 10, 11 through 18, and 22 through 24.

<sup>2</sup> Calves below the age corresponding to length of gestation (female < 219 cm, male < 223 cm).

Abbreviations: Preg.: pregnant; P. and L.: simultaneously pregnant and lactating; Lact.: lactating; Rest.: resting.

lactation and lactation and simultaneous pregnancy) from 3.99 to 3.48 years.

The difference is probably caused by the low number of lactating females in School 9, i.e. 35.1% of the resting females (*P*, 31; *R*, 37; *L*, 13 individuals) compared with 76.5% (*P*, 59; *PL*, 1; *L*, 61; *R*, 81 individuals) for the other 13 schools. At this stage, we have to conclude that the estimates produced by including School 9 are better, because they are based on a larger number of samples (Table 21).

The resultant estimate of the mean *length of lactation* (3.48 years) is about one year shorter than the mean *weaning age* (i.e. the age at which the number of suckling and weaned calves were equal (Section 7.2)). Half of this discrepancy (3.99 – 3.48 = 0.51 year) can be attributed to the low number of lactating females in School 9. We attribute the remaining 0.5 year to the fact that these analyses are dealing with two different biological phenomena. The mean *length of lactation* does not distinguish lactations terminated by weaning from those terminated prematurely by death, whereas the estimation of mean *weaning age* excludes those cases and thus should be longer. The mean *length of lactation* is more relevant to our analysis of the reproductive parameters of the population; the mean *weaning age* is a better indication of juvenile growth.

*Correction for post-reproductive females:* According to the criteria of Marsh and Kasuya (their Fig. 8, 1984), 15.5% of 71 lactating females and 49.0% of 100 resting females were post-reproductive. The sample on which Marsh and Kasuya's (loc. cit.) analysis was based was almost identical with that in Table 20. Therefore Marsh and Kasuya's estimates of the proportions of post-reproductive females are used to compute the mean lactating and resting periods for reproductive females only, as follows:

$$\text{lactation} = 3.43 \times (1 - 0.155)$$

$$= 2.90 \text{ years} \quad (\text{Equation 8.4})$$

$$\text{resting period} = 5.46 \times (1 - 0.490)$$

$$= 2.78 \text{ years} \quad (\text{Equation 8.5})$$

This reduces the mean calving interval to 6.92 years.

### 8.3. Age-specific reproductive cycle

As the pregnancy rate is strongly affected by maternal age, we have also computed the reproductive cycle on an age-specific basis. The analysis requires a large sample size, and so we have included School 9 data (appropriately corrected for the under-representation of young adult females). As the inclusion of School 9 changes the ratio of the number of pregnant (plus pregnant and simultaneously lactating) females to the total number of adult females from 60.7/209 (Table 21), to 91/283 (Table 20) the correction factor  $F_1$  required if School 9 is included is

$$F_1 = (60.7/209)/(91/283) = 0.903$$

(This correction factor is needed because the correction for the seasonality of pregnancy (see Table 15) was computed excluding School 9).

Corrections are also necessary because of the sample bias resulting from the segregation of pregnant and lactating females (Section 8.2) i.e. the frequency of the pregnant females has to be decreased by

$$F_2 = 19.0/59.7 = 0.318$$

Using these correction,  $Y_t$  (the mean length of one of the reproductive stages) and  $C_t$  (the mean calving interval), both at age  $t$  years, can be calculated as follows:

$$Y_t = \frac{X_t}{(PL_t + P_t \cdot F_2) F_1} \cdot \frac{452}{365} \text{ years} \quad (\text{Equation 8.6})$$

Table 22

Linear-regression equations ( $Y = aX + b$ ) describing the relationships between the length of the various reproductive stages ( $Y$ , years) or the annual pregnancy rate ( $Y$ , %), and age ( $X$ , years)

Y variable	Age range (years)	Constants		Correlation coefficient $r$
		$a$	$b$	
Lactation period (years)	< 24	0.186	-0.95	0.68
	> 21	0.597	-11.42	0.58
Resting period (years)	< 24	0.011	1.35	0.19
	> 21	0.381	-6.30	0.72
Calving interval (years)	< 24	0.196	1.64	0.70
	> 21	0.978	-16.48	0.65
Annual pregnancy rate %	< 18	-2.077	51.65	0.82
	> 15	-0.737	31.26	0.78

$$C_t = \frac{R_t + L_t + (PL_t + P_t \cdot F_2) F_1}{(PL_t + P_t \cdot F_2) F_1} \cdot \frac{452}{365} \text{ years} \quad (\text{Equation 8.7})$$

where  $X_t$  indicates the number of whales in age group  $t$  in one of the four reproductive stages. Other notations are as above. The annual pregnancy rate for the age group of  $t$  years is calculated as  $1/C$ . The calculations are based on data from 268 adult females grouped in three-year age classes as shown in Table 20.

Table 22 details the constants of the least-squares regression equations describing the relationships between age and each of the following parameters; annual pregnancy rate, lactation period, resting period, and calving interval.

Two regressions (one for age classes < 18 years, the other for classes > 15 years) are necessary to describe satisfactorily the relationship between annual pregnancy rate and age (Fig. 23 and Table 22). According to these equations, the annual pregnancy rate falls from 30.9% at 10 years to 4.7% at 36 years. The equations over-estimate the annual pregnancy rate for whales older than 36 years, which is zero.

Females attain sexual maturity between 7 and 12 years, and few give birth before 9 years of age. After the age of 9 years, lactating females start to appear, and the proportion gradually increases with increasing age. The mean length of lactation increases from 1.8 years at age 15 years to 3.2 years at age 24 years. After this, the rate of increase of the mean length of lactation increases, so that by the time a whale is 36 years old, the mean lactation period has increased to 9.4 years.

The mean resting period is almost constant at 1.5 years in the age range below 24 years. However, as in the case of the length of lactation, the resting period increases at a faster rate after age 24 years. The mean resting period at 36 years of age is estimated to be 7.4 years.

This method is not applicable to age classes over 36 years because of the absence of pregnant females as the standard for time calibration. However, comparison of the age composition of lactating females with that of pregnant females (Method 3 in Section 7.2) shows that females which are lactating at age 35.5 years will continue lactation for an average of 7.83 years. The mean length of lactation after 36 years is, therefore, estimated as

$$7.83 - (36 - 35.5) = 7.33 \text{ years} \quad (\text{Equation 8.8})$$

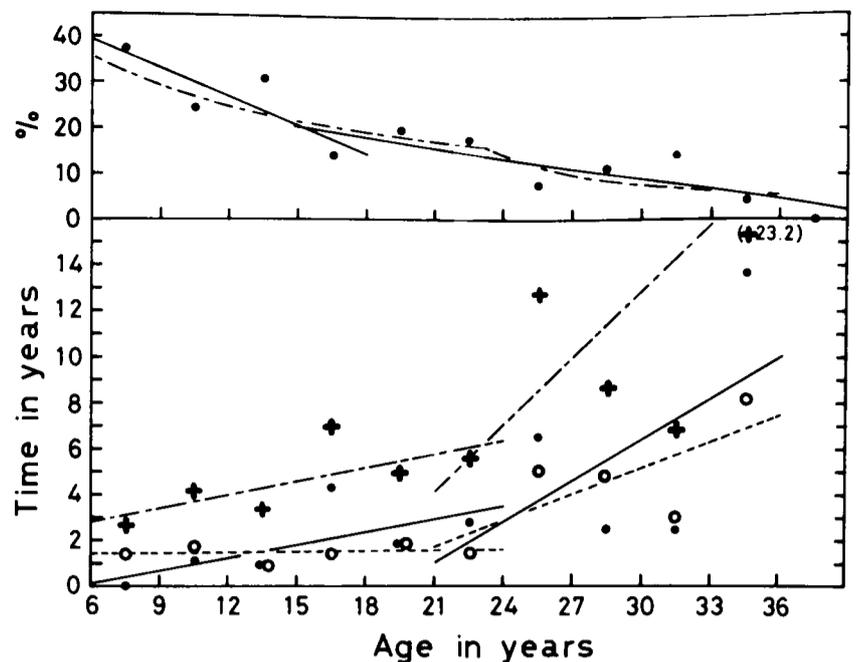


Fig. 23. Corrected age-specific reproductive parameters: annual pregnancy rate (top), mean calving interval (bottom, crosses and chain), mean length of lactation (bottom, closed circles and solid line), and mean length of resting period (bottom, open circles and dotted line). The dashed line at the top of the diagram indicates the annual pregnancy rate calculated as the reciprocal of the linear regression of mean calving interval.

An independent estimate of the mean length of lactation of females more than 36 years old is obtained from the relative proportion of lactating females younger and older than this age (Table 20). The lactation period for 58 females less than 36-years old is

$$\frac{57 + 1}{(1 + 85 \cdot 0.318) 0.903} \cdot \frac{452}{365} = 2.84 \text{ years} \quad (\text{using Equation 8.6})$$

The overall mean of the lactation period calculated for 70 individuals is 3.48 years (3.43 years (lactation period) + 0.05 years (lactation and simultaneous pregnancy)) (see Table 21). Thus we can estimate the mean lactation period ( $X$ ) after 36 years of age from the following equation:

$$2.84(57 + 1) + X \cdot 12 = 3.48 \cdot 70 \quad (X = 6.57 \text{ years}) \quad (\text{Equation 8.9})$$

This figure is close to 7.33 years, the estimate obtained independently above.

The mean resting period after the age of 36 years can also be calculated in this way. Using the data in Table 20, we can obtain the following estimate of the mean resting period for all animals less than 36 years old:

$$\frac{49}{(1 + 86 \cdot 0.318) 0.903} \cdot \frac{452}{365} = 2.37 \text{ years} \quad (\text{Equation 8.10})$$

Comparing this with the overall mean of the resting period (5.46 years), obtained from 14 schools (including School 9), we can obtain an estimate ( $X$ ) of the mean length of the resting period for the 64 females over 36 years of age using the following equation:

$$(2.37 \cdot 49) + (X \cdot 64) = 5.46(49 + 64) \quad (X = 7.83 \text{ years}) \quad (\text{Equation 8.11})$$

The mean life expectancy of a female at age  $n$  years is calculated using the following equation based on the

Table 23

 Outline of the age-specific reproductive cycle of *G. macrorhynchus* (based on data from Table 24, including School 9)

Age range (years)	6-12	12-18	18-24	24-30	30-36	≥ 36	Total
Corrected for sample bias (all adult females)							
Lactating period (years)	0.86	2.35	2.31	4.31	6.38	6.57	3.48
Resting period (years)	1.73	1.18	1.69	4.98	4.68	7.83	5.46
Calving cycle (years)	3.83	4.77	5.24	10.53	11.87	—	10.13
No. of ovulations/cycle <sup>2</sup>	2.43	2.23	1.80	2.66	2.20	—	—
Corrected for sample bias (post-reproductive females excluded)							
Lactation period (years)	0.86	2.35	2.31	4.31	4.91	0.66	2.86
Resting period (years)	1.73	1.18	1.69	4.60	3.83	1.51	2.78
Calving cycle (years)	3.83	4.77	5.24	10.15	9.51	—	6.88
No. of ovulations/cycle	2.43	2.23	1.80	—	—	—	—
Not corrected for sample bias (all adult females)							
Lactation period (years)	0.25	0.68	0.66	1.24	2.32	2.22	1.02
Resting period (years)	0.50	0.34	0.49	1.43	1.70	2.25	1.61
Calving cycle (years)	1.98	2.25	2.39	3.91	5.11	—	3.85
No. of ovulations/cycle	1.26	1.05	0.82	0.99	0.95	—	—

<sup>1</sup> For details of corrections for sample bias and School 9 see Section 8.

<sup>2</sup> Calculated as the product of the age-specific ovulation rate at the mid-point of the age range and the length of the calving cycle. The number of ovulations per year ( $y$ ) at age  $x$  years was calculated from the formula  $y = 1.008 (0.95)^x$  (Marsh and Kasuya, 1984).

Table 24

 Frequency of post-reproductive females in *G. macrorhynchus* constructed from Fig. 8 in Marsh and Kasuya (1984)

Age range (years)	Pregnant $N$	Lactating		Resting		Total	
		$N$	PRP (%)	$N$	PRP (%)	$N$	PRP (%)
With correction for sample bias <sup>1</sup>							
28-32	1.72	3	0.0	7	14.3	11.72	8.5
32-36	1.44	11	18.2	8	25.0	20.44	19.6
36-40	0	1	0.0	17	35.3	18.00	33.3
≥ 40	0	9	100.0	40	100.0	49.00	100.0
Without correction for sample bias							
28-32	6	3	0.0	7	14.3	16	6.3
32-36	5	11	18.2	8	25.0	24	16.7
36-40	0	1	0.0	17	54.5	18	33.3
≥ 40	0	9	100.0	40	100.0	49	100.0

<sup>1</sup> No. pregnant (corrected) = No. pregnant · 0.318 · 0.903.

Note: 0.318 (correction for sample bias); 0.903 (correction for School 9) see Section 8.

Abbreviations: PRP: post-reproductive.

annual survival rate in the life table constructed below (Section 9):

$$\left( \sum_{t=n}^m t(L_{t-0.5} - L_{t+0.5}) \right) / (L_{n-0.5}) - n \quad (\text{Equation 8.12})$$

where  $L_t$  indicates number of females at age  $t$  years, and  $m$  the maximum longevity (errors in the value of  $m$  cause no significant change in the result). If  $m = 63$ , the mean life expectancy of a 36-year old female is 14.1 years. Since we assume a stationary population, this figure should be close to the mean longevity of females that live to the age of 36 years, i.e. to the sum of the lactation and resting periods after this age, and is calculated from the above results as  $6.57 + 7.83 = 14.40$  years. The two figures are close.

Table 23 shows the results of the above analyses for

six-year age classes. The period of lactation and simultaneous pregnancy is included in lactation for the age group from 30 to 36 years. We calculated the mean number of ovulations per calving cycle by multiplying the length of the mean calving cycle by the mean ovulation rate at the mid-point of each age group, using the equation for ovulation rate developed by Marsh and Kasuya (1984).

*Correction for post-reproductive females.* Marsh and Kasuya (1984) identified post-reproductive females as (1) females below 40 years of age having old corpora albicantia only and no macroscopic follicles that were not atretic in their ovaries, or (2) any females older than 40 years. This standard is likely to underestimate the young post-reproductive females compared with those above 40 years of age. The proportions of post-reproductive females in various age groups (Table 24) were computed from Fig. 8 in Marsh and Kasuya using the corrections developed earlier. The youngest post-reproductive female appeared at the age of 29.5 years, and the proportion increased rapidly with age.

By correcting for the proportion of post-reproductive females in an age group, the length of the lactation or resting periods of the reproductive females in that age group are calculated (Table 23) using the following equation:

$$X_t = Y_t \cdot \frac{R_t}{(R_t + S_t)} \quad (\text{Equation 8.13})$$

where  $X_t$  indicates mean length of the resting period for reproductive females in each age group of  $t$  years,  $Y_t$  is mean length of the resting period for all adult females in the same age group,  $R_t$  the number of reproductive resting females in the age group, and  $S_t$  the number of post-reproductive resting females in the age group.  $Y_t$  was estimated from Equation 8.6 above, and  $R_t$  and  $S_t$  were calculated from data in Marsh and Kasuya (1984). The corresponding figures for the lactation period were also estimated using this method.

Since our criteria for classifying a female as post-reproductive are somewhat arbitrary and we do not know

exactly when each female became post-reproductive, these figures may not be very accurate. However, we can safely conclude that both the lactating and resting periods of reproductive females increase after the age of 24 years. We cannot estimate the mean number of ovulations per calving cycle for the reproductive females alone, because the annual ovulation rate calculated by Marsh and Kasuya is based on data for both reproductive and post-reproductive females.

#### 8.4. Other hypothesis tested and rejected

In our attempt to explain our apparently anomalous observation that the number of pregnant females in our sample was about three times the number of calves less than 452 days old, we tested several hypotheses. The only one that withstood this scrutiny was that pregnant females were over-represented in our sample. The other hypotheses and our reasons for rejecting them are discussed below.

*Alternative hypothesis 1: sample is not biased.* This hypothesis assumes that the difference between the numbers of fetuses (corrected estimate = 60.7 individuals) and of calves younger than the age of 452 days (20 individuals) was caused by mortality between birth and age 452 days, i.e. a mortality rate of 59.2% per year. If we accept this mortality rate, then we have to accept an extremely low or negative mortality rate between the second and the tenth year (assuming a stationary population) (see Section 9). Although such a high first-year mortality seems unrealistic, we do not consider this a valid reason to reject this hypothesis in the absence of data on mortality or population status.

Under this hypothesis, the mean reproductive cycle is estimated from the proportion of females at each reproductive stage using only the corrections for gestation length (452/365) and for School 9 ( $F_1 = 0.903$ ). The results are shown in Table 23. The mean length of lactation is estimated at about 0.6 to 0.7 year for females below 24 years of age and 1.02 years for all females. These figures contradict the results of (1) stomach-contents analysis (Section 7.2, Method 1) (which indicate that calves start to take solid food at about 0.5 year but may not be weaned until between 2 and 3 years of age, (2) school analysis (Section 7.2, Method 2) (which suggest that weaning will be completed at a variable age of between 2 and 15 years with a mean estimate of 4 or 5 years), and (3) the mean lactation length (7.33 years) for the 12 females that were still lactating after age 36 years (Equation 8.8). Assuming the mean lactation period in the population to be 1.02 years, the mean length of lactation for the 58 lactating females below 36 years ( $X$ ) is calculated as;

$$1.02 \cdot 70 = (58 \cdot X) + (7.33 \cdot 12) \quad (\text{Equation 8.14})$$

i.e.  $X = -0.29$  year, which is clearly impossible.

We also examined the possible effect of using cemental-layer counts to estimate the ages of these old lactating females (even though Kasuya and Matsui (in press) considered that the reading of cemental layers is not difficult in *G. macrorhynchus* and that the error is similar to that for dentine reading). Replacing the cemental ages by the corresponding dentinal-layer

counts reduced the ages of five lactating individuals in Table 20 the ages of three animals to less than 36 years. The resultant mean lactation period for the nine remaining females over 36 years old is 4.72 years. Assuming an overall mean lactation length of 1.02 years, the estimate of the mean lactation time for 61 females less than 36 years old is 0.47 years, which still contradicts the age at which the stomach-contents analyses indicate that solid food is first taken. Therefore we conclude that, even if the reading of cemental layers was inaccurate, the above discussion is not affected.

The mean number of ovulations per reproductive cycle (Table 23) is also inconsistent with this hypothesis. Correcting for the over-representation of pregnant females, the number of ovulations per cycle is greater than two for most age groups (Table 23). However, assuming that the sample is not biased, the numbers of ovulations per cycle is reduced to about one or less. This is unrealistic in view of the presence of a significant proportion of females with a corpus luteum of 'ovulation', and the other evidence of sterile cycles presented in Marsh and Kasuya (1984) (see also below).

The sum of the lactating and resting period for animals older than 36 years of age based on this hypothesis (4.47 years, Table 23) is also markedly different from the mean life expectancy of females at 36 years of age (14.1 years) (The mean lengths of the lactation and resting periods for animals older than 36 years of age have been calculated by the method outlined by Equations 8.9 to 8.11 using only  $F_1 = 0.903$  for inclusion of School 9). Replacing cemental ages by dentinal ages changes the age composition. The life expectancy of 36-years old females then becomes 10.9 years instead of 14 years as calculated above.

*Alternative hypothesis 2: Lactating females are under-represented.* In this case, the sample bias is corrected by increasing the number of females lactating, or pregnant and simultaneously lactating, by

$$F_3 = (59.7 + 1)/20 = 3.035$$

where 59.7 = No. of pregnant females

1 = No. of pregnant/lactating females,

20 = No. of calves less than 452 days old.

Then  $Y_t$ , the mean length of a reproductive stage, and  $C$ , the mean calving interval at the age of  $t$  years, are estimated as follows:

$$Y_t = \frac{X_t}{(P_t + PL_t \cdot F_3) F_1} \cdot \frac{452}{365} \text{ year} \quad (\text{Equation 8.15})$$

$$C_t = \frac{R_t + L_t \cdot F_3 + (PL_t \cdot F_3 + P_t) F_1}{(PL_t \cdot F_3 + P_t) F_1} \cdot \frac{452}{365} \text{ year} \quad (\text{Equation 8.16})$$

where  $X_t$  indicates the number of whales in age group  $t$  in one of the four reproductive stages,  $P_t$  the number of pregnant whales,  $PL_t$  the number of pregnant and simultaneously lactating,  $F_1$  the correction factor for inclusion of School 9 (0.903), and  $X_t = PL_t \cdot F_3$  or  $L_t \cdot F_3$  instead of  $X_t = PL_t$  or  $L_t$ .

The following estimates of the lactating and resting periods were then calculated as in Sections 8.2 and 8.3 based on the proportion of females at each reproductive stage:

Resting period, overall = 1.76 years  
 Resting period, < 36 years = 0.76 years  
 Resting period, > 36 years = 2.53 years  
  
 Lactation, overall = 3.31 years  
 Lactation, < 36 years = 2.74 years  
 Lactation, > 36 years = 6.07 years

This estimate of the mean resting period for females over 36 years (2.5 years) is obviously unrealistic for the 64 resting females, which include a significant proportion of individuals older than the oldest lactating female. The sum of the lactating and resting periods for females over 36 years is  $2.53 + 6.07 = 8.6$  years, much shorter than the mean life expectancy (14.1 years) of a 36-year-old female. We therefore consider that this hypothesis is inferior to the alternative assumption used in Sections 8.2 and 8.3, i.e. that pregnant females are over-represented.

*Alternative hypothesis 3: incorrect juvenile age estimates.* Another possible explanation of the disparity between the numbers of pregnant females and calves less than 452 days old is that the ages of young calves have been over-estimated. In order to investigate the implications of this explanation, we estimated the growth rate of neonates that would be necessary if (1) the sample was not biased and (2) the postnatal mortality during the period in which calves grew to lengths of 219 cm (female) or 223 cm (male) (the lengths corresponding to an age of 452 days, see Kasuya and Matsui, in press) were (a) zero or (b)  $\frac{1}{3}$  (i.e., annual mortality of 48%). The results are as follows:

Postnatal mortality	Estimated age at 219 cm (female), 223 cm (male)	Estimated daily growth rate cm/day
0	$452 \cdot \frac{20}{60} = 151$ days	0.52 (females) 0.55 (males)
48%	$452 \cdot \frac{20}{60} \cdot \frac{2}{3} = 226$ days	0.35 (females) 0.37 (males)

As these values are larger than 0.34 cm/day (the estimated rate during the linear stage of fetal growth), they are obviously unreasonable.

As discussed in Kasuya and Matsui (in press), the body length of *G. macrorhynchus* at 452 days estimated using the equation of Perrin *et al.* (1976) (assuming a gestation period of 452 days and a neonatal length of 139.5 cm) is 197.4 cm. The corresponding length on the mean growth curve for *G. macrorhynchus* developed by Kasuya and Matsui (in press) is approximately 228 cm. If the age estimates, and hence the growth curve, are modified in accordance with Hypothesis 3 above, the estimated body length at 452 days is 243 cm (0 mortality) and 265 cm (0.48 mortality per year) respectively. Thus the estimate based on the original growth curve is in closer agreement with the Perrin *et al.* (1976) prediction than either of the modifications.

Hypothesis 3 also assumes that the proportions of adult females at various reproductive stages in the sample are representative of those in the population. Thus all the problems discussed above for Hypothesis 1 also apply.

*Alternative Hypothesis 4: suckling calves were lost during the drive.* From the fishermen's accounts, it seems

improbable that both mothers and calves were lost during the drive. However, if this were the case, this situation becomes effectively identical to that discussed under Hypothesis 2 above.

If only the calves were lost, the proportions of adult females at the various stages in the reproductive cycle would be unaffected and the problems inherent in Hypothesis 1 remain. In addition, although the nursing-period analysis (Section 7.2, Method 2) becomes invalid, Hypothesis 4 does not affect the conclusions derived from the stomach-contents analysis (Section 7.2, Method 1) and the extended lactation of females older than 36 years (Section 7.2, Method 3).

Thus even if some suckling calves were lost during the drive, the relatively small number of lactating females in the sample is still inconsistent with the independent evidence of extended lactation.

*Alternative Hypothesis 5: rapid increase in pregnancy rate during sampling period.* If this happens, the proportion of pregnant females in the sample will be disproportionately higher than that of mature females at other reproductive stages. As indicated in Table 1 and the footnote to page 288, our sample was obtained over a seven-year period (longer than one reproductive cycle for most reproductive females), during which there was no significant change in the apparent pregnancy rate (0.37 in 1975, 0.26 in 1976, 0.32 in 1977, 0.33 in 1978, 0.18 in 1980, 0.23 in 1981, 0.25 in 1982). We therefore reject this hypothesis.

## 8.5. Discussion

The reproductive life of the short-finned pilot whale can be divided into three phases. Whales less than about 24 years old have a relatively high reproductive potential and a reproductive cycle which is fairly similar to that of most other odontocetes, except that the resting period tends to be about one year longer. We have called the period between 24 and 40 years the transitional period, because it is during this time that the proportion of post-reproductive females increases from about 9% (ages 28 to 32 years), to 20% (ages 32 to 36 years), to 33% (ages 36–40 years) and then to 100% (> 40 years). We have no direct evidence of conception in females over 35 years, even though some animals may ovulate up till the age of about 40 years (Marsh and Kasuya, 1984). Thus the post-reproductive stage starts when a female is between 29 and 40 years of age. Some females may have a post-reproductive life span of 20 to 30 years, and the mean post-reproductive life span is about 14 years.

As discussed in Marsh and Kasuya (1984 and in press) such a significant post-reproductive stage is very unusual in wild mammals. We have confirmed that about one sixth of the post-reproductive females appear to lactate for extended periods. (The oldest lactating female was 50.5 years). However, we have no knowledge of whether these old females participate in the other reproductive activities of their school.

*Comparison with G. melaena.* Sergeant (1962a) detailed the reproductive status of 500 adult females from a population of the closely related long-finned pilot whale, *G. melaena*. His data have been rearranged in Table 25 so that they can be compared with our data for *G. macrorhynchus*. (We have assumed a 16-month gestation

Table 25

Comparison of reproductive status of 500 specimens of *G. melaena* (rearranged from Sergeant (1962a) assuming a gestation period of 16 months) and 297 specimens of *G. macrorhynchus* (numbers in parentheses)

	Pregnant	Pregnant/ lactating	Lactating	Resting	Total
No. individuals	159 (86)	10 (1)	280 (69)	51 (113)	500 (269)
Proportion (%)	31.8 (32.0)	2.0 (0.4)	56.0 (25.7)	10.2 (42.0)	100.0 (100.0)
Length of phase (years)	1.25 (1.19)	0.08 (0.05)	2.21 (3.43)	0.40 (5.46)	3.94 (10.13)

period for *G. melaena*). A major difference between the reproductive cycles of the two pilot whale species lies in the abundance of resting females. Both the numbers of reproductive resting females and of post-reproductive resting females seem to be much lower in the long-finned pilot whale (but see also Marsh and Kasuya, 1984). Conversely, the pregnancy rate in *G. melaena* seems to remain high until the age of 50 years, the estimated age of the oldest female (Sergeant, 1962a).

*Evidence that the reproductive potential of G. macrorhynchus is suppressed.* Using the equation developed by Marsh and Kasuya (1984), we estimate that the ovulation rate of *G. macrorhynchus* is about 0.6 ovulations per year at 10 years, 0.36 at age 20 years and 0.21 at age 30 years. Females cease to ovulate by age 40 years, as discussed above. In comparison, the mean annual ovulation rate for striped and spotted dolphins is 0.41 ovulations per year (Kasuya, 1976b) while the mean annual ovulation rate for sperm whales less than 20 years old is 0.31 (Ohsumi, 1965). Thus the ovulation rate for specimens of *G. macrorhynchus* younger than 20 years is not less than that of the other odontocetes for which comparable figures are available.

However, an important between-species difference exists in the observed frequency of corpora lutea of 'ovulation'. The proportion of the total number of corpora lutea which were accompanied by a recognizable pregnancy (excluding those of recognized abortion) was 0.78 (91/(91+26)) in the short-finned pilot whale (Table 20), 0.75 (384/509) in the sperm whale (Best, 1967), 0.94 in the striped dolphin and 0.97 in the spotted dolphin (Kasuya, in press). The difference between the pilot and sperm whales and the dolphins is more pronounced if the difference in the gestation periods (14–16 months against 11–12 months) is taken into account. The relative frequencies of ovulation apparently not followed by pregnancy is approximately  $(1-0.778)/14.9 = 0.015$  in the short-finned pilot whale, 0.016 in the sperm whale off South Africa, 0.005 in the striped dolphin and 0.003 in the spotted dolphin. These figures suggest that the proportions of unsuccessful ovulations in short-finned pilot whales and sperm whales are similar and three to five times higher than those in the striped and spotted dolphins. These calculations are independent of calving-interval estimates. We conclude that the apparently high proportion of 'wasted' ova in *G. macrorhynchus* in comparison with the dolphins is a cause of the long calving interval and suggests that the reproductive potential may be suppressed in this population.

Further evidence of possible suppression is given by comparison of the estimated mean lengths of the resting period in several odontocetes. All estimates have been derived using similar methodology and are as follows: *G. melaena*: 0.4 year (Sergeant, 1962a); sperm whale: 0.67 year (Ohsumi, 1965) or 0.75 year (Best, 1968); spotted and striped dolphins: 0.2–0.6 year (Perrin *et al.*, 1976; Kasuya, in press). These estimates are all much less than 1.2–1.7 years, the mean resting period of *G. macrorhynchus*, even in its most fecund phase below 24 years of age.

These results suggest that the reproductive potential of this population of *G. macrorhynchus* may be suppressed by population density, food shortage, or other unknown environmental factors. It is also possible that the high proportion of adult females which are post-reproductive (about 25% of adult females) is suppressing breeding in the younger females.

*Comparison with the killer whale.* Bigg (1982) analysed the reproductive biology of a killer-whale population off Vancouver Island, based on eight years of observation of about 260 whales in 30 schools, some of which had a short history of selective cropping. Although the birth-rate of the cropped killer whale pods exceeded that of the unexploited pods by about 2–3%, the combined birth-rate was 9.17 or 11.43% per cow per year, depending on the method of calculation. The resultant estimates of mean calving interval are 10.9 years or 8.7 years, respectively. These values are very similar to the mean calving interval of the short-finned pilot whale calculated above (10.13 years). Bigg's observations on 26 individually-identified cows provide data on individual variation in the calving interval. The confirmed intervals were relatively short cycles and occurred only in the cropped pods. There were five intervals of three years and one interval of four years. These intervals are only slightly shorter than the mean interval of four to five years estimated for female pilot whales below 24 years. The density changes produced in the killer whale schools by cropping may have stimulated the possibly suppressed (Bigg, 1982) reproductive potential of young females in the school. However, Bigg recorded for both cropped and uncropped pods a total of 17 occasions where the minimum calving interval was six or seven years. Our data suggest that such a long lactation and/or resting period is very common in short-finned pilot whales older than 24 years. Although Bigg (1982) doubted that such a large component of the killer whale population was barren, we suggest that a significant proportion of females that

did not breed for long periods were probably post-reproductive.

In contrast to the population studied by Bigg (1982), the pregnancy rate of a killer whale population in Norwegian waters (Christensen, 1984) is considerably higher. This difference may reflect differences in food availability and/or social structure which may have resulted from the apparently larger-scale selective cropping by small-type whaling in Norwegian waters.

**Implications for management.** Bigg (1982) indicated that the effect of exploitation on the reproductive rate of killer whales might have appeared only in the schools where the cropping had occurred. Because of the cohesiveness of the school, the effect of the density change may not have been directly transmitted to other schools. This may be also true in the short-finned pilot whale schools, where the movement of members between schools is apparently less common than in striped dolphins (Kasuya, 1972; and Miyazaki and Nishiwaki, 1978). Thus the effect of the removal of an entire school, which is common in a driving fishery, may not produce a density-dependent change in the reproductive rate of the remaining schools. Although either selective cropping or whole-school cropping may increase the available food supply, the population reproductive rate may respond more rapidly to cropping individuals from many schools rather than the removal of a small number of entire schools. However, the social consequences of selective cropping are likely to vary with the age and sex of the cropped individuals, as discussed in the Workshop Report for the Conference on the Behaviour of Whales (IWC, in press).

## 9. LIFE TABLE

### 9.1. Litter size

A single foetus was present in all 141 pregnancies examined, indicating that multiplets are uncommon in this species and that the mean litter size is close to one.

### 9.2. Neonatal sex ratio

Table 26 shows the sex of all available foetuses (excluding those below 5 cm in body length, which cannot be sexed reliably) and of juveniles below 220 cm in body length. The 95% confidence interval for the age of calves of this length is about 0.5 to 1.5 years ( $\bar{X} = 1.1$  years (males); 1.2 years (females), (Kasuya and Matsui, in press). The difference between the sex ratios of foetuses and juveniles is not significant. If both stages are combined, 48.4% of neonates examined were female. This discrepancy from a 1:1 sex ratio is not statistically significant (chi-square test,  $P > 0.8$ ).

There are two reasons for using both foetal and juvenile sex ratios in order to estimate the neonatal sex ratio: (1) to increase the sample size and to improve the precision of the estimate, (2) to correct for any difference between foetal and neonatal sex ratios. If intrauterine mortality is different between sexes, the sex ratio may change with increasing foetal age and the foetal sex ratio may not necessarily represent the neonatal sex ratio. A similar phenomenon is expected for postnatal mortality. Even though nothing is known of any sexual difference in survival rates in the foetal and early postnatal periods,

Table 26  
Neonatal sex ratio

	Foetus > 5 cm		Postnatal < 220 cm		Total	
	Female	Male	Female	Male	Female	Male
<i>N</i>	58	61	17	19	75	80
% Female	48.7	—	47.2	—	48.4	—

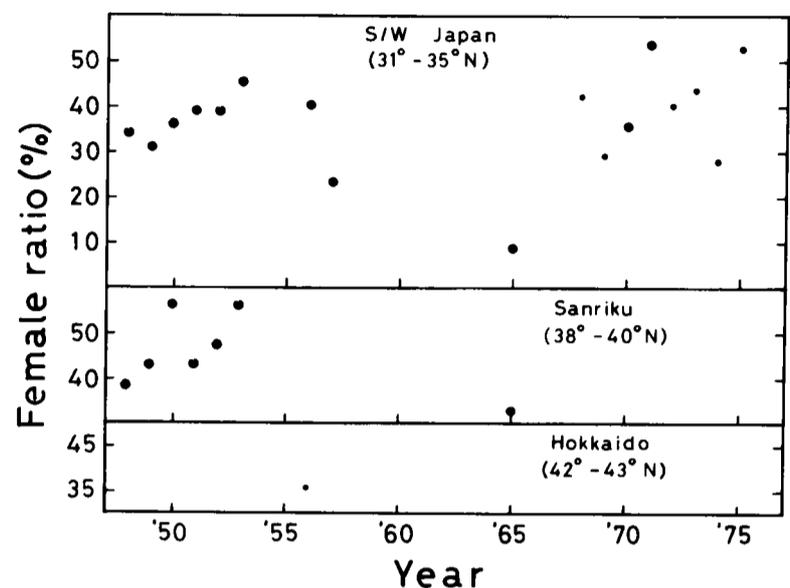


Fig. 24. Annual change of sex ratio of *G. macrorhynchus* in the catch of small-type whaling in Japan. Larger circles represent the total catches of over 100 whales and smaller circles the catches of between 50 and 100 whales inclusive. Catches of less than 50 whales are not listed. Data in Table 3.

both sets of data were tentatively combined in the present study.

### 9.3. Postnatal sex ratio

The postnatal sex ratio has been analysed separately for two sets of data: (1) the catch records of the small-type whaling and (2) the drive-fishery catch. The first data set is biased by the size of the animals caught (see below) but provides information from outside the geographical range of the drive fishery.

**Catch by harpoon gun ('small-type whaling').** The sex ratios for various years in Fig. 24 have been calculated from the data in Table 3. The proportion of females in the catch in southwestern Japan was about 30% in 1948 and gradually increased to about 45% in 1953. A similar pattern was observed in the catch off the Sanriku region on the Pacific coast of northern Honshu. The proportion of females gradually increased from about 40% in 1948 to about 55% in 1953. After 1953, the catch was small, and no trend was detected in either area (Table 27).

As shown by Kasuya and Matsui (in press), the body weight of a male at the mean asymptotic length (473.5 cm) is estimated to be 1,210 kg, approximately twice the weight of an adult female (569 kg) at the mean asymptotic length (364.0 cm). The difference in body size between sexes probably caused males to be fished selectively by the harpoon-gun fishery. However, this selectivity can also be affected by other factors, such as the capability of the gunner, the density of whales, the availability of other profitable species such as the minke whale, and consumer

Table 27

Sex ratio of *G. macrorhynchus* in the catch of small-type whaling off the Pacific coast of Japan

Year	South western Japan		Sanriku <sup>1</sup>		Total Pacific	
	Both sexes <i>N</i>	Female (%)	Both sexes <i>N</i>	Female (%)	Both sexes <i>N</i>	Female (%)
1948	104	33.7	321	37.7	425	36.7
1949	399	30.6	415	42.9	814	36.9
1950	361	36.0	289	56.4	650	45.1
1951	310	39.0	264	43.2	574	40.9
1952	194	39.2	120	46.7	314	42.0
1953	229	45.4	224	56.7	453	51.0
1954-57	377	34.7	111	36.9	575	35.0
1965-69	293	24.9	148	34.5	455	28.8
1970-75	455	43.7	62	46.8	541	43.6
1976-79	36	41.7	0	—	36	41.7

<sup>1</sup> Pacific coast of north-eastern Honshu, approximately between 38° N and 40° N.

preference. At Taiji, the people prefer to eat the meat of adult males, which is fattier than the meat from adult females. This may not be true, however, in other regions.

Thus the only definite conclusion we can make is that the true sex ratio of *G. macrorhynchus* must have been similar between southwest Japan and the Sanriku coast. In both regions, there was a steady increase in the female ratio from 1948 to 1953 followed by a reversion to initial levels after the 1954 season. There was little change in the number of pilot whales caught in the first six years. The number of fishing vessels was nearly constant, fluctuating slightly between 66 and 74 from 1949 to 1952 (Kasuya, 1975) and does not seem to have affected the sex ratio of the catch.

To examine the possibility that the increase over years in the proportion of females was due to the selective catch of males by small-type whaling, we shall assume (without proof) that the internal structure of the population in 1948 was similar to that being exploited by the present drive fishery. (The whales wintering at or south of southwestern Japan are considered to migrate in summer to the waters off northern Japan (Kasuya, 1975)). We shall also assume that the small-type-whaling operation hunted only sexually mature females and males. This assumption is probably not unreasonable, because few immature and early-maturing males exceed the mean asymptotic length for the female (see Kasuya and Matsui, in press). Recruitment is ignored. Then the intensity of the selection for males over females, (*b*), is calculated by

$$b = \frac{1}{c} \cdot \frac{\text{Male whaling catch 1948}}{\text{Female whaling catch 1948}} \quad (\text{Equation 9.1})$$

where *c* indicates the ratio of adult males to adult females in the population. Using data from the life table (Table 33) gives

$$c = (1 - 0.7742)/0.7742 = 0.292$$

therefore

$$b = \frac{1}{0.292} \cdot \frac{269}{156} = 5.91$$

If the selectivity remained the same until 1953, we get the following equation:

$$\frac{c \cdot P - M}{P - F} \cdot b = \frac{\text{Male whaling catch 1953}}{\text{Female whaling catch 1953}} \quad (\text{Equation 9.2})$$

where *P* equals the number of adult females in the population in 1948, *M* the total adult males caught from 1948 to 1953, and *F* the catch of adult females in the corresponding period.

The catch by harpoon gun in 1953 was 222 males and 231 females (Table 3). *M* is the sum of the adult-male catch by the small-type-whaling fishery (1890 whales, Table 3) and the drive fishery, for which total catch is uncertain. The annual catch off the Izu coast in 1948 and 1949 (statistics are not available) is assumed to be 412 (the mean annual catch in the area from 1950 to 1953). The catch of *G. macrorhynchus* at Nago (Okinawa) is assumed to be 183 per year (the mean of the catch of the 10 years from 1960 to 1969). Then the total catch by the two drive fisheries in the six years is estimated to have been  $(412 + 183) \times 6 = 3,750$  individuals. The proportion of adult females in the catch of the drive fishery was 0.5253, and that in the adults of both sexes was 0.7742 (Table 33). Therefore the catch of adult males is calculated as  $3,750 \cdot 0.5253 \cdot (1 - 0.7742)/0.7742 = 575$ , and the total catch of males by both fisheries as  $1,890 + 575 = 2,465$ . In the same way the catch of adult females is calculated as  $1,352 + (3,750 \cdot 0.5253) = 3,322$ . This calculation is based on the unrealistic simplification that the male proportion in the drive fishery catch was constant, thus over-estimating the male catch and consequently under-estimating the population.

Using the above figures to solve Equation 9.2 gives  $P = 15,200$ , the population of adult females in the 1948 season. Since the proportion of adult females is about 52% of the population, the size of the total exploited population is estimated as  $15,200/0.52 = 28,600$  individuals, which can be rounded to 30,000.\*

The above calculation suggests that the change of sex ratio in the catch of small-type whaling can be explained by the selective exploitation of adult males, if the above assumptions are correct and if the total population of the species was over 30 thousand in the 1948 season. This is of the same order as the population of the long-finned pilot whale in the Newfoundland area (less than 60,000, Mercer, 1975). Ignoring annual recruitment, the adult-male population,  $15,000 \cdot (1 - 0.7742) = 3,400$  in 1948, is estimated to have decreased during the exploitation to  $3,400 - 2,400 = 1,000$  by the 1953 season, while the population of adult females decreased from 15,200 to  $(15,200 - 3,300 =) 12,000$ . If it is assumed (without a definite basis) that the fishery has exploited a coastal population, the above catch figures may be large enough for the selective hunting to cause an obvious change in the sex ratio of the catch (but also see 'Fishing selection' below).

*Catch of the drive fishery:* Fig. 25 and Table 28 show the sex ratio of the short-finned pilot whales caught by the drive fishery from 1975 to 1981. Females comprised

\* Footnote: In view of information obtained after this study, this figure must include a population off the Pacific coast of northern Japan, from which no samples have been obtained in the present study (see footnote page 264).

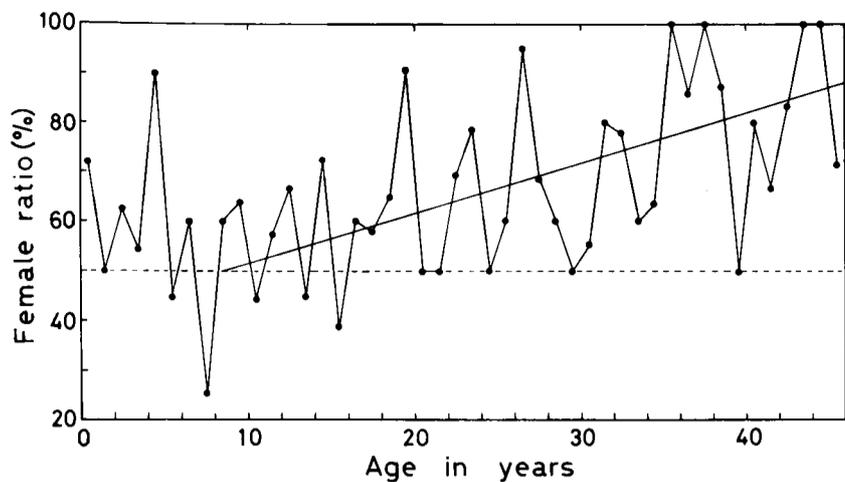


Fig. 25. Age-specific sex ratios of *G. macrorhynchus* in the catch of the driving fishery. The straight line indicates the least-squares regression between age and sex ratio (Equation 9.3).

Table 28  
Postnatal sex ratio in *G. macrorhynchus*<sup>1</sup>

Age range (years)	Male <i>N</i>	Female		$\chi^2$ probability <sup>2</sup>
		<i>N</i>	%	
0-10	46	69	60.0	0.2-0.3
10-20	49	71	59.2	0.2-0.3
20-30	40	74	64.9	0.01-0.02
30-40	17	54	76.1	0.02-0.05
40-46	6	31	83.8	< 0.001
46-63	0	26	100.0	< 0.001
Total	158	325	67.3	< 0.001

<sup>1</sup> Schools 7, 8, 9 (> 15 years), 10 through 18, 22 and 23.

<sup>2</sup> Chi-square test to see whether the sex-ratio is significantly different from 1:1.

67.3% of all postnatal individuals. This proportion is about 7% lower than the corresponding figure for the long-finned pilot whale, *G. melaena*, in the western-North-Atlantic drive fishery reported by Sergeant (1962a). The difference in male to female ratios between 158:325 (*G. macrorhynchus*) and 1,825:2,778 (*G. melaena*) is statistically significant (chi-square test,  $P < 0.01$ ).

Since the sample size is small, an irregular short-term fluctuation of the age-specific sex ratio (Fig. 25) is not significant, but the longer general trend may be important. The apparent decrease in the proportion of females between zero and eight years of age may not be significant, because both the neonatal sex ratio and the overall sex ratio between zero and 10 years are close to parity. However, it is possible that females comprise more than 50% of the age classes below 10 years (Table 28). The continual increase in the proportion of females starts somewhere between the ages of eight and fifteen years (Fig. 25). After age 16 years, females definitely exceed males, and they continue to increase in proportion until they attain 100% at 46 years and thereafter. The least-squares regression of the age-specific sex ratio (Fig. 25) is shown by

$$Y = 0.991X + 41.74 \quad 10 < X < 47 \quad (r = 0.59)$$

(Equation 9.3)

where  $Y$  indicates the proportion of females in %, and  $X$  the age in years. If this line is extrapolated towards the left it crosses the parity level at age 8.3 years (Fig. 25), the age which coincides with the start of the early-maturing

stage in some males. By the age of 16 years (when females definitely exceed males), most males have reached at least the early-maturing stage of their reproductive development. We therefore conclude that the disparate sex ratio is associated with the later arrival of puberty in the male.

The previous analysis showed that the small-type whaling selectively exploited the adult males until 1953 and could have changed the population sex ratio. At about age 13 years, the mean male growth curve exceeds 390 cm, which is the upper limit of female length (see Kasuya and Matsui, in press). Therefore the sex-ratio bias caused by small-type whaling is expected to occur in age classes above 13 years in 1953, i.e. this bias would have applied to whales born in 1940 or before. However, this bias would have been greater in older cohorts, because these males would have attained larger body sizes (growth lasts 25 years) and would therefore be more heavily selected. Also, animals in older cohorts would have been exposed to the selective fishery for longer than animals in the younger cohorts. However, the animals from cohorts before 1940 would have been 35 years or older in 1975 at the start of the collection of materials for this study, and 41 years in 1981 when it ended. Since the maximum age of males in our sample is 46 years, the male population which would have been hunted most severely by the small-type whaling would have almost died off when our data collection started. Accordingly, we conclude that the age-specific sex ratio indicated by our sample is not an artefact caused by selective whaling.

Although the drive fishery probably provides less biased information on school and population structure, it still leaves some possibility of sex-ratio bias (see Section 10). We offer the following explanations for the decreasing proportion of males with increasing age after puberty: (1) Adult males may segregate outside the driving fishery area (perhaps in the northern part of the range or in offshore waters), or leave the breeding school to assume a solitary life. (2) Males have a higher natural mortality rate. The analysis of the catch by small-type whaling revealed that the sex ratio is almost the same in the Sanriku region as in southwest Japan. This result is easily explained by the fact that, as indicated by Kasuya (1975), the individuals migrating between eastern Hokkaido and southwest Japan are following the seasonal movement of the northern boundary of the Kuroshio current and staying in the same oceanographic environment throughout the year.

Segregation of adult males out of the fishing ground, or into a solitary existence either inside or outside the fishing ground, cannot be confirmed. A drive fishery does not kill single individuals, and even small-type-whaling vessels would have had a smaller chance of finding solitary adult males. However, we consider that the disparate sex ratio is more likely to be due to higher natural mortality rate. The age of the oldest male in the present study is 17 years younger than that of the oldest female, and there are 26 females older than the oldest male. The continual and steady decrease of the male sex ratio with age also supports the above assumption. The slight excess of females in the age classes below 10 years (Table 28) also suggests that male mortality is slightly higher in the immature stage.

A similar between-sex difference in mortality was also

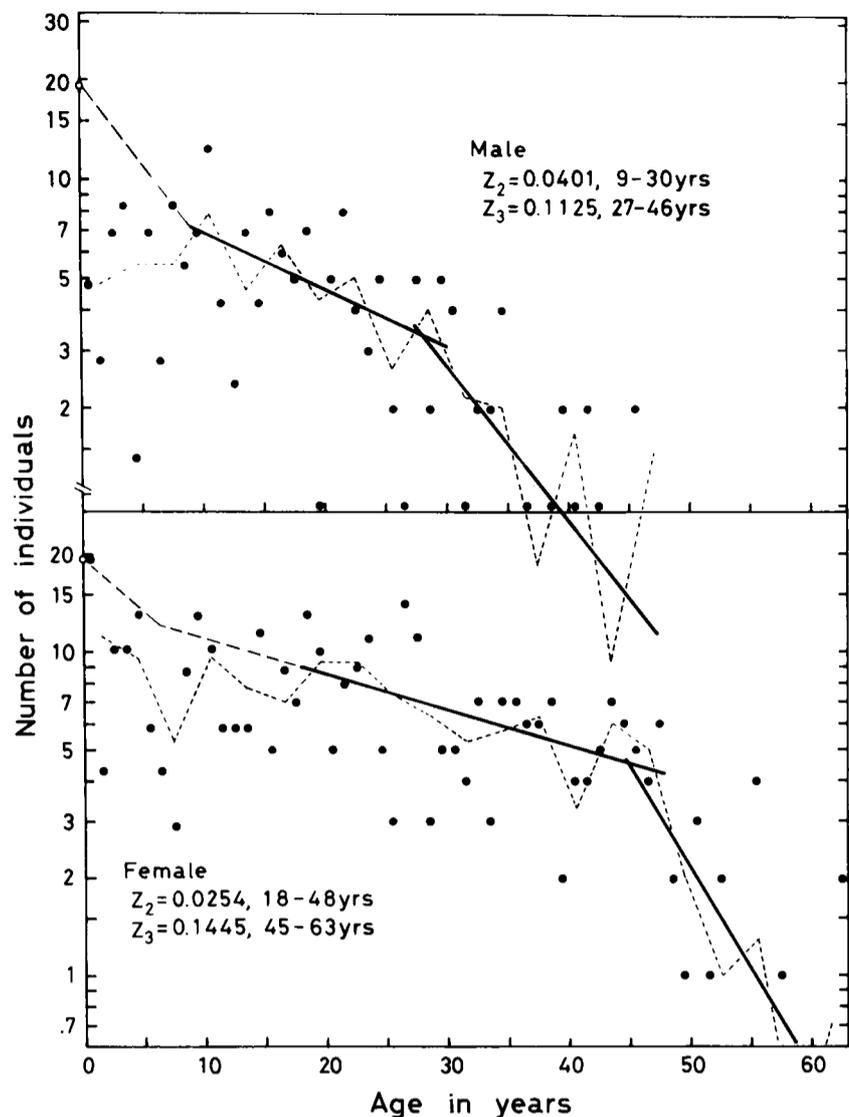


Fig. 26. Age frequency and total mortality coefficient ( $Z$ ) of *G. macrorhynchus* in the catch of the driving fishery. The closed circles and fine dotted lines indicate the frequency of each age and the means of each three-year age group respectively; the thick straight lines the least-squares regressions fitted to the means for the three-year age groups, the open circles the estimated annual production, and the straight dotted lines the hypothetical age frequencies of juveniles.

found in *G. melaena* in the western North Atlantic (Sergeant, 1962a). In this population, the age of the oldest male was 40 years, 10 years younger than the oldest female, and the male sex ratio was shown to decrease throughout the age series.

In another polygynous cetacean species, the sperm whale, there is no obvious difference in mortality between sexes. However, the sex ratio in the breeding schools is strongly skewed by the geographical segregation of adult males (Ohsumi, 1966; Best, 1979). A similar segregation would explain the skewed sex ratio of the short-finned pilot whale. However, the maximum age of the male sperm whale in the breeding area is not different from that of the females in the same area (Ohsumi, 1966). This is a distinctly different situation from that for the pilot whale, where the female lives much longer than the male. We therefore conclude that the skewed sex ratio in *G. macrorhynchus* is due to sex differences in mortality rather than to segregation.

#### 9.4. Age composition and mortality rate

The age-frequency diagram (Fig. 26) has been constructed from 150 males and 318 females in 14 schools (nos 7, 9 (> 15 years) through 18, and 22 through 24). In addition, the three juveniles of unknown sex less than one year of age have been arbitrarily divided equally between the

sexes. Among this total of 471 individuals, the ages of two males (5.5 and 8.5 years), three females (< 1 year), and three individuals of unknown sex (< 1 year) have been estimated from their body lengths. There are 21 females (18 adult and three of unknown growth stage), four males (immature, early-maturing, late-maturing, and mature), and three individuals of unknown sex (two suckling) missing from the 13 schools other than School 9. (For details see Fig. 27).

The School-9 data are biased more heavily. The school was composed of about 230 individuals. Each day the fishermen selectively killed the larger individuals. After 10 days, about 60 smaller whales were released. During this operation, the male ratio in the kill decreased gradually while the ratio of immature males increased. However, the number of immature females killed was negligible throughout. As shown in Figs 28 and 27 respectively, the lower range of body lengths of the whales slaughtered from this school is about 320 cm, while the youngest whales killed were aged eight years (female) and five years (male). Females measuring 320 cm in body length were below 15 years of age; males of the same body length were less than 11 years of age (see Kasuya and Matsui, in press). In the present analysis, it is assumed that the age frequency of the sample represents that of the school for age classes over 15 years for both sexes.

The age frequency of whales more than 15 years old (Fig. 26) has been constructed by combining all data from the 14 schools, while that below 15 years (Fig. 26) has been calculated as follows:

$$L_t = K \cdot B_t \quad (t < 15) \quad (\text{Equation 9.4})$$

$$K = \frac{\sum_{t=15}^{\infty} A_t}{\sum_{t=15}^{\infty} B_t} \quad (\text{Equation 9.5})$$

where  $L_t$  indicates the frequency at age  $t$  years corrected for the exclusion of School 9,  $A_t$  the number of individuals at age  $t$  including School 9, and  $B_t$  that without School 9. The value of  $K$  has been estimated empirically as 1.45 for females and 1.38 for males.

Because of the small sample size, there are large fluctuations in the age-frequency distribution. These fluctuations have been smoothed by using the means of three-year age classes (indicated by the dotted line on Fig. 26). For simplification, the age-frequency distribution for each sex has been divided into three portions (age groups) and the mortality coefficient ( $Z$ ) calculated separately for each. The least-squares regressions fitted to the age-frequency distribution based on the means of the three year age classes for the intermediate and oldest age groups are given here; those for the youngest age group will be considered below (Section 9.5).

Females:

$$\ln Y = -0.0254X + \log 14.23 \\ (18 < X < 48, r = 0.76) \quad (\text{Equation 9.6})$$

$$\ln Y = -0.1445X + \log 2,926.01 \\ (45 < X < 63, r = 0.87) \quad (\text{Equation 9.7})$$

Males:

$$\ln Y = -0.0401X + \log 10.34 \\ (9 < X < 30, r = 0.75) \quad (\text{Equation 9.8})$$

Table 29

Comparison of survival rate estimated from age composition by two different methods

Method		A	B
Female	18-47 years	0.9749	0.9751 ± 0.0164
	45-63 years	0.8655	0.8544 ± 0.0668
Male	9-30 years	0.9607	0.9567 ± 0.0315
	27-46 years	0.8936	0.9030 ± 0.0609

A: From  $Z_2$  or  $Z_3$  calculated by linear regression (Equations 9.6 through 9.9).

B: By segment analysis (Robson and Chapman, 1961), best point estimate with 95% confidence interval.

$$\ln Y = -0.1125X + \log 84.52$$

$$(27 < X < 46, r = 0.83)$$

(Equation 9.9)

where  $Y$  indicates the frequency, and  $X$  the age in years. The slope of each of these lines is an estimate of the total mortality coefficient  $Z$  for the respective sex/age class. The corresponding annual survival rates are listed in Table 29.

The merit of using the means of the three-year age classes is obvious for older ages. If the actual frequencies had been used in the calculations, the data for the age classes with a zero frequency would have to be excluded, with a resultant over-estimation of the survival rates.

Robson and Chapman (1961) detailed mathematical methods to estimate the survival rate and its confidence interval from the age-frequency distribution. The results of their segment-analysis method applied to each age frequency in our sample are listed in Table 29. Each of these figures is in good agreement with the survival rates calculated from the gradient,  $Z$ , of the corresponding least-squares regression (above).

The slopes of the linear regressions (Fig. 26) are the sum of the annual natural mortality coefficient at the time of recruitment to the fishery, the annual fishing mortality coefficient at the same time, and the annual change in the amount of recruitment. The last factor can probably be ignored, because, except for the post-war period, the present population seems to have sustained an annual catch of 200 to 500 individuals since the early 1920s (if this last assumption is untrue, the following analyses of mortality are invalid). It is obviously not possible to separate the natural mortality rate and the fishing mortality rate. Accordingly we referred only to the total mortality rate in this study.

In *G. macrorhynchus*, the mortality rate is higher in older animals than in young adults. In our sample, the difference is significant only in the female (Table 29), but the pattern is similar in both sexes. In males, the mortality rate starts to increase at about age 27 years, 15 years earlier than in females. This is consistent with the shorter maximum longevity of males. Each point estimate of male mortality is higher than the corresponding value for females of the same age. Although sexual differences in mortality are not always significant, we consider that this is probably an artefact of the small sample size.

There is little change in the age frequency of juvenile females during the first few years of life, but the frequency of males less than 10 years old is lower than that at 10

Table 30

Actual frequencies of juvenile males and females compared with expected frequencies calculated from life table

Age (years)	Actual frequency			Expected frequency
	Female	Male	$\Sigma$	
0.5	19.6	4.8	24.4	37.1
1.5	4.3	2.8	7.1	33.9
2.5	10.1	6.9	17.0	31.0
3.5	10.1	8.3	18.4	28.2
4.5	13.0	1.4	14.4	25.8
5.5	5.8	6.9	12.7	23.6
6.5	4.3	2.8	7.1	21.6
7.5	2.9	8.3	11.2	20.3
8.5	8.7	5.5	14.2	19.1
9.5	13.0	6.9	19.9	18.3
10.5	10.1	12.5	22.6	17.7
$\Sigma < 5$	57.1	24.2	81.3	156.0
$\Sigma 5-10$	34.7	30.4	65.1	102.9

years. The difference between sexes may not be significant. If the age frequencies of both sexes are combined (Table 30) and an exponential survival curve is fitted to the resulting points, using the least-squares method, the following equation is obtained:

$$\log Y = 0.0136X + \log 13.24 \quad (0 < X < 11)$$

(Equation 9.10)

where  $Y$  indicates the frequency and  $X$  age in years. The slope obtained here is greatly affected by minor changes in the age range included in the calculation (presumably due to the small sample size). However, this equation clearly suggests that the apparent mortality rate is negative or very close to zero in the immature stage. If juveniles are not under-represented in the present material, either juvenile mortality must be extremely low or the annual recruitment must have been decreasing in recent years. The first alternative is improbable, because the mortality between birth and weaning would be higher than that of the mother (2.5% per year, 18 to 46 years of age). We also reject the second explanation for the following reasons. Firstly, the recent catch increase started in 1975 coincident with the start of the collection of the present materials and is therefore too recent to be the cause of the recent reduction of recruits (see Sections 3.2 and 8.4 for the possible response of the population to the drive fishery). Secondly, although some years of high catch were recorded between 1954 and 1975, they were sporadic and could hardly have caused destruction of the population and thereby decreased recruitment in recent years. Accordingly, the only plausible explanation is a sampling bias against juveniles. Estimates of the true juvenile mortality rate and of the magnitude of the sample bias are made in the next section.

### 9.5. Life table

*Assumptions and equations used.* The mortality rate can only be legitimately estimated from an age-frequency distribution (as we have done) if the population is stable or has a known rate of increase (Caughley, 1977). We have assumed without supporting evidence that this population is stationary. Therefore, we regard our

estimates of the mortality rate for whales of various ages as tentative.

Caughley (1966, 1977) suggested that the typical mammalian mortality pattern is 'U-shaped', consisting of a juvenile phase in which the rate of mortality is initially high but rapidly decreases, followed by an initially low but steadily increasing rate of mortality. For simplification, we have divided the life of a female pilot whale into three stages;  $0 < t \leq 6.5$  years,  $6.5 < t \leq 46.5$  years, and  $46.5 < t < 70$  years; and have assumed that the mortality rates  $Z_1$ ,  $Z_2$ ,  $Z_3$  respectively are constant at each stage.

The female life table (Table 31) is constructed assuming a stationary population and is based on the following equations:

$$L_0 = \sum L_t \cdot A_t \cdot P_t \cdot F \cdot R \quad (\text{Equation 9.11})$$

$$L_t = L_0 \cdot e^{-Z_1 \cdot t} \quad (0 < t \leq 6.5) \quad (\text{Equation 9.12})$$

$$L_t = L_{6.5} \cdot e^{-Z_2(t-6.5)} \quad (6.5 < t \leq 46.5) \quad (\text{Equation 9.13})$$

$$L_t = L_{46.5} \cdot e^{-Z_3(t-46.5)} \quad (46.5 < t \leq 70) \quad (\text{Equation 9.14})$$

where

$F$ : mean litter size

$R$ : neonatal female sex ratio

$Z_1$ : total mortality coefficient below 6.5 years of age

$Z_2$ : total mortality coefficient between 6.5 and 46.5 years of age

$Z_3$ : total mortality coefficient above 46.5 years of age

$L_t$ : number of individuals at age  $t$  years

$A_t$ : proportion of sexually-mature individuals at age  $t$  years

$P_t$ : annual pregnancy rate at age  $t$  years

With the exception of the mortality rate of whales less than 18 years of age, all parameters have been calculated above as follows:

$$F = 1.0 \quad (\text{see Section 9.1})$$

$$R = 0.5 \quad (\text{see Section 9.2})$$

$$Z_2 = 0.0254 \quad (6.5 < t \leq 46.5) \quad (\text{see Equation 9.6})$$

$$Z_3 = 0.1445 \quad (46.5 < t < 70) \quad (\text{see Equation 9.7})$$

$$A_t = 0.2061t - 1.358 \quad (6 < t < 12) \quad (\text{from Equation 5.1})$$

$$P_t = -0.02077t + 0.5165 \quad (6 < t \leq 15) \quad (\text{from equation in Table 22})$$

$$P_t = -0.00737t + 0.3126 \quad (15 < t < 42) \quad (\text{from equation in Table 22})$$

All values for  $A_t$ ,  $P_t$  and  $L_t$  were calculated at the mid-point of each year class except for  $A_t$  at the extremes of its range (i.e. between six and seven years, and 11 and 12 years), when the function is integrated over the one-year range in each case.

As a simplification, the upper or lower boundaries of the equations for  $A_t$  and  $P_t$  were extended outside the actual ranges of the data in our model. For example, our sample suggests that the age of the youngest sexually mature female is between seven and eight years old, while the above equation is based on an estimate of between six and seven years. This bias is minimal. Similarly, all pregnant females in our sample were less than 35 years old, while the model assumes that females bear their last calf at age 42 years. The resultant overestimation of

Table 31

Simplified life table for females of *G. macrorhynchus* based on an imaginary cohort of 1,000 females. Only selected ages are listed here, but the total is based on all age classes

Age (years) ( $t$ )	Maturity rate	Annual pregnancy rate	Number of females			Dying in year between $t$ and $t+1$
			Immature	Adult	Giving birth	
0			(1,000)			
0.5	0	—	964	0	0	68
5.5	0	—	668	0	0	47
6.5	0.042	0.381	595	26	10	16
7.5	0.188	0.361	491	114	41	15
8.5	0.394	0.340	359	231	79	15
9.5	0.600	0.319	230	345	110	14
10.5	0.806	0.298	105	456	135	15
11.5	0.955	0.278	25	521	145	13
12.5	1	0.257	0	533	137	14
15.5	1	0.198	0	494	98	13
20.5	1	0.162	0	435	70	11
25.5	1	0.125	0	383	48	10
30.5	1	0.088	0	337	30	8
35.5	1	0.051	0	297	15	7
40.5	1	0.014	0	262	4	7
45.5	1	0	0	230	0	5
50.5	1	0	0	126	0	17
55.5	1	0	0	61	0	8
60.5	1	0	0	30	0	4
65.5	1	0	0	14	0	2
69.5	1	0	0	8	0	8
Total	—	—	6,660	15,591	2,003	1,000

Table 32

Simplified life table for males of *G. macrorhynchus* based on an imaginary cohort of 1,000 males. Only selected ages are listed here, but the total is based on all age classes

Age (years) ( <i>t</i> )	Maturity rate	Number of males		
		Immature	Adult	Dying in year between <i>t</i> and <i>t</i> +1
0		(1,000)		
0.5	0	946	0	98
5.5	0	545	0	56
10.5	0	349	0	13
12.5	0	322	0	12
13.5	0.023	303	7	13
14.5	0.208	235	62	11
15.5	0.425	164	122	11
16.5	0.642	98	177	11
17.5	0.858	37	227	11
18.5	0.997	1	252	10
19.5	1	0	243	9
20.5	1	0	234	9
25.5	1	0	191	7
30.5	1	0	136	15
35.5	1	0	77	8
40.5	1	0	49	5
45.5	1	0	25	3
49.5	1		16	16
Total	—	7,915	4,183	1,000

the number of births is only 58 out of 2,003 whales, an error which can be ignored.

Although the use of age at first ovulation instead of the age at first conception or at first parturition probably overestimates the true number of reproductive females, this does not bias our estimate of the reproductive rate, because the annual pregnancy rate has been calculated including those adult females. We also assumed that the mortality rate of females between the age of 6.5 years, the age when sexually-mature females are assumed by the model to first start to appear (see below), and 18 years is the same as that derived from the age-frequency distribution of females between 18 and 48 years of age ( $Z_2$ ).

The mortality rate of females less than 6.5 years of age ( $Z_1 = 0.0734$ ) was calculated assuming a uniform rate of decrease from  $L_0$  (calculated from Equation 9.11) to 12.06 (the actual frequency at 6.5 years of age extrapolated from Equation 9.6).

The life table for males (Table 32) has been constructed on the same principle as that for females. The total mortality rate between 0 and 9 years of age ( $Z_1 = 0.1102$ ,  $0 < t \leq 9$ ) was calculated assuming a constant rate of decrease from  $L_0$  (calculated from Equation 9.11 above) to 7.207 (the estimated frequency at nine years using Equation 9.8).

In the model, sexually mature males have been defined as those at the late-maturing stage or mature stages, because of the evidence that attainment of the histological 'late-maturing stage' coincides with functional maturity (see Section 4.5). The proportion of adult males at age  $t$  years was calculated from

$$A_t = 0.2166t - 2.932 \quad (13 < t < 19) \\ \text{(from Equation 4.7)}$$

*Comparison of the model with the original data.* The juvenile age frequencies observed in our sample are compared with those predicted by the model in Table 30. The total number of individuals between zero and five years of age in the sample (81.3 animals) is only 52% of the frequency estimated from the model. Similarly, the observed frequency for the 5- to 10-year age classes is only 63% of that predicted by the model. These discrepancies can be explained by the sample bias against females with young calves discussed in Section 8.

The mean ages calculated from the model using the equation

$$\frac{\sum ((n+0.5) \cdot (L_{n+0.5}))}{\sum L_{n+0.5}} \\ (n = \text{integer in this section}) \\ \text{(Equation 9.15)}$$

are about 20 years (female) and 13 years (male). The difference between these values and those calculated from our raw data is small in females but larger in males (Table 33). This may be because of a relatively greater fishing selection for adult males in the drive fishery (see 'Fishing selection' below).

The mean life expectancy of newborn calves, or the mean age at death,

$$\frac{(\sum n \cdot (L_{n-0.5} - L_{n+0.5}))}{L_0} \\ \text{(Equation 9.16)}$$

calculated from the model is 22 years in females and 12 years in males (Table 33). This value will be strongly affected by the errors in our estimate of juvenile mortality.

In the model, the ratio of adult females to functionally mature (late-maturing) males is 3.7:1 (Table 33). This value is not significantly different from the ratio in the original data (3.4:1), calculated assuming that males older than 16.0 years and females older than 9.0 years were at those stages. These values have been compared with Sergeant's (1962a) figures for *G. melaena* as detailed in his Table XXVII. In *G. melaena*, if (1) all females six years or older, (2) all males 11 years or older, and (3) all whales of both sexes with a closed pulp-cavity are considered to be sexually mature, the female to male ratio is 227:61 or 3.7:1, which is identical with the value in the present model.

In *G. macrorhynchus*, the ratio of adult females to total females is lower in the model than that in the sample (Table 33). This difference can be explained by the sample bias in favour of pregnant females (see Section 8).

The overall annual pregnancy rate of the sample (corrected only for the inclusion of School 9 (see Section 8)), is

$$(365 \cdot (P + PL)) / (452 \cdot (P + PL + L + R)) = 0.2345$$

This estimate (Table 33) decreases to the more reasonable value of 0.0961 when corrected for the sample bias in the pregnancy rate (see Section 8.3). The corresponding value estimated from the model (0.1285) is intermediate between these two figures. It is probably too high, because our extrapolation of the mortality rate for ages between 18 and 48 years back to the age of 6.5 years has increased the relative abundance of young adult females and thus the population pregnancy rate. If the mortality rate between 6.5 and 18 years of age is lower, the overall annual pregnancy rate will be close to 0.096, the observed

Table 33  
Summary of reproductive parameters of *G. macrorhynchus*

Parameter			Original data	Life-table data
1. Onset of sexual maturity,	female	year	9.02	—
	male	year	15.85	—
2. Mortality rate, annual,	female, 0.0–6.5 years	%	—	7.08
	6.5–18.0 year	%	—	2.51
	18.0–46.5 year	%	2.51	—
	46.5–70.0 year	%	13.45	—
	all ages	%	—	4.49
	male 0.0–9.0 year	%	—	10.43
	9.0–28.5 year	%	3.93	—
	28.5–50.0 year	%	10.64	—
	all ages	%	—	8.27
	in the population	%	—	5.82
3. Mean age,	female	year	21.98	19.98
	male	year	16.72	13.05
4. Mean longevity	female	year	—	22.26
	male	year	—	12.11
5. Sex ratio (female ratio),	neonatal	%	48.98	50.00
	all ages	%	67.26	64.78
	adult	%	77.42	78.85
6. Adult females	in the female population	%	78.11	70.07
	in the total population	%	52.53	45.39
7. Annual pregnancy rate		%	23.45	12.85
8. Gross annual reproductive rate,	female calves/female population	%	9.16	4.50
	all calves/total population	%	12.32	5.83
9. Average calf production per female living to post-reproductive age		no.	—	4.39
10. Reproductive females in the female population		%	58.31	52.36
11. Post-reproductive females in the adult female population		%	25.34	24.51

value (corrected for sample bias). We suggest that the overall annual pregnancy rate of this population is probably between about 9.6 and 13%.

The population pregnancy rate may be significantly altered by a minor change in age structure, even when the age-specific pregnancy rate is kept unchanged. This will be particularly important in the short-finned pilot whale, where the pregnancy rate is strongly dependent on age, especially in this population which contains a large proportion of old post-reproductive females.

The gross annual reproductive rates (the annual production of female calves by the female population), are calculated as above, based on previously derived parameters (Table 33). The value without correction for the sample bias in pregnancy rate (Section 8) is  $0.2345 \times 0.5 \times 0.7811 = 0.0916$ . This figure will be lowered to  $0.0916 \times 0.5 \times 0.7811 = 0.036$ , with correction for this bias. As the model assumes that the population is stationary, the corresponding figure estimated by the model ( $0.1285 \times 0.5 \times 0.7007 = 0.0450$ ) has to equal the overall annual mortality rate calculated for females from the equation

$$\frac{\Sigma(L_{n-0.5} - L_{n+0.5})}{\Sigma L_{n+0.5}} = L_0 / \Sigma L_{n+0.5} \quad (\text{Equation 9.17})$$

which is 0.045. The annual rate of female calf production by the female population is probably about 4–5%.

The sample suggests that the number of calves of both sexes produced annually by the entire population, the gross annual reproductive rate in the ordinary sense, is

$0.2345 \times 0.5 \times 0.7811 = 0.0916$ . This figure will be lowered to  $0.0916 \times 0.5 \times 0.7811 = 0.036$ , with correction for this bias. As the model assumes that the population is stationary, the corresponding figure estimated by the an estimate of 0.058 (Table 33). The gross annual reproductive rate of the population is probably about 5–6%.

The mean number of calves produced by an adult female living to the post-reproductive stage is estimated as the sum of age-specific pregnancy rates,  $\Sigma P_{n+0.5}$ . Assuming sexual maturity at 9.0 years (the mean for the population) and the age of the last parturition at 42 years (possible maximum from the age/pregnancy rate-regression equation), the number of calves is estimated as 4.39. If breeding longevity is assumed to be 35 years, then the calf production is estimated at 4.19. The difference is negligible.

The age-specific abundance of post-reproductive females given in Section 8 can be used to calculate the number of post-reproductive females as  $\Sigma(A_t \cdot S_t)$ , where  $S_t$  indicates the proportion of post-reproductive females at age  $t$  years. The approximate number of post-reproductive females, 25% of the adult females (Table 33), is calculated using the corrected abundance of these females, i.e. 8.5% (28–32 years), 19.6% (32–36 years), 33.3% (36–40 years) and 100% (over 40 years) in Table 24. The values observed from the data and predicted by the model are very similar.

Table 34

Criteria used to allocate individual specimens of *G. macrorhynchus* to the appropriate growth stage when gonad data incomplete

Order of preference	1	2	3
	Single-testis weight (g)	Age (years)	Body length (cm)
Male			
Immature	< 100	≤ 14.5	≤ 401
Early-maturing	100 to 170	15.5	402 to 413
Late-maturing	170 to 400	16.5	414 to 422
Mature	≥ 400	≥ 17.5	≥ 423
Female	Age (years)	Body length (cm)	
Immature	< 9	≤ 320	
Mature	≥ 9	≥ 321	

### 10. SCHOOL STRUCTURE, SOCIAL MATURITY AND FISHING SELECTION

#### 10.1. Materials and methods

The analysis is based on data from 18 schools (Nos. 7 through 24, see Table 1). The 13 schools shown in Table 36 are the most important with respect to the quality of the information obtained from them. Since these data were collected during six years, from 1975 to 1980, we

firstly examined whether the school structure had changed during this period by plotting various school parameters against the year of catch and calculating the resultant least-squares regression equations. In no instance was the regression coefficient significantly different from zero (*T*-test,  $P > 0.05$ ). The parameters tested were (1) school size,  $n = 18$ ,  $a = -2.73$ ,  $r = -0.4$ ,  $0.05 < P < 0.1$ , (2) proportion of adult males,  $n = 13$ ,  $a = 1.98$ ,  $r = 0.2$ ,  $0.3 < P < 0.5$ , (3) proportion of immature individuals of both sexes,  $n = 13$ ,  $a = -1.69$ ,  $r = -0.2$ ,  $0.3 < P < 0.5$ , (4) proportion of females,  $n = 17$ ,  $a = -0.01$ ,  $r = -0.001$ ,  $P > 0.9$ , (5) proportion of pregnant females,  $n = 14$ ,  $a = -3.64$ ,  $r = -0.3$ ,  $P > 0.9$ , (6) proportion of lactating females,  $n = 14$ ,  $a = -0.77$ ,  $r = -0.77$ ,  $r = -0.07$ ,  $P > 0.9$ , (7) proportion of resting females,  $n = 14$ ,  $a = 4.11$ ,  $r = 0.3$ ,  $0.3 < P < 0.5$ , (8) proportion of post-reproductive females,  $n = 12$ ,  $a = 6.16$ ,  $r = 0.4$ ,  $0.1 < P < 0.2$  (all proportions are in %, and those in (5)–(8) relative to number of total adult females). We therefore discounted any change in school structure during the sampling period.

The composition of the 18 schools of *G. macrorhynchus* classified on the basis of age, body length and reproductive status is illustrated in Figs. 27 and 28. Ages were estimated using annual growth layers in dentine or cementum, except for eight whales for which the

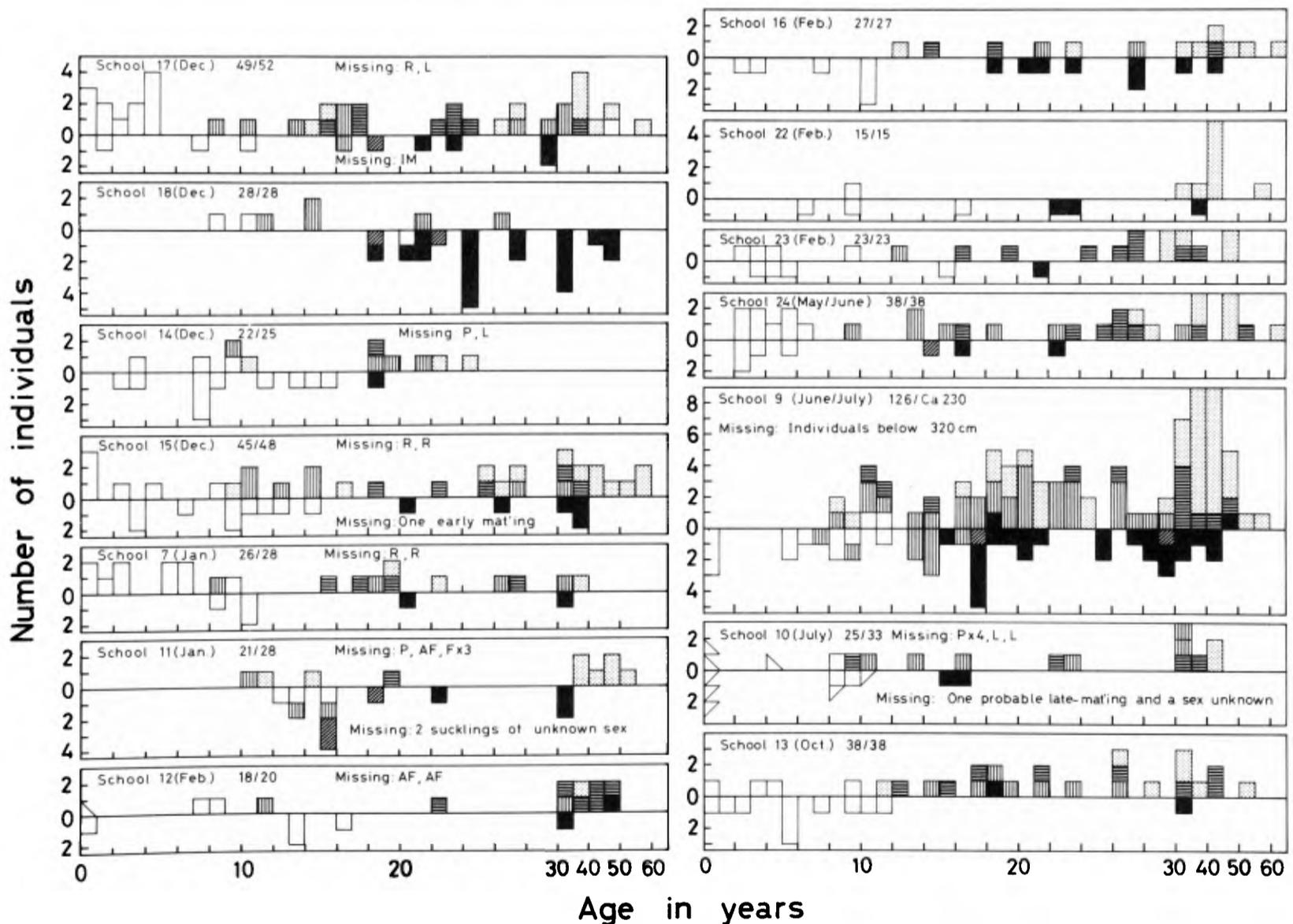


Fig. 27. School structure of *G. macrorhynchus* plotted against age. The school number, month of catch, number listed/number caught, and number and reproductive status of missing individuals are indicated at the top (IM-immature, AF-adult female, AM-adult male, F-female, M-male, L-lactating, P-pregnant, R-resting). Triangles indicate whales the ages of which have been estimated from body length. The frequency histograms for the females are on the top of the lines, those for males below the lines. Code for females. White: immature; vertical lines: pregnant; horizontal lines: lactating; dots: resting; black: known only as mature. Code for males. White: immature; vertical line: early-maturing; oblique line: late-maturing; black: mature.

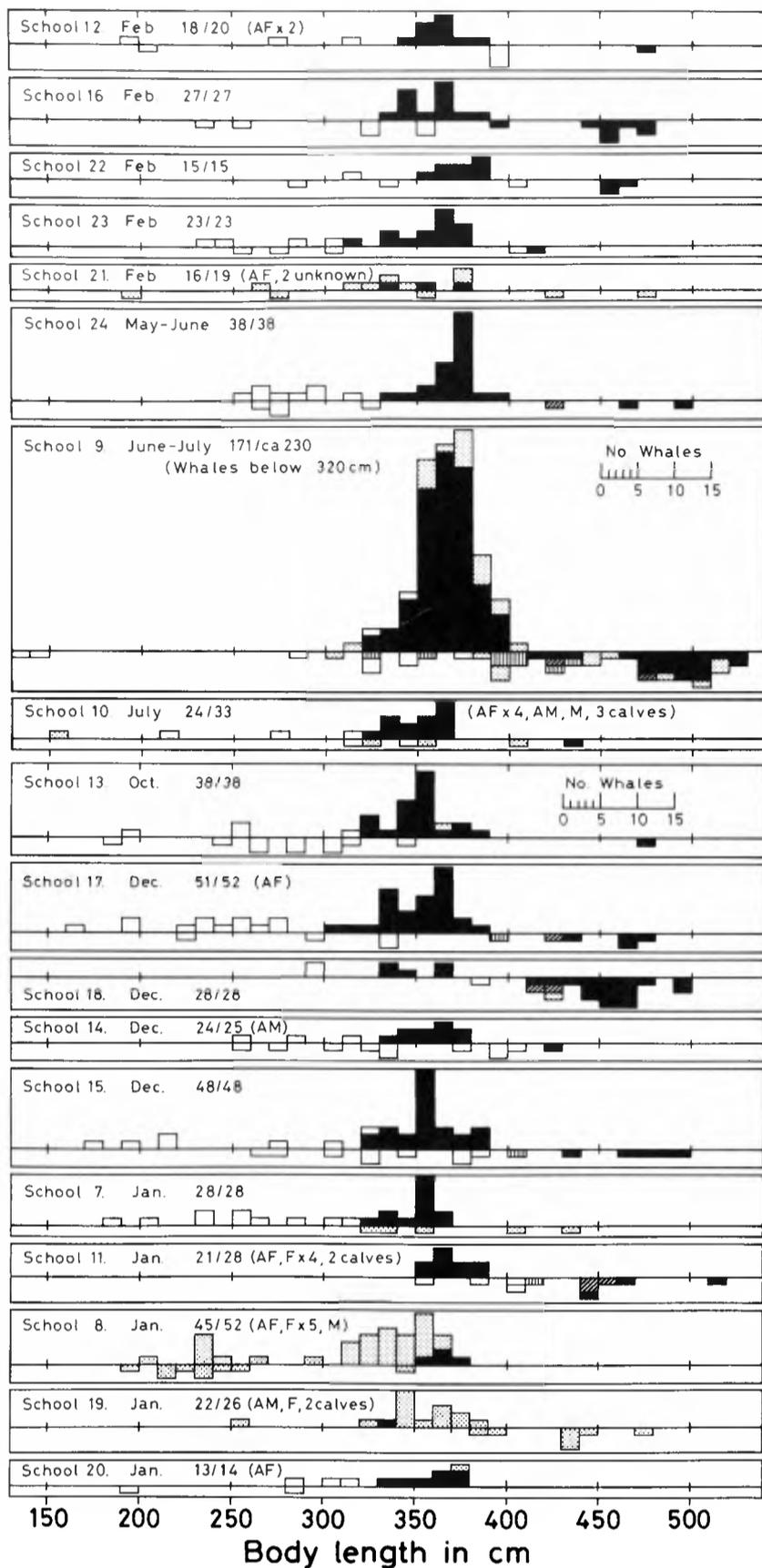


Fig. 28. School structure of *G. macrorhynchus* plotted against body length. Code for females (on the top of lines): white: immature; black: mature; dots: unknown. Code for male (below the lines): white: immature; vertical lines: early-maturing; oblique lines: late-maturing; black: mature; dots: unknown. Other marks (as in Fig. 27) are school number, month of catch, number listed/number caught, and number and reproductive status of missing individuals indicated at the top (IM-immature, AF-adult female, AM-adult male, F-female, M-male, L-lactating, P-pregnant, R-resting).

length-age relationship was used (see Kasuya and Matsui, in press). This method was applied to females under 290 cm or males under 385 cm, which correspond to ages of 6.0 and 14.0 years, respectively. The ages of 21 individuals (excluding those in School 9) were not estimated, either because their body lengths were not known (two calves in school 11) or because they were greater than the range for which the age-length relationship can usefully be applied. The sexual maturity of 11 males and three females was estimated using the

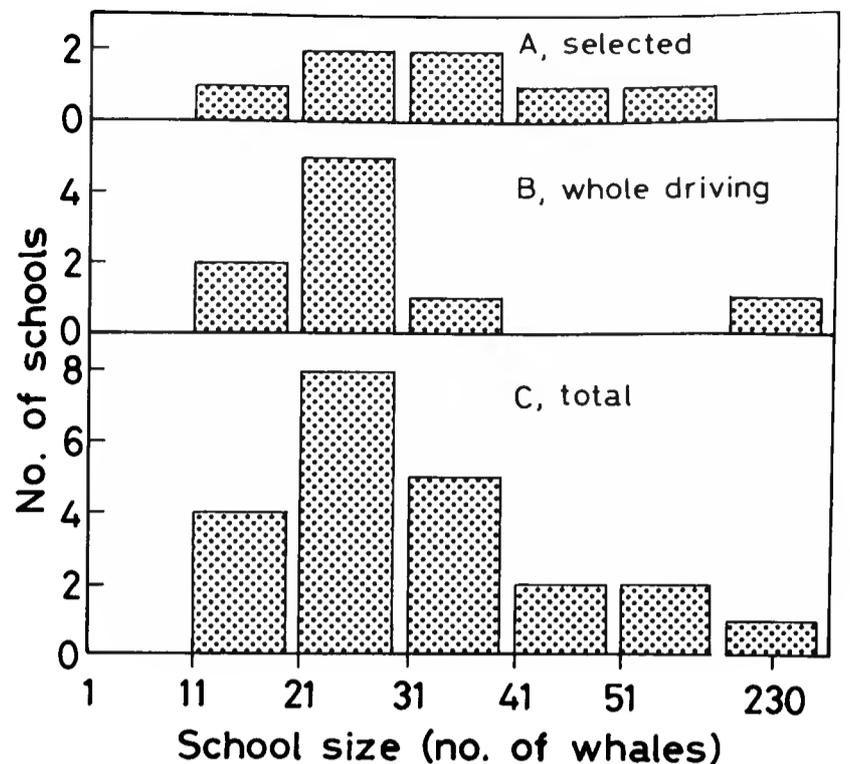


Fig. 29. School-size frequencies of *G. macrorhynchus* caught by the driving fishery. A: eight schools selected from aggregations, B: seven schools found alone, C: total of 21 schools including six schools of unknown status.

criteria in Table 34, while the reproductive status of most whales was determined by examining reproductive organs (Sections 4 and 5).

## 10.2. School size

As indicated in Section 2, eight schools were found alone and driven to shore (nos. 7, 11, 13, 14, 19, 20, 22 and 23), while seven schools were each driven from aggregations of several schools (nos. 10, 12, 15, 16, 17, 18 and 24). The fishermen reported that these aggregations were scattered over an area of several square nautical miles but that the smaller groups ('school', ordinary unit of driving) were more tightly grouped and distinct. The aggregations also often contained school(s) of another delphinid species, as analysed below.

School 9 was actually an aggregation containing, at first sighting, eight schools of *G. macrorhynchus* and one or more schools of *Tursiops truncatus* scattered over a wide area. Later the aggregation became tighter (presumably because of a nearby killer whale school) and was driven to port. The total number of pilot whales caught was about 230 ( $\bar{x} = 29$  whales per school, close to the mean school size calculated below).

Fig. 29 shows the school-size frequency for 22 drives, for 16 of which information was available about the school before driving commenced. The sizes of these 21 schools (excluding School 9) ranged from 14 to 52 whales ( $\bar{x} = 30.9$ ). The eight schools found alone consisted of 14 to 38 whales ( $\bar{x} = 24.6$ ) and were often smaller than seven schools taken from aggregations, which contained 20 to 52 whales ( $\bar{x} = 35.1$ ). Although the difference between the two means is not significant, we believe that the selected schools tend to be larger than the schools found alone, because the fishermen tend to select one of the larger schools in an aggregation if they can.

Kasuya (unpublished) has 21 shipboard observations of schools of *G. macrorhynchus* in the western North

Pacific with reliable estimates of school size. On two occasions, two schools were found 100 to 200 m apart. These groupings may correspond to the aggregations mentioned above. The school sizes ranged from five to 50 whales ( $\bar{x} = 20.6$ ;  $SD = 12.8$ ). Admitting inaccuracy in the shipboard estimation of school size, we conclude that this figure is close both to the sizes discussed above, and to the mean school size (25) reported for *G. macrorhynchus* off the coast of southern California (Brown and Norris, 1956).

Sergeant (1962a) reported that the 'herd' size of *G. melaena* averaged about 20 whales in pelagic waters and rarely exceeded 100, but that the size of schools stranded or driven ashore averaged about 85 whales and frequently exceeded 200. Sergeant also observed that many small 'groups' of about 15 to 25 whales scattered in Trinity Bay, Newfoundland, tended to come together when alarmed by aircraft.

We conclude that the groupings of short-finned pilot whales vary from solitary schools to loose aggregations of several schools and may comprise tight aggregations in certain (alarm) situations, e.g. when disturbed by aircraft (Sergeant, 1962a) or killer whales (School 9). The 'school' discussed below is probably the only long-lasting identifiable social unit of this species. Aggregations may provide member schools with occasional opportunities to mate or exchange individuals.

### 10.3. Effect of fishing bias on school composition

Tables 35 and 36 detail the differences in the composition of six schools found alone and seven schools taken from aggregations. (The incomplete data available from School 9 have been excluded).

The reproductive status of the males in aggregations and solitary schools is significantly different (chi-square test,  $0.02 < P < 0.05$ ) because of the higher number of adult males in the schools selected from aggregations (range 1 to 18;  $\bar{x} = 5.7$ ) compared with that in solitary schools (range 1 to 3;  $\bar{x} = 2.0$ ) (Table 36). This fishing bias is due to the fishermen's preference for adult males because of their large body size and preferred meat. The proportion of immature and maturing males is not different between the two catch types.

The proportion of the total females that are pregnant is higher in the schools taken from aggregations, while the proportion of resting females is lower, but the differences are not statistically significant (chi-square test on actual number of whales,  $0.3 < P < 0.5$ ). We know of no reasons why pregnant females would be caught in preference to resting females and consider that there is probably no conscious fishing bias in their favour.

Thus we conclude that the drive fishery may select (1) larger schools and (2) schools containing a higher number of adult males. This will cause the number of adult males in the population in Section 9 to be over-estimated. The ratio of mature males to mature females in the schools taken from aggregations is  $40/128 = 0.31$ , in contrast to  $12/80 = 0.15$  in the solitary schools (Table 35).

### 10.4. Inter-relationship of school members

The composition of the schools of *G. macrorhynchus* in our sample was highly variable with respect to the sex,

Table 35  
Comparison of schools taken from aggregations and solitary schools

Sex and reproductive status	Aggregations		Solitary schools	
	No. of whales	%	No. of whales	%
<b>Male</b>				
Immature	33.5 <sup>1</sup>	41.6	34 <sup>2</sup>	66.7
Early-maturing	2	2.5	2	3.9
Late-maturing	5	6.2	3	5.9
Mature	40	49.7	12	23.5
Total	80.5	100	51	100
<b>Female</b>				
Immature	36.5 <sup>1</sup>	22.2	23 <sup>2</sup>	22.3
Resting	45	27.4	36	35.0
Lactating	38	23.1	23	22.3
Pregnant	42	25.5	19	18.4
Mature unclassified	3	1.8	2	1.9
Total mature	128	77.8	80	77.7
Total	164.5	100	103	100
Missing (♀ and ♂)	1		0	

<sup>1</sup> Half of three calves of unknown sex included.

<sup>2</sup> Half of two calves of unknown sex included.

age and reproductive status of school members (Table 36, Figs 27 and 28).

**Mature males.** With the exception of School 20, each of the 27 schools examined contained at least one mature male. The number of mature males in solitary schools ranged from one to three. In contrast, four of seven schools taken from aggregation contained four to 18 mature males. We consider that these schools were selected and that they may be over-represented in our sample. Thus in the thirteen schools for which detailed figures are available (Table 36) the ratio of mature females to mature males varies from 1.6 to 23.0 (excluding 0.3 in School 18, which contained 18 adult males). When the apparently post-reproductive resting females are excluded, the mature male: mature female ratios of 11 schools in Table 36 are between 1.1 and 21.0 (excluding 0.3 values for unusual Schools 18 and 22). Since all these 11 schools contained both pregnant and lactating females, they are certainly breeding schools. Thus we conclude that there is usually an excess of reproductive females over mature males in breeding schools of *G. macrorhynchus*, and that the species is polygynous like *G. melaena* (Sergeant, 1962a).

School 18 was exceptional, with 18 mature and two 'late-maturing' males. Only one of the five pregnant females in School 18 was classified as being in 'recent oestrus', the remaining four females being in various stages of pregnancy (Fig. 30 and Table 36). In contrast, Schools 13, 10 and 24 had more oestrous females than school 18 but fewer mature males. Thus it seems unlikely that males congregate around oestrous females. We also tested the correlation between the number of adult males and that of other members in the school. None of the correlations was statistically significant. These results suggest that either mature males stay in the same breeding school for a period exceeding one female breeding cycle, or that their movement between breeding schools is controlled by (unknown) factors other than the female reproductive cycle.

Table 36  
School composition in *G. macrorhynchus*

School no.	School taken from aggregation							Solitary school					
	10 <sup>2</sup>	12	15	16	17	18	24	7	11	13	14	22	23
<b>Male maturity</b>													
1. Immature	5.5 <sup>3</sup>	4	9	6	4	1	4	3	4 <sup>5</sup>	10	10	3	4
2. Early-maturing	0	0	1	0	1	0	0	0	2	0	0	0	0
3. Late-maturing	1	0	0	0	1	2	1	0	3	0	0	0	0
4. Mature	2	1	5	8	4	18	2	2	3	1	2	3	1
5. Unclassified	0	0	0	0	0	0	0	0	0	0	0	0	0
6. Total	8.5	5	15	14	10	21	7	5	12	11	12	6	5
<b>Female maturity</b>													
7. Immature	5.5 <sup>3</sup>	3	6	0	12	2	8	10	1 <sup>5</sup>	4	3	1	4
8. Mature	18	12	27	13	30	5	23	13	12	23	10	8	14
9. Unclassified	0	0	0	0	0	0	0	0	3	0	0	0	0
10. Total	23.5	15	33	13	42	7	31	23	16	27	13	9	18
<b>Reproductive status of adult female</b>													
11. Oestrous <sup>1</sup>	3	0	1	0	0	1	5	2	0-4	5-6	0	0	0
12. Pregnant	10 <sup>4</sup>	2	7	2	9	5	7	4	2-6	7-8	5	0	1
13. Lactating, all	7 <sup>4</sup>	6-9	5	3	10	0	8	4	1-5	8-9	2	0	8
14. Lactating, post-reproductive	0-2	3-4	0	1	1	0	1	0	0-4	2	0-1	0	2
15. Resting, reproductive	0	0-2	9	4	8	0	3	5	4-8	6-7	3	1	3
16. Resting, post-reproductive	2	1-2	6	4	3	0	5	0	4-8	1	0	7	2
17. Unclassified	0	3	0	0	0	0	0	0	4	1	0	0	0
18. Total	18	12	27	13	30	5	23	13	12-15	23	10	8	14
<b>Age composition, male</b>													
19. < 9 years	3.5 <sup>3</sup>	1	3	3	3	0	4	1	1 <sup>5</sup>	7	6	1	3
20. 9 to 23 years	4-5	3	8	6	4	7	3	3	9	3	5-6	3	2
21. > 23 years	0-1	1	4	5	3	14	0	1	2	1	0-1	2	0
22. Unclassified	1	0	0	0	0	0	0	0	0	0	1	0	0
23. Total	8.5	5	15	14	10	21	7	5	12	11	12	6	5
<b>Age composition, female</b>													
24. < 9 years	5.5 <sup>3</sup>	3	6	0	13	1	8	10	1 <sup>5</sup> -4	3	2-4	0	3
25. 9 to 35 years	9-15	4-6	17-19	7	19-21	6	15	10-12	4-8	20	9-11	2	12
26. > 35 years	3-9	6-8	8-10	6	8-10	0	8	1-3	6-10	4	0-2	7	3
27. Unclassified	6	2	2	0	2	0	0	2	4	0	2	0	0
28. Total	23.5	15	33	13	42	7	31	23	16	27	13	9	18

<sup>1</sup> Females with corpus luteum of 'ovulation' or with foetus smaller than 10 cm in body length.

<sup>2</sup> One individual of unknown sex excluded.

<sup>3</sup> Half of three suckling calves of unknown sex included.

<sup>4</sup> One pregnant and simultaneously lactating female included.

<sup>5</sup> Half of two suckling calves of unknown sex included.

The wide variation in the proportion of mature males in breeding schools (Table 36) and the polymodal mature-male age frequency in some schools (Schools 9 and 24) (Fig. 27) suggest that males do not necessarily stay in one breeding school for their entire lifetime but may aggregate (School 18) or move away from a school (as in Schools 13 and 20) to another breeding school. However, as mentioned below, there is no indication that any particular component of the adult male population is geographically segregated from the sampling area (also see Section 9.3).

**Maturing male.** The maturing stage (early and late-maturing stages combined) includes whales ranging from the immature to the fully sexually-mature stages. We expect the social behaviour of these individuals to vary widely. The 13 schools contained a total of only 12 maturing males.

As shown in Table 36, the maturing males were not evenly distributed among schools. Only six schools contained males at this stage; five maturing males were

present in School 11. This school contained an additional three immature males of similar age (Fig. 27). These findings suggest that males may tend to aggregate at the arrival of puberty (usually between 10 and 20 years of age) and may occasionally leave their mothers' school to join with other pubertal males. This is also supported indirectly by the occasional lack of males in these age ranges (Schools 13, 16 and 18).

**Adult females and immature individuals.** As expected, the number of lactating females in a school shows significant positive correlation with the number of immature individuals (Spearman rank correlation coefficient,  $P < 0.025$ ). The number of pregnant females is also positively correlated with the number of immature individuals ( $P < 0.025$ ), presumably because a calf remains in the breeding school for some time after weaning. The significant positive correlation between the number of immature individuals and the number of reproductive resting females in a school also supports this conclusion ( $P < 0.025$ ).

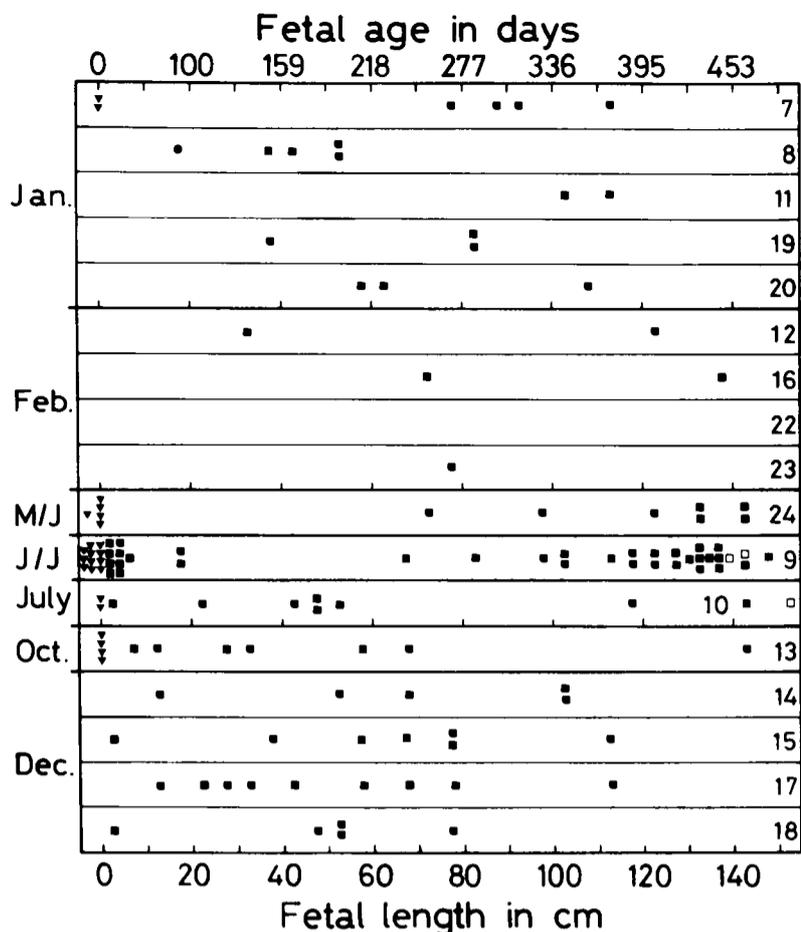


Fig. 30. Body-length frequencies of foetuses (black squares) and newborn calves (white squares) below 155 cm in body length. The school number is indicated at the right. Nonpregnant females with corpus luteum of 'ovulation' (triangles) are plotted on 0 cm length. The foetal age indicated at the top has been calculated from foetal length using the equation at the base of Table 9.

The age composition of the females within schools of *G. macrorhynchus* (Fig. 27) suggests that pubertal females, unlike males, do not aggregate or move between schools. Thus a female probably remains in its mother's school for life.

Fig. 30 shows the body-length frequency of foetuses and calves under 155 cm. The corpus luteum of 'ovulation' of non-pregnant females is plotted on zero body length. This is an obvious over-simplification, because a corpus luteum of 'ovulation' persists for an unknown (but probably short) time (Marsh and Kasuya, 1984). In contrast to the pattern in *Stenella attenuata* (Kasuya *et al.*, 1974) and *S. coeruleoalba* (Kasuya, 1972), the calculated dates of conceptions are not synchronized in most schools of *G. macrorhynchus* but dispersed over several months. This lack of synchrony could occur either when a school is a cohesive long-term unit in which oestrus is not synchronized, or when school members are recombined randomly at frequent intervals. In view of the results discussed above, we reject the second explanation.

The number of post-reproductive resting females in a school is not correlated with the number of immature whales ( $P > 0.05$ ). We suggest that this is because the last lactation ( $> 6$  years) and the post-reproductive life time (about 14 years on average) of females is long enough for most of their calves to attain puberty or sexual maturity.

The number of resting females classified as post-reproductive per school ranged from zero to seven individuals, with modes at zero and four. However, the number of such females is almost certainly higher than

this because (1) our classification of a female as post-reproductive is conservative (Section 8), and (2) information is incomplete for some whales (Table 36 and Figs 27 and 28). Our results certainly do not suggest that the presence of post-reproductive resting females and/or old ( $> 40$  years) lactating females is essential for a school (Table 36).

Post-reproductive females usually seemed to be associated with adult females of other reproductive stages. School 22 is an exception to this pattern, with eight resting females, one immature female (9.5 years), three immature males (ages six to 17 years) and three mature males. Seven of the eight resting females were classified as post-reproductive, using the criteria of Marsh and Kasuya (1984). The ovaries of the remaining adult female, aged 35.5 years, contained one large follicle (15.1 mm) and a young corpus albicans, indicating that it had ovulated recently. School 22 might be the result of a recent school split. Alternatively, the immature whales might have been the offspring of the youngest two or three adult females (aged 33.5, 38.5 and 40.5 years at capture), none of which had managed to bear and rear a calf for the previous six years. Thus even this unusual school is not inconsistent with our thesis that each school is a stable matrilineal kinship group.

### 10.5. Social maturity

We estimated in Section 4.5 that males attain 'functional maturity' when their testes reach the 'late-maturing' stage. We will now attempt to identify when males reach 'social maturity', the stage when they can successfully impregnate females, as defined by Best (1969) and Ohsumi (1971) for another polygynous species, the sperm whale.

The data available are limited to 14 breeding schools (13 schools in Table 36 and School 20 in Fig. 28). One school (no. 20) contained neither mature nor maturing males (by histological criteria), but all of the remainder contained at least one mature male, while only four had both mature and maturing males. No school was found with maturing but no mature males. This suggests that maturing males cannot substitute for mature males.

We examined the age of the youngest histologically-mature male in relation to the number of males at this stage in the same school. Their ages ranged from 18.5 to 34.5 years ( $\bar{x} = 26.8$ ) for the four schools containing one mature male; 15.5 to 20.5 years ( $\bar{x} = 17.5$ ) for three schools having two mature males; 22.5 years for both schools having three mature males; and from 18.5 to 21.5 years ( $\bar{x} = 19.8$ ) for four schools with more than three mature males. If the lower range of the first group was higher than those of the latter groups, it could be suggested that some of the histologically mature males may not be socially mature. However the similarity of the lower ranges suggests that 'social maturity' is not different from 'histological maturity'. The sperm whale is similar (Best, 1969). In *G. macrorhynchus*, therefore, 'social maturity' (= histological 'mature stage') is attained at about 17 years, or two years after the start of puberty (= histological 'early-maturing stage') and 10 years before the cessation of growth in mean body length.

### 10.6. Interspecific aggregations

Five of the 12 drives of pilot whales for which this information was available were not accompanied by other cetaceans. (Four of these drives were of solitary schools.)

Bottlenose dolphins were found near the pilot whales in six drives, five of which were of aggregations of pilot whale schools. One solitary school (no. 14) was found near schools of both bottlenose dolphins and Pacific white-sided dolphins, *Lagenorhynchus obliquidens*.

Twenty-three schools (21 encounters) of *G. macrorhynchus* in the western North Pacific were observed from ships (Kasuya, unpublished). Bottlenose dolphins were observed near the pilot whales on seven occasions, including one aggregation of two schools. Pacific white-sided dolphins were also seen near one pilot whale school. Thirteen encounters (14 schools) were with pilot whales only. Interspecific aggregations were limited to coastal waters, perhaps because of their higher productivity and the relatively coastal habitat of *Tursiops* and *Lagenorhynchus*.

We conclude that short-finned pilot whale schools are often associated with bottlenose dolphins or Pacific white-sided dolphins, particularly when in a large aggregation, and suggest that such an aggregation is a temporary concentration of schools, probably in a feeding area.

### 10.7. Discussion

*School structure.* We conclude from the above analyses that the *G. macrorhynchus* school is usually a breeding unit composed of adult males, adult females of various reproductive stages (including post-reproductive individuals), and immature and pubertal individuals of both sexes. At puberty, some males may leave the school where they were nursed to join with other males of the same stage, presumably when schools aggregate in a feeding area. Adult males, usually one to three per school, may also move between schools occasionally and form schools dominated by adult males. We have no evidence of social or geographical segregation of pubertal or mature males. Females probably attain sexual maturity in their mother's school. The association of females persists for a long time, at least for more than one calving cycle, and presumably usually for life. Females and juvenile males in one school are probably consanguineous.

We tentatively suggest that the school structure of *G. macrorhynchus* differs from that of the sperm whale (Ohsumi, 1971; Best, 1979) as follows: (1) some immature male and female sperm whales apparently segregate from their breeding schools; (2) some adult male sperm whales segregate from the breeding schools socially and geographically. Although the sperm whale is polygynous, there appears to be little difference between the natural mortality rates in the two sexes (Ohsumi, 1966) and there are large numbers of 'surplus' males which segregate geographically from the breeding area (Ohsumi, 1971; Best, 1979). This segregation perhaps allows the surplus adult males to avoid competition for resources with the breeding population. In contrast, our results for *G. macrorhynchus* suggest that the male mortality rate is

much higher than that of the female, so that there does not appear to be many 'surplus' males in the population. Therefore, assuming that intrasexual competition among adult males is not a major source of mortality, we suggest that such competition is not great in *G. macrorhynchus*, as already indicated for *G. melaena* (Sergeant, 1962a). It is of course possible that our results are an artefact of a sampling bias caused by geographical segregation. However, the sex differences we have observed in maximum longevity (46 years for males, 63 years for females) suggest that this is not the case and contrast with Ohsumi's (1966) results for sperm whales in the breeding areas off Japan. As both pilot whales and sperm whales have been subjected to fishing pressures which have selected for adult males, it does not seem likely that these results are historical consequences of the respective fisheries.

*Fishing selection.* Adult males are probably over-represented in our sample because of the selection of schools with a large number of adult males from aggregations. The adult male/female ratio in the 'solitary' schools is 0.15, in contrast to 0.29 for the whole sample (Tables 35 and 36). Assuming that the ratio in the 'unselected' catch is close to the true population parameter we suspect that the ratio obtained in Section 9 (Table 33) is nearly twice the true figure. Although this bias may actually cause an under-estimation of the male mortality rate and of the population size in the 1940's (Section 9), we consider that we do not have enough data to make meaningful corrections.

*Over-representation of pregnant females.* Our analyses of school structure indicate that the percentage of adult females that were lactating varied from 0 to 50% ( $\bar{x} = 26.5\%$ ;  $SD = 17.3\%$ ) but do not suggest fishery selection for pregnant females or against lactating females. Thus we conclude that the sample bias discussed in Section 8 may have been caused by the geographical concentration of schools that contain a high proportion of pregnant females in our sampling area, which was limited to coastal waters near the northern limit of the range.

The drive fishery for striped dolphins also shows a similar but less intense bias towards pregnant females. However, the fishery for the spotted dolphin shows the opposite bias (Kasuya, in press). In Dall's porpoise (*Phocoenoides dalli*) in the western North Pacific, mother and calf pairs are known to segregate from the other animals in August in the northern part of the range of this species (Kasuya and Jones, in press). There is also some evidence of segregation in the white whale (Brodie, 1971). In Mysticeti, reproductive status affects the timing of the migrations of humpback and gray whales (Lockyer and Brown, 1981; Lockyer, 1984).

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# Changes in the Ovaries of the Short-Finned Pilot Whale, *Globicephala macrorhynchus*, with Age and Reproductive Activity

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## ABSTRACT

Macroscopic examination of the ovaries of 298 specimens of *Globicephala macrorhynchus* obtained from a driving fishery off the Pacific Coast of Japan was supplemented by histological and histochemical study of a representative series of ovarian structures. The patterns of follicular development and atresia and corpora-luteum development and regression are described. The atresia of macroscopic follicles was frequently accompanied by thecal luteinization producing conspicuous corpora atretica which did not persist. We could not separate corpora lutea of pregnancy from those of 'ovulation'. The corpus luteum persisted throughout the gestation period but with apparent change(s) in lipid metabolism. Some corpora albicantia regressed fully within two years, but the rate of regression probably varied with hormonal status. Corpora albicantia persisted for life as a record of ovulations.

Almost all the whales were aged using dentinal and/or cemental growth-layer groups. The age-specific decline in the pregnancy rate was paralleled by a decline in the ovulation rate, and infertile ovulations were more common in older females. Females ceased to ovulate before age 40 years. About 25% of mature females had senescent ovaries which were severely depleted of oocytes (presumably because of the exceptionally high atresia rate) and histologically similar to post-menopausal human ovaries. Female short-finned pilot whales in this population thus had a definite post-reproductive phase in their life cycle.

## INTRODUCTION

The ovaries of various cetaceans have been studied as indices of relative age and terminal reproductive status and as records of reproductive history. However, with few exceptions, scientists have had no direct information on the species' reproductive physiology or life history. Thus the interpretation of cetacean ovaries has been rather like running an experiment without a control.

Research methods have been determined largely by specimen availability. Harrison and his co-workers have made detailed macroscopic and histological examination of the ovaries of mostly fairly small samples of a large variety of odontocete species (e.g. Harrison, 1949, 1972; Harrison, Boice and Brownell, 1969; Harrison and Brownell, 1971; Harrison and Ridgway, 1971; Harrison, Brownell and Boice, 1972; Harrison and McBrearty, 1973-74, 1977; Collet and Harrison, 1981). This approach gives precise information about each ovary, but interpretation has usually been hampered by sample size and/or lack of information about the ages of the animals.

Interpreting ovaries on the basis of macroscopic examination alone is less precise, but much less time-consuming, and has been the usual method of studying ovaries from a large series of conspecifics obtained from a fishery. Interpretation of these data has been facilitated by an independent estimate of each animal's absolute age in some studies (e.g. Ohsumi, 1965; Kasuya, Miyazaki and Dawbin, 1974; Perrin, Coe and Zweifel, 1976; Miyazaki, 1977; Perrin, Holts and Miller, 1977), but not others (e.g. Chittleborough, 1954; Sergeant, 1962; Gambell, 1968, 1972).

Laws (1958, '59, '61), Best (1967), Fisher and Harrison (1970), Hirose, Kasuya, Kazihara and Nishiwaki (1970),

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Zimushko (1970) and Harrison, Bryden, McBrearty and Brownell (1981) have combined the advantages of both these approaches. They have macroscopically examined the ovaries of a large series of conspecifics and have used histology as a supplementary tool. Unfortunately, these studies were hampered by a lack of absolute-age data.

In this study, we have attempted to maximize the information value of the ovaries from each pilot whale by examining them macroscopically and, where necessary, histologically. An independent estimate of the whale's absolute age was subsequently used to enhance our ability to interpret these observations.

## MATERIALS AND METHODS

The ovaries examined were collected from 298 specimens of *Globicephala macrorhynchus* caught in the driving fishery off the Pacific Coast of Japan between 1975 and 1981 in the following months: January, February, May, June, July, October and December. Each whale was assigned an accession number which is a hyphenated combination of the school number and the number of the animal within the school, e.g. whale 13-24 refers to whale 24 in School 13. The methods used to collect and preserve specimens from each whale are outlined in our companion paper (Kasuya and Marsh, 1984). The ovaries from 298 whales from Schools 7, 9 to 18, 20, 22 to 27 (Kasuya and Marsh, loc. cit.) were examined by Marsh (those from Schools 7 and 17 were also checked by Kasuya) without knowledge of the age estimate for each whale, which was obtained by Kasuya by counting dentinal and/or cemental growth layers as described by Kasuya and Matsui (1983).

Each formalin-fixed ovary was trimmed of its bursa and weighed to the nearest 0.1 g. The number of corpora lutea, corpora albicantia, and corpora atretica were

Table 1

The characteristics on which the macroscopic classification of corpora albicantia was based

Characteristic	Class of corpus albicans		
	Young	Medium	Old
<i>External structure</i>			
Protuberance from ovarian surface	As small corpus luteum	Usually slight except for stigma	Stigma only
Shape	As small corpus luteum	May be round or flattened against surface	Irregular, may be round or flattened against surface
Stigma	Obvious as on corpus luteum	Smaller than young corpus albicans	White, usually puckered plaque
Nature of surface	Smooth	Smooth	
<i>Internal structure</i>			
Trabeculae	Obvious	Less obvious	Not visible
Periphery	Obvious	Obvious	Traced with difficulty
Colour	Pale orange to white	Usually white, may have orange/brown pigment especially near centre	White, may have trace of brown pigment
Blood vessels	Mainly around periphery	Relatively much more obvious	Form bulk of structure
Avascular connective tissue	Forms bulk of structure (although still vascular in very young CA)	Much less	Very reduced, may be almost absent

counted by hand-slicing the cortex and medulla at one- to two-mm intervals. The hilar region was left intact to hold the slices together.

On the assumption that the macroscopic appearance of a corpus albicans was likely to be a more reliable index of its age than its diameter would be, each corpus albicans was classified as young, medium, or old according to the characteristics outlined in Table 1 before it was measured.

Three diameters of all corpora lutea, corpora albicantia, corpora atretica, and the largest follicles present in each ovary were measured to the nearest 0.1 mm with vernier calipers. The mean diameter of each structure was calculated as the cube root of the product of the three diameters.

Each sample for histology was dehydrated through a graded series of ethanols, cleared in xylene, embedded in *Paraplast* and sectioned at 5  $\mu$ m. One section from each sample was stained with *Mayer's* haemalum and *Young's* eosin-erythrosin (Marsh, Heinsohn and Spain, 1977); another with either a variant of Gomori's trichrome (Gomori, 1950), or van Gieson's stain (Curtis, 1905) with celestin blue haemalum.

A cryostat was used to cut frozen sections of selected formalin-fixed follicles, corpora lutea, corpora albicantia, and corpora atretica at 8  $\mu$ m. These sections were stained for lipids with a modification of Herxheimer's method using Oil-Red 0 and Sudan IV (Drury and Wellington, 1967); or with haematoxylin and eosin as above.

The ovaries of the whales in School 17 were examined first. During the macroscopic examination of these ovaries we sampled a wide range of structures for histology. Each of these ovaries was then re-examined along with the corresponding histological slides. This provided a check on our macroscopic identifications and a firm basis for the subsequent macroscopic examination of the remaining ovaries, which was also supplemented with histology as required. After all the ovaries had been

sliced and examined, the corpora albicantia count for each was rechecked macroscopically. This was facilitated by marking each corpus albicans with a pin as it was counted.

The Non-Linear Regression Program from IMSL (Anon., 1975) was used to fit the curve describing the relationship between corpus count and age.

## RESULTS

### Weight of ovaries

#### *Immature whales*

The ovaries of immature specimens of *G. macrorhynchus* are lozenge-shaped organs about 3 cm long by 0.8 cm high by 1.5 cm wide in a three-month old animal and about 3.5 cm long by 1 cm high by 2 cm wide in a nine-year old female approaching maturity. In our sample of 36 immature females, the weight of both ovaries (Figs 1 and 2) ranged from 2.5 g (at 0.5 year) to 11.5 g (8.5 years old)

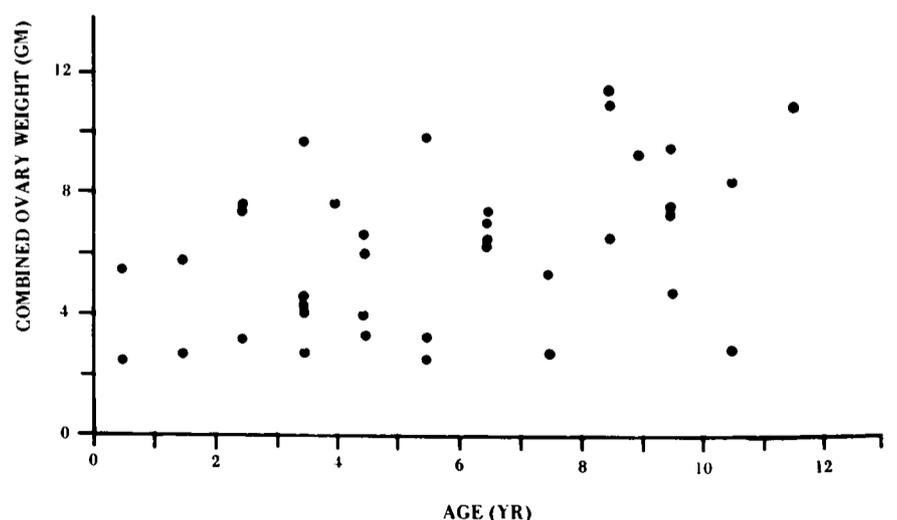


Fig. 1. Scatterplot of combined ovary weight against age for immature females of *G. macrorhynchus*.

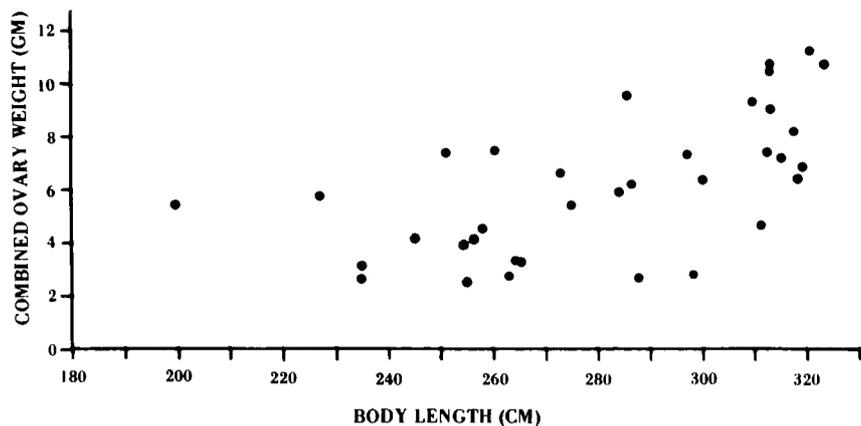


Fig. 2. Scatterplot of combined ovary weight against body length for immature females of *G. macrorhynchus*.

(mean ( $\bar{x}$ ) 6.2 g; standard deviation ( $s$ ) 2.6 g). Even though there was considerable variation in ovary weight for animals of the same age (Fig. 1) or body length (Fig. 2), combined-ovary weight was positively correlated with both factors. (Age:  $r = 0.45$ ;  $P < 0.01$ ; Body length:  $r = 0.63$ ,  $P < 0.001$ ).

*Mature whales*

The ovaries of mature whales were usually readily distinguishable from those of immature animals by the presence of the obvious surface scars of the corpora albicantia (CAs) (e.g. Fig. 3E). The size of mature ovaries varied greatly with age and reproductive status.

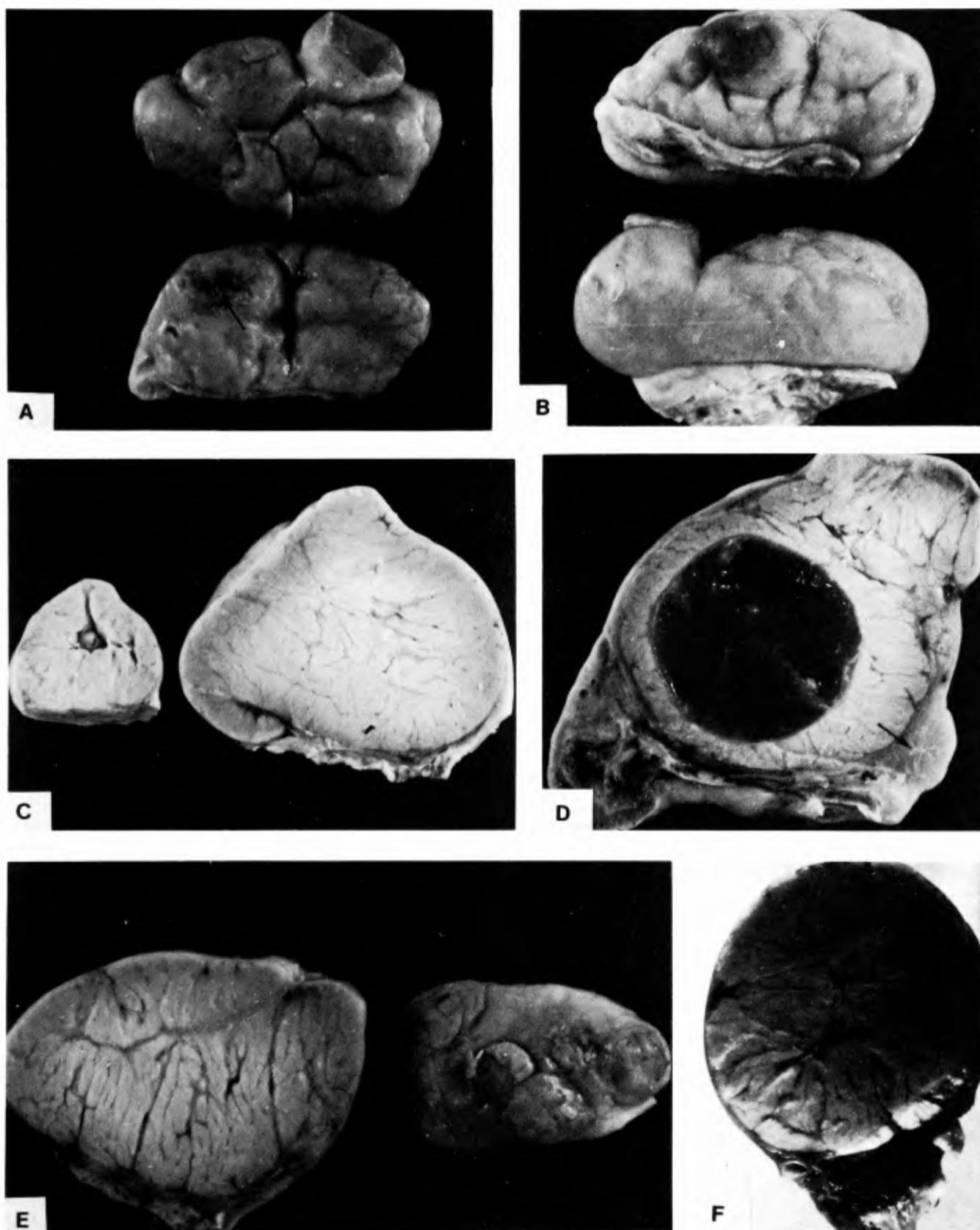


Fig. 3. Ovaries of *G. macrorhynchus* actual size. A. Ovaries of resting Whale 13-35 (11.5 years). The upper (left) ovary contained a large follicle (mean diameter 13.6 mm): the lower (right) ovary, a recent rupture point (arrowed) and a medium corpus albicans (at right end). B. Ovaries of lactating Whale 13-36 (21.5 years). The stigma of a corpus atreticum *a* can be seen in the upper (right) ovary. A young corpus luteum of 'ovulation' is visible at the left end of the lower (left) ovary. C. Median slices through a young corpus luteum of 'ovulation' (right) in the right ovary of lactating Whale 10-1 (22.5 years) and a corpus luteum of late pregnancy (fetal length 146 cm) in the left ovary of Whale 9-101 (23.5 years). D. Median slice through a young corpus luteum of early pregnancy (fetal length 1.2 cm) with an unusually large jelly-filled centre. An adjacent medium corpus albicans is arrowed (from Whale 9-79, 14.5 years). E. Ovaries of Whale 9-113 (23.5 years) which was pregnant with a 3-mm fetus. The corpus luteum (median slice at left) was in the right ovary and was already well-established. The left ovary contained one young and six old corpora albicantia; five of these are visible in the photograph. F. Median-slice through a large corpus luteum of 'ovulation' in the right ovary of resting Whale 25-32 (18.5 years).

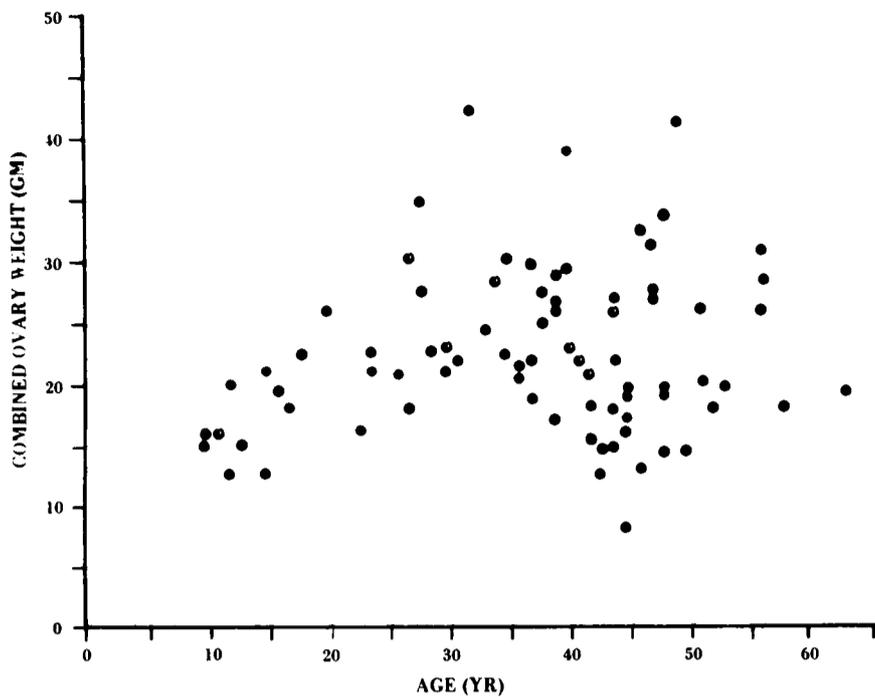


Fig. 4. Scatterplot showing the combined ovary weights of resting females of various ages. Note the lack of a generalized reduction in ovary weight for females over 40 years old, all of which were classified as post-reproductive.

For the 69 pregnant whales, the weight of both ovaries ranged from 32.7 g (in a newly-mature 8.5-year old animal) to 109.3 g (in a 22.5-year old female with a particularly large corpus luteum (CL) that was 44.9 mm in mean diameter) ( $\bar{x}$  56.8 g;  $s$  15.8 g). The pregnant ovaries were significantly heavier ( $t$  test;  $P < 0.01$ ) than those from 14 females with a CL but no detectable fetus; the latter ranged from 16.6 g to 79.4 g in combined weight ( $\bar{x}$  42.9 g). The mean weight of the smaller ovary (i.e. the ovary without a CL) of 78 pregnant whales was 10.5 g ( $s$  4.82 g). This was significantly heavier than the smaller ovary of 128 whales which were neither pregnant nor ovulating (i.e. no CLs or large follicles present) ( $\bar{x}$  9.1 g,  $s$  3.3 g) ( $t$  test;  $P < 0.05$ ). This result suggests that even the inactive ovary undergoes some enlargement during pregnancy.

The weights of both ovaries of the 55 lactating females (excluding those with a CL) ranged from 9.3 g to 50.5 g ( $\bar{x}$  23.2 g;  $s$  7.8 g), significantly lighter ( $t$  test;  $P < 0.0005$ ) than the pregnant ovaries but not significantly different in weight ( $t$  test;  $P > 0.2$ ) from the ovaries of 80 resting

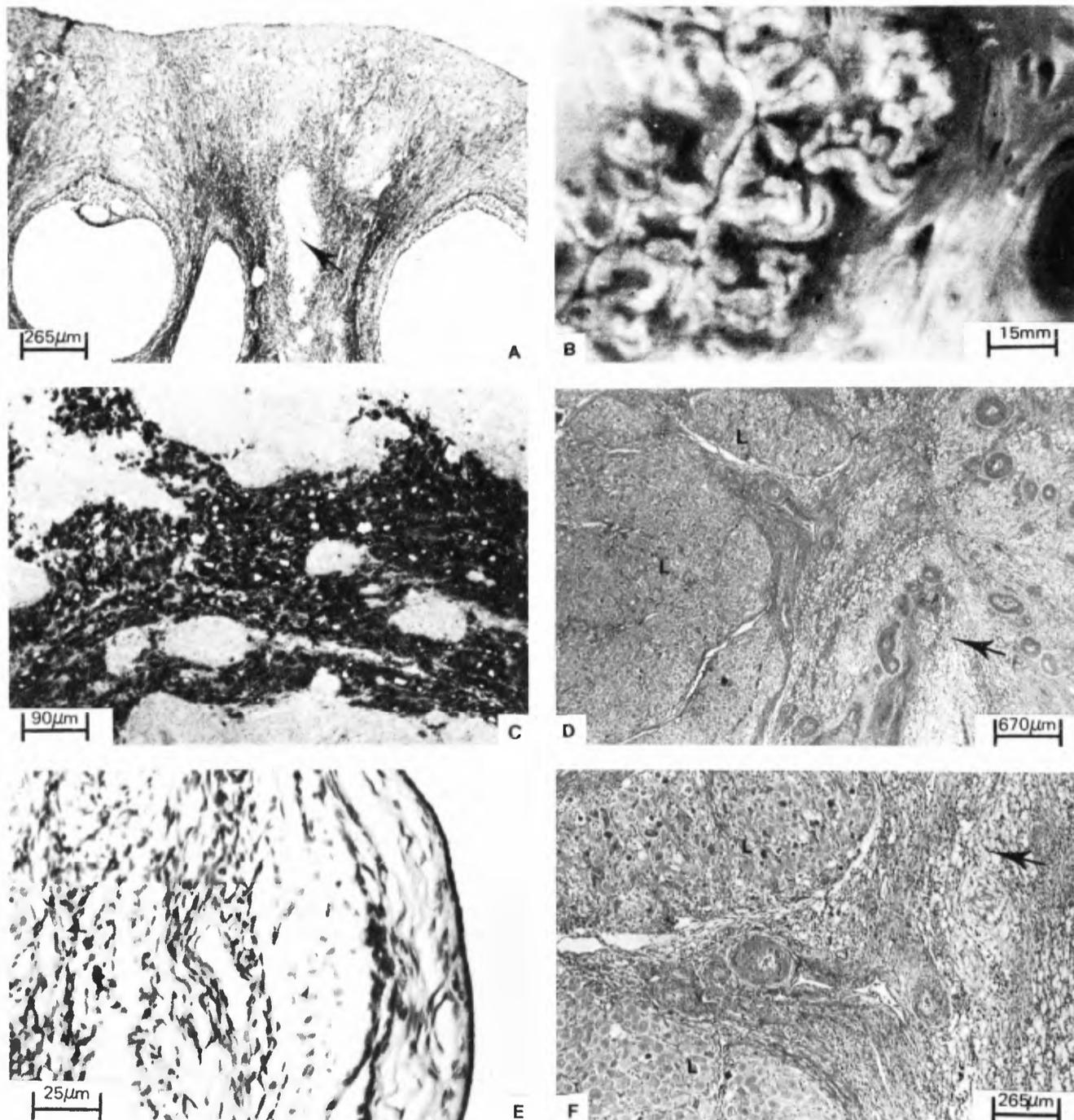


Fig. 5. Different forms of follicular atresia in *G. macrorhynchus* (see also Fig. 11B). A. Cortex of the ovary of immature Whale 17-33 (4.5 years) showing numerous primordial and antral follicles and one corpus fibrosum (arrowed) stained with haematoxylin and eosin. B, D, F. Corpus atreticum *a* (mean diameter 6.2 mm) in the ovary of lactating Whale 17-17 (15.5 years). B. Part of a median slice showing the irregular outline of the corpus. D, F. Histological preparations stained with Gomori's trichrome showing that some lobes of the well-vascularized corpus are still composed of luteal cells (L) while others (arrowed) are undergoing 'fatty' degeneration. C. Part of a corpus atreticum *b* in the ovary of resting Whale 16-9 (40.5 years) stained for lipid with Oil-Red O. E. The wall of one of three cystic follicles in the ovary of resting Whale 25-31 (34.5 years). The granulosa and theca cells have been replaced by fibrous tissue. Stained with haematoxylin and eosin.

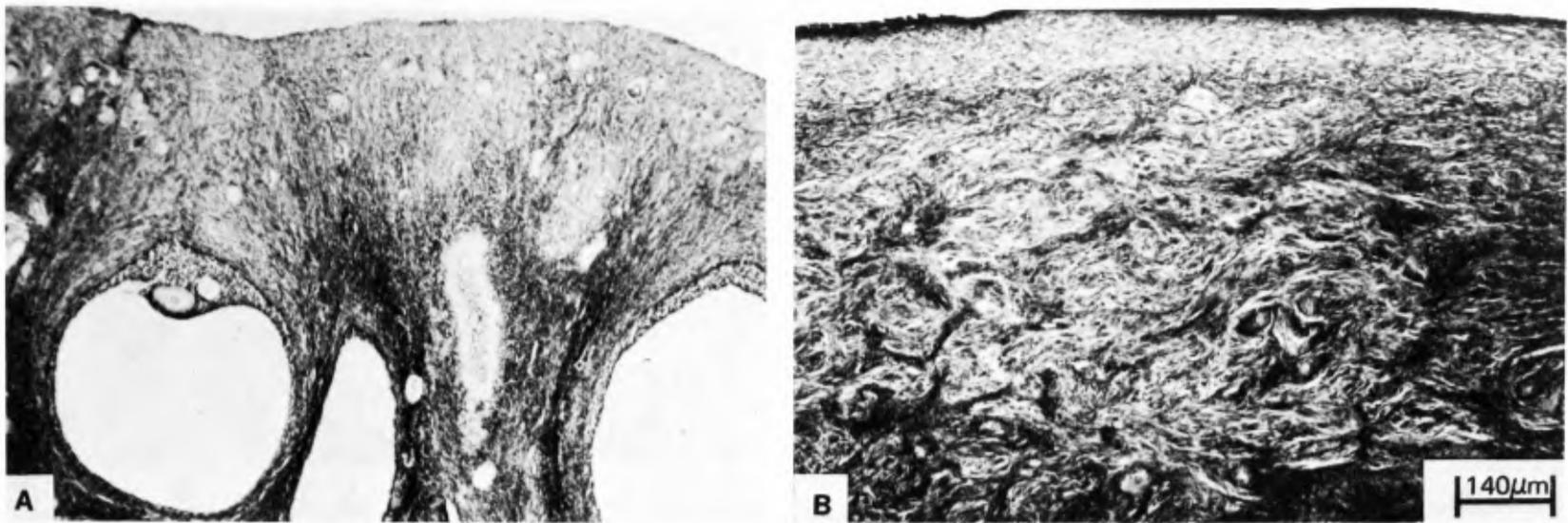


Fig. 6. Age-related changes in the histology of the ovarian cortex in *G. macrorhynchus*. Both photos same scale. A. Part of the cortex of immature Whale 17-33 (4.5 years) showing numerous primordial and antral follicles. Stained with haematoxylin and eosin. B. Cortex of lactating Whale 17-41 (47.5 years) and probably post-reproductive. No follicles can be seen. The cortex is reduced in thickness and composed mainly of fibrous tissue. Stained with van Gieson and celestin blue haemalum.

females (excluding those with a CL) which ranged from 8.4 g to 42.5 g ( $\bar{x}$  22.3 g;  $s$  6.72 g). The combined ovary weight of resting females (Fig. 4) was positively correlated with the age of the whale for animals less than 30 years old ( $r = 0.65$ ,  $P < 0.01$ ) but was highly variable in animals older than this. Both ovaries of some of the females over 40 years appeared shrivelled and had a combined weight of less than 15 g (e.g. No. 17-24 aged 44.5 years had a combined ovary weight of 8.4 g). However, we have no evidence for a reduction in the ovary weight of all old females, and the average combined ovary weight of 44 females older than 40 years was 21.8 g ( $s$  7.0 g) which was not significantly different from the average combined ovary weight ( $\bar{x}$  23.9 g;  $s$  6.7 g) of 31 females (without a CL or young CA) aged between 20 years and 40 years ( $t$  test;  $P > 0.1$ ).

### Follicular development

Primordial follicles occurred scattered throughout the periphery of the cortex in young specimens of *G. macrorhynchus* (Figs 5A, 6A). The mean of the diameters of 10 such follicles was  $58 \mu\text{m}$ , and the mean size of the oocyte was about  $20 \mu\text{m}$ . Follicle growth followed the usual pattern outlined in Appendix B of Perrin and Donovan (1984). The smallest follicles with an obvious antrum had a diameter of 150 to  $200 \mu\text{m}$ . By this stage, the granulosa layer was several cells thick and the capillaries in the theca interna were obvious. In macroscopically-visible (i.e.  $> 1$  mm in diameter) antral follicles, the theca interna and theca externa were much more clearly differentiated. As most of the antral follicles larger than 1 cm in diameter that we examined histologically were atretic, we have no information on whether the granulosa and theca cells start to luteinize before the follicle ruptures.

A frequency histogram of the diameter of the largest follicle present in 297 pairs of ovaries is presented in Fig. 7. No macroscopic follicles were seen in 44% of ovary pairs; the proportion of mature animals with no macroscopic follicles being greater in old animals (Fig. 8).

In immature animals, there is a seasonal cycle of follicle

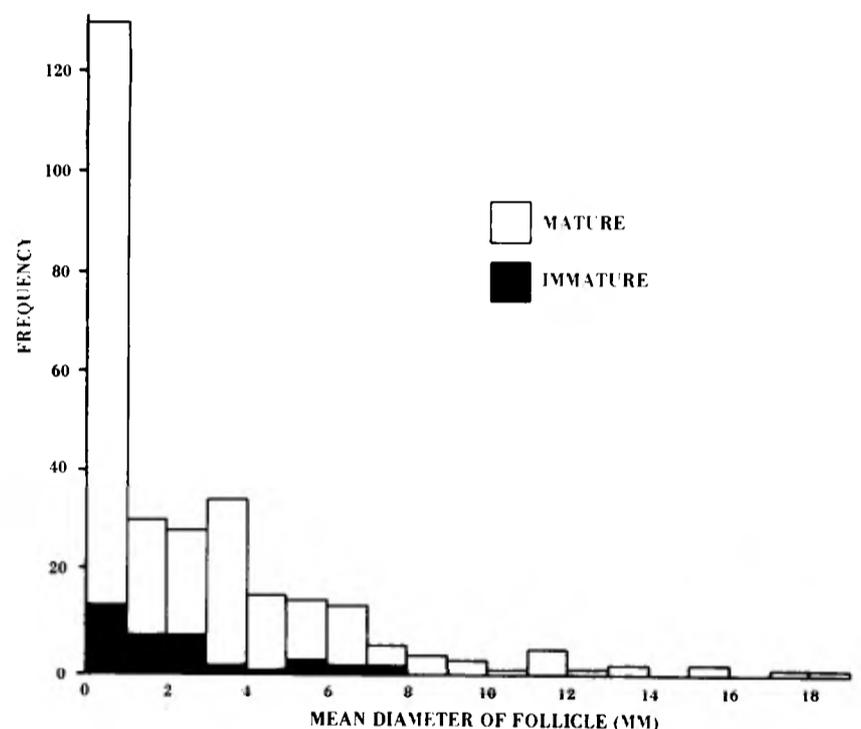


Fig. 7. Frequency histogram showing the size distribution of the largest follicle present in immature and mature ovaries of *G. macrorhynchus*.

growth. Although immature animals had follicles up to 7.1 mm in diameter (Fig. 7) (e.g. No. 24-31 aged 3.5 years), the presence of follicles greater than 4 mm was limited to the period 31 May to 23 July inclusive (Fig. 9).

In immature females, many follicles tended to be enlarging, so that the surface of the ovary was covered with bulges. In older females approaching oestrus, fewer follicles tended to enlarge. The three whales which had a corpus luteum of 'ovulation' ('CLO') but no macroscopic follicles were all estimated to be between 36 and 38 years old.

The frequency histogram illustrating the maximum follicle diameter of whales at different stages of pregnancy (Fig. 10) indicates that the presence of large ( $> 5$  mm diameter) follicles was limited to animals with fetuses less than 50 cm long. At all stages in the gestation period, there tended to be some whales with no macroscopic follicles and some with medium-sized follicles (1 to 5 mm in diameter).

Macroscopic follicles below 8 mm in diameter were

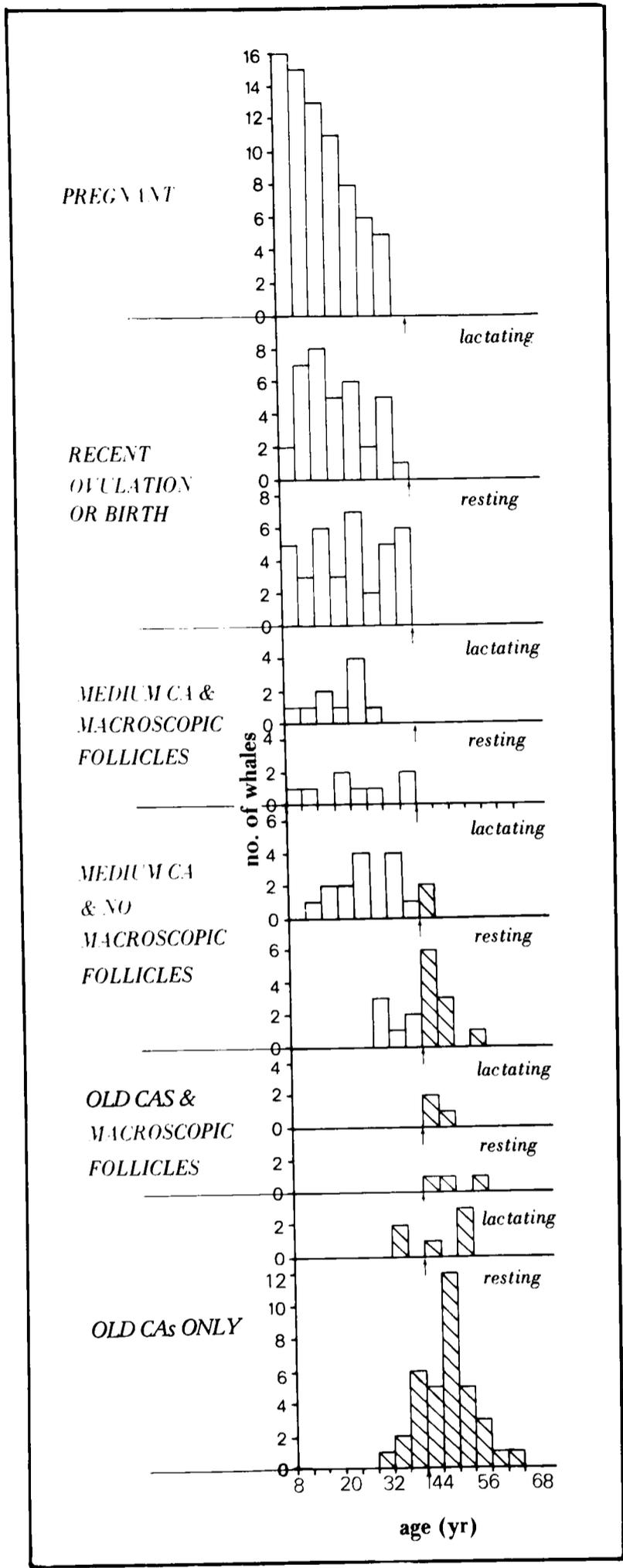


Fig. 8. Reproductive status and ovarian condition of 245 mature females of *G. macrorhynchus* aged from 8.5 to 62.5 years. The hatching represents the whales that we classified as post-reproductive. All 'non-pregnant' pilot whales with a corpus luteum or young corpus albicans (CA) have been classified as 'recent ovulation or birth'. Macroscopic follicles were discounted if they were obviously atretic (even without histology). Animals classified as having old corpora albicantia (CAs) only had no macroscopic follicles.

observed in some of the lactating females in all months for which specimens were available (Fig. 9). Larger follicles were observed in only four lactating females, all

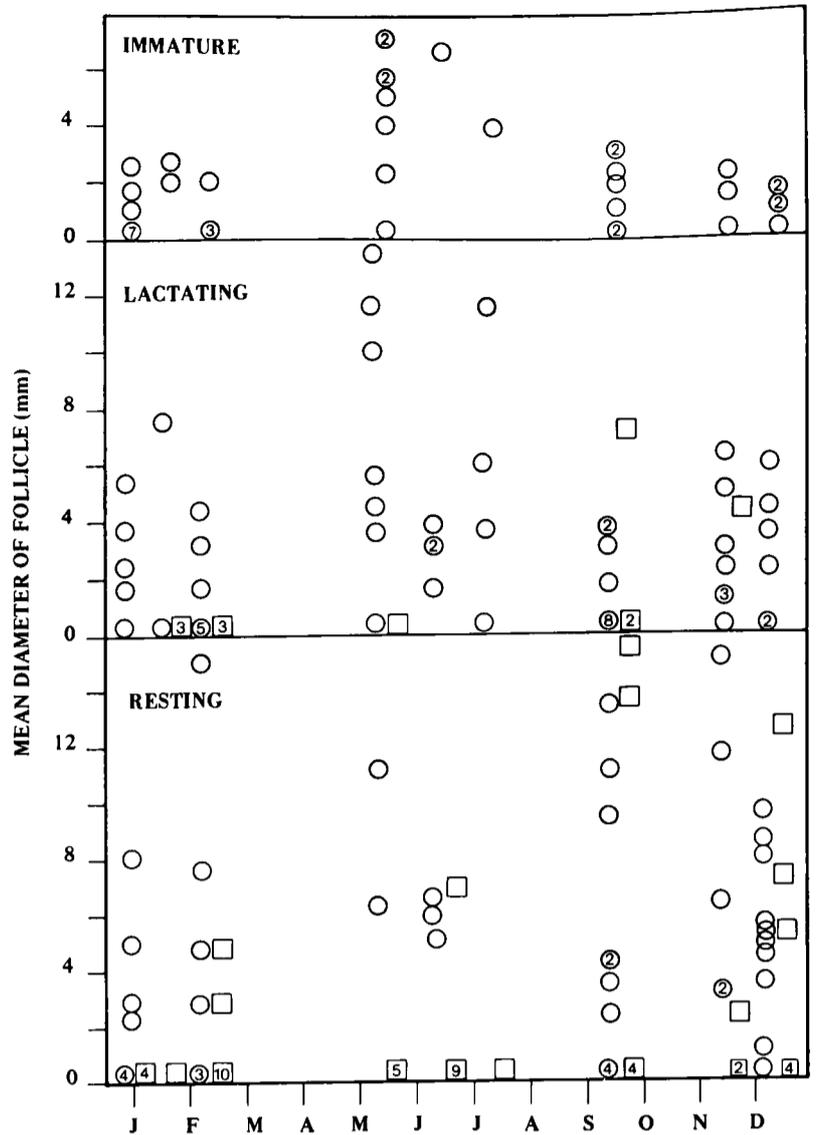


Fig. 9. Seasonal changes in the diameter of the largest follicle present in immature, lactating and resting pilot whales. Data for postreproductive (□) animals are presented separately from the remainder (○) as the large follicles present in these whales tend to be atretic. □ or ○ 1 whale, □ or ○ n whales.

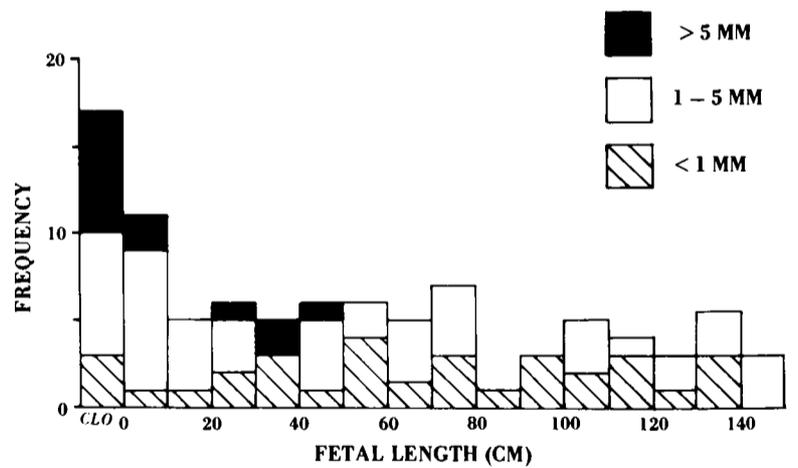


Fig. 10. Frequency histogram of the mean diameter of the largest follicle in *G. macrorhynchus* ovaries with corpora lutea of 'ovulation' and at various stages of pregnancy.

of which were examined in the period 31 May to 23 July inclusive, the same period in which the largest follicles (> 4 mm in diameter) were observed in immature whales.

This seasonal pattern was much less clear in resting females (Fig. 9). Macroscopic follicles 8 mm in diameter and smaller were observed in some animals in all months. Larger follicles were not limited to the May-July period but were also observed in some animals in February, October and December. This pattern persisted even when we distinguished between the reproductive and post-reproductive females using the criteria outlined below.

Many of the largest (> 10 mm) follicles were thick-

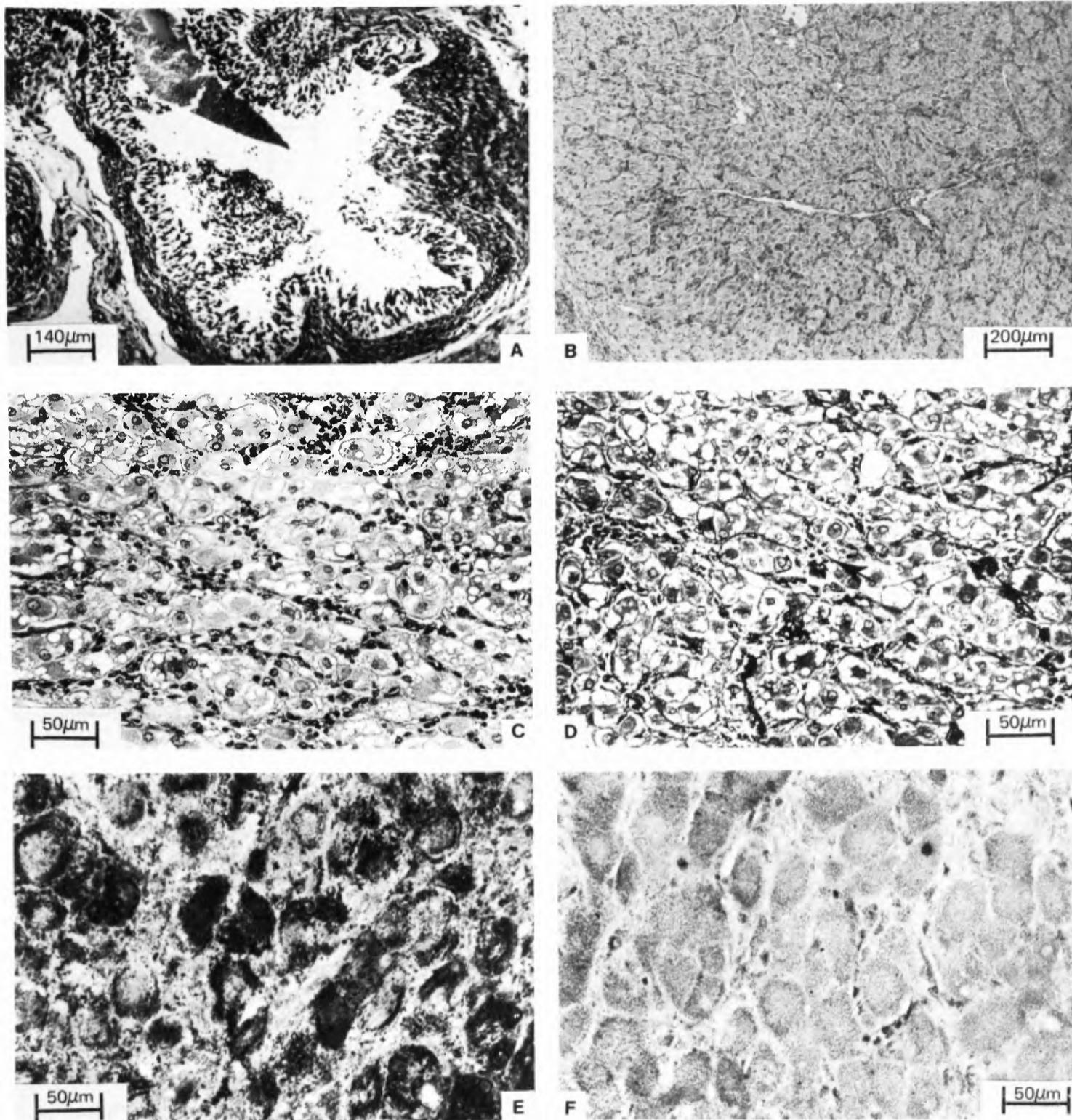


Fig. 11. Histology of corpora lutea in *Globicephala macrorhynchus* ovaries. A. Recently ruptured follicle in the right ovary of Whale 13-35 (aged 11.5 years) (see also Fig. 3A). The granulosa and theca layers are very developed and there has been some haemorrhage into the antrum. (Haematoxylin and eosin). B. Small accessory corpus luteum (3.6 mm in diameter) in the left ovary of Whale 17-31 (10.5 years) which was pregnant with a 23.3-cm fetus. Note the primary and secondary luteal cells. This ovary also contained one normal-sized corpus luteum (31.3 mm in diameter) and another accessory corpus luteum (11.0 mm in diameter). Neither accessory corpus luteum had a stigma. (Haematoxylin and eosin). C, D. Sections from a large corpus luteum of 'ovulation' (45 mm in diameter) in the right ovary of Whale 25-32 (18.5 years) stained with haematoxylin and eosin (C) and Gomori's Trichrome (D). The large pale primary luteal cells with vacuolated cytoplasm lie in rows within the network of secondary luteal cells which have darkly staining nuclei. The tissue is highly vascular and the erythrocytes (arrowed) are clearly visible in (D). E, F. The lipid metabolism of a corpus luteum appears to change during pregnancy. The primary luteal cells in (E) (Whale 13-28, 19.5 years, with 6.3-cm fetus) are packed with lipid granules and droplets in contrast to those in (F) (Whale 9-102, 26.5 years, with 124-cm fetus). Stained with Oil-Red O and Sudan IV.

walled and obviously atretic. It is very difficult to (1) be sure without histological examination that a large follicle is not atretic, and (2) measure large antral follicles (Fig. 3A) accurately. We cannot therefore make a definite statement about the usual size of follicles at ovulation. However, our observations that all follicles were below 8 mm in diameter for the immature period of seven or more years (Kasuya and Marsh, 1984) and that follicles larger than this were seasonally limited in lactating females suggest that a follicle probably stays at or below about 8 mm in diameter before the pre-ovulation growth spurt.

#### Follicular atresia

Coupled with the normal follicular development cycle is the concurrent normal phenomenon of follicular atresia. This is not necessarily simply a degenerative process. The metamorphosis of the follicle wall into a different kind of probably functional tissue occurs without ovulation as a normal and essential event in the ovarian cycle (Weir and Rowlands, 1977). Atresia may lead to the development of secondary interstitial tissue (which we did not study in *G. macrorhynchus*) and accessory corpora lutea, both of which are probably hormonally active (Weir and

Table 2

Details of specimens of *G. macrorhynchus* with accessory corpora lutea

## A. Accessory corpora lutea of pregnancy

Accession no.	Age (years)	Foetal length (cm)	Mean diameter(s) accessory corpora lutea (mm)	
17-31	10.5	23.3	11.0	3.2
25-2	11.5	29.5	7.0	3.9
18-27	21.5	< 0.5	7.0	
17-8	32.5	57.5	7.1	
20-8	N/A	63	5.0	3.9

## B. Accessory corpora lutea in post-reproductive ovaries

Accession no.	Age (years)	Mean diameter(s) of accessory corpora lutea (mm)		
26+27-43	36.5	4.4		
10-15	37.5	6.5		
13-31	40.5	10.2		
22-3	40.5	3.6	3.1	
22-12	41.5	5.4	4.0	
9-106	41.5	6.4		
9-98	43.5	4.2	3.9	3.0
24-12	48.5	7.6		
17-1	55.5	4.2		

Rowlands, 1977). Atresia may lead to the development many more become atretic.

Follicles may become atretic at any stage of their development (Byskov, 1979). We did not study the atresia of small follicles in *G. macrorhynchus*, as this did not appear to modify the macroscopic structure of the ovary. However, the atresia of medium and large follicles is conspicuous and presents a variety of appearances depending on the stage of the follicle and the hormonal status of the whale at the time it begins. These are discussed below.

*Atresia without luteinization*

*Corpora fibrosa*: The atresia of follicles in immature females and of some medium-sized follicles in mature specimens occurred without luteinization, i.e. without accumulation of lipids in the granulosa or theca cells. Small corpora fibrosa (Fig. 5A) were derived from the basement membrane of atretic medium-sized follicles. These fibrous bodies appeared to be slowly resorbed and were not evident in large numbers in the cortex of old whales (e.g. Fig. 6B).

*Cystic follicles*: Many of the large follicles we examined histologically (especially those from old females) had become cystic (e.g. Fig. 5E). In some cases the walls were obviously unusually thick even when examined macroscopically, the granulosa and theca cells having been replaced by fibrous tissue.

*Atresia with luteinization*

Atresia of Graafian follicles of various sizes often progressed via different stages of luteinization. These will be discussed separately below.

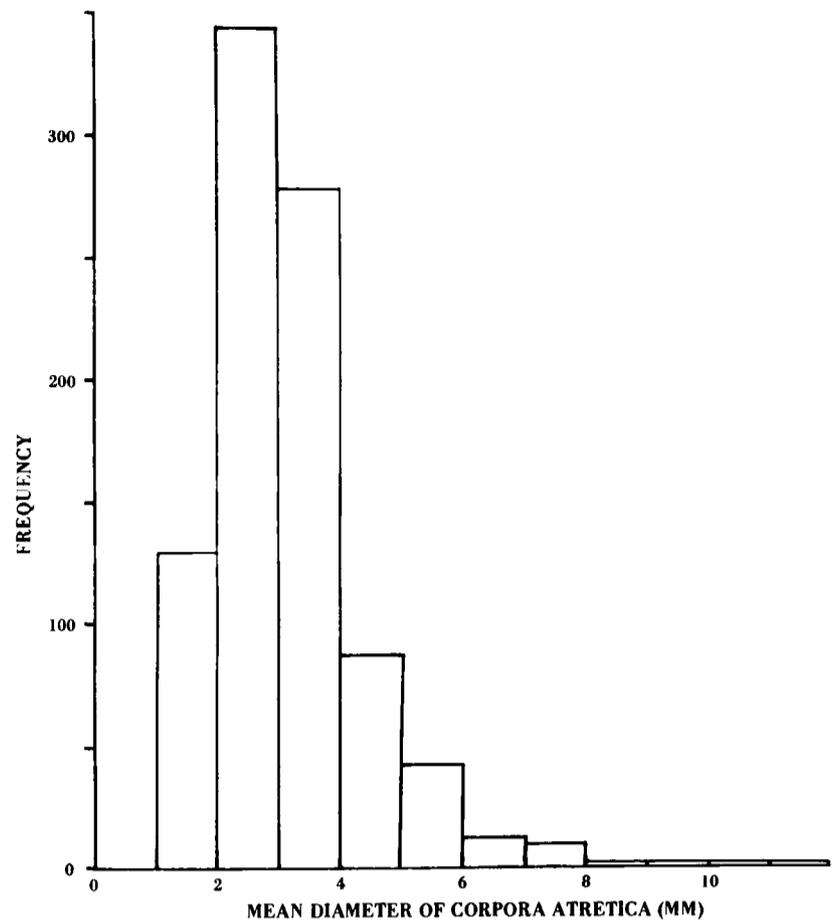


Fig. 12. Frequency histogram showing the size distribution of corpora atretica b in *G. macrorhynchus*.

*Accessory corpora lutea*: In several whales we found one or more follicles that had behaved as if ovulation had occurred but without the egg being released, thus forming an accessory corpus luteum (accessory CL) on which no stigma was visible. Details of the animals in which accessory CL were found are summarized in Table 2. The ovaries of five animals (aged 10.5 to 32.5 years) contained accessory corpora lutea of pregnancy which were 5.0 to 11.0 mm in diameter (Fig. 11B). The ovaries of nine old females aged from 36.5 to 55.5 years also contained yellow structures without stigmata which were 3.0 to 10.2 mm in diameter and histologically identical to corpora lutea, even though these ovaries showed no signs of having ovulated recently.

*Corpora atretica b*: We observed irregularly-shaped masses of yellow-brown pigmented tissue ranging from 1 to 12 mm in mean diameter (modal mean diameter 2 mm to 3 mm) (Fig. 12) in about 75% of the mature ovaries examined. None were seen in immature ovaries. A total of 938 such bodies were recorded in 235 pairs of mature ovaries. The surface trace associated with these structures was slight or absent.

Histological study indicated that these bodies were formed from atretic follicles of various sizes in which lipid accumulation had started in some of the granulosa cells and in the cells of the theca interna. As atresia continued, the granulosa cell members became reduced by lysis and phagocytosis with concomitant collapse of the follicle. During the atretic differentiation, few thecal cells became necrotic. Rather they had hypertrophied and accumulated lipid droplets (Fig. 5C), undergoing a type of 'fatty' degeneration. The resulting lipid pigment (which resembled ceroid) was pale yellow at first and readily soluble in fat solvents but gradually oxidized, becoming darker and more insoluble. Best (1967) reported similar bodies in

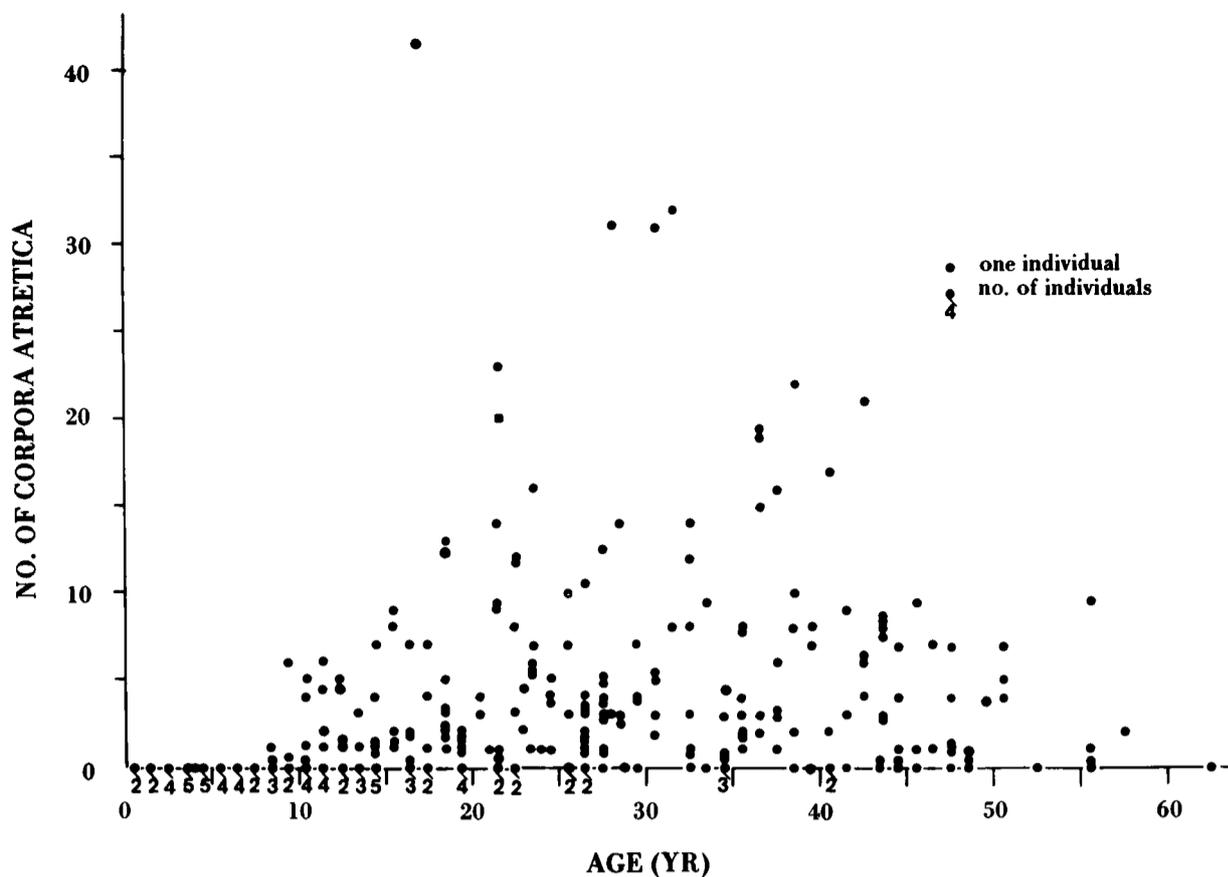


Fig. 13. Scatterplot of corpora atretica *b* number against age for *G. macrorhynchus*.

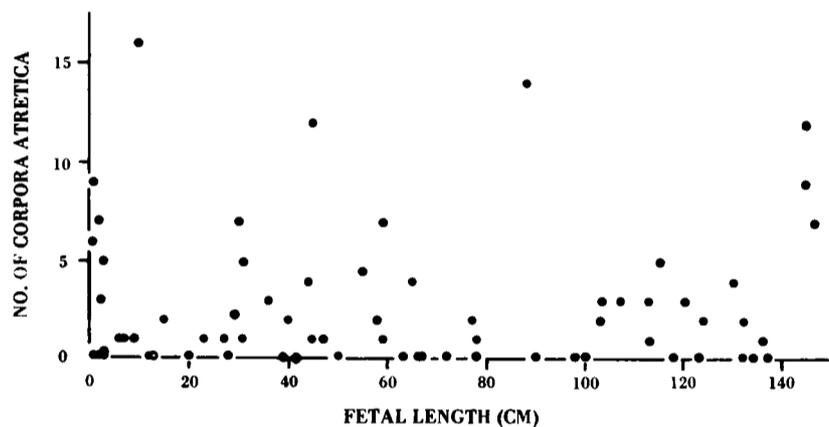


Fig. 14. Number of corpora atretica *b* present per pair of ovaries of *G. macrorhynchus* at various stages of pregnancy.

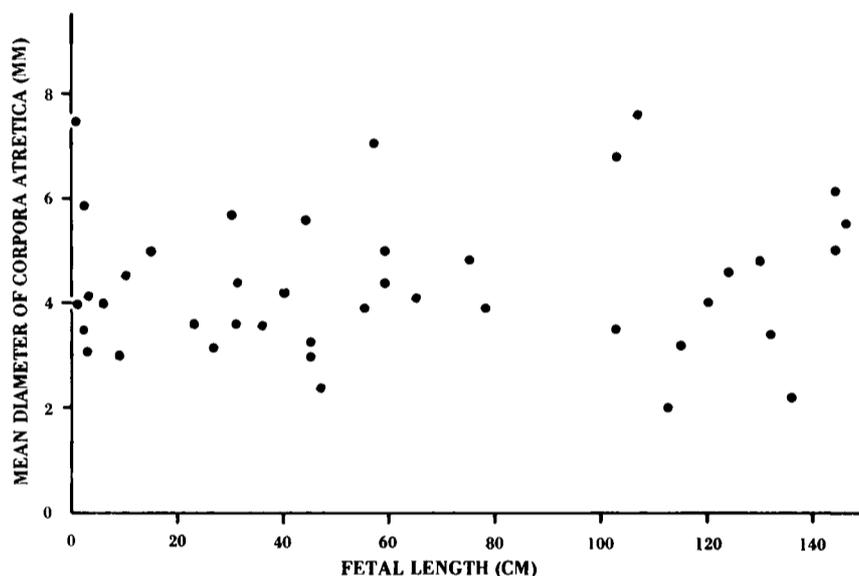


Fig. 15. Scatterplot showing the size of the largest corpus atreticum *b* present in the ovaries of *G. macrorhynchus* at various stages of pregnancy.

sperm whale, *Physeter macrocephalus*, ovaries and called them 'corpora atretica *b*'. We have followed his terminology.

Fig. 13 illustrates the relationship between corpora-atretica count and age of the whale. Animals with one or more corpora atretica *b* were less likely to be aged less than 20 years ( $\chi^2$ ,  $P < 0.01$ ) or more than 40 years ( $\chi^2$ ,  $P < 0.05$ ) than between 20 and 40 years.

When the incidence of corpora atretica *b* was studied within an age group of whales, their presence/absence was found to be independent of pregnancy status ( $\chi^2$ ,  $P > 0.5$ ; both for whales aged less than 20 years and between 20 and 36 years).

Corpora atretica *b* were present in pilot whales at all stages of pregnancy (Fig. 14), and the likelihood of an animal having one or more was independent of the stage of pregnancy ( $\chi^2$ ,  $P > 0.05$ ). There was no evidence that the maximum diameter of corpora atretica *b* changed during the gestation period (Fig. 15). The distribution of corpora atretica *b* within a pair of ovaries was also independent of their current activity as measured by the presence of a corpus luteum or young corpus albicans ( $\chi^2$ ,  $P > 0.05$ ). There was no significant difference in the

proportion of ovaries with corpora atretica *b* between the periods December–February and June–July ( $\chi^2$ ,  $P > 0.05$ ), suggesting that their occurrence was independent of the time of year.

Within a pair of ovaries, the ovary with the larger number of CAs was also likely to have more corpora atretica *b* ( $\chi^2$ ,  $P < 0.05$ ).

The number of corpora atretica *b* per ovary pair ranged from 0 to 43 ( $\bar{x}$  4); most whales had less than 10 (Fig. 13). Animals with one or more such bodies had an average of 5.4 per ovary pair. Table 3 details the reproductive status of the 23 whales with more than 10 corpora atretica *b*. Nearly half of this group had a corpus luteum of 'ovulation' or large follicles suggesting that when large-scale atresia with luteinization occurred, it tended to be around the time of oestrus and in pilot whales older than about 17 years. The oldest whale with 10 or more corpora atretica *b* was aged 42.5 years, suggesting that these bodies do not persist.

Table 3

Details of the ovaries of 23 specimens of *G. macrorhynchus* (age 17.5 to 42.5 years) with more than 10 corpora atretica *b*. (*R* = resting, *L* = lactating)

Structures present in ovaries	No. of whales	
	Total mature whales in category	No. with > 10 corpora atretica <i>b</i>
Corpus luteum of pregnancy (fetal length 10.5 to 144 cm)	77	5
Corpus luteum of 'ovulation'	17	5 <i>R</i> * + 1 <i>L</i>
Macroscopic follicles > 5 mm in diameter	32†	3 <i>R</i> * + 1 <i>L</i>
Macroscopic follicles 1 to 5 mm in diameter	40†	1 <i>R</i>
No macroscopic (i.e. > 1 mm in diameter) follicles	88†	5 <i>R</i> * + 2 <i>L</i>

\* One whale also with one corpus atreticum *a*.

† Excluding animals with a corpus luteum.

*Corpora atretica a*: Other yellow bodies which were histologically similar to corpora atretica *b* but better-defined and usually larger structures were also observed in the ovaries of *G. macrorhynchus* (Fig. 5B). These irregularly-shaped bodies were placed superficially in the ovary and often had an obvious stigma (Fig. 3B) suggesting that they had originated from ruptured follicles. Best (1967) described similar structures in sperm whale ovaries. He called them 'corpora atretica *a*' and we have followed his terminology (for a discussion of alternative terminologies, see Appendix B of Perrin and Donovan (1984)).

Fig. 5(D, F) illustrates the start of the process of degeneration of one of these bodies. We have not observed extensive fibrous replacement of the luteal cells like that seen in fin whale (Laws, 1961), sperm whale (Best, 1967) or minke whale (Appendix B, Perrin and Donovan, 1984) corpora atretica *a*. We therefore consider that it is likely that most degenerate pilot whale corpora atretica *a* eventually virtually disappear from the ovary, leaving at most a surface scar. Thus they are probably less likely to be confused with CAs than the corresponding structures which have been described from the ovaries of large whales.

Corpora atretica *a* (ranging from 3.2 mm to 13.3 mm in mean diameter;  $\bar{x}$  7.1 mm; *s* 2.6 mm) were found in the ovaries of 23 pilot whales. The reproductive status of the whales whose ovaries contained these bodies is detailed in Table 4. Thirteen of these animals had ovulated recently (two were pregnant with a small fetus; 10 had a 'CLO', and one a young CA). More than half of the animals with a 'CLO' also had a corpus atreticum *a*. Five animals with large follicles in their ovaries suggesting approaching oestrus also had a corpus atreticum *a*. Whale 9-116, which had given birth the day before her death, had seven old corpora atretica *a* (all with obvious stigmata) in her left ovary, which also contained the corpus luteum.

We did not include corpora atretica *a* in our corpora counts, as we consider that they resulted from follicle ruptures which were not followed by normal corpus-luteum development.

Table 4

Details of the ovarian status of 23 *G. macrorhynchus* females (age 11.5 to 40.5 years) with at least one corpus atreticum *a*. (*R* = resting; *L* = lactating)

Structures present in ovaries	No. of whales	
	Total mature whales in category	No. with corpus atreticum <i>a</i>
Corpus luteum of pregnancy (foetal length < 5 mm to term)	77	5
Corpus luteum of 'ovulation'	17	5 <i>R</i> + 5 <i>L</i> *
Macroscopic follicles (> 5 mm in diameter)	32†	4 <i>R</i> + 1 <i>L</i>
Young corpus albicans	51†	1 <i>R</i> *
Medium corpus albicans	50†	1 <i>R</i> * + 1 <i>L</i> *

\* One corpus atreticum *a* degenerating.

† Excluding animals with a corpus luteum.

### The corpus luteum

A corpus luteum (CL) (*sensu* Appendix B of Perrin and Donovan, 1984) was observed in the ovaries of 95 pilot whales. A fetus was found in the uterus of 73 of these animals, confirming that these were CLs of pregnancy (CLPs). Another two whales with a CLP had recently aborted; two more had recently given birth. All four were from School 9, which was held for several days between capture and slaughter (Table 1, Kasuya and Marsh, 1984). A cystic placental mole (Jubb and Kennedy, 1970), presumably derived from the remains of a very small embryo (Dr P. Ladds, Department of Tropical Veterinary Science, James Cook University, pers. comm.), was found in the uterus of another whale with a CL (No. 25-1, 28.5 years).

No fetus could be found in the uteri of the remaining 17 whales. We shall refer to the CLs of all these animals as 'CLOs' even though some may have been from animals which had recently aborted a fairly small fetus or which contained a very small embryo missed in dissection.

### The corpus luteum of 'ovulation'

Fourteen 'CLOs' (excluding collapsed, recently ruptured follicles, e.g. Fig. 3A) ranged from 12.5 mm to 45 mm in mean diameter ( $\bar{x}$  25.1 mm). As can be seen from Fig. 16, all but four were below the size range of the CLPs. All had a conspicuous stigma (Fig. 3B). In cross-section, most of the ochre-coloured 'CLOs' were loose-structured, the cords of glandular tissue being separated by hollow fissures (Fig. 3C). However, some 'CLOs' (e.g. the 45-mm diameter CL of Whale 25-32 (18.5 years) (Fig. 3F) and the 40-mm diameter CL of Whale 24-9 (37.5 years)) were compact structures similar morphologically and histologically to all but the youngest CLPs. Thus we were unable to separate all 'CLOs' from CLPs using criteria of size or morphology. Five of the 'CLOs' were found in lactating whales (age range 21.5 to 37.5 years) and 12 in resting whales (age range 11.5 to 39.5 years).

As discussed below, we have no evidence of recent ovulation by any specimen of *G. macrorhynchus* more than 40 years old. The proportion of lactating and resting females less than this age with a 'CLO' is significantly

Table 5

Seasonal incidence of corpora lutea of 'ovulation' ('CLO'). (All animals over 39 years old excluded, but animals from School 9 whose ovaries were examined in the field only (see Kasuya and Marsh, 1984) included)

Month	School no(s)	Number of whales				% with 'CLO' (Lactating and resting)
		Lactating		Resting		
		With 'CLO'	Total	With 'CLO'	Total	
January	7, 11	0	5	2	8	15.4
February	12, 16, 22, 23	0	13	0	10	0
May/June	24	2	7	3	5	41.7
June/July	9, 10	3	17	12	24	36.6
October	13, 25, 26, 27	1	12	5	10	27.3
December	14, 15, 17, 18	0	16	0	19	0

higher in May/June (41.7%) June/July (36.6%) and October (27.3%) than in the other months for which data are available ( $\chi^2$ ,  $P < 0.001$ ) (Table 5).

*The corpus luteum of pregnancy*

The 77 CLPs ranged in mean diameter from 30.4 mm to 47.5 mm ( $\bar{x}$  37.6 mm;  $s$  3.4 mm; mode 37.5 mm). Although there is no evidence for a consistent change in the mean diameter of CLPs throughout the gestation period (Fig. 16), we tested whether CLPs tended to shrink during early pregnancy by examining the relationship between fetal length and the mean diameter of the CLP for 17 whales, each of which had a fetus 20 cm or less in length. However, no change was detected, as neither the linear nor quadratic relationship between these two variables was significant ( $r = -0.39$ ,  $P > 0.20$ ; Regression ANOVA: neither Regression Mean Square (MS) or Curvature MS was significantly different ( $P > 0.10$ ) from the Residual MS).

Besides being larger than most 'CLOs', the appearance of all but the youngest CLPs (Fig. 3E) was different in cross-section, the luteal tissue being held more closely together by the more extensively developed connective tissue network. However, the stigma was generally still very obvious although morphologically highly variable.

About 15% of CLs had a 'jelly-filled' centre,

exceptionally up to 30 mm in diameter (Fig. 3D) but usually much smaller. This was formed from fibrin resulting from blood entering the antrum as the follicle ruptured. The 'jelly' was replaced by fibrous connective tissue in older CLs.

Only three pregnant whales were simultaneously lactating. Their ovarian condition is summarized in Table 6.

*Development of the corpus luteum*

The following description of the histological appearance of the developing CL was built up from the examination of two recently-ruptured follicles, eight 'CLOs' and 13 CLPs (from whales with fetuses 3 to 146 mm long).

The two recently-ruptured follicles we studied histologically were 8 mm and 15 mm in maximum diameter. Ovulation had been followed by haemorrhage from the blood vessels of the theca interna. Luteinizing cells lining the antrum were interspersed with erythrocytes and fibrinous material (Fig. 11A). The theca interna and membrane granulosa were clearly separated by a distinct basement membrane and were both deeply folded. The granulosa cells each had a rounded nucleus about 7  $\mu$ m in diameter, surrounded by varying but small amounts of eosinophilic granular cytoplasm, which was irregularly

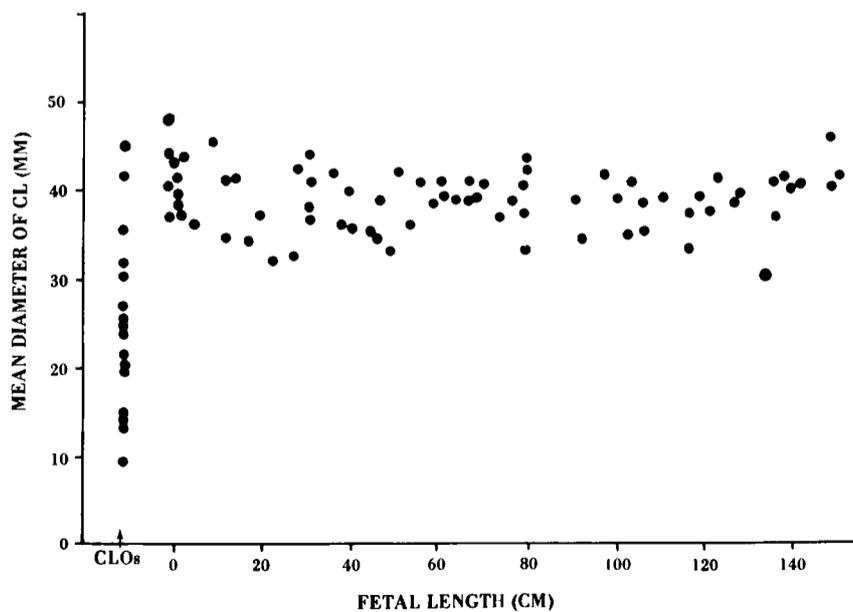


Fig. 16. Scatterplot of the diameters of corpora lutea of 'ovulation' ('CLO') (including two recently ruptured follicles) and of corpora lutea of pregnancy through the gestation period.

Table 6

Details of ovaries of three specimens of *G. macrorhynchus* which were simultaneously pregnant and lactating

Accession no.	Age (years)	Fetal length (cm)	Estimated <sup>1</sup> length of pregnancy (days)	Mean diameter CA (mm)		
				Young	Medium	Old
26-8	12.5	19.3	98			7.9
						7.4
						5.8
25-38	13.5	39	156		9.2	
10-12	34.5	20	100		10.3	7.7
						5.8
						5.5
						5.0

<sup>1</sup> Calculated from formula derived from Laws (1959).

$$\text{Length of pregnancy in days} = \left(452 \times 0.91 \times \frac{\text{F.L.}}{139.5}\right) + (452 \times 0.09)$$

(F.L. = fetal length).

positive for lipid. Cell boundaries were difficult to see. The theca cells had round to oval nuclei about  $10\ \mu\text{m}$  long and cytoplasm which did not stain for lipid. Both layers were much more developed than in large, intact follicles.

Two morphologically-distinct types of luteal cells (Fig. 11C) were observed in all the fully-formed CLs we examined histologically. We refer to these as primary and secondary luteal cells *sensu* Mossman and Duke (1973). Similar cells have been referred to as granulosa and theca luteal cells by various authors (e.g. Harrison, 1949; Harrison *et al.*, 1981). We have avoided this terminology, as it is impossible to verify the origin of these cell types without a more complete series.

The secondary luteal cells (Fig. 11C) formed a lattice which radiated throughout the CL and was continuous with an interrupted layer of cells around the periphery. These cells followed the trabeculae into the substance of the CL and were obvious where they surrounded capillaries. The secondary cells were fusiform. Each had a distinct ovoid, basophilic nucleus about  $5$  to  $8\ \mu\text{m}$  long and a small amount of cytoplasm which did not stain with fat stains, even though it tended to be vacuolated in older CLs (e.g. old 'CLPs' from animals with fetuses  $> 15$  cm long). The primary luteal cells occurred in rows within the network of secondary luteal cells and connective-tissue fibres. Primary luteal cells (Fig. 11C) were rounded or polyhedral, ranging from about  $25$  to  $50\ \mu\text{m}$  in diameter, and contained a pale-staining, rounded nucleus about  $10\ \mu\text{m}$  in diameter with a prominent nucleolus. Cells containing two nuclei were sometimes seen in young CLs.

In young CLs, the cytoplasm of the primary luteal cells tended to be lipid-rich and granular (Fig. 11E). In animals with small embryos (3 to 10 cm long), an increasing proportion of the lipid component of the cytoplasm of the primary luteal cells tended to be concentrated in large droplets up to  $15\ \mu\text{m}$  in diameter. In older CLPs (from animals with fetuses 15 to 146 cm long) the cytoplasm stained palely or not at all with Oil-Red 0 and had a fairly uniform appearance (Fig. 11F). These results suggest that the lipid metabolism of the primary luteal cells of a CLP alters when the fetus is between 10 and 15 mm long. In our material, this was the most obvious change in the primary luteal cells to occur during pregnancy. Other changes may have occurred but if so, they were masked by inadequate fixation.

The connective-tissue strands separating areas of luteal tissue (Fig. 3C) are highly developed in all but the youngest CLPs. This correlates with the more compact appearance of older CLPs. All CLs had a very well-developed blood supply with an extensive network of capillaries (Fig. 11D).

### The corpus albicans

In this paper, we refer to regressing and regressed CLs as corpora albicantia (CAs) irrespective of their colour. We have recorded and measured 1,737 CAs from *G. macrorhynchus* ovaries, up to 18 per pair, the modal number being six (Fig. 17). Each CA was classified as young, medium or old according to the criteria outlined in Table 1. As regression is essentially a continuous process, these categories are somewhat arbitrary, but we consider them a useful guide to the state of regression.

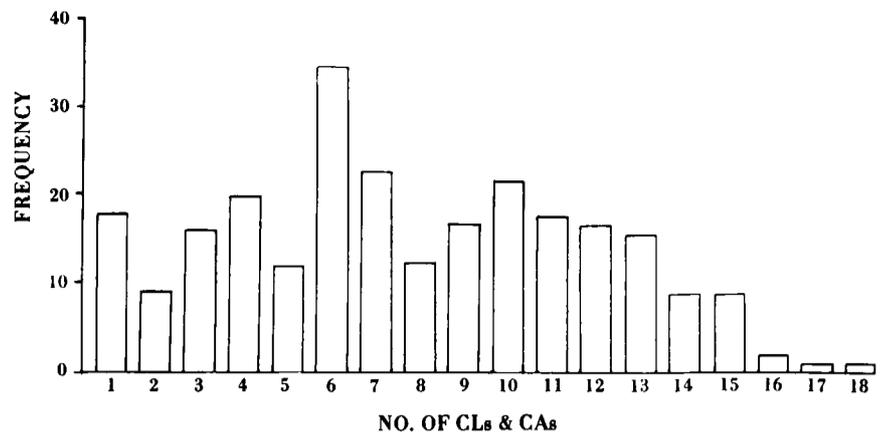


Fig. 17. Frequency histogram showing the distribution of corpora counts (number of corpora lutea (CLs) plus corpora albicantia (CAs) for *G. macrorhynchus*.

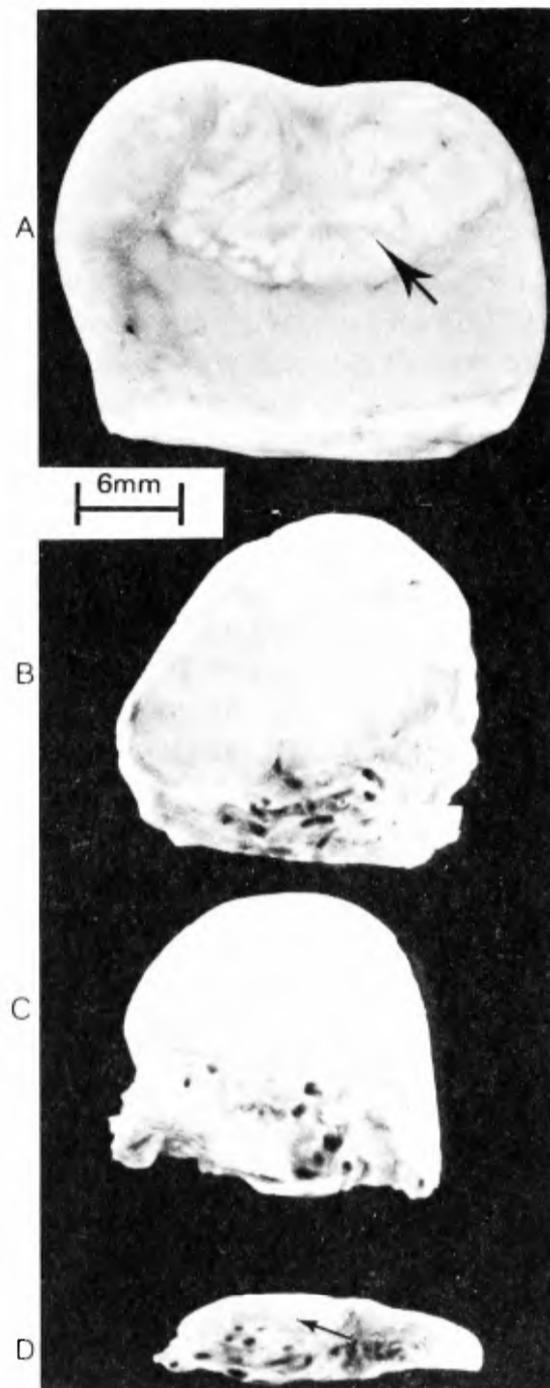


Fig. 18. Median slices through various corpora albicantia to show the pattern of regression. A. Initial stage in the regression of a corpus luteum of 'ovulation', some lobes (arrowed) were still active (Whale 13-23, 32.5 years). B. Young corpus albicans of pregnancy from 9-100 (aged 10.5 years and lactating). C. Slightly older corpus albicans from 9-95 (aged 30.5 years and lactating). D. Old corpus albicans (arrowed) also from Whale 9-95.

Eighty CAs were classified as young (Figs. 18A, B, C; 19A). Their size distribution is shown in Fig. 20, the range of mean diameters being from 8.5 to 28.5 mm ( $\bar{x}$  15.2 mm;  $s$  3.27 mm). These young CAs can easily be distinguished from CLs on the basis of colour (young CAs

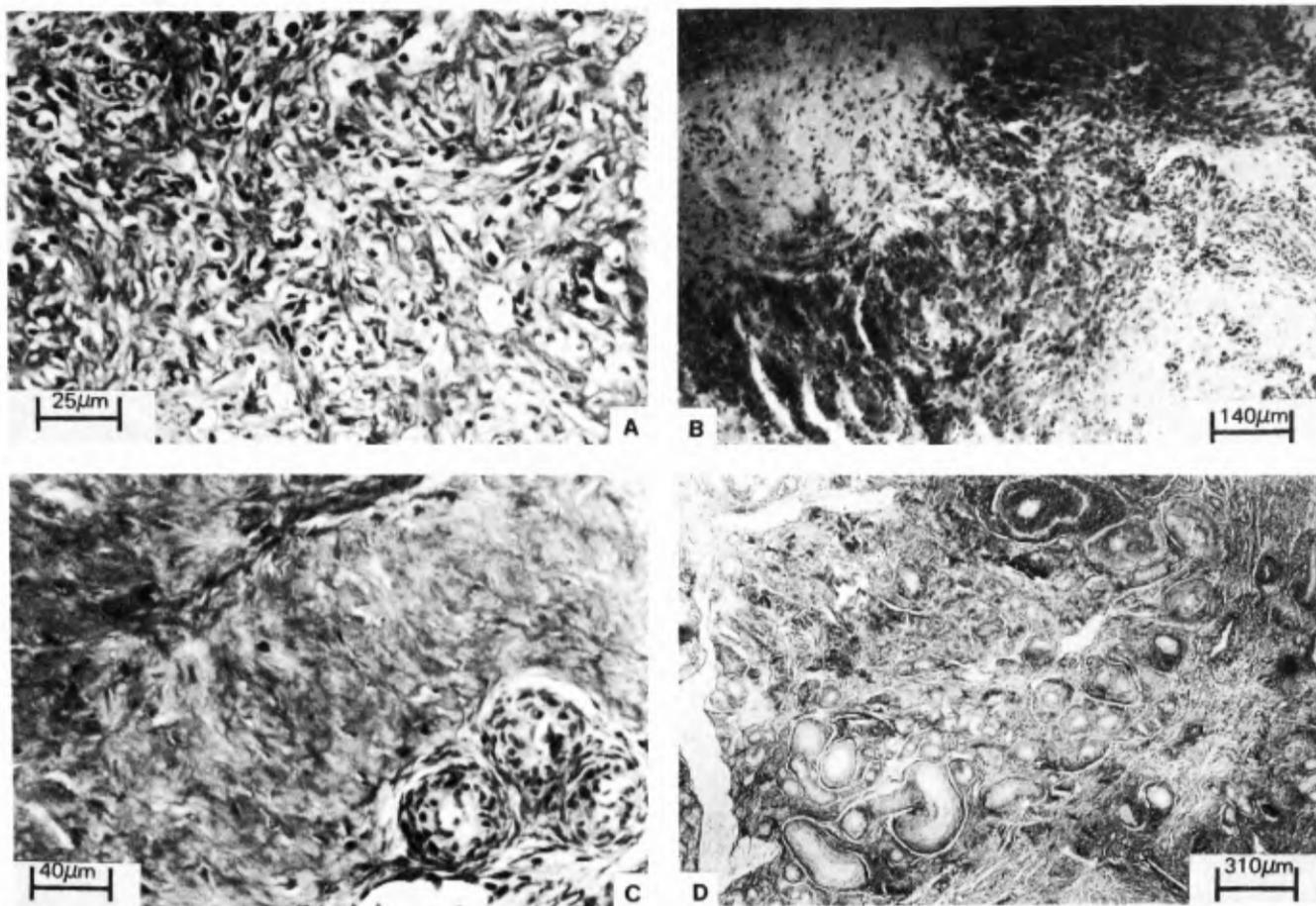


Fig. 19. Histology of regressing corpora albicantia in ovaries of *G. macrorhynchus*. A. Histology of regressing lobe of young corpus albicans of Whale 13-23 shown in Fig. 18A. The primary luteal cells have been replaced by cellular fibrous tissue but some presumed secondary luteal cells with dark nuclei are still visible (Gomori's trichrome). B. Macrophages filled with lipid in the brown central area of a medium corpus albicans (10.5 mm in diameter) in the ovary of Whale 11-21 (14.5 years). (Haematoxylin and eosin). C. Hyaline connective tissue forms the bulk of this medium corpus albicans (11.9 mm in diameter) in the left ovary of pregnant Whale 17-44 (16.5 years). Erythrocytes are still present in the blood vessels. D. Part of one of the 12 old corpora albicantia of lactating Whale 26-12 (48.5 years). This corpus albicans, which was 7.5 mm in diameter, consisted mainly of thick-walled blood vessels (van Gieson and celestin-blue haemalum).

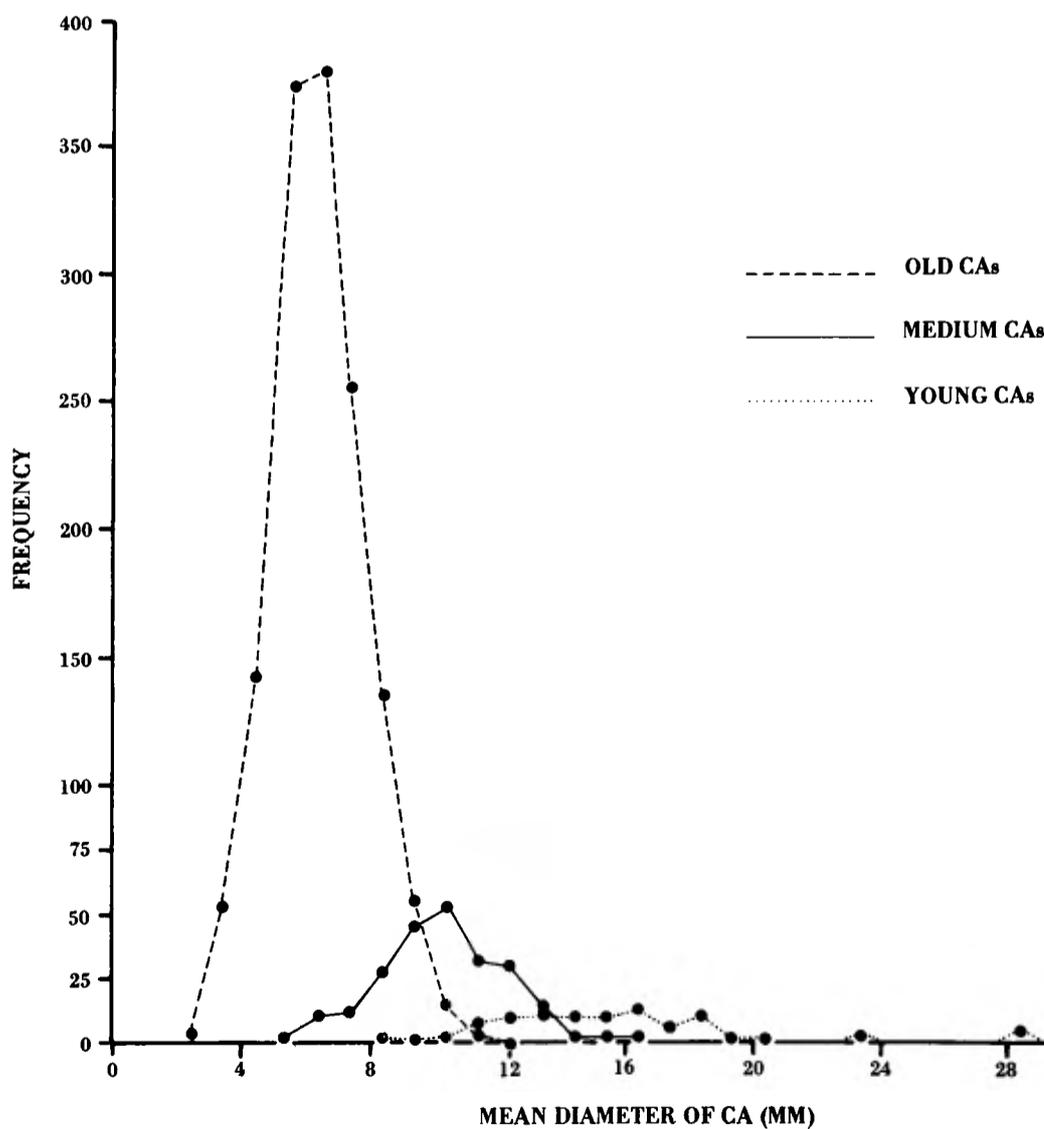


Fig. 20. Size-frequency distributions of young, medium and old corpora albicantia (CAs) in ovaries of *G. macrorhynchus*.

Table 7

Details of whales on which the histological comparison of young corpora albicantia derived from corpora lutea of pregnancy and presumed ovulation was based. (P = pregnant; L = lactating; F.L. = fetal length)

Accession no.	Age (years)	Reproductive status	Number of corpora			
			CL	Young CAs	Medium CAs	Old CAs
<i>Corpora of pregnancy</i>						
9-100	10.5	L		1		
9-99	11.5	L		1		
<i>Probable corpora of 'ovulation'</i>						
9-92	10.5	P (F.L. 137 cm)	1	1		
9-115	22.5	P (F.L. 1.2 cm)	1	2	0	7

are pale orange or white; CLs are ochre) and texture (CAs are much more fibrous), as well as size. Two hundred and thirty-one medium CAs (Figs. 3D; 19B, C) were measured. They ranged from 5.5 mm to 16.5 mm in mean diameter ( $\bar{x}$  10.4 mm;  $s$  1.99 mm) (Fig. 20) and were significantly smaller than the young CAs ( $t$  test;  $P < 0.0005$ ). The 1,426 CAs classified as old (Figs. 3E, 18D; 19D) ranged from 2.5 mm to 12 mm in mean diameter ( $\bar{x}$  6.4 mm;  $s$  1.5 mm) (Fig. 20). The mean diameter of the old CAs was significantly less than that of medium CAs ( $t$  test;  $P < 0.0005$ ).

#### *The pattern of regression*

The CLs of the two whales from School 9 that had recently given birth (one of them only the day before its death) were macroscopically and histologically indistinguishable from the CLPs of late pregnancy. The youngest CA in our series was a regressing 'CLO' 23.5 mm in diameter (Figs 18A; 19A), in some lobes of which a large proportion of primary luteal cell were still recognizable, although few had visible nuclei and these were all pyknotic. Fibrous replacement of the primary luteal cells was obviously progressing rapidly and many fibroblasts were visible. In the remaining lobes, most of the primary luteal cells had been replaced by cellular fibrous tissue (Fig. 19A) within which occasional primary luteal cells and groups of presumed secondary luteal cells were still visible. This young CA was a very vascular structure with an extensive network of capillaries and larger vessels. The trabecular arrangement of the former CL was still obvious. The other young CAs (e.g. Fig. 18B, C) were all slightly older and less vascular, and the density of cells was much lower.

We compared the macroscopic structure and histology of several young CAs. Two were definitely derived from CLPs, the other two were probably derived from 'CLOs' (see Table 7). We could not separate the two groups.

The connective tissue of the CAs classified as medium was shrunken and hyalinized, making the blood vessels appear much more prominent (Fig. 19C). Some blood vessels were occluded; most contained erythrocytes. The trabeculae were less obvious.

In old CAs (Fig. 19D), the shrinkage and hyalinization of the connective tissue had progressed even further. The trabeculae were no longer obvious, and thick-walled blood vessels made up the greater part of the structure. However, many of the blood vessels were patent.

The histological structure of all 12 CAs of Whale 26-12, which was 48.5 years old, corresponded to the above description of old CAs. As discussed below, our data suggest that (1) CAs persist and (2) this whale had probably not ovulated for at least nine years. As this animal was lactating, we presume she had been pregnant at least once and conclude that the bodies we have classified as old CAs represent the end-point in the degeneration of all CLs.

Some CAs in all three categories had a brown central area full of lipid-laden cells (presumably macrophages) (Fig. 19B). The lipid inclusions were histochemically and morphologically similar to those in corpora atretica, and we suggest that they may have derived from secondary luteal cells, which are probably of thecal origin (see Harrison *et al.*, 1981) and which have undergone 'fatty' degeneration.

#### *The rate of regression*

We have studied the rate of regression of CAs by considering the ovaries of sexually mature whales less than 13 years old (Table 8). As pointed out by Kasuya and Marsh (1984) our sample suggests that short-finned pilot whales begin to ovulate at a minimum of about 7.5 years (see No. 7-17, Table 8). The youngest animals with old CAs were Nos. 14-15 and 15-25, both aged 9.5 years. We therefore conclude that it is possible for a CL to degenerate into an old CA within two years.

However, it is likely that the degeneration rate is dependent on hormonal status. Fig. 21 shows the diameters of the largest young CA observed in various females at different stages of pregnancy. Assuming that ovulation does not occur during pregnancy (which is estimated to last 14.9 months (Kasuya and Marsh, 1984)) it is obvious that the degeneration of a young CA must be greatly reduced or halted during this time, a conclusion supported by histological study of the young CAs present in the ovaries of Whales 9-115 (pregnant with a 1.2-cm fetus) and 9-92 (pregnant with a near-term fetus) (Table 7).

It is also likely that the rate of regression is slower in old animals, although we have no data bearing directly on this. As discussed below, the oldest pregnant whales we have examined had an expected age of parturition of 35.5 years, and we have no evidence of ovulation occurring in whales older than 40 years. Yet medium CAs were recorded in animals as old as 55.5 years (Table 9 and

Table 8  
Details of the ovaries and reproductive status of *G. macrorhynchus* females 12.5 years and younger

Accession no.	Reproductive status	Fetal length (cm)	Estimated time <sup>2</sup> since last ovulation (days)	Mean diameter CA (mm)		
				Young	Medium	Old
<i>8.5 years (3 immature; 4 mature)</i>						
9-122	P	3	50 <sup>3</sup>	15.1	11.2 8.8	
26-9	P	40.5	160 <sup>1</sup>			
17-2	P	66.5	237 <sup>1</sup>			
7-17	P	90	306 <sup>1</sup>			
<i>9.5 years (5 immature; 5 mature)</i>						
14-15	P	100	336		10.4	7.3
24-25	P	132	430 <sup>1</sup>			
10-14	L		> 452 <sup>1</sup>		11.1	
15-25	R			13.3	10.2	5.6
26-21	R			17.8		
<i>10.5 years (2 immature; 9 mature)</i>						
9-114	P	1	43.6 <sup>3</sup>	15		
10-8	P	2.8	49 <sup>1,3</sup>			
17-31	P	23.3	109		12.2	
15-15	P	65.5	234		15.4	11.5 7.2 7.0 5.0
15-47	P	78	271 <sup>1</sup>			
11-16	P	100	336 <sup>1</sup>			
9-92	P	137	445	12.7		
9-100	L		> 452 <sup>1</sup>	20.3		
14-3	R				11.8 10.8	7.5
<i>11.5 years (1 immature; 7 mature)</i>						
25-2	P	29.5	128		14.0 8.0	3.7
12-5	P	31	132		10.5	9.6
18-47	P	50	188 <sup>1</sup>			
9-99	L		> 452 <sup>1</sup>	18.5		
20-2	R or L			16.7	9.2	
13-35	R (ovd)		several		11.6	4.5
11-5	R			16.9		
<i>12.5 years (6 mature)</i>						
26-8	P/L	19.3	98			7.9 7.4 5.8
15-44	P	75	262		11.3	
23-4	P	78	271 <sup>1</sup>			
26+27-42	L		> 452		13.3 7.6	6.7
13-29	L		> 452	15.5	9.2	8.3
16-10	R				12.5	7.9 6.2 5.0

<sup>1</sup> Pregnant at first ovulation.

<sup>2</sup> Calculated from formula derived from Laws (1959).

$$\text{Length of pregnancy (in days)} = \left(452 \times 0.91 \times \frac{\text{F.L.}}{139.5}\right) + (452 \times 0.09)$$

<sup>3</sup> Probably over-estimated.

P = pregnant; L = lactating; R = resting; R (ovd) = resting with large follicles; P/L = pregnant and lactating; F.L. = fetal length.

Fig. 8). The rate of resorption of CAs is also known to be reduced in post-menopausal human ovaries (Peters and McNatty, 1980).

*Evidence for the persistence of corpora albicantia*

If old CAs disappeared from the ovary, we would expect their size distribution to be negatively skewed and the modal value to decrease with age. Figs 20 and 22 indicate

that neither of these expectations was fulfilled in *G. macrorhynchus*. The mean diameter of the smallest CA in each ovary pair also showed no evidence of changing after about age 20 years (Fig. 23). As discussed below, we have no evidence for ovulations occurring in animals over 40 years old. Thus for example, No. 24-7 (aged 62.5 years) probably had not ovulated for more than 20 years yet had ten old CAs clearly visible in her ovaries. On the

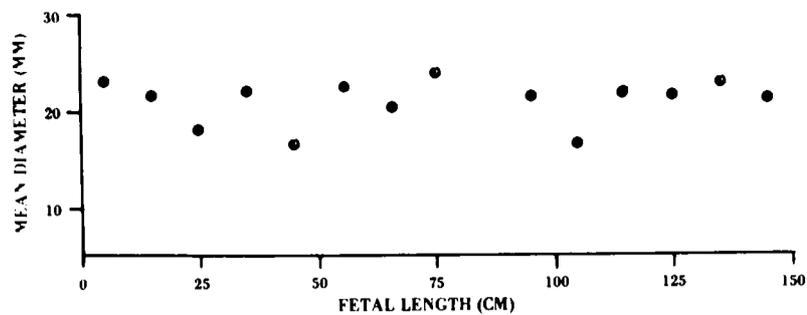


Fig. 21. Diameter of the largest young corpus albicans present per pair of ovaries of *G. macrorhynchus* at various stages of pregnancy.

basis of all this evidence, we concluded that CAs persist in this species.

The frequency distribution of corpus counts (Fig. 17) is somewhat at odds with this conclusion. For if the CAs do not disappear, and if the population of whales is stable and our sample unbiased with respect to age, we would expect the modal number of corpora to be one (rather than six as in Fig. 17) and the frequency to fall off with increasing numbers of corpora (which it does but only after the mode). There are several explanations for the frequency distribution in Fig. 17. Firstly, our sample of

whales is biased with respect to age. Females under 15 years old are under-represented in our sample from the largest school (School 9) and the reproductive status of the sample is not representative of the population (see Kasuya and Marsh, 1984). Further, the range of ages at which sexual maturity is reached (7 to 12 years), the reduction of ovulation rate with increasing age (Fig. 25), the wide individual variation both in ovulation rate (Table 8 and Fig. 25) and in the age at which ovulation declines and ceases (see Fig. 8) will also affect the frequency distribution of corpus counts. In view of these confounding influences, we conclude that we would be unjustified in rejecting the conclusion that CAs persist on the basis of Fig. 17 alone.

#### Bilateral ovarian activity

Even though ovulation appeared to take place from any point on the surface of either ovary, more ovulations occurred from the left ovary in animals of all ages (Fig. 24). The first ovulation occurred from the left ovary in eight whales and from the right in four whales. (The difference is not significant,  $\chi^2$ ,  $P > 0.25$ ). Of 1,521 CLs

Table 9

Results of histological examination of ovarian cortex to obtain an index of follicle abundance

Accession no.	Age (years)	Reproductive status <sup>1</sup>	Follicle abundance ranking <sup>2</sup>	Age of youngest CL or CA <sup>3</sup>	Macroscopic follicles present	No. of corpora artretica and accessory CLs found on macroscopic examination
17-33	4.5	Im	4	—	✓	0
17-9	4.5	Im	4			
17-31	10.5	P	4	CLP	✓	1
17-5	14.5	R	4	young CA	✓	
17-3	15.5	R	3	young CA	✓	1
17-17	15.5	L	3	medium CA	✓	9
17-35	17.5	L	3	young CA	✓	1
7-22	22.5	R	3	'CLO'	✓	
17-18	22.5	L	3	medium CA	✓	3
23-18	24.5	L	3	young CA		5
17-37	24.5	L	3	medium CA	✓	4
24-22	26.5	L	3	medium CA		1
7-8	27.5	L	3	young CA	✓	4
17-13	27.5	R	3	young CA	✓	12
23-3	29.5	R	1	old CA		4
17-29	35.5	L	3	young CA	✓	1
17-20	38.5	R	1	old CA		8
16-9	40.5	R	3	medium CA		17
22-12	41.5	R	1	medium CA		9
9-85	43.5	R	1	old CA	✓	8
17-24	44.5	R	1	old CA		
22-9	44.5	R	1	old CA		
24-12	45.5	R	1	old CA		9
24-19	46.5	R	1	old CA		1
24-1	47.5	R	1	old CA		7
15-5	47.5	R	1	old CA	✓	
17-41	47.5	L	1	old CA	✓	1
15-4	55.5	R	1	medium CA <sup>4</sup>	✓	
17-1	55.5	R	1	old CA	✓	2
24-7	62.5	R	1	old CA		

<sup>1</sup> Im = immature; P = pregnant; L = lactating; R = resting.

<sup>2</sup> 1: < 2 follicles per 10 fields each 2.7 mm<sup>2</sup>; 2: < 10 follicles per 10 fields; 3: 10 > 50 follicles per 10 fields; 4: > 50 follicles per 10 fields.

<sup>3</sup> CLP = corpus luteum of pregnancy; 'CLO' = corpus luteum of 'ovulation'; CL = corpus luteum; CA = corpus albicans.

<sup>4</sup> Classified as medium on macroscopic examination; mean diameter 9.5 mm.

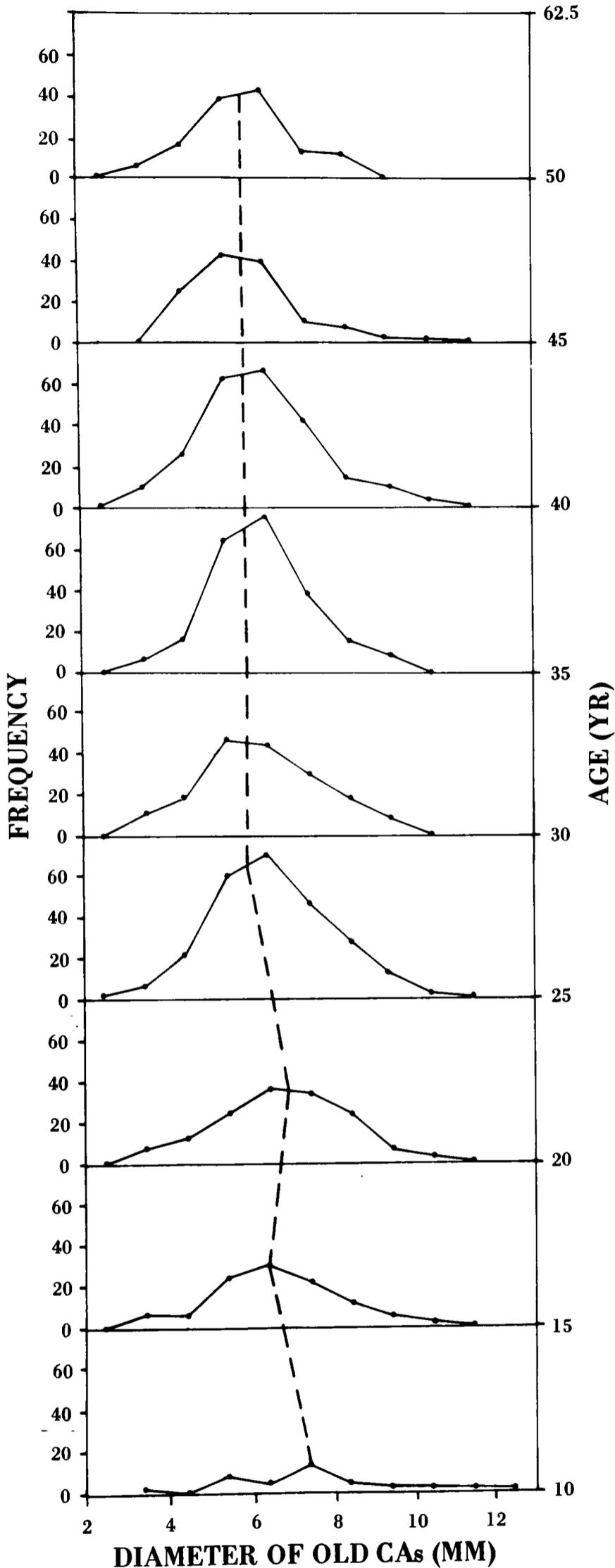


Fig. 22. The size distribution of old corpora albicantia (CAs) in the ovaries of *G. macrorhynchus* at various ages. The dotted line traces the change in the mode.

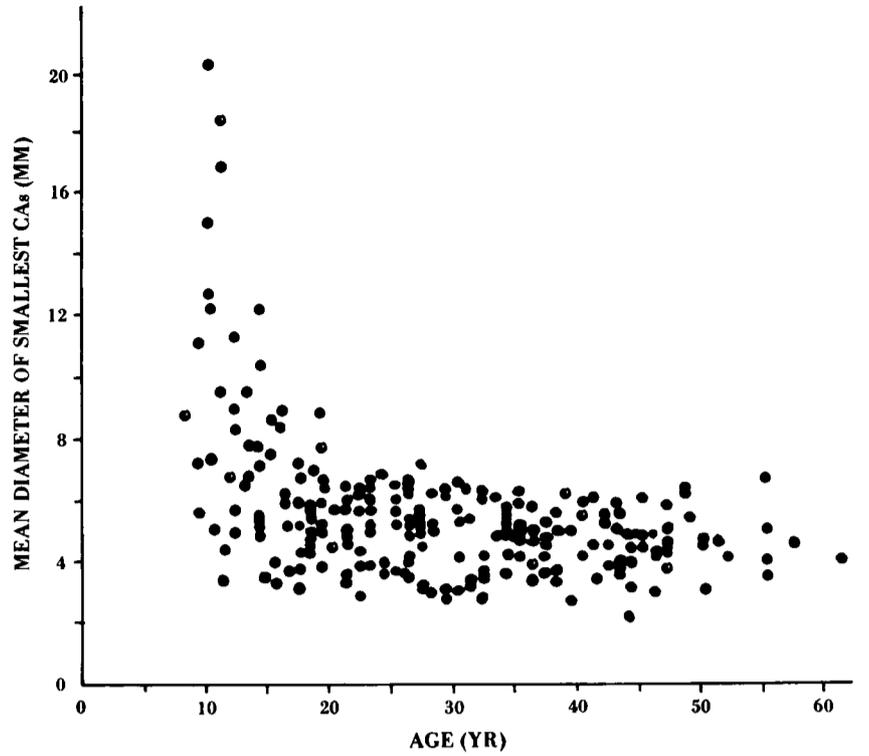


Fig. 23. Scatterplot showing the size of the smallest corpus albicans (CA) in the ovaries of *G. macrorhynchus* at various ages.

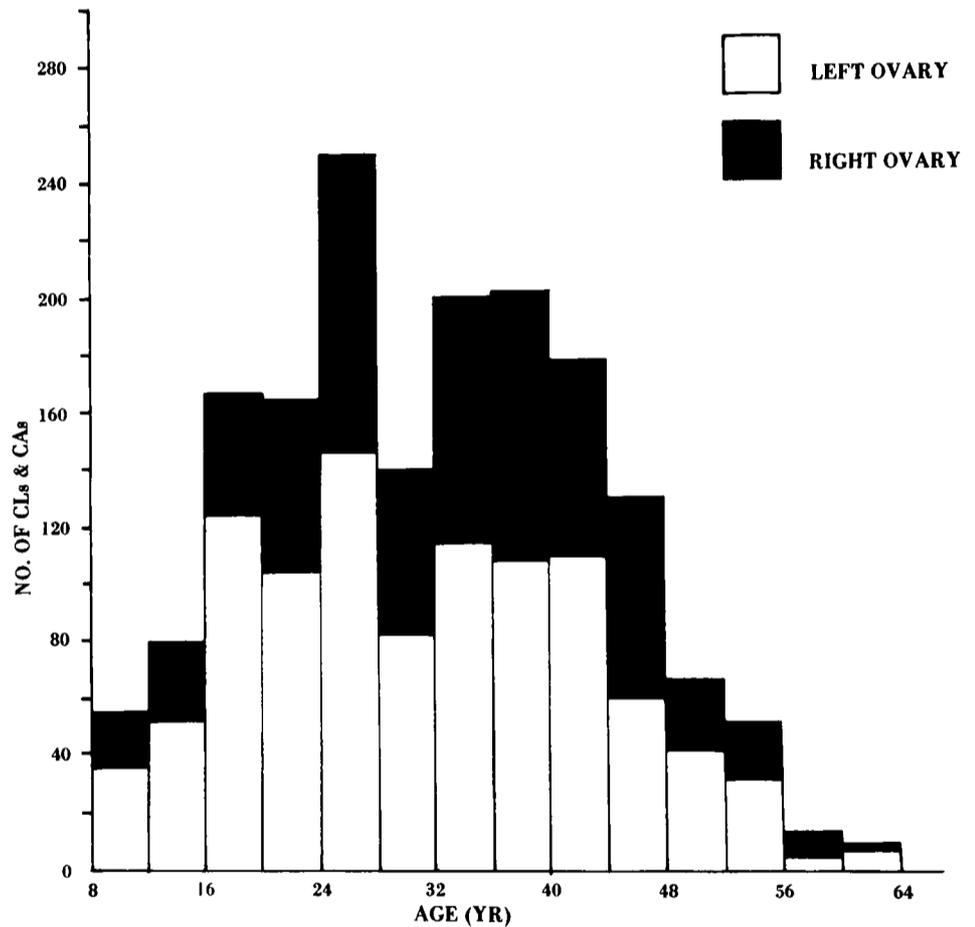


Fig. 24. Numbers of corpora lutea (CLs) and corpora albicantia (CAs) in the left and right ovaries of *G. macrorhynchus* at various ages.

and CAs scored, 61% were found in the left ovary, the proportion being significantly higher (71%) in animals less than 20 years old than in older whales (59%) ( $\chi^2$ ,  $P < 0.001$ ). However, there was no difference in the bilateral distribution of corpora between animals aged between 20 years and 40 years and those older than 40 years ( $\chi^2$ ,  $P > 0.05$ ), providing further evidence that CAs are not lost from the ovary.

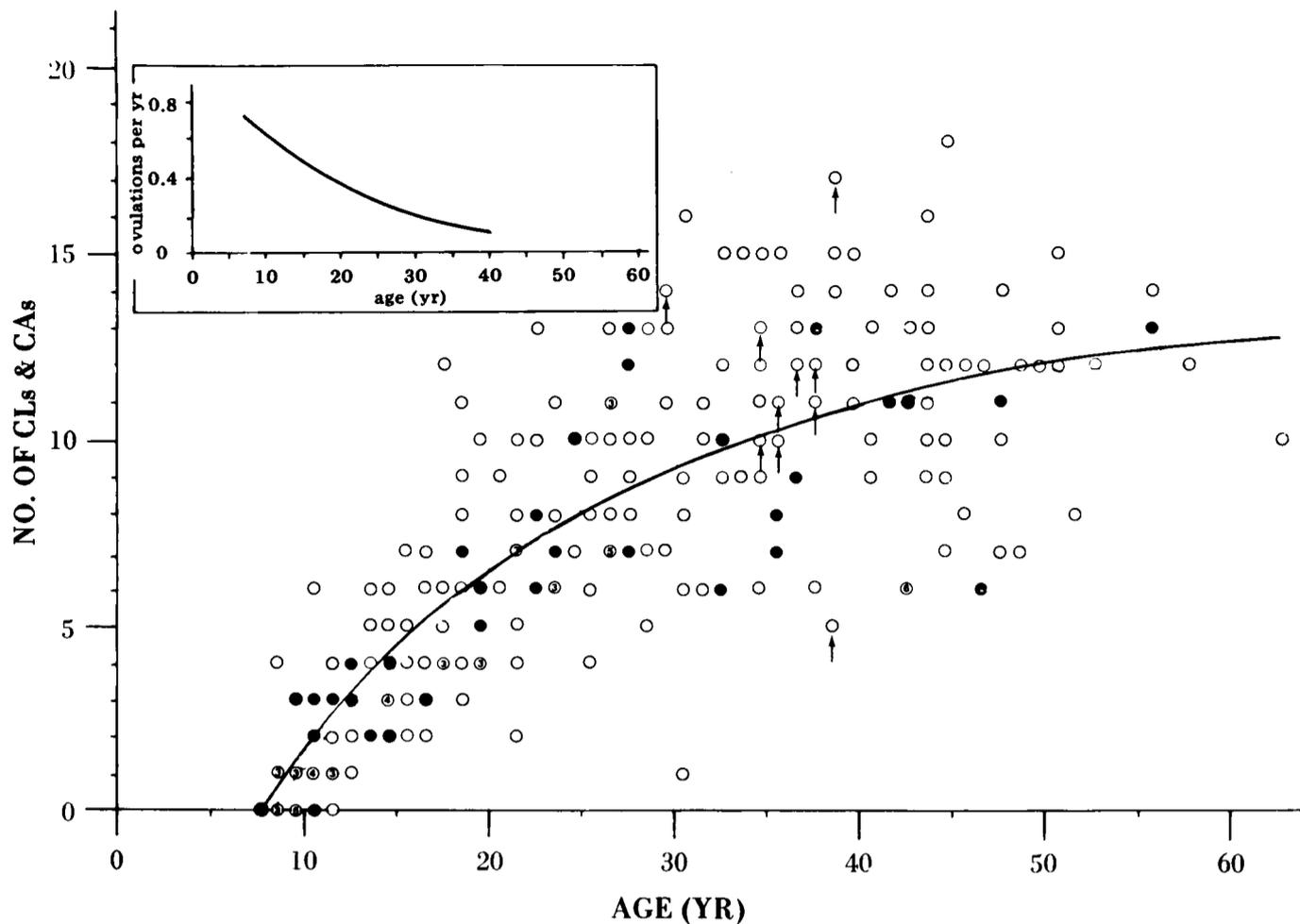


Fig. 25. Relationship between corpus count (number of corpora lutea (CLs) plus corpora albicantia (CAs)) and age in *G. macrorhynchus*. The fitted regression line is

$$y = 13.39 - 19.65 (0.95)^x$$

where  $y$  is the number of corpora at age  $x$ .

○ one whale; ● two whales; ⊙ whales

The arrows indicate the whales less than 40 years old which have been classified as post-reproductive. (All whales more than 40 years old were also classified as post-reproductive). Inset: change in ovulation rate with age calculated using the formula

$$\frac{dy}{dx} = 1.008 (0.95)^x \text{ up to age 40 years.}$$

Where  $dy/dx$  is the number of ovulations per year at age  $x$ . The mean of the corpora count at each age is given in Table 10.

### Ovulation rate

Even assuming that CAs persist as a record of ovulations, estimating the rate of accumulation is difficult because of (1) variation in the age at attainment of sexual maturity; (2) change in ovulation rate during an individual's reproductive life span and (3) individual variation in the accumulation rate. All of these factors contribute to the scatter in the plot of number of corpora (CLs plus CAs) against estimated age (Fig. 25).

As discussed by Kasuya and Marsh (1984) and illustrated in Table 8, females of *G. macrorhynchus* ovulate for the first time between the ages of 7 and 12 years. The ovulation rate obviously changes with age (Fig. 25) and, as discussed below, we have no evidence of recent ovulations occurring in any whale over 40 years old. The number of corpora in 45 whales 40 years old and older was independent of age ( $r = 0.12$ ,  $P > 0.2$ ). The spread of values for the number of corpora counted in the ovaries is considerable irrespective of the age of the whale (Fig. 25; Table 10). The magnitude of the standard deviation of corpus counts for a given age is highly variable (probably due to the small sample sizes) but shows no systematic increase after about age 17 years.

The individual variation in the accumulation rate is illustrated by Table 8, which summarizes the details of 31

Table 10  
Mean ( $\bar{x}$ ) of corpus counts (corpora lutea and corpora albicantia) for *G. macrorhynchus* females of various ages

Age (years)	Corpus count		Age (years)	Corpus count		Age (years)	Corpus count	
	$n^*$	$\bar{x}$		$n^*$	$\bar{x}$		$n^*$	$\bar{x}$
8.5	7	1.0	24.5	3	9.0	40.5	3	10.7
9.5	10	0.9	25.5	5	7.4	41.5	3	12.0
10.5	11	1.8	26.5	11	9.0	42.5	4	9.0
11.5	8	1.9	27.5	9	10.1	43.5	7	12.1
12.5	6	2.8	28.5	4	8.8	44.5	5	11.2
13.5	5	3.8	29.5	4	11.3	45.5	2	10.0
14.5	10	3.5	30.5	5	8.0	46.5	3	8.8
15.5	5	4.2	31.5	3	9.0	47.5	5	10.6
16.5	6	4.2	32.5	7	9.7	48.5	2	9.5
17.5	6	5.8	33.5	2	12.0	49.5	1	12.0
18.5	8	6.9	34.5	7	9.4	50.5	3	13.3
19.5	8	5.5	35.5	7	9.4	51.5	1	8.0
20.5	2	7.5	36.5	5	11.4	52.5	1	12.0
21.5	8	6.3	37.5	5	11.0	55.5	3	13.3
22.5	6	8.5	38.5	4	12.8	57.5	1	12.0
23.5	7	7.3	39.5	3	12.7	62.5	1	10.0

\*  $n$  = Sample size.

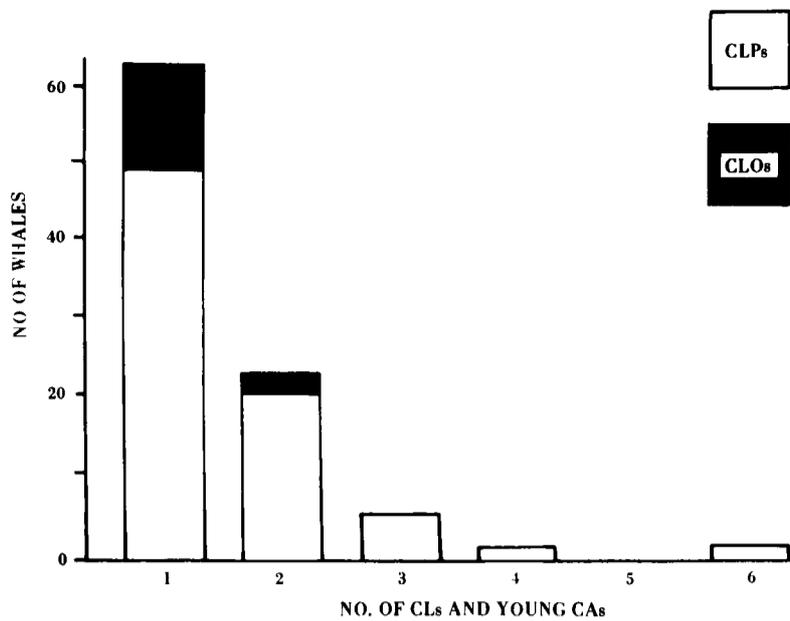


Fig. 26. Frequency histogram of the number of recent ovulations (corpora lutea (CLs) plus young corpora albicantia (CAs)) in female *G. macrorhynchus* with at least one corpus luteum. CLP = corpus luteum of pregnancy; 'CLO' = 'corpus luteum of ovulation'.

newly-mature whales aged between 8.5 and 12.5 years inclusive. Although 14 of these animals had only 1 corpus, one of the youngest (No. 9-122, 8.5 years) had four; another (No. 15-15, 10.5 years) had six. Fig. 26 provides further evidence of individual variation in the ovulation rate. Counts of the number of CLs and young CAs in the 95 animals with an active CL showed that although about two-thirds of these animals had no young CA, the remainder had one to five, suggesting that they had ovulated several times shortly before becoming pregnant. (The whale with one CL and 5 young CAs was No. 17-44 aged 16.5 years).

When Perrin *et al.* (1976) calculated ovulation rates for the spotted dolphin, *Stenella attenuata*, they corrected for individual differences in age at first ovulation and calculated ovulation rates in terms of reproductive age rather than absolute age. We decided not to do this because the sample size was rather small (Table 8) to make a meaningful correction.

The relationship between age and number of corpora obviously cannot be satisfactorily described by a single straight line (Fig. 25). Mizroch (1981) attempted to overcome this problem for a corresponding (but much larger) data set for fin whales by fitting a series of straight lines, each for an arbitrarily-selected, non-overlapping age range. We attempted this initially but ultimately rejected the approach because (1) the data are so variable that the results obtained were greatly affected by the way in which the age range was subdivided and (2) the corpus counts at a given age (especially for low ages) do not meet the assumptions of least-squares curve-fitting (see Zar, 1974), which makes the validity of comparing the slopes of a series of different lines rather dubious.

While acknowledging that the data do not meet all the assumptions, we decided to fit a single curve to the corpus count/age data of 243 females (including immature individuals) seven years old or older. (This sample was not corrected for bias; see Kasuya and Marsh, 1984). A single-phase, exponential curve of the form

$$Y = 13.39 - 19.65 (0.95)^x$$

where  $Y$  = number of corpora at age  $x$  had an  $r^2$  of 0.66, i.e. the curve explained about two-thirds of the variation

in corpus count with age. The residuals showed no systematic bias. The estimates of all the parameters were significantly different from zero at the 0.001 level. This curve suggests that the ovulation rate falls continuously throughout life from about 0.7 ovulations per year for seven-year-olds to about 0.14 per year for 39-year-olds (inset, Fig. 25). Obviously this curve is not completely satisfactory, as it does not model the complete cessation of ovulation after age forty, but the value it gives for the annual ovulation rate for animals older than 40 years is very low ( $< 0.13$ ).

An alternative approach is to fit an exponential curve to the corpora counts of animals between 7 and 40 years old. This curve is, however, less satisfactory, as it gives a higher ovulation rate at age 40 years (i.e. 0.22 ovulations per year).

### Changes in ovarian condition with age

As discussed by Kasuya and Marsh (1984) the percentage of pregnant females decreases with age. The oldest pregnant female in our sample was 34.5 years old, with a predicted age at parturition of 35.5 years. This was also the age of the oldest female which had recently given birth (the day before her death). Even though 12 whales older than 35 years (the ovaries of 10 of which were studied in detail) were still lactating, consideration of the ages of their probable calves suggests that these animals might also have given birth to their last calf when, at most, 37 years old (see Table 19, Kasuya and Marsh, 1984).

The ovaries of seven females aged between 36.5 and 39.5 years, inclusive, showed evidence of recent ovulation (including one with bilateral ovarian papilloma (K. Benirschke, pers. comm.)). Four of these whales had one 'CLO', two had one young CA, and one had two young CAs. However, we could find no evidence of recent ovulation in the ovaries of any of the 49 females 40 years old or older (Fig. 8). We therefore investigated the possibility that the infertility of these old females might be due to age-related changes in their ovaries.

Fig. 8 summarizes the reproductive status and ovarian condition of 245 mature females. Although the ovaries of no female over 40 years old contained both medium CAs and macroscopic follicles, 12 had medium CAs and no follicles that were not obviously atretic on macroscopic examination. As discussed above, although we have evidence that a CL can degenerate into an old CA within two years, we suspect that this rate of regression is greatly reduced in old animals and do not consider that the presence of medium CAs in the ovaries of animals older than 40 years is proof that they have ovulated within the preceding two years.

Six whales over 40 years old had at least one macroscopic follicle in their ovaries, even though all their CAs were classified as old. It is likely that most, if not all, of these follicles were atretic or destined to become so. The large follicles from older females that we investigated histologically were all atretic (e.g. No. 25-31 aged 34.5 years had three large follicles 18 mm, 10.3 mm and 7.9 mm in mean diameter; all were cystic (Fig. 5E)).

Thirty-one of the 49 females over 40 years old (63%) had only old CAs and no macroscopic follicles in their ovaries (Fig. 8). Six of the 18 animals (33.3%) aged between 36 and 40 years also had ovaries in this condition, as did five of the 40 animals (12.5%) aged

between 28 and 36 years. All animals younger than 29 years had a CL or medium or younger CA in their ovaries.

Semi-quantitative histological study of samples from the ovarian cortex of 30 whales spanning an age range of 4.5 to 62.5 years (Table 9), indicated that the number of follicles was significantly reduced in older females. All 12 females studied which were 41 years old or older had a follicle abundance rating of one (i.e. < 2 follicles per  $10 \times 2.7 \text{ mm}^2$  fields) as did two younger animals (Nos. 23-3 aged 29.5 years and 17-20 aged 38.5 years), both of which had only old CAs and no macroscopic follicles in their ovaries (No. 23-3 was the youngest animal with this ovarian status).

We tentatively suggest that all females older than 40 years and all with only old CAs and no macroscopic follicles in their ovaries are post-reproductive. According to these criteria, about one quarter of the 245 mature females whose ovaries were studied and for whom age estimates were available were post-reproductive.

Apart from the very low number or absence of follicles, the ovaries of old females showed evidence of other histological changes (Fig. 6B). The cortex was reduced in thickness and very fibrous and the tunica albuginea was very thick. The walls of blood vessels were thickened and sclerosed. Parts of the ovarian surface were calcified in four animals (9-127 aged 38.5 years; 11-19, 44.5 years; 26-12, 48.5 years; 24-7, 62.5 years). The germinal epithelium of the ovaries of two whales (9-123, 38.5 years; 12-3, 48.5 years) had extensively ingrown towards the medulla. No. 23-16 (34.5 years) had a pendulous cyst on one ovary, and No. 13-6 (34.5 years) had a granulosa cell tumour in one ovary. Some of this pathology has been detailed by Benirschke and Marsh (1984).

#### *Decline in the fertility of ovulating whales with increasing age*

Table 11 compares the incidence of 'CLOs' (excluding 'recent ruptures') and CLPs in whales 20 years old and younger with that in older whales. The proportion of the well-established corpora lutea which were classified as CLPs was significantly lower in the older whales ( $\chi^2$ ,  $P < 0.005$ ), indicating that ovulation is less likely to be followed by pregnancy in older females.

Table 11

Incidence of corpora lutea of 'ovulation' and pregnancy in both females twenty years old and younger and in older females. ('CLOs' classified as 'recent rupture' and animals which had recently aborted were not included)

	Age (years)	
	≤ 20	> 20
No. of whales with a 'CLO'	2	13
No. of whales with a CLP	44	29

## DISCUSSION

The ovarian changes associated with varying reproductive status are not completely separable from those due to advancing age, as reproductive status is partially age-dependent. However, this macroscopic and histological study of the ovaries of a large sample of short-finned

pilot whales for which independent absolute age estimates were available does permit some distinction along these lines as discussed below.

### Changes in the ovary associated with reproductive status

#### *Follicular development and atresia*

Follicular development in *G. macrorhynchus* follows the usual mammalian pattern outlined in this volume (Appendix B of Perrin and Donovan, 1984).

The various products of follicular atresia, a particularly conspicuous feature of the ovaries studied, were also substantially similar to structures described in other mammals, including cetaceans (Figs 1 and 2, Appendix B of Perrin and Donovan, 1984). Best (1967) described and figured structures in sperm-whale ovaries similar to corpora fibrosa (Fig. 5A). Corpora atretica *b* (atretic luteinized follicles) (Fig. 5C) have been recorded from mature females of several cetacean species. Different terms have been used by different workers to describe different stages in the development and regression of these bodies (for references see Appendix B of Perrin and Donovan, 1984). In this study we have shown (1) that corpora atretica *b* are formed when the thecal cells of an unruptured antral follicle luteinize and subsequently go through a process of 'fatty' degeneration (Fig. 5C) while accumulating a 'ceroid-type' pigment and (2) that corpora atretica *b* do not persist (Fig. 13). These results should overcome previous confusion about the etiology and persistence of these bodies.

Corpora atretica *b* appear to be much more common in *G. macrorhynchus* than in the other odontocetes for which figures are available. We recorded 938 corpora atretica *b* in 235 pairs of mature ovaries (about 4 per pair), compared with means of 0.28 per pair (Perrin *et al.*, 1976) and 0.27 per pair (Kasuya *et al.*, 1974) in *Stenella attenuata*. We found one or more corpora atretica *b* in about 75% of mature ovary pairs; in contrast, Best (1967) recorded them in about 50% of sperm whale ovaries. Corpora atretica *b* were found in *G. macrorhynchus* at all stages of pregnancy (Fig. 14). This is not surprising. In our sample, although the presence of large (> 5 mm in diameter) follicles was limited to pilot whales with fetuses less than 50 cm long, there were whales with medium-sized follicles (1 < 5 mm in diameter) at all stages in the gestation period (Fig. 10). As Miller and Campbell (1978) point out (for cattle, *Bos taurus*), although the normal oestrus cycle does not occur during pregnancy, follicles can still undergo (limited) development and atresia.

At least one corpus atreticum *a* (Fig. 5B) was recorded in about 10% of mature ovaries (Table 4), a proportion similar to that in the sperm whale (Best, 1967). In both species, the recently ovulated females have the highest incidence of these bodies. The general morphology of a corpus atreticum *a* in *G. macrorhynchus* (Figs. 5B, D, F) is very similar to the corresponding structures in other species as discussed in Appendix B of Perrin and Donovan (1984). However, pilot-whale corpora atretica *a* are, not unexpectedly, smaller than their counterparts in large whales, and we consider that they may not produce a persistent scar of connective tissue such as the corresponding structures do in the larger species (*loc. cit.*).

Accessory corpora lutea (*sensu loc. cit.*) (Fig. 11B) are

not common in *G. macrorhynchus*, occurring in about 6% of ovaries. A similar structure was described in *Globicephala melaena* by Harrison (1949). Cystic atresia similar to that recorded in *G. macrorhynchus* (Fig. 5E) has also been described in the long-finned pilot whale, *G. melaena*, by Sergeant (1962).

#### *The corpus luteum*

The general development of the corpus luteum (CL) of the short-finned pilot whale is similar to that in the franciscana, *Pontoporia blainvillei*, as described by Harrison *et al.* (1981). When fully formed, the CL contained two distinct types of luteal cells (Fig. 11C), a feature reported for several cetaceans (van Lennep, 1950; Best, 1967; Hirose *et al.*, 1970; Mossman and Duke, 1973; Harrison *et al.*, 1981), including *G. melaena* (Harrison, 1949). Although the basic morphology of the CL is similar in the two species of pilot whale, CLs of *G. melaena* (Sergeant, 1962) are generally larger than those of *G. macrorhynchus*. The difference probably reflects the larger body size of *G. melaena*. About 10% of CLs had a jelly-filled centre in *G. melaena* (Sergeant, 1962), which is lower than the 15% incidence of this feature in *G. macrorhynchus* (Fig. 3D).

In both species, some of the 'CLOs' were within the size range of CLPs, while most were smaller (Fig. 16; Sergeant, 1962). Sergeant considered that 'CLOs' in the larger size group were probably corpora of early pregnancy or the result of early embryonic death. We agree with Benirschke, Johnson and Benirschke (1980) that the placental membranes of even very small odontocete embryos are of appreciable size and not easily overlooked and consider that probably only the youngest of the structures that we classified as 'CLOs' were associated with a pregnancy. This conclusion is supported by our observation that 'CLOs' were relatively more common in older whales. We were unable to reliably separate 'CLOs' from CLPs in *G. macrorhynchus* on morphological or histological grounds (see also Appendix B, Perrin and Donovan, 1984).

Sergeant (1962) reported that in *G. melaena* 'CLOs' were particularly noticeable in the young first-maturing females, implying that these animals were sub-fertile. In contrast, it appears that a high proportion of *G. macrorhynchus* in our sample became pregnant at their first ovulation (Table 8). This may be a result of the difference in the age of sexual maturation for the two populations studied rather than an inherent specific difference. Sergeant (1962) estimated that the long-finned pilot whales in the population he studied first conceived at 4.5 to 8 years; whereas our estimate of the pre-reproductive period for this population of *G. macrorhynchus* is 7 to 12 years (Kasuya and Marsh, 1984). Perrin *et al.* (1977) noticed a parallel difference in the fertility rates of very young mature females of *Stenella attenuata* and *S. longirostris*. As they pointed out, such differences in the fertility of young females may reflect inherent differences or may reflect differential population status with respect to exploitation. If females in a more heavily exploited population tend to become sexually mature at an earlier age, they could still be less fertile in terms of pregnancies per ovulation than if they had matured when older.

Sergeant (1962) considered that the CLP of *G. melaena* reaches a maximum diameter in the early part of fetal life

and shrinks again thereafter. However, his evidence for a reduction in the size of a CLP during the gestation period is much less convincing than the evidence of a similar phenomenon in *S. attenuata* (Kasuya *et al.*, 1974; Perrin *et al.*, 1976) and *S. coeruleoalba* (Miyazaki, 1977). We have no evidence that the CLP of *G. macrorhynchus* changes size during the gestation period (Fig. 16), although the evidence for a change in the lipid metabolism of a CLP during this time is convincing (Fig. 11E, F). Histological evidence of a change in the activity of a CL during pregnancy has also been reported for blue and fin whales, *Balaenoptera musculus* and *B. physalus* (Mackintosh and Wheeler, 1929); the sperm whale (Chuzhakina, 1961); the harbour porpoise, *Phocoena phocoena* (Fisher and Harrison, 1970) and *S. graffmani* (= *S. attenuata*) (Harrison *et al.*, 1972).

Multiple CLPs are fairly rare in both *G. macrorhynchus* (Table 2) and *G. melaena* (Sergeant, 1962) as in most other cetaceans with the exception of the white whale, *Delphinapterus leucas* (Brodie, 1972; Sergeant, 1973) and the narwhal, *Monodon monoceros* (K. Hay, pers. comm., 1981) (see Appendix B of Perrin and Donovan, 1984).

#### *The corpus albicans*

The pattern of regression of CAs in *G. macrorhynchus* is very similar to that reported for many other cetaceans, including *G. melaena* (Sergeant, 1962). The connective-tissue elements in the walls of the arteries of the original CL are particularly resistant to change and make up the greater part of the structure of old CAs (Fig. 19D).

Several workers have separated the CAs observed in various cetaceans into two types (usually on histological grounds) and have suggested that one type might have developed from CLOs and the other from CLPs (e.g. Peters, 1939; Sleptsov, 1940; van Lennep, 1950; Robins, 1954; Zemskiy, 1956; Ivashin, 1958; 1984; Hirose *et al.*, 1970; Fisher and Harrison, 1970; Zimushko, 1970; Harrison and Brownell, 1971; Harrison *et al.*, 1969; Harrison *et al.*, 1972; Collet and Harrison, 1981). The essential distinguishing feature of the two types is usually held to be the amount of amorphous, relatively acellular, hyaline material present.

Several workers (e.g. Fisher and Harrison, 1970; Collet and Harrison, 1981) have suggested that CAs which consist of little more than coils of obliterated blood vessels with sparse hyaline material may be the end point in the regression of CLOs, while those with a considerable quantity of acellular material result from CLPs. However, as all 12 CAs of a lactating 48.5-year old female *G. macrorhynchus* (which almost certainly had not ovulated for at least nine years) consisted of little more than coiled blood vessels (e.g. Fig. 19D), we consider that previous workers have been confused by the stages in the regression of CLs to old CAs. We could make no histological distinction between young CAs derived from CLPs and those derived from presumed 'CLOs' (Table 7) and agree with most other cetologists who have studied the CAs from a large series of conspecifics (e.g. Laws, 1961; Sergeant, 1962; Best, 1967; Gambell, 1968, 1972; Kasuya, 1972; Kasuya *et al.*, 1974; Perrin *et al.*, 1976; Miyazaki, 1977; Harrison *et al.*, 1981), that it is not possible to separate CAs of pregnancy from those of ovulation.

Laws (1961) found that for cetaceans the diameter of the fully regressed CA tended to be a constant percentage

of the diameter of the CLP. He calculated that the regression ranged from between 82.6 and 84.1%. The mean diameter of old CAs in *G. macrorhynchus* was 6.4 mm, while the mean diameter of the CLPs was 37.6 mm. Thus the shrinkage was 83%, within the range suggested by Laws.

In *G. macrorhynchus*, CAs can regress to the 'old CA stage' within two years in at least young animals (Table 8). This time is comparable to that suggested for *G. melaena* by Sergeant (1962) who suggested that the rate of regression of a CA may be influenced by the hormonal status of the animal. Our results (Fig. 21) suggest that the rate of regression of young CAs is very slow during pregnancy. A similar result was obtained for sperm whale CAs by Best (1968).

We counted up to 18 CAs per pair of ovaries in *G. macrorhynchus*; Sergeant (1962) found a maximum of 16 per pair in *G. melaena*. Figs 20, 22, and 23 provide convincing evidence that CAs persist in the ovaries of *G. macrorhynchus* as a permanent record of ovulations. This conclusion is supported by our study of the CAs present in old post-reproductive females that had probably not ovulated for up to 20 or more years. In contrast, Harrison (1949) suggested that in *G. melaena*, the CAs may regress to such a degree that they cannot be detected without serial histological sectioning of the ovaries. Sergeant (1962) also considered that some of the small CAs of ovulation may be lost in this species. However, most cetologists working on species for which a large series is available (e.g. Mackintosh and Wheeler, 1929; Mackintosh, 1942; Chittleborough, 1954; Chuzhakina, 1961; Laws, 1961; Ohsumi, 1965; Best, 1967; Gambell, 1968, 1972; Kasuya, 1972; Kasuya *et al.*, 1974; Perrin *et al.*, 1976; Miyazaki, 1977) have considered that CAs persist.

#### *The pattern of ovarian activity*

Both Harrison (1949) and Sergeant (1962) agreed that ovulation could take place from any point on the surface of either ovary in *G. melaena*. *G. macrorhynchus* appears to be similar in this regard. In contrast, Best (1967) reported a definite polarity of ovulation sites in sperm whale ovaries. Both *G. melaena* and *G. macrorhynchus* show some bilateral difference in ovarian activity, more ovulations tending to occur from the left ovary in both species. However, the dominance of the left ovary is much less dramatic in *Globicephala* spp. than in many other odontocetes (for references see Appendix B of Perrin and Donovan, 1984).

There is no good evidence that either *G. melaena* or *G. macrorhynchus* can be polyovular. Multiple CLs of pregnancy have occasionally been observed in both species, but the supernumerary CLPs were probably derived from unruptured follicles. However, it seems likely that pilot whales can be polyoestrous. We have evidence of up to six ovulations occurring in fairly quick succession in *G. macrorhynchus* (Fig. 26). Harrison (1949) and Sergeant (1962) also report instances of two or more CAs of about the same size in *G. melaena* ovaries.

#### *Seasonality of oestrus*

Kasuya and Marsh (1984) concluded from their data on estimated parturition dates and the length of gestation that conceptions in this population of *G. macrorhynchus*

occurred in all months of the year, with a single peak in April/May. The ovarian data on the seasonality of oestrus fit this picture reasonably well. Follicle size seemed to be greatest in both immature and lactating females in the months May to July, while 'CLOs' were most commonly observed both during this period and in October. Some resting females also had large (> 8 mm in diameter) follicles in February, October and December, suggesting that oestrus activity may be prolonged in resting females that fail to conceive in the main part of the mating season.

### **Changes in the ovaries of *G. macrorhynchus* with age**

#### *Follicle abundance*

The age-related decline in follicle abundance in the ovaries of *G. macrorhynchus* is conspicuous both macroscopically and histologically (Fig. 6). Chuzhakina (1961) documented a similar decline in sperm whale ovaries and claimed that follicles were completely absent from whales with 13 or more corpora. These results are not surprising if we accept the evidence presented by Zuckerman (1956) (which albeit is based on very few species, none cetaceans), that there is no renewed proliferation of oocytes beyond fetal or early post-natal life in mammals. The decline in the population of female germ cells in the ovary begins prior to birth in the species that have been studied and continues until the cells are exhausted or the animal dies (Talbert, 1977). However, the relationship between exhaustion of developing oocytes and normal life span is extremely variable among the few mammalian species, and even strains of species, that have been studied (Talbert, 1977). We observed no CLs or young CAs in any of the 49 short-finned pilot whales aged over 40 years, suggesting that none of these animals had ovulated recently.

Although our assessment of the oocyte population in the ovaries of specimens of *G. macrorhynchus* of various ages (Table 9) can, at best, be regarded as semi-quantitative, it is obvious that the oocyte population of whales over 40 years old is severely depleted. (To obtain a numerical estimate of the oocyte stock of such animals is impracticable: about 6,000 histological sections would be needed per ovary).

Sergeant (1962) noted that there may be only a single enlarging follicle in older long-finned pilot whales 'approaching oestrus'. We have also observed older short-finned pilot whales with only one large follicle. Such animals are unlikely to conceive. Research on other mammals has shown that during the fertile part of the life span, antral follicle production is always in excess of the number ovulated. Those follicles which remain may, however, serve an important hormonal function and give rise to the oestrogen that seems essential for the continued growth of those that ovulate (Jones, 1970). According to Nalbandov (1964), if all but one or two of the developing follicles are destroyed during the follicular phase, none of the remainder ovulates normally. Thus the presence of a small number of macroscopic follicles in the ovaries of *G. macrorhynchus* females over 40 years of age is not inconsistent with our classification of these animals as post-reproductive. Although menopause can

occur in women before the stock of oocytes is completely exhausted, it is generally agreed that post-menopausal ovaries show little or no follicular response to exogenous gonadotrophins (Talbert, 1968).

#### *Follicular atresia*

Large follicles that do not ovulate, degenerate (Jones, 1970). The follicles that have been studied in short-finned pilot whales aged 40 or more years were all atretic. Cystic atresia of macroscopic follicles was common (Fig. 5E). Accessory corpora lutea were present in the ovaries of nine non-pregnant whales (Table 2). Similar bodies in the ovaries of old mice, *Mus musculus*, have been described as 'examples of total failure of the ovarian mechanism' (Jones, 1970).

Atresia accompanied by thecal luteinization to produce corpora atretica *b* is a conspicuous feature of mature *G. macrorhynchus* ovaries. Although the incidence of these bodies was significantly lower in females over 40 years old than in those aged between 20 and 40 years old, we consider that this reflects the much lower number of follicles in the ovaries of these older whales (Table 9) rather than a reduction in the tendency for follicles to become atretic.

The incidence of follicular atresia has also been shown to be age-related in other mammals. Best (1967) reported a sudden and rapid increase in the proportion of sperm whales exhibiting follicular atresia after 13 CAs had accumulated in the ovaries (unfortunately, absolute age estimates were not available). Ageing rodents show an increasing tendency for follicles to luteinize prematurely so that ovulation cannot take place (Talbert, 1968). Ceroid associated with regressing luteal bodies (corpora atretica *b*) was present in greater amounts in the ovaries of aged pigtail macaques, *Macaca nemestrina*, than in younger animals (Graham, Kling and Steiner, 1979).

Factors which control the rate of follicular atresia have the greatest influence on the rate of loss of oocytes (Talbert, 1977). In all mammals the loss of follicles by ovulation is insignificant compared to the 'devastating effects of atresia' (Jones, 1970). The rate of follicular atresia in mature *G. macrorhynchus* ovaries (which, as discussed above, seems to be unusually high) is probably an immediate cause of the high proportion of females in our sample which were post-reproductive. Follicular atresia accompanied by luteinization is also a conspicuous feature of the ovaries of mature pigtail macaques (Graham *et al.*, 1979), one of the few non-human primates in which a menopausal condition has been convincingly documented.

#### *Other changes*

In addition to the decline in follicular abundance and increase in atresia discussed above, other age-related changes occur in the histology of the ovaries of *G. macrorhynchus*. These are similar to those which have been documented in post-menopausal humans. Such changes include a general decrease in volume of the cortex and thickening and sclerosis of arterial walls (Graham *et al.*, 1979), ingrowth of the surface epithelium (Peters and McNatty, 1980) and increased pathology (Labhsetwar, 1970). Chuzhakina (1961) observed some of these

features in the ovaries of sperm whales with 13 to 16 CAs which also exhibited no evidence of recent ovulations or primordial follicles. However, as discussed below, the evidence for a climacteric in the sperm whale is far from conclusive.

We were surprised to find no generalized reduction in ovarian weight in the females which were classified as post-reproductive (Fig. 4). Ovaries have been reported to become atrophic in menopausal women, rats, mice and hamsters (for references see Labhsetwar, 1970), but actual data on the weight changes are scanty. As Labhsetwar (1970) points out, the accurate determination of weight changes is complicated by the tendency of old gonads to undergo pathological changes and by the positive correlation between body weight and ovarian weight. We have not attempted to separate these confounding influences on ovarian weight in *G. macrorhynchus*.

#### *Comparison with other odontocetes*

A small percentage of adult female spotted dolphins, *S. attenuata*, (Perrin *et al.*, 1976) and spinner dolphins, *S. longirostris*, (Perrin *et al.*, 1977) were classified as post-reproductive or senile by criteria including (1) being neither pregnant nor lactating; (2) having small withered ovaries; (3) having no macroscopic ovarian follicles and (4) having no young CAs. As most of the specimens of *G. macrorhynchus* that we have classified as post-reproductive do not satisfy these criteria (Figs 4 and 8), we cannot make a meaningful comparison between the incidence of post-reproductive females in these species.

Sergeant (1962) considered that about 5% of mature specimens of *G. melaena* were post-reproductive. Again it is difficult to make between-species comparisons as Sergeant apparently assumed that lactating females had not reached the climacteric. However, as the relative proportions of pregnant, lactating and resting females in Sergeant's sample of *G. melaena* are very different from the values we have obtained for *G. macrorhynchus* (Kasuya and Marsh, 1984), it seems likely that the proportion of post-reproductive females is lower in *G. melaena* than in *G. macrorhynchus*. (It is, of course, possible that the differences observed merely reflect population differences in age composition and/or history of exploitation).

As discussed above, anatomical studies of sperm whale ovaries reveal clear indications of a drop in fertility with age. Age-specific differences are also found in the proportions of the various reproductive classes in the catch. Age-specific pregnancy rates have been demonstrated by Ohsumi (1965), Best (1968; 1980) and Gambell (1972), but only Ohsumi's rates are expressed in terms of absolute age rather than relative age estimated from corpus counts. As the number of corpora present at a given age in the sperm whale is highly variable (see Ohsumi, 1965), the latter approach has obvious limitations. Ohsumi's data are also potentially misleading in that he has assumed that all females with a CL are pregnant. However, Ohsumi (1965) has aged a 'pregnant' sperm whale at 59 to 60 years, not much younger than the oldest animals he recorded, aged 63 to 64 years. We conclude that, at present, there is no evidence for an age-specific climacteric in the sperm whale, even though fertility seems to be significantly reduced in old animals.

### *Other anatomical changes associated with reproductive senescence*

Age-related changes in pregnancy rate are not dependent solely on ovarian status but on the sum of the total age changes in the reproductive tract. Although primary ovarian failure is thought to contribute significantly to the age-related decline in reproductive capacity in women (Jones, 1970), in laboratory rodents reproductive decline has been shown experimentally to be primarily due to the uterus (Finn, 1970). Sergeant (1962) described degenerative changes in the uterus of 'senile' specimens of *G. melaena*. We have not yet established whether there are parallel changes in the uterine morphology of *G. macrorhynchus*, but they cannot be ruled out as a possible cause of the decline in fertility observed in ovulating whales older than 20 years (Table 11). Partial uterine failure is suggested as one of the causes of the low incidence of pregnancy in pre-menopausal women (Finn, 1970).

### Concluding remarks

Krohn (1964) claimed that there is 'no reasonable doubt that the likelihood of conceiving declines with increasing age in all species (of mammal) for which there is any information at all'. Unfortunately such information is difficult to obtain, especially for marine mammals with life spans similar to our own. One of the best ways to obtain this information is to use the carcass-salvage approach on a large sample of conspecifics obtained through a fishery, as has been done for a number of cetacean species. However, if age-specific reproductive rates are to be measured accurately, reliable estimates of absolute age are essential. It should also be remembered that data on the age-specific abundance of fetuses are (with suitable corrections) likely to be much more valuable to management than inferences based on the study of the ovaries alone. Unfortunately most studies of cetaceans do not meet these criteria.

As reviewed by Marsh and Kasuya (in press), a decline in pregnancy rate with advancing age seems likely for at least several odontocetes. However, at this stage there is no firm evidence that the post-reproductive phase occupies a major portion of the total life span of the females of any wild mammal other than *G. macrorhynchus* which (in this population) ceases to produce calves by the age of about 36 years when it still has a life expectancy of about 14 years (Kasuya and Marsh, 1984). Kasuya and Marsh also point out that the behaviour work of Bigg (1982) and his co-workers suggests that killer whales may be similar. These species certainly present the closest parallel to the situation in humans, where even in societies, such as India in the 1880's, which did not have the benefits of 'modern medicine', the life expectancy for women of menopausal age was about 15 years (Dublin, Lotka and Spiegelman, 1949).

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# Possible Biases in Estimates of Reproductive Rates of the Spotted Dolphin, *Stenella attenuata*, in the Eastern Pacific

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## ABSTRACT

Reproductive rates for the spotted dolphin have been estimated from field samples in two ways:

1. Directly from the fraction of pregnant females in the samples and the estimated duration of gestation.
2. Indirectly from estimates of the length of the calving cycle – the sum of the estimates of the duration of gestation, lactation and the post-weaning interlude.

Both methods are subject to bias from the estimate of the gestation period, and perhaps from the seasonality of the sampling. The second method is subject to additional bias from estimation of the ages of calves at weaning. Both methods are subject to errors caused by stock misidentification, changes in fishing procedure (changes in sample method), and incorrect determination of reproductive state. The second method is subject to additional errors associated with the sampling of the suckling calves. Examination of these biases and errors indicates that both methods are likely to underestimate annual pregnancy rate with the first method providing a more precise estimate.

Annual pregnancy rate is strongly correlated with annual kill rate. One interpretation of this relation is that the reproductive rates for the stock have changed in response to changes in fishing mortality. If true, a further implication is that historical changes in the net reproductive rate in the range of 5 to 12% have occurred, which are higher than values assumed in the current stock assessment model.

## INTRODUCTION

This paper examines the basis of the estimated reproductive rates for 'stocks' of eastern-Pacific spotted dolphin, *Stenella attenuata*, used by the United States Government for setting management regulation for this species (and other species) to limit the incidental mortality associated with tuna-fishing activities in the eastern Pacific. Errors in the estimates of reproductive rates may result in improper management advice and therefore adversely affect the populations or the fishery.

Estimates of annual replacement rates were used by the National Marine Fisheries Service in developing a management model for dolphin stocks. For this purpose, the gross annual reproductive rate (GARR), the annual production of calves as a fraction of the total population number, was calculated (Henderson, Perrin and Miller, 1980). However, their estimates were not used for the stock assessment model, which required an estimate of the maximum net reproductive rate ( $R_{max}$ ), because estimates of net reproductive rates from the data base collected by NMFS were not considered practical (Smith, 1979).<sup>2</sup>

Several species and stocks of dolphins are involved with the fishery for tunas in the eastern tropical Pacific Ocean (Au, Perryman and Perrin, 1979), but the spotted dolphin is the most important species to this fishery, and one putative stock, the 'northern offshore spotted dolphin' is the most important. Because of heavy fishing on this stock, it provides the best data base in terms of sample size: about 10,000 (Henderson *et al.*, 1980, Fig. 5) and time series (1971–78)). For these reasons, this stock is

used here to evaluate the available data on reproductive rates for eastern Pacific dolphins and the effects of fishing mortality on these rates.

## METHODS

The calculation of GARR requires at least an estimate of the length of the gestation period and the fraction of the population that is pregnant. How these estimates were obtained is discussed below.

### The gestation period

Direct determination of the length of gestation for the spotted dolphin has not been possible. Perrin, Coe and Zwiemel (1976) estimated the gestation period for the spotted dolphin (porpoise) from collected material. The stock was not specified, but the map of the sample locations on page 233 of their paper indicates most of the animals were from the northern-offshore stock. Their method assumed that both fetal growth (length) after the first few weeks of pregnancy and early postnatal growth were linear with time. Average length at birth was estimated as 82.5 cm from the regression of length on percent of sample postnatal.

Fetal growth was estimated to be 8.283 cm/month from a computer-forced modal progression (NORMSEP) using fetus-length data collected between January and October 1972, yielding an uncorrected gestation period of 9.96 months. A correction of 1.55 months was added to account for the period of nonlinear growth during early pregnancy, giving an estimated gestation period of 11.5 months  $\pm$  0.2 months. The uncertainty applies to the estimate of the length of the period of nonlinear growth and does not include errors from any other source.

No estimates of the uncertainties for the total gestation period have been made. A comparison of estimated fetal growth rate for the spotted dolphin with those for other

<sup>1</sup> Present address: c/o Living Marine Resources, Inc., 7169 Construction Court, San Diego, CA 92121, USA.

<sup>2</sup> The range for  $R_{max}$ , a hypothetical parameter used in a density-dependent reproductive model for the stocks, has been taken as 0.02 to 0.06 and 0.00 to 0.04. The former range is currently used, with 0.04 being the point estimate used. The rationale for these ranges will be found in Smith, 1979.

Table 1  
 Reproduction statistics for the northern offshore spotted dolphin<sup>a</sup>

Year	1971	1972	1973	1974	1975	1976	1977	1978
Sample size mature females	86	455	159	112	125	63	31	32
GARR	0.17	0.15	0.18	0.10	0.10	0.09	0.06	0.08
Fraction mature females pregnant	0.51	0.43	0.52	0.32	0.30	0.30	0.23	0.22
Fraction mature females lactating	0.49	0.43	0.34	0.59	0.59	0.60	0.58	0.69
Fraction of population immature (nursing and young) <sup>b</sup>	N/A	N/A	0.40	0.43	0.42	0.51	0.48	0.40
Young <sup>c</sup>	—	—	0.31	0.28	0.31	0.41	0.39	0.25
Nursing	—	—	0.09	0.15	0.11	0.10	0.09	0.15

<sup>a</sup> 1971–72 from Perrin *et al.*, 1976, p. 262, Table 8; all-set data, all females pregnant and lactating are included in fraction pregnant. 1973–78 from Henderson *et al.*, 1980, sets with 40 or more animals killed.

<sup>b</sup> This is taken to be the same as the fraction of females immature; however, some bias may exist because of departure from a 1:1 male:female sex ratio.

<sup>c</sup> The fraction young was obtained by subtracting half the number of lactating females from the number of immature females, which sample presumably includes the associated nursing calves.

Cetacea indicates that the rate for this species may be underestimated and gestation period overestimated (Perrin, Coe and Zweifel, 1976, p. 238). The same conclusion can be derived from comparison of gestation period for this species with those of other species and from brain-weight data (Perrin, Holts and Miller, 1977, p. 734 ff). Further, an attempt to determine reproductive seasonality in this species did not confirm the existence of well-defined fetal length modes (Barlow, 1979), which may indicate that the rates derived from the NORMSEP fit are less reliable than previously believed. Therefore, the 11.5-month estimate of gestation period for this species should be considered provisional and possibly an overestimate.

### Gross Annual Reproductive Rate

Several methods can be used to estimate GARR. The simplest is to determine the number of pregnant animals as a fraction of the total population and apply a correction for gestation period

$$\left(\frac{12}{11.5} = 1.04\right).$$

The sample data, from animals collected from purse-seine sets, are believed biased because of the greater vulnerability of nursing females and their calves to capture (Powers and Barlow, 1979). This bias reportedly can be reduced by limiting the data set to stations where 40 or more animals are taken (Powers and Barlow *op. cit.*). If this does not remove all of the bias then the estimate of GARR will still be an underestimate.

Henderson, *et al.* (1980) used two other methods for estimating GARR. Their Method I, which is a derivative of the above method, requires that the sample data provide estimates of: (a) the proportion of the population that is female; (b) the proportion of those females that are reproductively active; and (c) the proportion of the reproductively active females that are pregnant. The product of these three fractions, corrected for the length of gestation provides an estimate of GARR (see Perrin *et al.*, 1976).

Their Method II is also an extension of the method of Perrin *et al.* (1976, p. 261 ff) and Perrin, Miller and Sloan (1977, p. 632), who suggested that there was reason to believe both nursing calves and lactating females were over-represented in the samples because of a strong mother-calf bond and less stamina for the nursing calves. At that time they believed that the bias from this source could be at least partially corrected by estimating GARR as the reciprocal of the calving interval.

Calving interval was estimated as the sum of the gestation period, the lactation period and the resting period. Gestation was taken to be 11.5 months as noted above. Resting period was estimated from the sample as the ratio of the number of mature females resting, i.e. not pregnant, lactating or senile (post-reproductive), to the number pregnant times the length of gestation. The duration of lactation was estimated by the method of 'cumulative calves'.

The cumulative-calf estimate assumed a nursing calf exists in a sample for each lactating female. The length (age) at which the cumulative frequency of calves in a sample equals the number of lactating females is assumed equal to the average length (age) at weaning. The age of the longest calf, the duration of lactation, was calculated from growth curves developed by Perrin *et al.* (1976).

There are several problems associated with Method II estimation, and there appears little reason for its continued use if the bias from over-representation of nursing calves and lactating females is reduced or corrected by setting a sample kill criterion of 40 or greater (Powers and Barlow, 1979; Henderson *et al.*, 1980). Method II contains all the uncertainties of Method I (estimation of age, gestation period, sampling errors) as well as uncertainties associated with sampling lactating females and nursing calves. As a probable result, Method II at times produces unreasonable estimates of GARR.<sup>3</sup>

Because of these uncertainties with Method II, the

<sup>3</sup> For example, Henderson *et al.*, 1980, p. 20 reported a calculated calving interval of 4.38 years for the southern offshore spotted dolphin in 1976 based on Method II (cumulative calf). The sample, however, contained 69 pregnant females out of 138 sexually mature females, which indicates a calving interval of less than two years.

Method I approach is used in this paper to provide the GARR estimates given in Table 1. The uncertainties associated with the data preclude error estimates. The precision of the GARR estimates might be improved by using the 1973–78 estimate for proportion female (0.557) given in Henderson *et al.* 1980, p. 16. Inspection of the other estimates – proportion pregnant, etc. – indicates that pooling or averaging is not warranted because of the apparent time-related trends.

**Replacement rates**

Some attempts have been made to derive estimates of replacement rates (net reproductive rates) from GARR. These included defining net reproductive rate as the difference between the gross reproductive rate and an estimate of natural mortality rate (Smith, 1979). Estimates of natural mortality rates for a Japanese population of spotted dolphins, which was assumed to be nearly unexploited, were used for this purpose in 1976 at a NMFS workshop to estimate a net reproductive rate of about 4% for the eastern Pacific population of spotted dolphins. This approach was abandoned at the 1979 workshop (Smith, 1979). Two reasons were given: the Japanese population ‘may have been more heavily exploited than previously thought’ (Smith, 1979, p. 41) and males were believed under-represented in the samples.<sup>4</sup>

Another attempt to estimate net reproductive rate was made at the 1979 workshop using the estimated GARR for a lightly fished eastern Pacific stock of *Stenella attenuata*, the so-called southern offshore spotted dolphin. The assumption again, was that GARR for a lightly fished stock should approximate the natural mortality rate. However, some very serious sampling biases are evident in the data (seasonality of samples and high variability among proportion pregnant in samples), and the GARR for the southern stock could not be used. The workshop abandoned the available data in favor of selecting a range with a lower limit of zero and an upper limit of 4%, which was asserted to be the maximum value reported for cetaceans (Smith, 1979, p. 43).<sup>5</sup>

**DISCUSSION**

The observational data, such as those summarized in Table 1, provide the only species-specific information from which to calculate reproductive rates for this species. As mentioned above, these data are subject to several sources of error or bias. Perhaps the statistic least subject to error is the fraction of mature females pregnant, being independent of the assumptions about

<sup>4</sup> Net reproductive rate for the eastern stock was estimated as GARR-eastern (an ‘exploited stock’) minus GARR-Japanese (an ‘unexploited stock’). These reasons would result in an overestimate of GARR for the Japanese population and hence underestimate the net rate for the eastern Pacific population. This fact escaped the workshop, which chose to use an even lower estimate of the net rate than 4%.

<sup>5</sup> Such a low upper-limit for net reproductive rates of cetaceans is obviously in error. Smith himself (1977) suggested an annual rate of increase of 4.9% to 6.2% for sei whales, Chapman (1979) provided estimates of exponential growth rates for two species of whales, and these range from 0.08 to 0.154. More recently, Fowler (1981) has estimated the net reproductive rate for Dall’s porpoise, *Phocoenoides dalli*, to be 12%, and Reilly (1984) suggests 6–8% for gray whales.

Table 2  
Correlation between estimated kill and pregnancy rate, northern offshore spotted dolphin

Year	Kill	Fraction pregnant
1970	371,328 <sup>a</sup>	—
1971	184,326	0.51
1972	298,154	0.43
1973	131,863	0.52
1974	95,643	0.32
1975	105,564	0.30
1976	47,400	0.30
1977	22,549	0.23
1978	19,241	0.22
d.f. = 6		
r <sup>1971-71</sup> = 0.730* <sup>b</sup>		
r <sup>1970-71</sup> = 0.967**		

<sup>a</sup> From Smith, 1979.

<sup>b</sup> Note: r<sup>1971-71</sup> is the correlation coefficient for same-year comparisons of kill and fraction pregnant; r<sup>1970-71</sup> is the comparison of fraction pregnant (1971) to kill (1970), etc.

\* Significant at the 0.05 level.

\*\* Significant at the 0.01 level.

gestation period, age, growth, and selective kill. It is subject to seasonal and spatial sampling error and to histological misclassification; the last should result in an underestimate if early-stage pregnancies are missed in the laboratory.<sup>6</sup>

An inspection of the annual estimates of pregnancy rate shows a declining trend with time from 1971 through 1978 rather than random variation as would be expected if each were an independent estimate subject to sampling error. This trend appears to be correlated with the decline in kill rate resulting from protective actions by tuna fishermen. An estimate of annual kills for this stock of dolphin is provided in Smith (1979) and is included here in Table 2. The correlation between kill number and pregnancy rate is significant when compared on an annual basis, and highly significant if a one-year lag between the year of kill and the year of estimated pregnancy rate is allowed.

It is tempting to suggest that the correlation is related, in some way, to population density or stress that has produced a compensatory change in reproductive rate.<sup>7</sup> The response suggested by the data seems too rapid to be solely density dependent. Instead, it may represent a response to the decline in the total mortality rate, or it may be an artifact and the correlation spurious.

An artificial trend in the data could result from:

- (a) *Chance*. However, the probability of this is very low based on the correlation coefficient, even though it must be noted that the sample size for recent years is small.
- (b) *Changes in the time and area of sampling*. Barlow

<sup>6</sup> The GARR could be adjusted if an estimate of the time period for undetected early pregnancies were available. Lacking one, the only adjustment made is for length of gestation:

$$\frac{12}{11.5} = 1.04.$$

Missed pregnancies, if assessed, would increase the adjustment and estimate of GARR.

<sup>7</sup> A non-linear density-dependent model for predicting the response of this dolphin population to fishery mortality was used by the 1979 Workshop (Smith, 1979).

(1979) shows that neither seasonality nor location of sampling affects the estimates of pregnancy rate for this stock sufficiently to account for a trend of this magnitude.

- (c) *Changes in the sampling of pregnant females relative to lactating or resting females in recent years.* This has been discussed by Powers and Barlow (1979). Aside from the bias with small-kill sets (less than 40), another bias may result from changes in the length of the chase period during fishing. If a speed or endurance differential exists among resting, pregnant and lactating females with calves, the proportions captured may have changed as schools become more wary of fishing operations in recent years. If females with calves tended to fall behind during the chase, the proportion pregnant captured might increase with length of chase (which presumably has increased in recent years), but the reverse appears to have occurred. Questions of possible sampling bias should be examined by reanalysis of the fishing log and kill data.

If instead the trend is a response of the population to the decrease in kill and lower mortality rate, again, several causes are possible:

- (a) *The population may be undergoing a decline in reproductive capacity as the result of years of pursuit and capture by the fishing fleets.* The available evidence, however, suggests that reproductive failure has not occurred; for if it had, the fraction of immature animals in the samples should have declined, as should the fraction of lactating females, yet the data show the fraction of immature animals to be stable, and the fraction of lactating females to have increased, which suggests that the length of lactation has increased.
- (b) *During the period of high kills, that is prior to 1974, a higher number of very young calves died.* The resulting reimpregnation of the mothers increased the fraction pregnant. However, the numbers of neonates in the sample are too few to account for such an increase in proportion of the females pregnant owing to reimpregnation. This problem needs to be studied by reexamination of the complete, unpublished data set.
- (c) *The population may be responding to changes in mortality rate by changing the reproductive rate.* The response appears to be closely coupled with kill rate (mortality rate) rather than with population size (density).

From the summarized data, it seems likely that the reproductive rate (but not necessarily stock size) of the offshore spotted dolphin is responding to the decreased kill rate. A better assessment of this possibility perhaps can be had by reworking the archived data. Changes in the fishery and the current, legally mandated, low kills make it unlikely sufficient additional material will be collected to add further to the statistical base. Improved population counts, however, if they can be made, will allow the overall status of the stock to be assessed.

If the stock is responding to a decline in total mortality by altering its reproductive behaviour, with the resulting increase in length of lactation, as the data suggest, then it is possible to make some inferences of possible net reproduction rates. Estimates of possible net reproductive

rates made in this manner are less affected by bias from errors in estimating age, growth, gestation period, and other reproductive parameters and population statistics. The estimated GARR appears to have changed from a high of 0.15–0.18 during the period of higher kills to a lower level of 0.06–0.10 in recent years. If one assumes the present growth of the population to be zero, the difference between GARR for the two stanzas suggests that a maximum net recruitment rate of at least 0.05–0.12 is possible, which is in keeping with rates observed in other marine mammal populations (Chapman, 1979; Fowler, 1981; and Reilly, 1984) and higher than the 0.04  $R_{max}$  assumed for the current stock assessment model.

## SUMMARY AND CONCLUSIONS

1. A data base on more than 10,000 animals has been collected over an eight-year period (1971–78) and used to estimate reproduction statistics for the northern offshore spotted dolphin.

2. Gross annual reproductive rates (GARR) for this stock have been calculated, but the estimates are likely biased. Net reproductive rates have not been calculated.

3. The fraction of mature females sampled that were pregnant shows a significant decline over the eight-year period. This decline in pregnancy rate is highly correlated with the decrease in fishing mortality over the same period. Calculated GARR exhibits a similar trend.

4. Therefore, for modeling purposes, a reasonably unbiased estimate  $R_{max}$  can be derived by subtracting the GARR for recent years (low fishing mortality) from the GARR for years with a higher associated mortality. The results suggest net annual recruitment rates of 5–12% are possible. The 4% value for  $R_{max}$  used in the present assessment model is unsupported and possibly low.

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# Further Analyses of Reproduction in the Striped Dolphin, *Stenella coeruleoalba*, off the Pacific Coast of Japan

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## ABSTRACT

Analysis of reproduction in *Stenella coeruleoalba* (Meyen, 1833) was carried out based on data for 3,456 animals aged by means of examination of dentinal growth layers for animals younger than 10 years old and of cemental growth layers for the older animals. The ages when 50% of animals attain sexual maturity are calculated at 8.9 years in the female and 8.8 years in the male. Males over 17 years of age appear to reach full sexual maturity and to attain social maturity. Adult females are composed of 33.8% pregnant, 1.9% pregnant and lactating, 42.6% lactating and 21.7% resting. One reproductive cycle is 3.2 years and consists of 1.1 years in pregnancy, 1.4 years in lactation and 0.7 years in resting. The annual ovulation rate is 0.5. Older females that have experienced 12 ovulations or more show a higher proportion of resting. The pregnancy rate of animals taken by harpoon is slightly lower than that in the drive-in fishery. The overall sex ratio (male/female) is 1.06. Gross annual production is estimated to be 9.2% of the population.

## INTRODUCTION

The striped dolphin, *Stenella coeruleoalba* (Meyen, 1833), is distributed widely in tropical and subtropical waters in the Atlantic and Pacific Oceans and the Mediterranean Sea. The species is annually caught by the driving method (*Oikomi*) at Kawana (34° 57' N, 139° 08' E), Futo (34° 52' N, 139° 06' E) and Taiji (33° 36' N, 135° 56' E) on the Pacific coast of Japan. At Taiji the catch of striped dolphins by hand harpoon was carried out until 1973. The striped dolphins caught off the Pacific coast of Japan are thought to belong to one population (Ohsumi, 1972; Miyazaki, Kasuya and Nishiwaki, 1974; and Nishiwaki, 1975).

Reproduction of the species have been studied by Hirose, Kasuya, Kazihara and Nishiwaki (1970), Hirose and Nishiwaki (1971), Kasuya (1972), Kasuya and Miyazaki (1976), Kasuya (1976) and Miyazaki (1977). Histological examinations of gonads without regard to age were made by Hirose *et al.* (1970) and Hirose and Nishiwaki (1971). Kasuya (1972) analyzed reproduction based on age determination by examination of dentinal growth layer. By this method, Kasuya and Miyazaki (1976) estimated the calving interval over a long period of time and suggested that it has become shorter with a decrease in population level. Kasuya (1976) reconsidered the life history parameters based on cemental growth layers. Miyazaki (1977) reported on reproduction of the species based on histological examination of testes and age determination by means of examination of dentinal growth layers in a large sample of both sexes.

Combining samples collected in December 1978 (school no 47), December 1979 (school no. 48) and June 1980 (school no. 49) with the samples of Miyazaki (1977), further analyses of reproduction of the striped dolphin were carried out, using age determinations derived from dentinal growth layers for animals younger than 10 years and from cemental growth layers for the older animals.

## MATERIALS AND METHODS

The data presented in this study were obtained from 6,389 animals from 49 schools taken at Kawana, Futo and Taiji during 11 fishing seasons, 1963–80 (Table 1). In addition, data from 271 animals taken by hand harpoon were also used. Out of 6,660 animals, the ages of 3,456 individuals (1,779 males and 1,677 females) were estimated from the number of growth layers in the teeth.

For age determination, teeth were prepared by staining with haematoxylin after decalcification of thin ground sections (10 to 20  $\mu\text{m}$ ) in a 5% water solution of formic acid. Although reading of growth layers in the dentine is easier than reading those in the cementum for the younger animals, it becomes more difficult for animals of 16 years or more because of the formation of osteodentine inside the pulp cavity. For this study, age was determined mainly by counting the growth layers in dentine for animals younger than 10 years and by counting them in cementum for animals 10 years old or older. The teeth collected from schools 44 and 45 were prepared by T. Kasuya and their growth layers counted by myself. Revised age compositions of 30 schools taken by the driving method are shown in Fig. 1 together with age composition of animals caught by harpoon. Testes were collected from most of the males, fixed in 10% formalin and weighed in the laboratory. A block sample of one cubic cm was taken from the center of a cross section at midlength of the testis. Sections were mounted and stained with Mayer's haematoxylin and eosin, and examined histologically. The mean diameter of 20 seminiferous tubules was used as an index of tubule diameter.

The ovaries were collected from most of the females and fixed in 10% formalin. In the laboratory, the ovaries were weighed, the number of corpora albicantia and corpora lutea counted, and three diameters of corpora measured. The mean diameter of the corpus luteum or albicans was obtained as the cube root of the product of the three diameters. Corpora atretica were separated from corpora albicantia and excluded from the present analysis.

Body length was measured to the nearest centimeter in

Table 1  
List of materials used in this study

School no.	Location	Date of kill	No. of dolphins		No. of dolphins aged		Researcher <sup>1</sup>
			Caught	Examined	Males	Females	
1	Futo	22 Oct. '63	453	30	—	—	T
2	Futo	5 Nov. '63	242	54	—	—	T
3	Kawana	9 Nov. '63	34	31	—	—	T
4	Futo	14 Nov. '64	36	36	—	—	T
5	Futo	16, 18, 22 Nov. '68	1,700	413 <sup>2</sup>	—	—	K
6	Kawana	17 Nov. '68	344	322	—	—	K
7	Kawana	18 Nov. '68	423	168	—	—	T
8	Futo	12 Oct. '70	265	89	—	—	M & K
9	Kawana	13 Oct. '70	293	64	—	—	M
10	Futo	21 Oct. '70	324	68	—	—	M
11	Kawana	24 Oct. '70	49	44	—	—	M
12	Kawana	29 Oct. '70	48	34	—	—	
13	Kawana	22 Nov. '70	1,832	125	18	60	H
14	Futo	25 Nov. '70	365	16	—	—	M
15	Kawana	2 Dec. '70	260	260	—	—	M
16	Kawana	10 Dec. '70	84	84	—	—	M
17	Futo	2 Oct. '71	393	176	30	15	M
18	Kawana	4 Oct. '71	101	58	13	29	M
19	Futo	5 Nov. '71	25	25	13	12	M
20	Kawana	17, 18 Nov. '71	636	362	241	74	M
21	Futo	20 Nov. '71	140	100	57	42	M
22	Kawana	15 Dec. '71	903	306	225	61	M & K
23	Kawana	3 Oct. '72	31	30	19	9	M
24	Kawana	4 Oct. '72	225	96	65	27	M
25	Futo	7 Oct. '72	120	32	18	13	M
26	Kawana	8 Oct. '72	94	41	23	14	M
27	Futo	13, 15, 16 Oct. '72	574	217	97	98	M
28	Kawana	14, 18, 19 Oct. '72	305	124	53	61	M
29	Kawana	17, 19, 20 Oct. '72	238	124	38	80	M
30	Kawana	23 Oct. '72	48	48	24	4	M
31	Kawana	26 Oct. '72	54	40	27	13	M
32	Futo	1 Nov. '72	63	63	40	20	M
33	Kawana	5 Nov. '72	284	122	39	81	M
34	Futo	9 Nov. '72	239	127	39	65	M
35	Futo	10 Nov. '72	45	27	18	9	M
36	Kawana	15 Nov. '72	243	126	16	96	M
37	Futo	16 Nov. '72	200	76	14	54	M
38	Kawana	17, 20 Nov. '72	372	212	55	101	M
39	Futo	21 Nov. '72	293	132	54	74	M
40	Kawana	23, 26 Nov. '72	535	140	63	74	M
41	Kawana	26 Nov. '72	2,327	415	—	—	M
42	Kawana	26 Nov. '72					
43 (42) <sup>3</sup>	Futo	7, 9 Dec. '72	912	180	78	90	M
44 (43) <sup>3</sup>	Kawana	19 Nov. '73	414	251	141	92	M & K
45 (44) <sup>3</sup>	Kawana	20, 22 Nov. '73	1,724	470	112	112	M & K
46	Taiji	8, 9 Jan. '75	—	137	—	—	M
47	Taiji	19, 20 Dec. '78	—	79	—	—	M
48	Taiji	15 Dec. '79	150	133	42	34	M
49	Taiji	20 June '80	150	82	20	47	M
—	Taiji	20 Jan. '73–15 Feb. '73	271 <sup>4</sup>	271	87	116	M
Total			18,861+	6,660	1,779	1,677	

<sup>1</sup> H, K, M, M & K, and T indicate Hirose, Kasuya, Miyazaki, Miyazaki & Kasuya, and Tobayama, respectively.

<sup>2</sup> Additional data to those in Miyazaki (1977) were obtained.

<sup>3</sup> Figures in parentheses indicate school nos of Miyazaki (1977).

<sup>4</sup> Animals caught by harpoon.

a straight line from the tip of the upper jaw to the notch of the tail flukes.

## GROWTH

### Foetal growth

Length frequencies for 874 fetuses and 785 newborn calves less than 178 cm long are shown in Fig. 2. Data for 21 individuals taken in May were included from

Nishiwaki and Yagi (1953). These frequencies were separated into several normal distributions by statistical analysis. Means of the normal distribution of length frequencies were calculated and plotted by month (Fig. 3). A linear regression line weighted by sample size was calculated by the least squares method based on the following five mean values: 8.1 cm in May, 72.5 cm in October, 79.8 cm in November, 80.1 cm in December and 94.0 cm in January. The correlation coefficient is

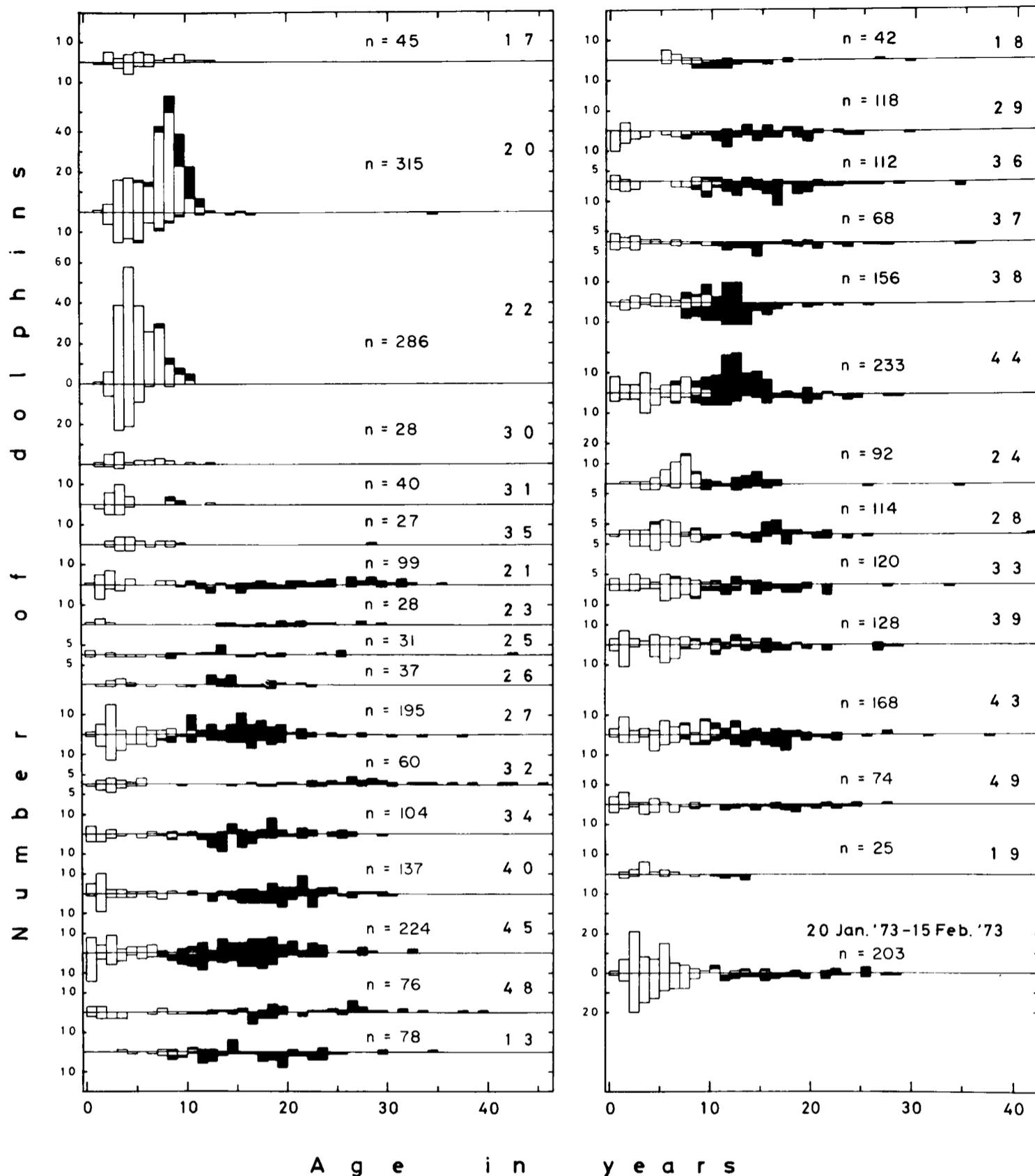


Fig. 1. Age compositions of 30 schools of *Stenella coeruleoalba* caught by the driving method and 271 striped dolphins caught by harpoon. White areas indicate immature or pubertal dolphins and black mature. Areas above the horizontal line indicate males and those below it females. School number indicated at the right, and sample sizes in parentheses.

statistically significant ( $P < 0.01$ ). The linear foetal growth rate (slope of the line) is calculated to be 0.29 cm per day. Mean body length at birth of the species is about 100 cm (Miyazaki, 1977). Laws (1959) showed that foetal growth in Odontoceti can be described by a linear plot of length except for the very early stage of growth. If  $L_{t_0}$  of Laws (1959) is approximated by  $0.15 \times$  gestation length ( $L_{t_g}$ ), the total gestation length is estimated to be 408.9 days (13.6 months). A second linear regression line obtained from the other four points of foetuses in Fig. 3 has a slope of 0.30 cm per day and yields an estimate of gestation length of 393.5 days (13.1 months). Considering the two estimates, the gestation period is calculated to be 401 days (13.4 months). The mean date of conception is

estimated in about January from the first regression line, and that from the second regression is in about July. Bimodal length frequencies were seen in the foetal data for 3 months, October to December. The separation between the two modes ranged from 54.5 to 62.9 cm with a mean of 58.7 cm. If the foetal growth rate is taken as 0.3 cm per day, the two mating seasons are estimated to be separated by 195.6 days (6.5 months). This suggests that the striped dolphin has two mating seasons during the year, in the winter and in the summer.

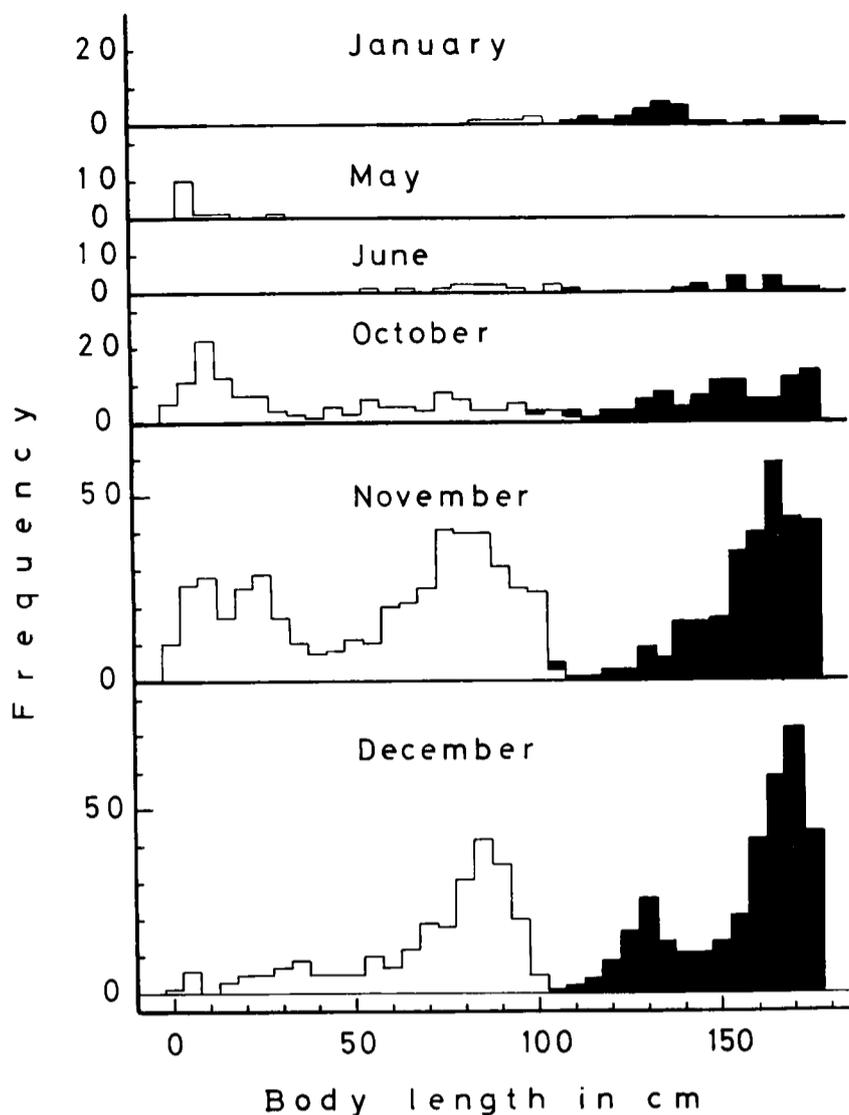


Fig. 2. Length frequencies of fetuses and calves of *Stenella coeruleoalba* by months. White areas indicate fetuses and black calves.

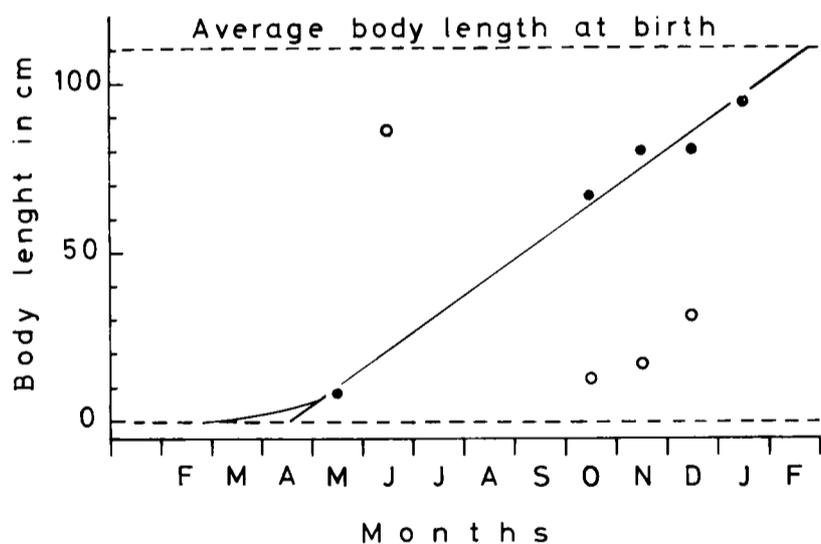


Fig. 3. Linear least-squares regression line (weighted) of growth in *Stenella coeruleoalba*. Closed circles indicate the mean length frequency of fetuses which will be born in the winter season, open circles that of fetuses in the summer, and closed squares that of calves. Numbers are sample sizes.

### Postnatal growth

The estimated growth curves (Figs 4 and 5) are based on samples of 1,763 males and 1,599 females. In the first two years, the striped dolphin grows rapidly, attaining 166 and 180 cm in the first and the second year, respectively. As the mean body length at birth is about 100 cm (Miyazaki, 1977), the mean growth rate in the first year is estimated at 5.5 cm/month and in the second year at 1.2 cm/month. Growth rate of the striped dolphin is

higher in the foetal stage (about 9 cm/month) than in neonates and decreases rapidly with age. Mean body length of males appears to exceed that of females beginning at the age of three years. The growth rate seems to be constant between ages 3 and 9 years in females, and 3 and 12 years in males. Between 3.5 and 8.5 years of age, the difference in mean body lengths between the sexes ranges from 1.7 to 3.2 cm, with an average of 2.4 cm. The increase in mean body length stops in females at about the age of 11.5 years, and in males at about 16.5 years. The oldest male was 45.5 years old and the oldest female 37.5 years old. The mean body length of 313 males over 16.5 years old was 238.9 cm (an estimate of asymptotic length) which is larger by 13.2 cm than 225.7 cm, the mean of 734 females over 11.5 years old.

### REPRODUCTION IN THE MALE

The testes of 350 males were analyzed histologically. Immature, pubertal and mature males were defined as animals having testes containing only spermatogonia, both spermatogonia and spermatocytes and spermatozoa, respectively. The mature males were classified into three types, MI, MII and MIII, based on the histological examination of 20 tubules selected randomly. Types MI and MIII were mature males having testes containing spermatozoa in 5% or less and in 100% of tubules examined, respectively. Mature males of Type MII were defined as the animals at stages intermediate between types MI and MIII.

### Testis weight

There is no significant difference in weight between the right and left testes (Miyazaki, 1977). In this study the weight of the left testis was used. When the weight of the left testis was not available, the weight of the right testis was used.

Testis weight in immature males gradually increases with age and reaches the maximum of 19.4 g at the age of 13.5 years (Fig. 6). Pubertal animals in the range of 2.5–4.5 years had testes weighing from 4.0 to 30.7 g. The youngest mature male was 6.5 years old. As shown in Fig. 6, a rapid increase in testis weight occurs at the age of 7 to 10 years. After 10 years of age, wide variation in testis weight is seen. This variation is due to seasonal changes in testis activity, as discussed below. The largest left testis weighed 225.2 g. Most mature males of type MIII had left testis weight of 80 g or more and were 20 years old or older. In the old mature males, type MI maturity was not found. Monthly fluctuation of mean testis weight in two age groups is shown in Fig. 7. The males of 8.5 years or younger have larger testis weight in October–November. In the males over 8.5 years of age, the mean testis weight increases from February to October, then decreases sharply to December. Although there are limited samples in certain months, it can be safely said that the striped dolphin probably undergoes month-to-month change of testis weight. Among 6 months examined, October showed the largest mean testis weight in the two age groups.

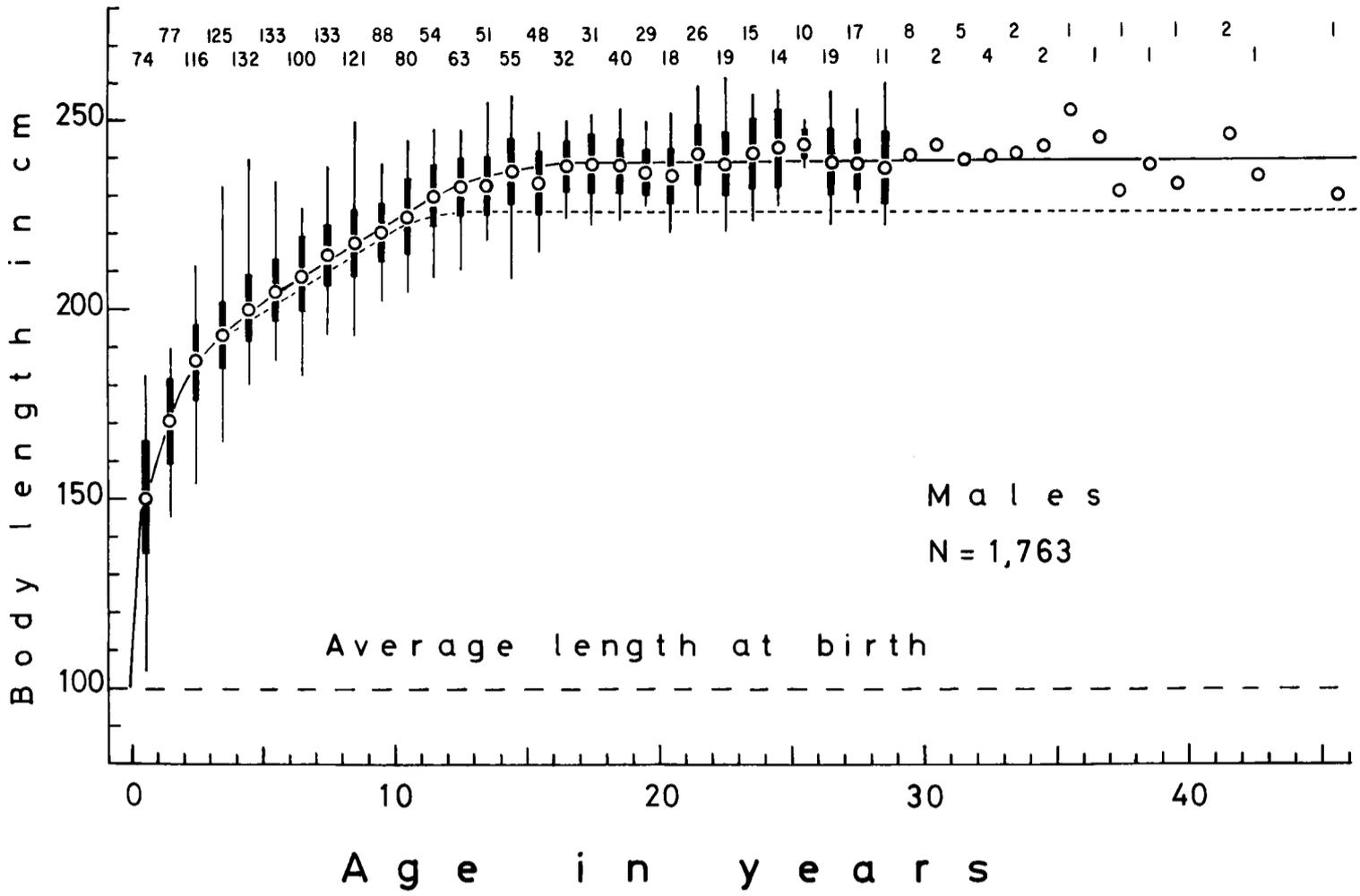


Fig. 4. Mean growth curve of males of *Stenella coeruleoalba*. Open circles indicate mean, vertical line range, and black box two standard deviations. Numbers are sample sizes. Broken line is the mean growth curve of females.

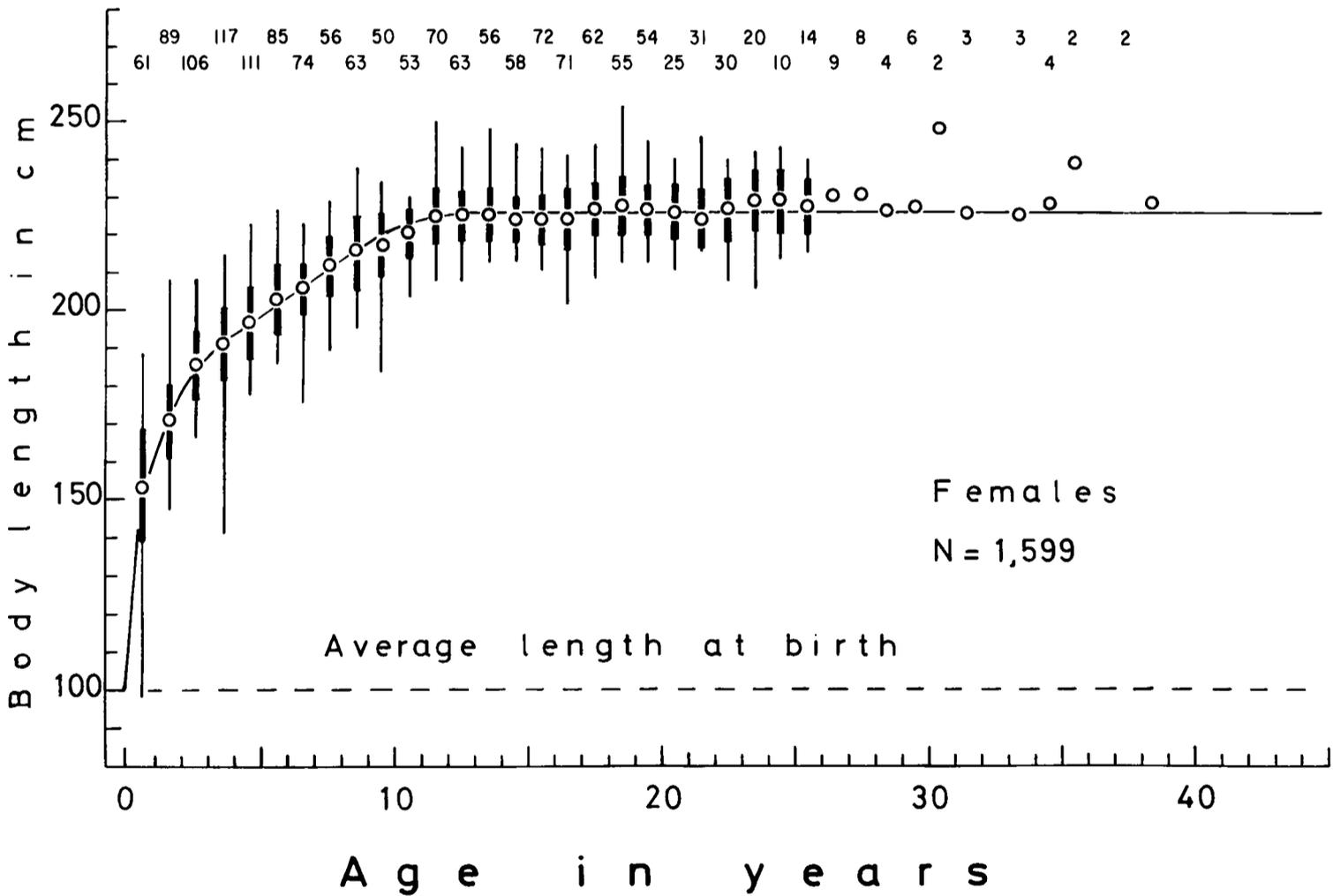


Fig. 5. Mean growth curve of females of *Stenella coeruleoalba*. Symbols defined in Figure 4.

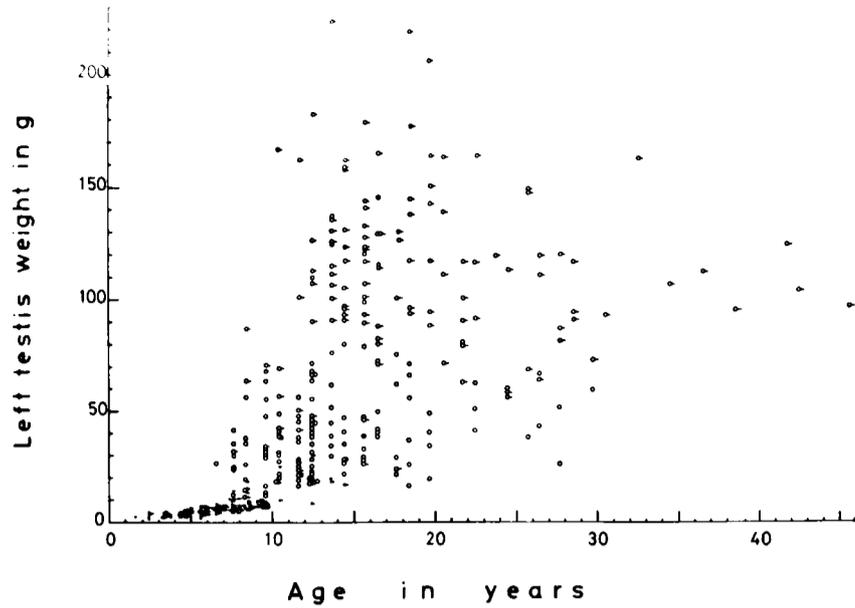


Fig. 6. Scatterplot of testis weight on age in *Stenella coeruleoalba*. Open circles indicate mature males, open circles with bar mature males of type MIII, closed circles immature males, and closed circles with bar pubertal males.

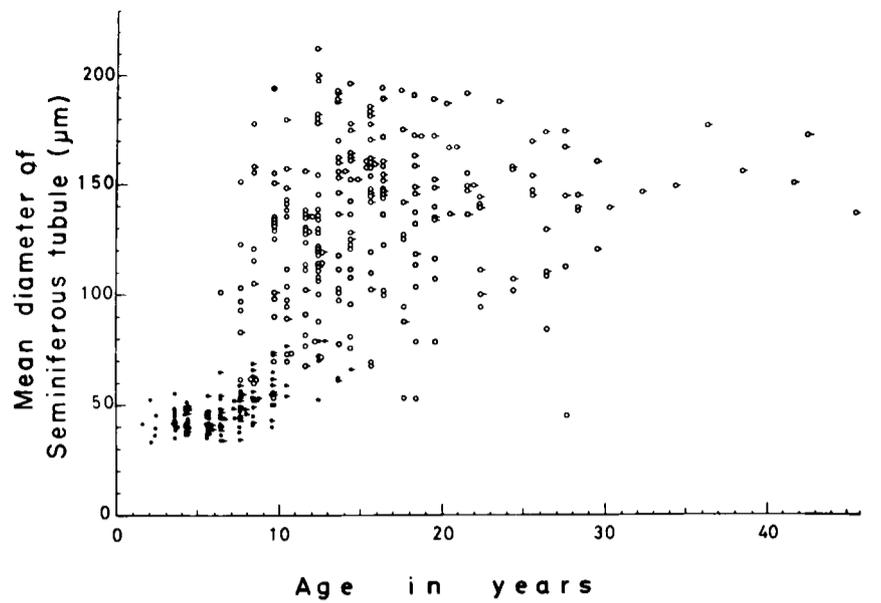


Fig. 8. Scatterplot of seminiferous tubule diameter on age in *Stenella coeruleoalba*. Symbols defined in Fig. 6.

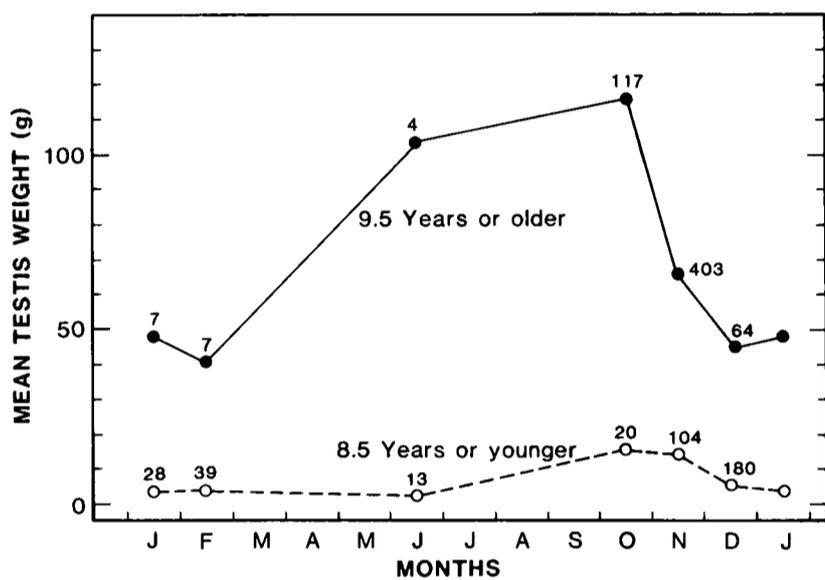


Fig. 7. Mean testis weight of *Stenella coeruleoalba* on months by two age groups. Numbers are sample sizes.

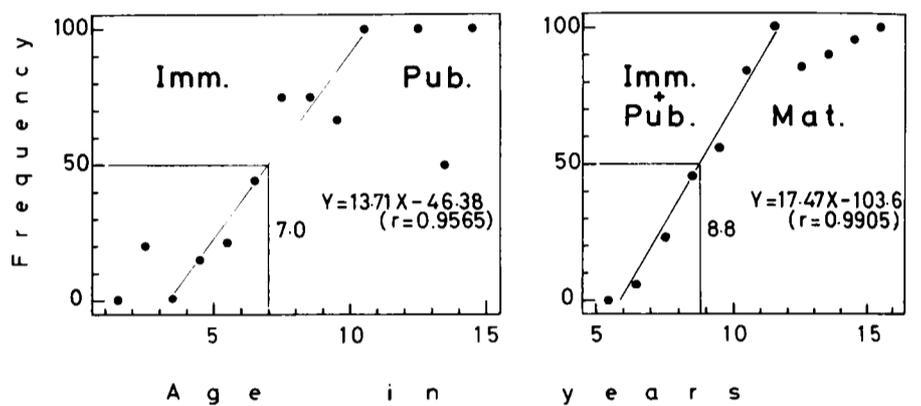


Fig. 9. Sexual maturity of male *Stenella coeruleoalba* by age. Numbers are sample sizes.

of mature males/number of total males) increases linearly (Fig. 9). The age when 50% of males attain sexual maturity is estimated to be 8.8 years. The slope of the regression line is 17.5% per year, lower than the value of 19.3 for females.

### Seminiferous tubule size

The diameter of the seminiferous tubules in immature males ranges from 33 to 65  $\mu\text{m}$  (Fig. 8). For pubertal males, the tubules are from 34 to 79  $\mu\text{m}$  in diameter and increase in size during the age interval 7–11 years. Mature males have tubules 45 to 214  $\mu\text{m}$  in diameter, markedly wider variation than in the immature and pubertal males. The tubule size in mature males increases rapidly during the period from 7 to 15 years of age and seems to be constant thereafter. Rapid development of tubule diameter is observed at the same time as the onset of rapid increase in testis weight at 8 to 10 years. After 30 years of age, all of the mature males in the seven samples had seminiferous tubules larger than 130  $\mu\text{m}$  in diameter. The mean diameter of the tubules in this group was 155.7  $\mu\text{m}$  (Fig. 8).

### Attainment of sexual maturity

The youngest mature male was 6.5 years old and the oldest immature male was 14.5 years old. Most of the mature males were 11.5 years old or older. For the period from 5.5 to 11.5 years of age, the maturity rate (number

### Attainment of social maturity

The proportion of males of type MIII increases with age (Fig. 10). The age when 50% of mature males attain the stage of type MIII is about 16.5 years. This suggests that the male reaches full sexual maturity on the average around the age of 16.5 years.

Miyazaki and Nishiwaki (1978) studied the school structure of the striped dolphin and concluded that the dolphin moves between three types of schools: a juvenile school, a mating school and a non-mating adult school, in accordance with age and sexual condition. They estimated that males older than 13.5 years have attained full sexual maturity and have become socially mature. However, the analysis discussed above indicates that full sexual maturity is attained on the average at 16.5 years. Re-analysis of school structure in the species was therefore carried out, using Miyazaki and Nishiwaki's (1978) criteria for school classification (Fig. 11). Seven mixed schools (numbers 19, 24, 28, 33, 39, 43 and 49) were excluded from the present analysis. A juvenile school contains almost no adult females. The few 'adult' males can be considered to have not yet reached social maturity, except for the very few (1 in Fig. 11) over 17 years of age.

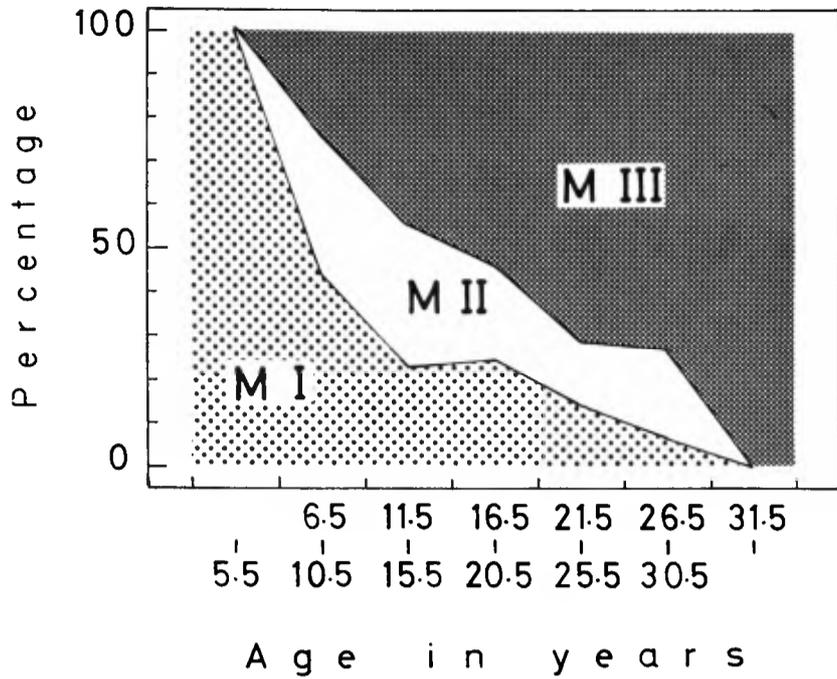


Fig. 10. Percentage of mature males of types MI, MII and MIII by age. For definition of types MI, MII and MIII see text.

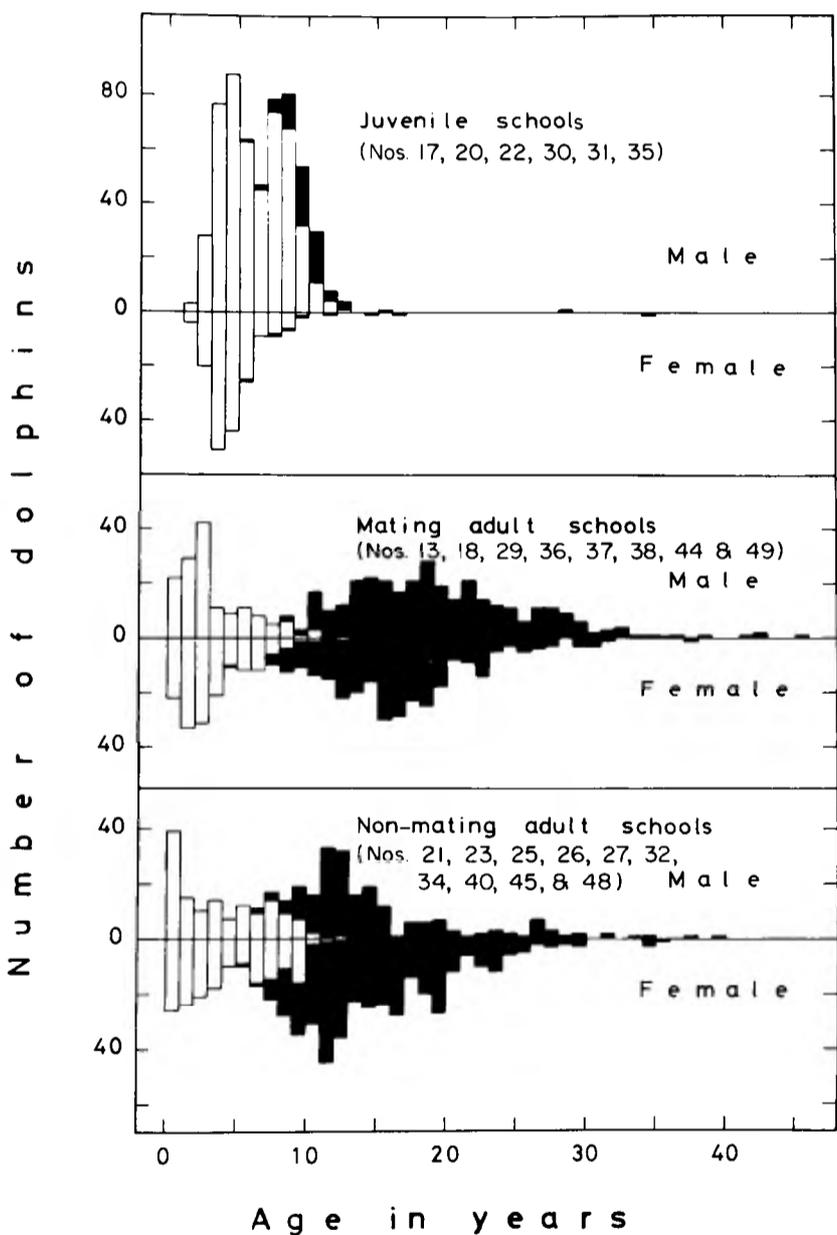


Fig. 11. Age compositions of juvenile, mating and non-mating adult schools of *Stenella coeruleoalba*. Symbols defined in Fig. 1.

Comparison of age compositions of males between the mating school and the non-mating adult school suggests that the mature males above 16.5 years might leave the non-mating school, where most females are engaged in calving, and move into the mating school, where most of the mature females are participating in mating. The age when the bulk of mature males moves from the

non-mating adult school to the mating school coincides well with the estimated mean age of males at the attainment of full sexual maturity, 16.5 years. This suggests that the male of the striped dolphin might attain social maturity at the age of 16.5 years or older.

### REPRODUCTION IN THE FEMALE

#### Attainment of sexual maturity

Mature females were defined as those with at least one corpus luteum or corpus albicans. Resting females were defined as adults neither pregnant or lactating. Mature non-lactating females having a corpus luteum and no foetus were included in the resting category.

The youngest mature female was 4.5 years old and the oldest immature female was 12.5 years old. The age at onset of maturity is lower by two years in females than in males. Most of the mature females were 10.5 years old or younger. This tendency is almost the same as that in the males. Regression of mature on age (Fig. 9) yields an estimate of the age when 50% of females are sexually mature of 8.8 years. Thirty-nine primiparous females (pregnant, with corpus luteum but no corpus albicans) were estimated to have conceived at an average age of 10.3 years, based on back projection of age using the estimated foetal growth curve. This age is very close to the age of 10.5 years by which most females have attained sexual maturity.

#### Ovulation

The largest number of corpora was 25. However, the age of this animal was unknown. The mean number of corpora on age increases linearly during the period from 7.5 to 28.5 years (Fig. 12). A linear regression line weighted by sample size was calculated by the least squares method. The annual ovulation rate was estimated to be 0.50. When one reproductive cycle is estimated to be 3.17 years (discussed below), 1.6 corpora are estimated to be accumulated in one reproductive cycle. Some younger mature females appear to ovulate much more frequently than expected from the estimated average ovulation interval. One female 7.5 years old with 14 corpora and three females 10.5 years old with 13, 14 and 22 corpora are considered to be anomalous individuals that possibly ovulated many times before they conceived. The mean number of corpora for 15 females over 29.5 years was 8.5. This value is lower than expected from the average ovulation rate.

A regression of the logarithm of number of mature females on number of corpora (Fig. 13) yields a slope of  $-0.858$ . Since the annual ovulation rate is 0.50 and the age when 50% of females attain the sexual maturity is 8.8 years, corpora frequency can be converted into the following age frequency of mature females;  $\log y = -0.0988X + 5.58$  ( $r = 0.984$ ), where  $x$  = age in years,  $y$  = number of mature females, and  $r$  = correlation coefficient. From this equation, the annual mortality rate of mature females was calculated to be 9.41%.

#### Changes in size of corpora

A plot of mean diameter of the corpus luteum on fetal length shows that diameter appears to increase from

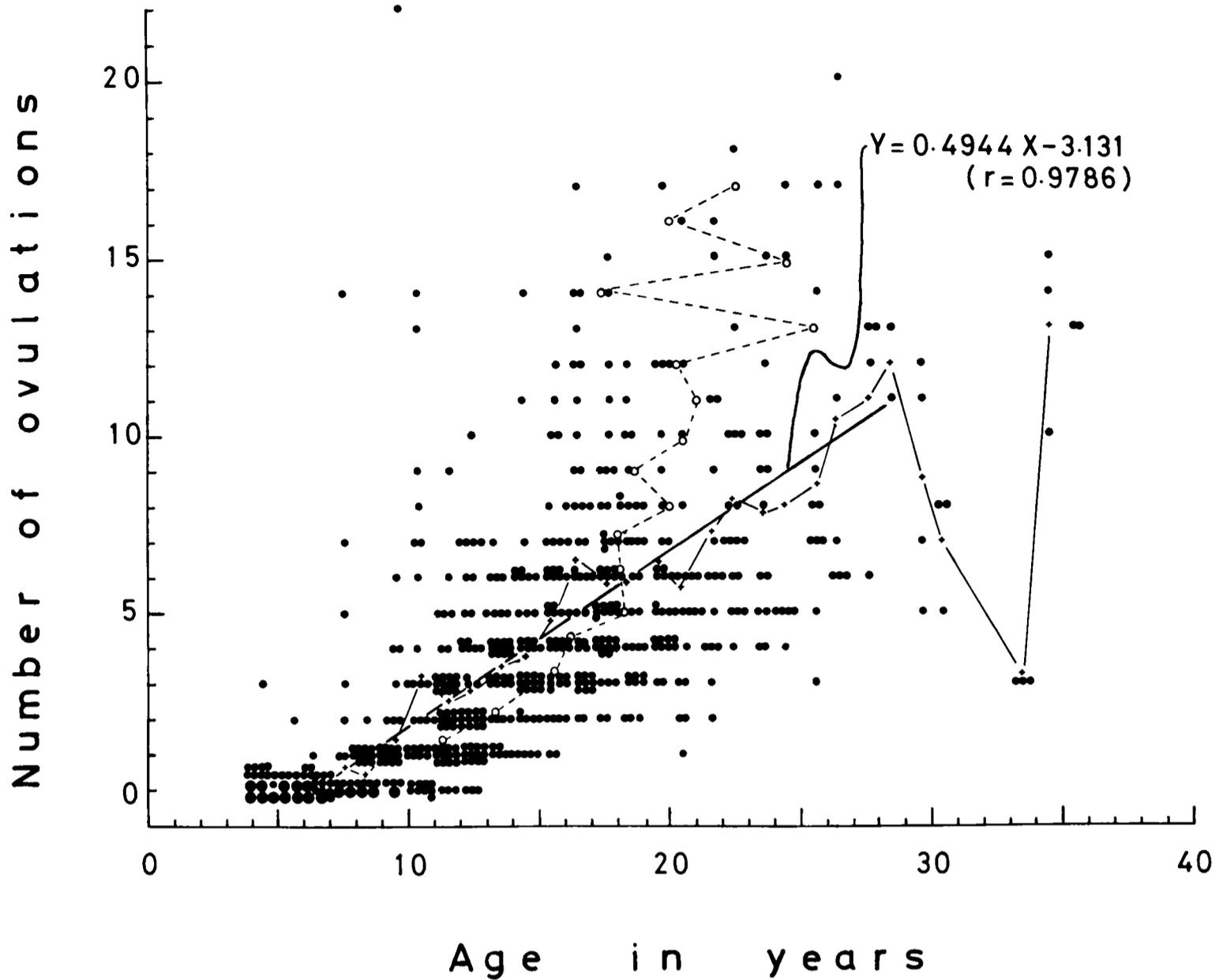


Fig. 12. Scatterplot of number of corpora on age in *Stenella coeruleoalba*. Larger closed circles indicate 10 animals, smaller circles one animal and double crosses mean number of corpora at each age. The linear regression line weighted by sample size was calculated by the least squares method during the period from 7.5 to 28.5 years.

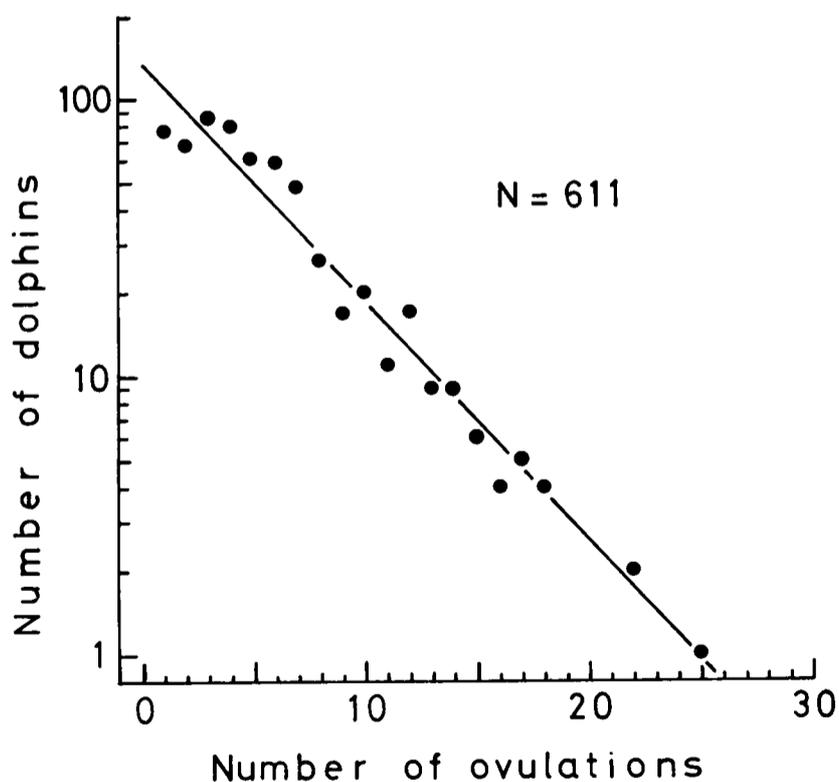


Fig. 13. Frequency of corpora in *Stenella coeruleoalba*. The linear regression line was calculated by the least squares method.

about 27 to about 29 mm in early pregnancy and then decreases to about 24 mm in late pregnancy (Fig. 14). The corpus luteum in pregnant females ranges from 17 to 40 mm in diameter, with a mean of 25 mm (Fig. 15). Lactating females show a single pronounced mode at about 8 mm in diameter of the largest corpus albicans. This mode can be easily separated from the mode for pregnant animals by about 17 mm. The considerable separation of these sharp modes suggests that regression of the corpus luteum after parturition is quite rapid. There are two modes in the size distribution of the largest corpus in resting females. The first mode, at about 21 mm, is composed of corpora lutea which are from undetected very early pregnancy, from very recent abortion, or from ovulation. The second mode, at about 7 mm, is composed of corpora albicantia showing no significant difference in mean size from those in lactating females. The minimum size for the largest corpus albicans is the same in lactating as in resting females, suggesting that the corpus luteum may regress to near-minimum size during lactation.

#### Reproductive condition

The distribution of reproductive conditions changes with age (Fig. 16). All adult females 4.5 to 6.5 years old were pregnant. Between 7.5 and 11.5 years, the proportion of females pregnant decreases with age, corresponding to

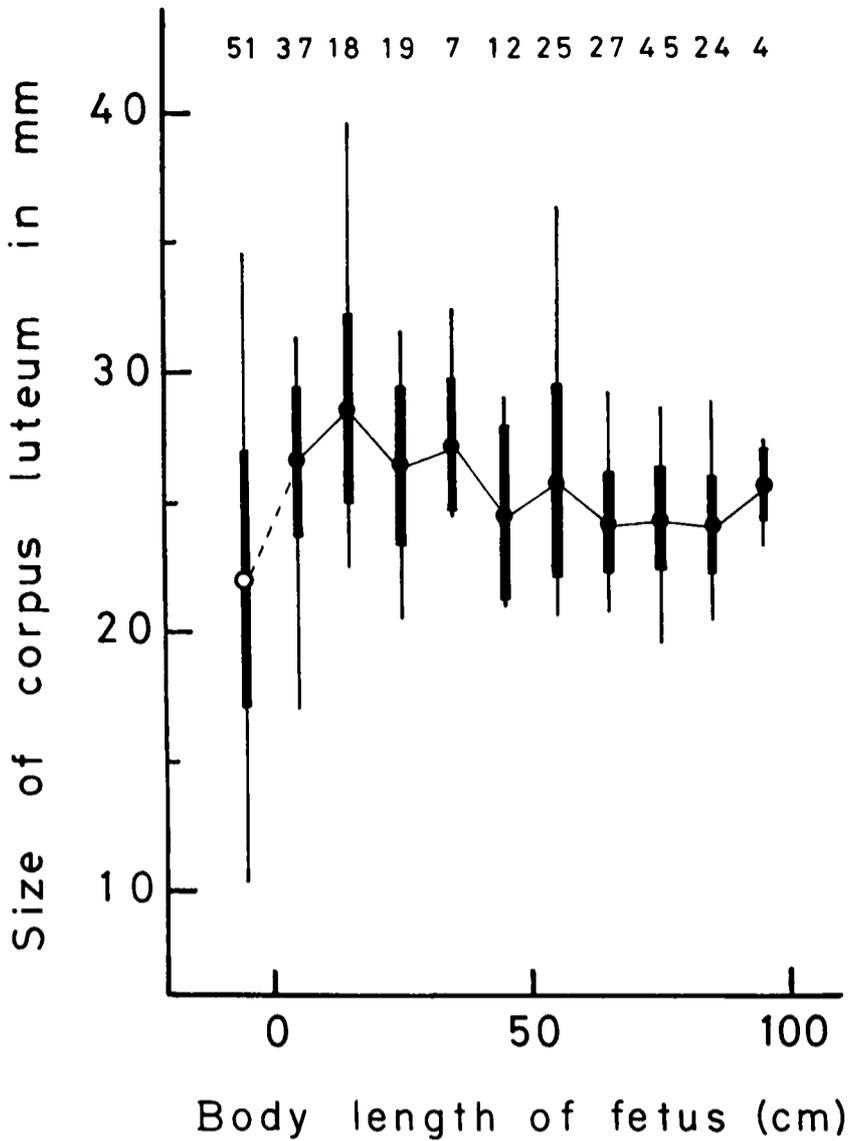


Fig. 14. Fluctuation of the diameter of the corpus luteum in *Stenella coeruleoalba*. Vertical line indicates range, black box two standard deviations, closed circles mean of the corpus luteum of pregnancy at each foetal length and open circles mean of the corpus luteum of resting females having no foetus.

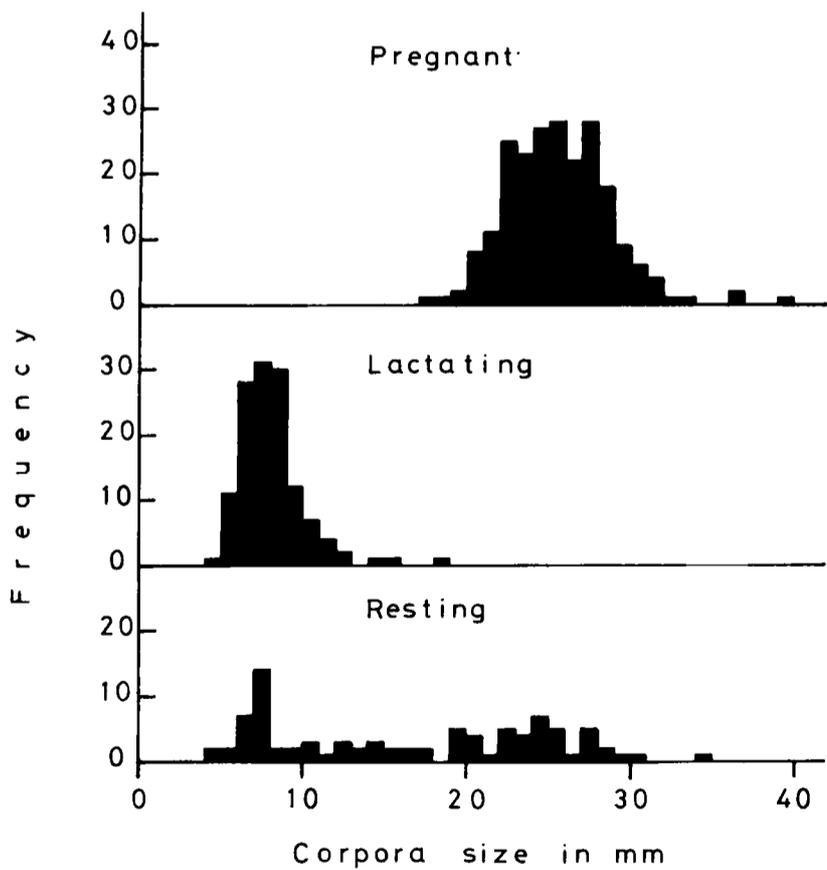


Fig. 15. Size frequencies of corpora in *Stenella coeruleoalba* by reproductive conditions. Black areas indicate corpora lutea and white corpora albicantia.

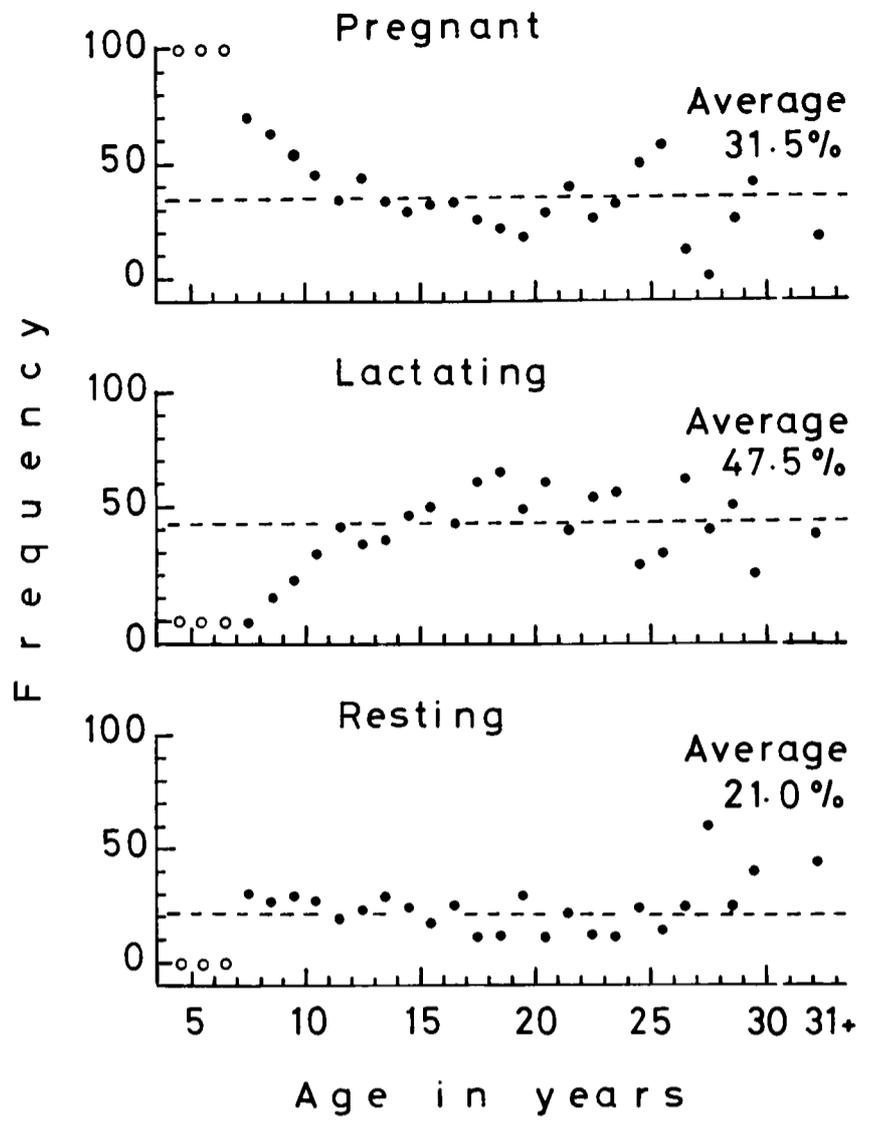


Fig. 16. Fluctuation of reproductive conditions of mature females of *Stenella coeruleoalba* by age. Numbers are sample size.

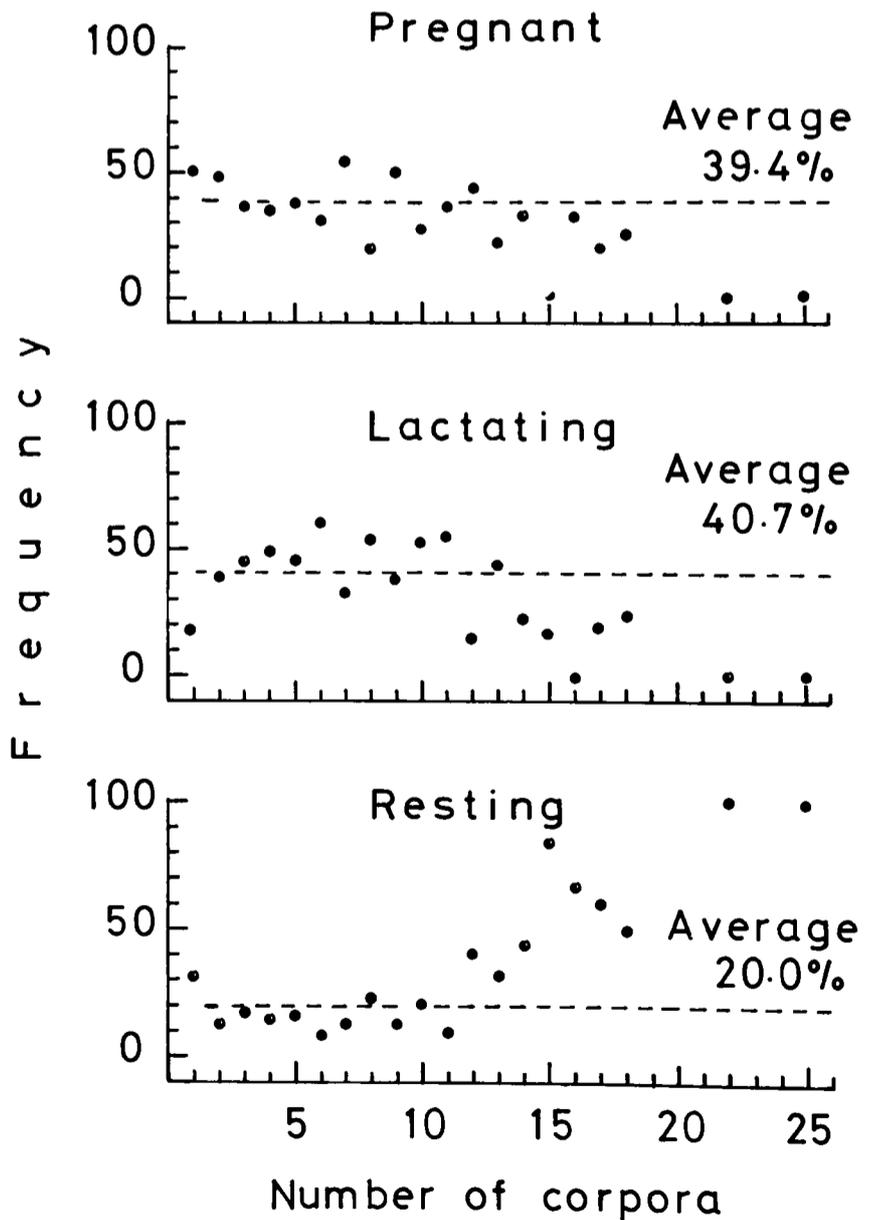


Fig. 17. Fluctuation of reproductive conditions of mature females of *Stenella coeruleoalba* by corpus count. Numbers are sample size.

Table 2  
Sex ratio in *Stenella coeruleoalba*

Age	Sex ratio (male/female)
Foetuses	1.09 (n = 516)
0.5	1.21
1.5	0.85
2.5	1.09
3.5	1.08
4.5	1.20
5.5	1.59
6.5	1.52
7.5	2.34
8.5	1.64
9.5	1.40
10.5	1.33
11.5	0.69
12.5	0.86
13.5	0.82
14.5	0.89
15.5	0.65
16.5	0.43
17.5	0.49
18.5	0.73
19.5	0.52
20.5	0.69
21.5	0.84
22.5	0.63
23.5	0.75
24.5	1.40
25.5	0.67
26.5	2.11
27.5	2.13
28.5	2.75
29.5	1.33
30.5	0.67
31.5	1.33
32.5	—
33.5	0.67
34.5	0.40
35.5	0.50
36.5	—
37.5	0.50
38.5	—
39.5	—
41.5	—
42.5	—
45.5	—
Total	1.06 (n = 3,972)

increase in the proportion of females lactating. The proportion of females resting is almost constant until around 27 years of age, then appears to increase with age. The initial very low lactation rate compared to pregnancy rate, of course, reflects the fact that a very high percentage of the young females are primiparous. The lactation rate climbs rapidly to a level about equal to the pregnancy rate at about 12 years of age and behaves like the pregnancy rate thereafter.

The proportions for 699 adult females were 33.8% pregnant, 1.9% pregnant and lactating, 42.6% lactating and 21.7% resting. Since the length of gestation is about 13.2 months, the period of lactation is estimated to be about 1.36 years based on the proportion of lactating females to pregnant females. The resting period is estimated at 0.69 year by the same method. Adding these estimates, one reproductive cycle is estimated to be 3.17 years long. As the proportion of lactating and resting females in relation to pregnant females becomes larger with increase in age, it can be said that both lactating and

Table 3

Comparison of catch composition on *Stenella coeruleoalba* between driving and harpooning methods

	Driving method	Harpooning method
No. of males (%)		
Immature	926 (55.4)	97 (89.0)
Mature	744 (44.6)	12 (11.0)
Total	1,670 (100)	109 (100)
No. of females (%)		
Immature	672 (43.6)	101 (74.8)
Mature	870 (56.4)	34 (25.2)
Total	1,542 (100)	135 (100)
No. of mature females (%)		
Pregnant	227 (34.1)	9 (26.5)
Pregnant and lactating	12 (1.8)	1 (2.9)
Lactating	284 (42.7)	14 (41.2)
Resting	142 (21.4)	10 (29.4)
Total	665 (100)	34 (100)
Sex ratio (male/female)		
Immature	1.38	0.96
Mature	0.86	0.35
Total	1.08	0.81

resting periods may lengthen with age, and the reproductive cycle seems to become longer in older animals.

Relative numbers of pregnant and lactating females decrease with number of corpora (Fig. 17). After 12 corpora the proportion of females resting increases from about 20% to 100% at 22 corpora or more. This suggests that the striped dolphin may stop conceiving at about 22 corpora, although the sample is very small.

### Sex ratio

The sex ratio (male/female) in fetuses is 1.09, close to the 1.06 overall ratio for postnatal animals (Table 2). In the postnatal animals there is change in sex ratio with age. The sex ratio in animals less than 4 years old is 1.05, but in the animals from 4 to 11 years of age the ratio is 1.54. In the animals older than 11 years, the number of females greatly exceeds that of males, for a ratio of 0.75, despite the greater ages attained by males.

### Comparison of catch composition

Proportion sexually mature in striped dolphins caught by harpoon is lower in each sex than for the animals caught by the driving method (Table 3). Comparison of sex ratio of the catch between the driving and the harpooning methods indicates that the driving method takes relatively more males. Mature females exceed mature males in numbers in both types of fishery. Although the lactation rate was almost the same for the two fisheries, the pregnancy rate in animals taken by harpoon is slightly lower than that in the driving fishery.

### Gross annual production

Average gross annual production was calculated as the product of annual pregnancy rate, proportion female and the sexual maturity rate of females. Of the 3,456 postnatal animals whose age was determined, 48.5% were females.

The proportion of females mature was 54.6%. Average annual pregnancy rate was 34.8%. Gross annual production was calculated as 9.22% of the population.

### DISCUSSION

Kasuya (1976) reported that the striped dolphin attains asymptotic length at 21 years in males and at 17 years in females. The present study indicates that increase of body length stops at 16.5 years in males and 11.5 years in females. The mean age at attainment of sexual maturity for females is estimated to be 8.8 years. The proportion mature of females older than 11.5 years was 99.2%. This suggests that cessation of growth in body length in females may be closely correlated with attainment of full sexual maturity. In males, the age of attainment of full sexual maturity and social maturity is around 16.5 years. This age coincides with the age at which asymptotic length is attained.

Kasuya (1972) reported two mating seasons: in November–December and in May–June. Miyazaki (1977) reported three mating seasons: in February–May, July–September and in December. Based on the present analysis of large samples of fetuses, it can be said that the striped dolphin has two mating seasons, in the summer and in the winter. The foetal length frequencies suggest that about  $\frac{2}{3}$  of the pregnant females give birth in the winter season and the remainder in the summer season. The fact that the proportion of pregnant females having larger-size fetuses (50 cm or more in body length) is 67.7% suggests that these pregnant females are more frequently captured than pregnant females having smaller-size fetuses.

Seasonal variation of testis weight of mature males may be considered as an indication of level of sexual activity. If there is a seasonal increase of testis weight of mature males, it would be expected to occur around the time of the mating season. However, there is a difference between the time of the mating season (January and July) and the month (October) of the largest mean value of testis weight for mature males. This may be because the main sampling season of October to December is outside the mating season.

According to Miyazaki and Nishiwaki (1978), males 4 to 11 years old are thought to stay in the juvenile school until attainment of sexual maturity. Females of this age have already left the juvenile school before attainment of sexual maturity. The sex ratio (males/females) of 1.54 in this age range suggests that some of the females having left the juvenile school may not join adult schools captured near the coast but instead segregate from the other animals until the attainment of sexual maturity.

Although Kasuya (1972) reported that the gestation length of the striped dolphin is estimated at about 12 months, the present analysis indicates gestation length of about 13 months. From this estimate and the proportions of the various reproductive phases in adult females, one reproductive cycle of the striped dolphin is estimated to be 3.17 years, including 1.38 years lactating and 0.69 years resting. The estimated lactating period is close to the 1.5 years mean weaning age estimated by Miyazaki (1977). For the present study, mature females with corpus luteum

which were neither pregnant nor lactating were classified as resting. However, as reported by Perrin, Coe and Zweifel (1976), these corpora lutea may have represented an undetected very early pregnancy, a very recently aborted pregnancy or loss of a calf shortly after birth, or may have been corpora lutea of ovulation. If some of 76 resting females having a corpus luteum were in the state of an undetected very early pregnancy, the present gross annual production would be underestimated.

### ACKNOWLEDGEMENTS

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# Preliminary Study of the Male Reproductive Cycle in Common Dolphins, *Delphinus delphis*, in the Eastern North Atlantic

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## ABSTRACT

Morphometric data and histological studies of testes have allowed us to describe different stages of the male reproductive cycle for *Delphinus delphis* in the northeastern Atlantic. Animals from 190 cm long are in a prepubertal period and sexual maturity is reached at 200 cm (which corresponds to at least six or seven dentinal layers). Different stages of spermatogenesis have been described from testes weighing from 150 to 1,600 g. Spermatogenesis seems to follow a seasonal pattern. Its duration and timing appear to differ from stock to stock, and probably also from one male to another. The individual cycles are not synchronous, thus the period of testicular activity for the whole population spreads over about 10 months (from the end of December to the end of October).

## INTRODUCTION

Reproduction of the odontocetes has been the subject of numerous studies dealing mainly with the female. General works such as those of Slijper (1962), Tomilin (1957), Anderson (1969), Harrison (1972) and Ridgway (1972) give information on the reproduction of different species, but to our knowledge, very few authors have sought to precisely describe testicular activity in the dolphins. Moreover, those studies of the male cycle which have been made have come to differing conclusions, depending on the species and populations involved (Sergeant, 1962; Fisher and Harrison, 1970; Harrison and Ridgway, 1971; Hirose and Nishiwaki, 1971; Kasuya, 1972; Perrin, Coe and Zweifel, 1976; Perrin and Henderson, 1979; and Gaskin and Blair, 1977). For the common dolphin, the results obtained by Sleptsov (1941) for the Black Sea population differ from those of Harrison (1972), Oliver (1973), Gurevich and Stewart (1978) and Hui (1979), who worked with populations in the eastern Pacific. Some workers recognize a cycle of testicular activity, while others believe that spermatogenesis continues throughout the year.

The purpose of the work described here was to examine the cycle of testicular activity in *Delphinus delphis* through morphometric and histological analysis of gonads.

## MATERIALS AND METHODS

The gonads of 26 males stranded on the Atlantic coasts of France or captured offshore (map 1) were fixed and preserved in saline 10% formalin. After each testis was measured and weighed, samples of the testes and epididymides were placed in Bouin's solution for 24–36 hours. The samples were then dehydrated in ethanol and imbedded in paraffin after prolonged immersion in butanol. Finally, 5 to 10- $\mu$ m sections were stained in Groat's haematoxylin. The seminiferous epithelium was usable up to 10 or 15 days after death. The epididymis, like most of the other tissues, deteriorated much more rapidly.

## RESULTS

The morphometric data from the gonads (Table 1) were used to examine the following relationships: variation of the sum of the lengths of the testes with total body length (Fig. 1), variation of the combined weight of the testes with body length (Fig. 2), and variation in the ratio of the sum of testis lengths and combined weight ( $\Sigma L/\Sigma W$ ) with total length (Fig. 3).

The histological analyses allowed determination of the average length at attainment of sexual maturity and the state of spermatogenic activity in adult males. The results are presented below under three development categories: immature, prepubescent and mature.

### Immature

The seminiferous tubes are narrow (40–60  $\mu$ m in diameter) and imbedded in abundant interstitial tissue. The seminiferous epithelium is bordered by a regular Sertolian syncytium on which rest the spermatogonia, which have clear spherical centres. Other stages of germinal cells were not observed (Plate Ia). The epididymis, poorly developed, has a large and completely empty lumen. This scenario, typical of immature gonads, was observed in nine individuals between 117 and 187 cm long. Their testes were less than 15 cm long and weighed 5 to 20 g each.

### Prepubescent

The interstitial tissue occupies very little space between the seminiferous tubules. The tubules appear to have elongated but retain a small diameter (about 50  $\mu$ m). The Sertoli cells, regularly distributed, alternate with very numerous spermatogonia. In the majority of the tubules, one can find some spermatocytes around a small central lumen. The epithelium of the epididymis is well developed; the lumina are well defined but optically void (Plate Ib). Two dolphins of 192 and 194 cm, with testes 8.5 to 11.5 cm long weighing 30 to 40 g each, presented this histological picture; they are considered to have been in a prepubescent phase.

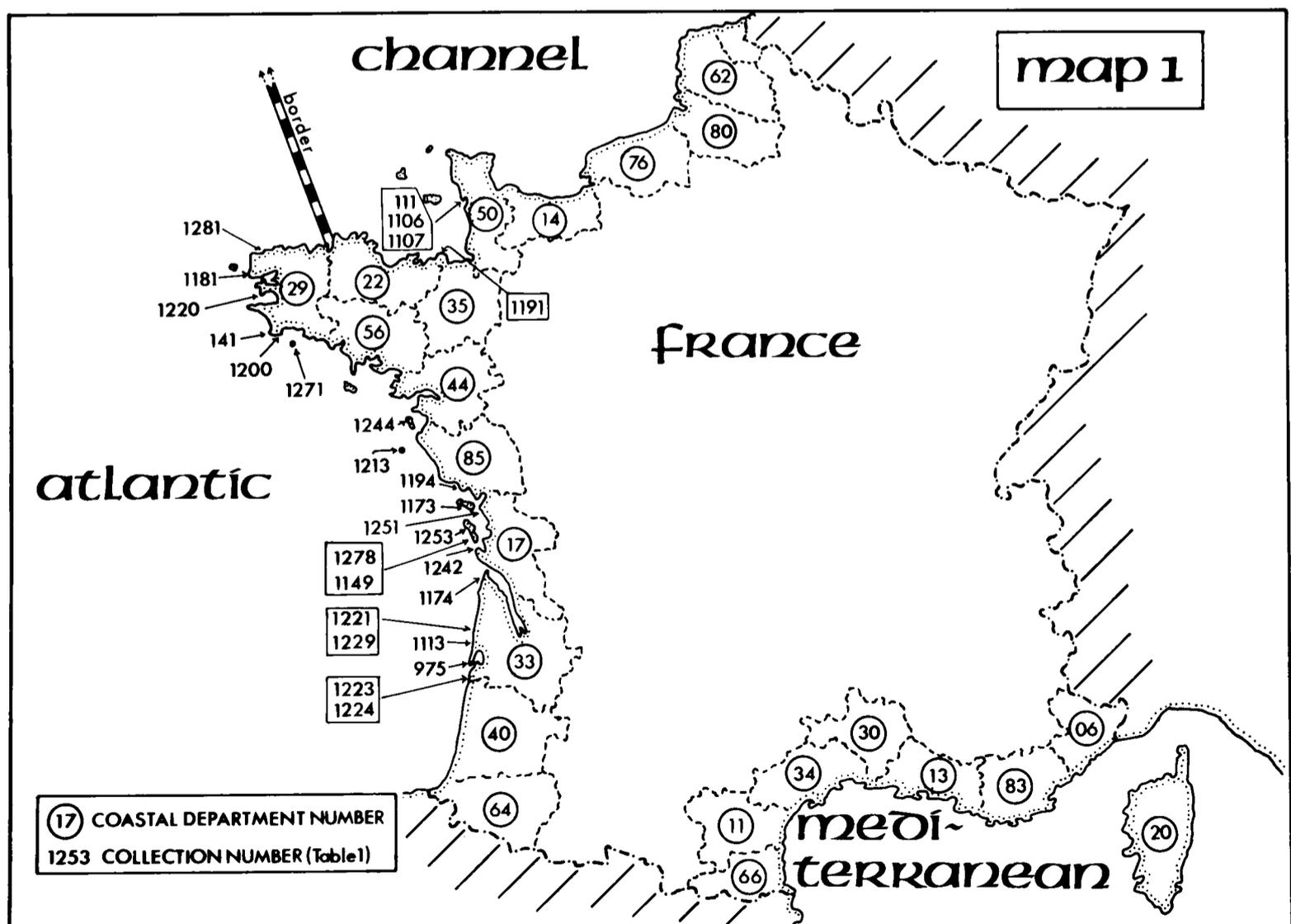
Table 1

Data on testes of *Delphinus delphis* from the northeastern Atlantic. Arrows mean that the testes have been collected without making a distinction between the left and the right one. Bold weight and length sums have been extrapolated from data for one testis

Collection no., date and locality*	Testes										Histological findings
	Animal		Left		Right		$\Sigma L$	$\Sigma W$	$\frac{\Sigma L}{\Sigma W}$		
	L (cm)	W (kg)	L (cm)	W (g)	L (cm)	W (g)					
1220 3/1/81 Saint-Nic (29)	117	±20	5.5	5.5	6.0	4.7	11.5	10.2	1.13	—	
975 10/12/73 Arcachon (33)	148	—	—	—	—	—	—	—	—	Immature	
(141) 29/12/79 Penmarch' (29)	160	55	7.4	9.0	7.6	10.0	15.0	19.0	0.79	—	
1213 6/11/80 Ile d'Yeu (85)	173	72	13.0	10.0	12.0	7.0	25.0	17.0	1.47	Immature	
1173 29/3/80 Ste Marie en Ré (17)	175	±70	7.8	12.8	7.7	11.8	15.5	24.6	0.63	—	
1244 14/3/81 Noirmoustier (85)	180	±60	8.4	19.0	8.8	17.0	17.2	36.0	0.48	Immature	
1194 12/8/80 St Vincent/Jard (85)	180	65	10.5	15.0	9.5	18.0	20.0	33.0	0.61	Immature	
1224 18/1/81 Mimizan (33)	180	±60	11.5	19.9	12.0	14.6	23.5	34.5	0.68	—	
1242 4/3/81 Ronce-les-bains (17)	187	63	11.0	16.0	11.7	17.0	22.7	33.0	0.69	—	
1200 7/9/80 Le Guilvinec (29)	192	—	8.5	30.0	9.0	40.0	17.5	70.0	0.25	Prepubescent	
1113 9/2/79 Lacanau (33)	194	71	11.5	32.0	11.5	34.0	23.0	66.0	0.35	Prepubescent	
1271 17/8/81 Les Glénans (29)	206	±100	15.0	70.0	15.5	80.0	30.5	150.0	0.20	End of activity	
1107 5/1/79 Règneville (50)	206	108	24.0	570	—	—	<b>48.0</b>	<b>1,140</b>	<b>0.04</b>	Spermiogenesis	
1174 22/3/80 Soulac (33)	209	—	18.0	120	18.0	100	36.0	220	0.16	Spermatocytogenesis	
1221 8/1/81 Lège (33)	210	—	27.0	350	29.0	320	56.0	670	0.08	Resting phase	
.251 21/3/81 Aytré (17)	210	—	30.0	370	34.0	430	64.0	800	0.08	Resting of spermatocytogenesis	
1229 21/1/81 Lège (33)	211	—	25.0	—	27.0	—	52.0	—	—	—	
1149 16/11/79 Boyarville (17)	213	±100	33.0	425	33.0	420	66.0	845	0.08	Resting phase	
1181 5/2/80 Le Conquet (29)	215	—	29.0	—	—	—	<b>58.0</b>	—	—	—	
1191 3/7/80 Saint Malo (35)	220	—	22.5	265	26.0	260	48.5	525	0.09	Resting phase	
1253 20/3/81 St Pierre d'Ol. (17)	220	—	30.0	—	—	—	<b>60.0</b>	—	—	—	
(111) 5/1/79 Règneville (50)	220	132	28.0	800	—	—	<b>56.0</b>	<b>1,600</b>	<b>0.04</b>	—	
1223 17/1/81 Biscarosse (33)	222	±100	25.0	470	27.0	470	52.0	940	0.06	Resting phase	
1281 18/2/82 Landéda. (29)	222	±100	—	530	33.0	515	<b>66.0</b>	1,045	<b>0.06</b>	Spermatocytogenesis	
1106 5/1/79 Règneville (50)	223	127	23.0	760	25.0	575	48.0	1,335	0.04	Spermiogenesis	
1278 17/12/81 Oléron (17)	223	130	26.0	285	27.0	330	53.0	615	0.09	Resting phase	

L = Length; W = Weight;  $\Sigma L$  = Summed lengths of both testes;  $\Sigma W$  = Summed weights of both testes.

\* The numbers in parentheses after the locality refer to the departments shown in Map 1.



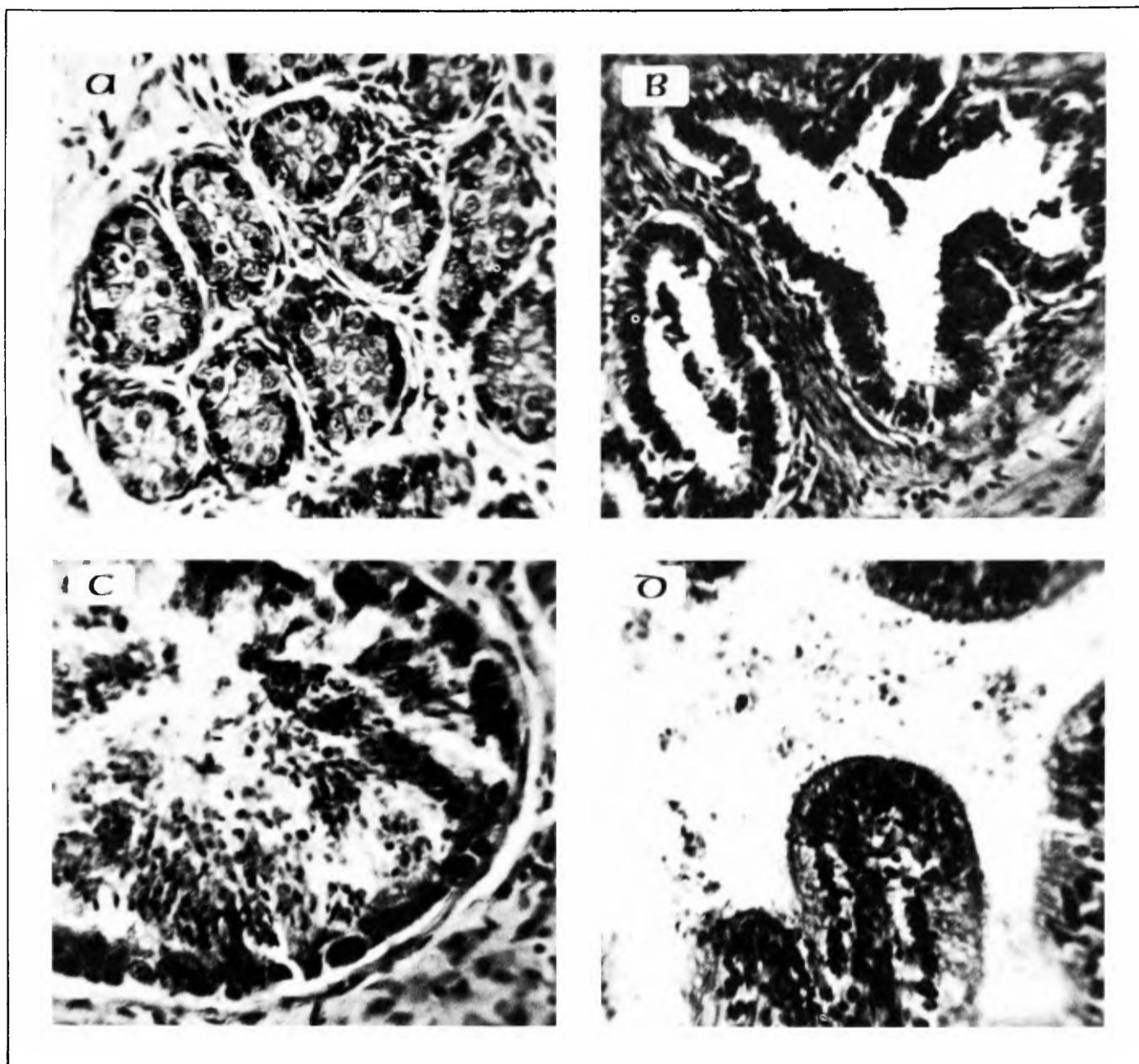


Plate I. Histological sections of *Delphinus delphis* testis (H.  $\times 300$ ).

- a: seminiferous tubules (mean diameter =  $45 \mu$ ) of an immature male, 173 cm long.  
 b: epididymis of a prepubertal male, 192 cm long.  
 c: seminiferous tubules (mean diameter =  $200 \mu$ ) of a mature male, 206 cm long.  
 d: epididymis of a mature male, 206 cm long.

### Mature

In our sample, the size of sexually mature males varied from 206 to 223 cm. Their gonads were 15 to 34 cm long and weighed 70 to 800 g each. Their histological appearances varied considerably from individual to individual. The smallest seminiferous tubules had an average diameter of  $100 \mu\text{m}$ , but some attained 200 to  $250 \mu\text{m}$ . All degrees of maturation of the germinal cells were visible, and the relative proportions of spermatogonia, spermatocytes, spermatids, spermatozoa, Sertoli cells, and the distension of the epididymal lumen all indicated the stage of spermatogenesis.

The beginning of sexual activity is characterized by multiplication of spermatogonia and by production of spermatocytes. Then spermatogenesis goes into full sway, and one can observe spermatogonia, spermatocytes and spermatids in ranked order. The number of spermatogonia and spermatocytes tends to diminish during the course of the active phase (Plate Ic). The young spermatids have spherical nuclei and little pigmentation, those of medium age have round and darkly pigmented nuclei, and the mature spermatids are elongated and exhibit a flagellar opening but remain attached to the epithelium. Full testicular activity is characterized by the presence of

spermatozoa in the lumina of the seminiferous tubules and the epididymis. The presence of only spermatids (young or mature) in the epididymis is evidence of the end of activity, or of a period of abortive spermatogenesis at the end or beginning of testicular activity (Plate Id).

In the resting phase, the diameters of the seminiferous tubules ( $100$  to  $150 \mu\text{m}$ ) and of the epididymis diminish, but they never become as narrow as in immature animals. At the beginning of the resting phase, the Sertoli cells appear more numerous than the spermatogonia, and some spermatids of greater or lesser maturity can remain in the seminiferous tubules and the epididymis. In complete cessation of testicular activity, the Sertolian syncytium is appreciably diminished, to the point that the spermatogonia occupy a greater volume than does the syncytium.

### DISCUSSION

#### Size and age at attainment of sexual maturity

We have examined three relationships between morphometrics of the testes and body length.

Differences in length and weight between the right and left testes were not significant, and no correlation was found between these differences and body length. Hui

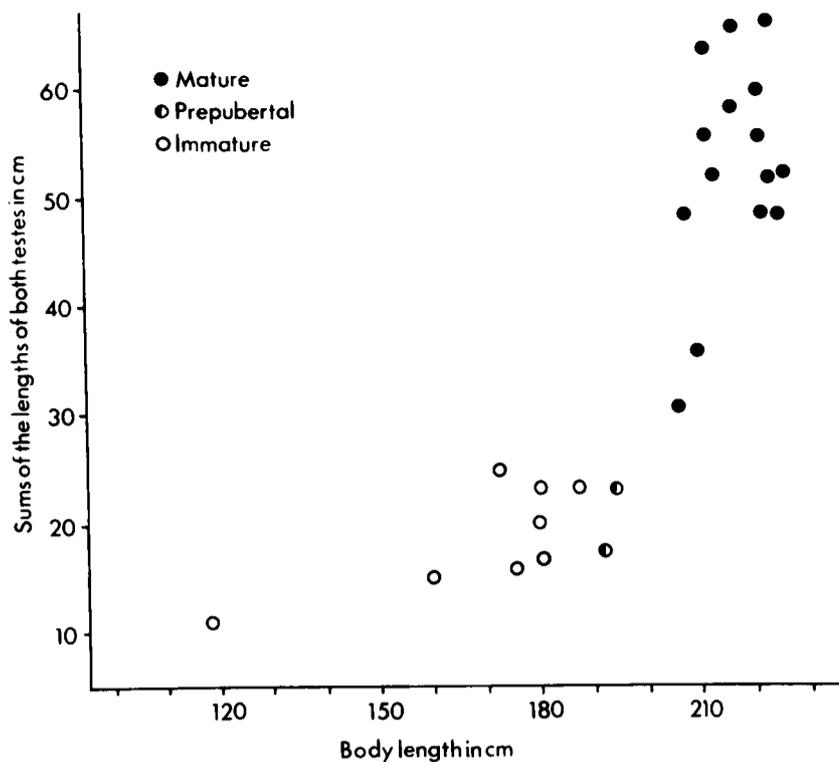


Fig. 1. Relationship between the sums of the lengths of both testes and total body length.

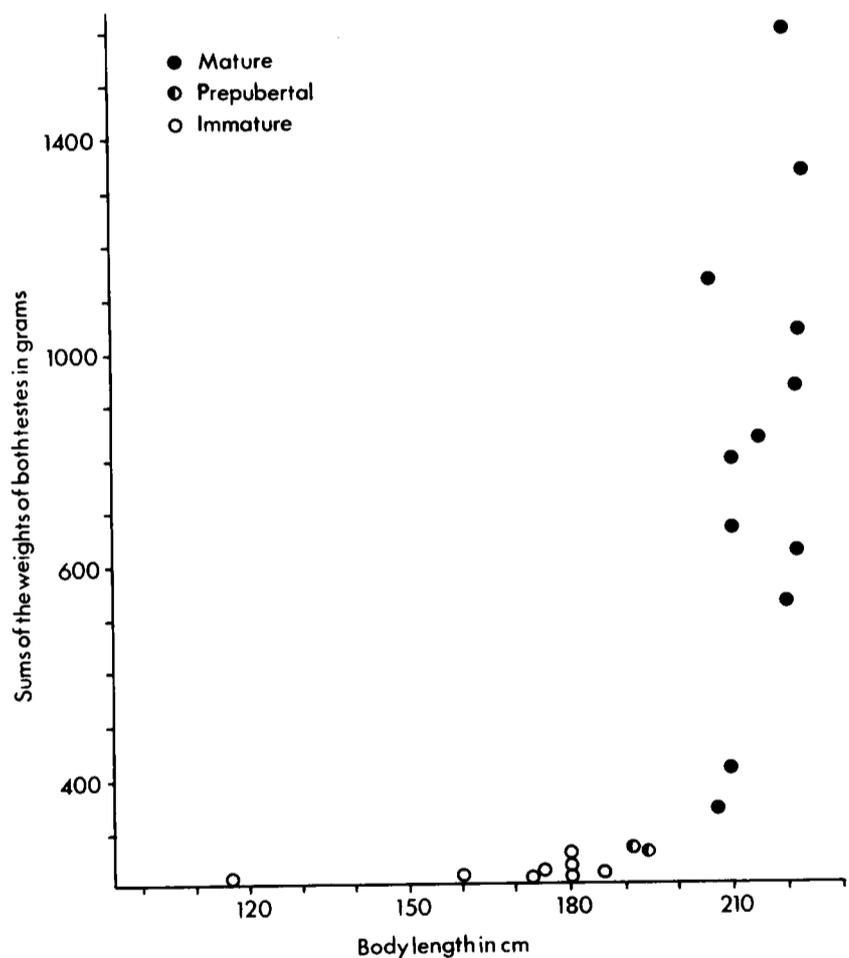


Fig. 2. Relationship between the sums of the weights of both testes and total body length.

(1979) found the same for *Delphinus delphis* in the eastern North Pacific. We therefore have used the summed lengths or weights; this allows comparisons with the findings of other workers.

Fig. 1 shows an increase in the size of the gonads beginning at body length of about 180–190 cm then a very rapid increase after 200 cm. The weight of the gonads begins to increase at about 190 cm (50 to 100 g) and increases very rapidly (although very variably) from 150 to 1,600 g after 200 cm (Fig. 2).

These two relationships indicate that, for our study area, male common dolphins of less than 190 cm are completely immature, those of 190 to 200 cm can be

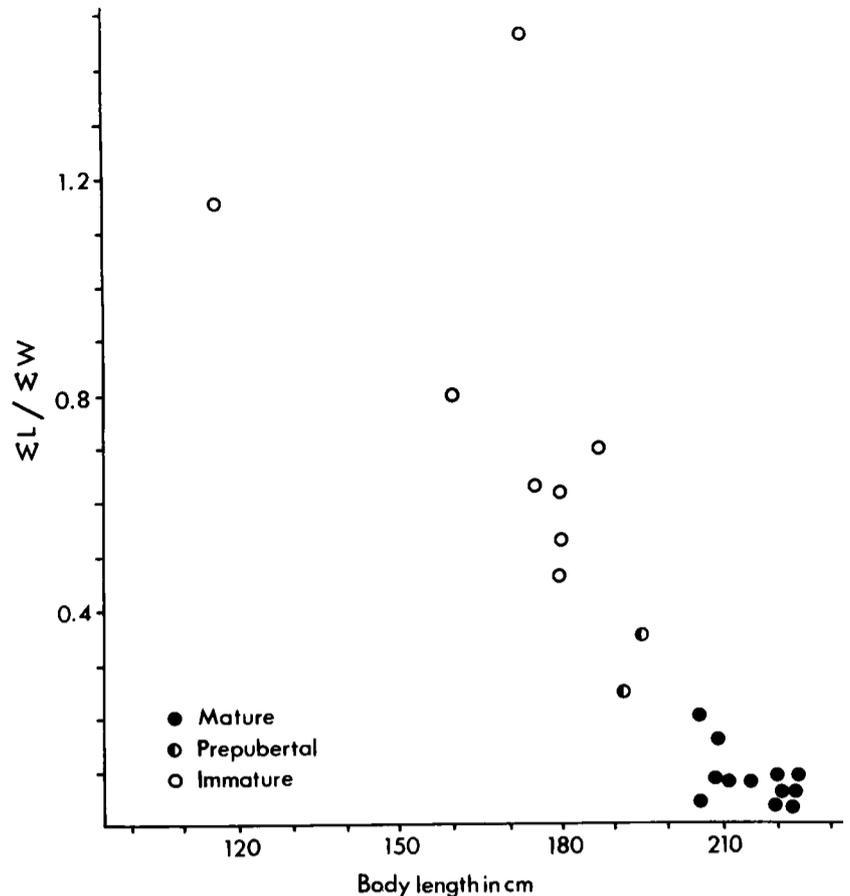


Fig. 3. Relationship between the sums of the lengths of both testes/sums of the weights of both testes ( $\Sigma L/\Sigma W$ ) and the total body length.

considered prepubescent, and those over 200 cm long are sexually mature, with combined testes weights of at least 150 g.

This hypothesis appears confirmed by our histological analyses, which identified four males of 148, 173 and 180 cm (2) as immature, two of 192 and 194 cm as prepubescent, and 11 of 206 (2), 209, 210 (2), 215, 220, 222 (2) and 223 cm (2) as mature.

In addition, one of us has noted (Collet, 1982) that the pelvic bones of *Delphinus* males thicken and increase abruptly in weight over a body length of 200 cm. Since these bones are connected to the male reproductive organ by the ischiocavernous and bulbocavernous muscles (Ridgway and Green, 1967), it appears very probable that this rapid increase in their robustness is related to sexual maturation.

Finally, Fig. 3 shows that the ratio of summed testes length to summed testes weight ( $\Sigma L/\Sigma W$ ) decreases uniformly as the size of the dolphin increases. One exception is an individual of 173 cm that had exceptionally long testes (12 and 13 cm) for their low weight (10 and 7 g), yielding a high  $\Sigma L/\Sigma W$  ratio. Histological examination showed these testes to be immature.

It appears then that the ratio  $\Sigma L/\Sigma W$  is either above or a little below 1 for immature individuals, diminishes progressively in prepubescent animals, and is equal to or less than 0.2 for sexually mature males. Based on histological examination, the ratio is less than 0.1 in males at the onset of spermatogenic activity and decreases further (to less than 0.05) in males in full sexual activity. If this finding holds for a larger sample of animals, it will allow determination of sexual status from the  $\Sigma L/\Sigma W$  ratio. The states of onset and cessation of activity, however, cannot be differentiated by the above method.

According to counts of dentinal layers (Collet, 1981), males of 200 cm have at least 6–7 growth layer groups (GLGs). If the GLGs are annual, which has not yet been confirmed, males of *Delphinus delphis* in the northeast

Atlantic do not attain sexual maturity before 6 or 7 years of age. This finding is very tentative, however, mainly because the body of data is small.

According to Tomilin (1957), male common dolphins in the Black Sea become mature at about 165 cm and 2<sup>1</sup> years of age. Sleptsov (1941) considered them mature at 157 cm and 4<sup>1</sup> years, even though some were still immature at 180 cm. The common dolphin of the Black Sea, however, is of a smaller size than those of the Atlantic and Pacific (Perrin and Reilly, 1984). Even so, sexual maturity at 2 years appears quite precocious when compared to ages at maturity obtained more recently for other species of dolphins (7–13 years old, see below).

For the common dolphins of the Pacific, some authors indicate that sexual maturation occurs at 180–190 cm and 3–4 years of age (Harrison, 1969; Nishiwaki, 1972; Harrison, 1972; and Evans, 1976), but others have come to different conclusions. Oliver (1973) estimated sexual maturity to occur at 202 cm (200–204 cm), when the combined testis and epididymis weight is 100–150 g for each side. Gurevich and Stewart (1978) noted that the weight of the gonads increases greatly between 6 to 10 GLGs, as does also the diameter of the seminiferous tubules. Finally, according to Hui (1979), sexual maturity is attained at about 170 cm and 8–12 GLGs.

We note that some studies (notably that of Walker, 1981 on *Tursiops* of the eastern Pacific) have demonstrated that size at sexual maturity can differ between populations.

If our estimates of age at sexual maturity seem higher than those obtained for other populations, it should be taken into consideration that estimated ages at sexual maturity for males of other species of dolphins are even higher, e.g. 9–13 years in *Tursiops truncatus* (Harrison and Ridgway, 1971; Sergeant, Caldwell and Caldwell, 1973; and Ross, 1977), 9–12 years in *Stenella* spp. (Kasuya, 1972; Perrin *et al.*, 1976), nearly 12 years in *Globicephala melaena* (Sergeant, 1962) and 7–11 years in *Hyperoodon ampullatus* (Benjaminsen and Christensen, 1979).

Finally, it seems reasonable to conclude that at least 3 factors are responsible for the variation in the estimates: the species studied, the population involved, and, above all, the uncertainties concerning the definition of and real time represented by a GLG, for which even the reading varies from one investigator to the other.

Our results indicate that the combined testes weight for mature individuals varies between 150 and 1,600 g. Oliver (1973) obtained comparable results for *D. delphis* in the northeastern Pacific; maturity was attained at 100–150 g. Sleptsov (1941) considered common dolphins of the Black Sea mature at gonadal weight of 300 g. Hui (1979) noted the beginning of spermatogenesis at 140 g, but according to this author, the testes of mature *D. delphis* in the northeastern Pacific weigh at least 350 g. Finally, according to Harrison (1972) spermatogenesis in common dolphins of the northeastern Pacific begins at testis weight of 380 g, but spermatozoa do not appear in the seminiferous tubules until weight of 900 g.

Our results, then, broadly agree with those obtained by the different studies on *D. delphis* from the northeastern Pacific, with the onset of spermatogenesis at about 150 g.

<sup>1</sup> The method used by the author for age determination is unclear.

The apparent differences are due to the fact that we consider individuals with a combined testes weight of over 150 g as mature but in a resting phase, while Harrison (1972) and Hui (1979) consider mature only those animals with spermatozoa, which, as we also found, have much higher testis weights. These authors do not recognize a phase of complete inactivity but believe that activity is continuous, with perhaps a period of greater activity during rut. The dolphins they considered prepubescent with a combined testes weight of 150–350 g could thus have been mature individuals in a resting phase.

It is also interesting to note in this context that it has been found for other species (in particular for *Stenella longirostris* in the eastern tropical Pacific – Perrin and Henderson, 1979) that mature testis weight can vary greatly between populations, possibly as a function of degree of exploitation.

Maximum testis weight can vary considerably on an individual basis, probably as a function of age, hierarchal position in the social unit, and certainly with the cycle of testis activity. The highest combined testes weight recorded for *Delphinus* was noted by Nishiwaki (1965); 8 kg in a male of 75 kg. (Such observations may not be rare in Japan; one of the Japanese names for *Delphinus delphis* is *kintama-iruka*, or 'the testicle dolphin').

#### DETERMINATION OF A CYCLE OF TESTIS ACTIVITY

The great variation in testis size among mature common dolphins of similar size led us to consider the existence of a cycle of testis activity. Histological analysis of the gonads of 11 individuals showed different stages of spermatogenesis.

In no specimen did we find with certainty spermatozoa in the seminiferous tubules or in the epididymis. We therefore have no data on *Delphinus* in full sexual activity.

Of 8 animals from the Bay of Biscay, we recognized 3 as being in a phase of complete inactivity in December and January, the onset of spermatogenesis in two at the end of February and in March, a decline of activity in one in August, and the near-end of activity in one in November. These results suggest a period of activity lasting from April to August and perhaps prolonged into the autumn. Of three dolphins stranded on the Channel coast, two were in a phase of active spermatogenesis in January and one was in a recent resting phase in July. This leads to an hypothesis of an earlier season of activity, between December and June–July, in the dolphins of the Channel.

Therefore it appears that testis activity in common dolphins of the northeastern Atlantic may be seasonal. This cycle of activity, which extends for 6–8 months, starts earlier or later in the year depending on the groups or stock involved (Channel or Atlantic dolphins, i.e. northern or southern Brittany), so that the total period of testis activity in the northeastern Atlantic lasts more than 10 months. This extension of the season for the whole population could mask the individual seasonal cycle, as has been noted by Hirose and Nishiwaki (1971) for *Stenella coeruleoalba* in Japan.

The distinction that we have drawn between the

northern and southern Brittany animals is based on only a few data, and the differences we see could in fact be due to individual variation. We must also recognize that our study is primarily based on dead stranded animals (only 6 of 26 were captured or stranded alive) that may or may not be representative of the population(s). Necropsies of the dead stranded dolphins revealed pathological lesions (most notably in the lungs). Certain histological anomalies that suggest disturbed spermatogenesis could therefore have been related to illness suffered by the animals.

The results of research on male seasonality in small cetaceans have varied with species, the population involved and the investigator. Thus, male seasonality has been proposed in *Stenella coeruleoalba* (in Japanese waters – Hirose and Nishiwaki, 1971), in *Delphinus delphis* (in the Black Sea – Sleptsov, 1941 and Tomilin, 1957; in waters around Great Britain – Fraser, 1953; and the eastern North Pacific – Ridgway and Green, 1967 and Gurevich and Stewart, 1978), in *Globicephala melaena* (in the western North Atlantic – Fisher and Harrison, 1970 and Gaskin and Blair, 1977). Finally, Simpson and Gardner (1972), claimed that the 'majority' of cetaceans exhibit a cycle of testicular activity. Other authors have concluded that spermatogenesis occurs year-round, with perhaps a period of more intense activity during rut (proposed for *Delphinus delphis* in the eastern North Pacific – Harrison, 1972 and Hui, 1979; *Phocoenoides dalli* in the North Pacific – Morejohn, 1979; and for odontocetes in general – Slijper, 1962).

As we have noted for the common dolphin of the eastern North Atlantic, cycles of testis activity with different timings and lengths depending on stocks, and possibly individuals, could be masked by a total long season of activity for the whole population. This may partially explain the differences between results obtained in several studies of *Delphinus* in the eastern North Pacific (Ridgway and Green, 1967; Harrison, 1972; Gurevich and Stewart, 1978; Hui, 1979) and also explain similarly varying estimates of the timing of rut.

This preliminary study has permitted us to determine the probable size and age at attainment of sexual maturity and to suggest a cycle of spermatogenesis activity that includes a complete resting phase.

These results must be confirmed by study of a larger number of animals, collected throughout the year and more certainly representative of the population(s).

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# Preliminary Analysis of Reproductive Parameters of the Boutu, *Inia geoffrensis*, and the Tucuxi, *Sotalia fluviatilis*, in the Amazon River System

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## ABSTRACT

Examination of the reproductive organs of 27 specimens of *Sotalia fluviatilis* and 21 of *Inia geoffrensis*<sup>1</sup> incidentally captured in commercial fisheries operations in the central Amazon region of Brazil allows preliminary estimation of reproductive parameters in these species. *Sotalia* males with body lengths of greater than 140 cm may show greatly enlarged testes (up to 5% of body weight) although only half of our adult sample ( $n = 6$ ) had testes characteristic of sexually 'active' animals. *Sotalia* females attain sexual maturity, as indicated by ovarian scars, at body lengths of between 128.5 and 138.5 cm, with a distinct left-hand polarity of ovarian function. Calves are born at lengths between 71 and 83 cm after a calculated gestation period of 10.2 months, and calving is apparently seasonal, with a peak between October and November (the low-water period of the Amazon River system). *Inia* males over 198 cm in length are probably reproductively mature; testes size increases in proportion to body size (maximum of 1.2% of body weight). Females of *Inia* over 183 cm long are mature and show no evidence of polarity in ovarian function. Calf size at birth is  $79.4 \pm 3.3$  cm and the calving season is apparently during the months of May through July, coincident with the peak water levels of the river system. This seasonality in the calving period in both dolphins is linked to relative food availability in relation to the river flooding cycle. The difference in relative testes size between *Sotalia* and *Inia* males may be related to contrasting breeding systems.

## INTRODUCTION

Neither species of Amazon freshwater dolphin, *Inia geoffrensis* or *Sotalia fluviatilis*, has been systematically studied in its natural habitat and very little is known about their reproduction. Observations of their behavior and natural history may be found in Layne (1958), Layne and Caldwell (1964), Pilleri (1969), Pilleri and Gihl (1977), Gewalt (1978), and Trebbau and van Bree (1974). Specimens that died after being collected for live display were the basis of the reproductive anatomical studies of Harrison and Brownell (1971) and Harrison, Brownell and Boice (1972). Captive live births of 2 *Inia* calves have been described by Huffmann (1970), McCuster (1973) and Caldwell and Caldwell (1972). Comparative reproductive characteristics of platanistid dolphins are reviewed by Brownell (1984).

The marked annual floods of the Amazon River system impose a seasonal rhythmicity on nearly all the aquatic fauna, particularly in terms of the availability and relative abundance of food (Goulding, 1980, 1981; Lowe-McConnell, 1979; Welcomme, 1979). The amplitude of the floods is about 10 m. The fish populations are concentrated in the river channels and deeper lakes during the dry season and dispersed through the vast flood plains during the flood season. It is reasonable to suppose that the energetically 'costly' reproductive period of the dolphins might be thus synchronized with the greatest availability of foods, as in other mammals (Low, 1978; Sadlier, 1969).

In this paper, we present a preliminary analysis of reproductive data from specimens of *Inia* and *Sotalia* collected in the central Amazon region near Manaus,

Brazil (Fig. 1), as part of a recently initiated study of the biology of these species undertaken by the Instituto Nacional de Pesquisas da Amazônia (INPA).

The collection of specimens is relatively difficult in the Amazon, as many myths exist about these dolphins and the fishermen of the region generally avoid contact with them because of such superstitions (Allen and Neill, 1975; Smith, 1981; personal observations).

## MATERIALS AND METHODS

Dolphins were collected as incidental captures in the regional fisheries by local fishermen and fishermen from our Institute and, as such, do not represent a systematic, balanced collection. The characteristics of each animal are presented in Table 1. Each specimen was necropsied and the reproductive material weighed and measured before being sliced in  $\sim 3$  mm sections and preserved in Bouin's solution or 10% formalin. Due to time restrictions, we have not attempted histological analysis of these gonads nor have we aged the dolphins using dentinal layering. Each ovary was inspected macroscopically for scars or obvious corpora lutea or c. albicantia associated with reproductive events, while the uterus was inspected for small fetuses if the animal was not obviously gravid. Total testes weight as a percentage of body weight is used as an index of relative maturity or sexual activity.

## RESULTS

### *Sotalia*

#### *The male*

Males of less than 139 cm in length were not found with the disproportionately large testes apparently characteristic of reproductively active males (Fig. 2a) and only 50% of the 6 males  $> 139$  cm possessed greatly enlarged testes.

<sup>1</sup> We provisionally call these species by their most commonly used names but recognize that there is taxonomic confusion involving both genera (Pilleri and Gihl, 1977; Casinos and Oçaña, 1979; van Bree and Robineau, 1977; van Bree, 1974).

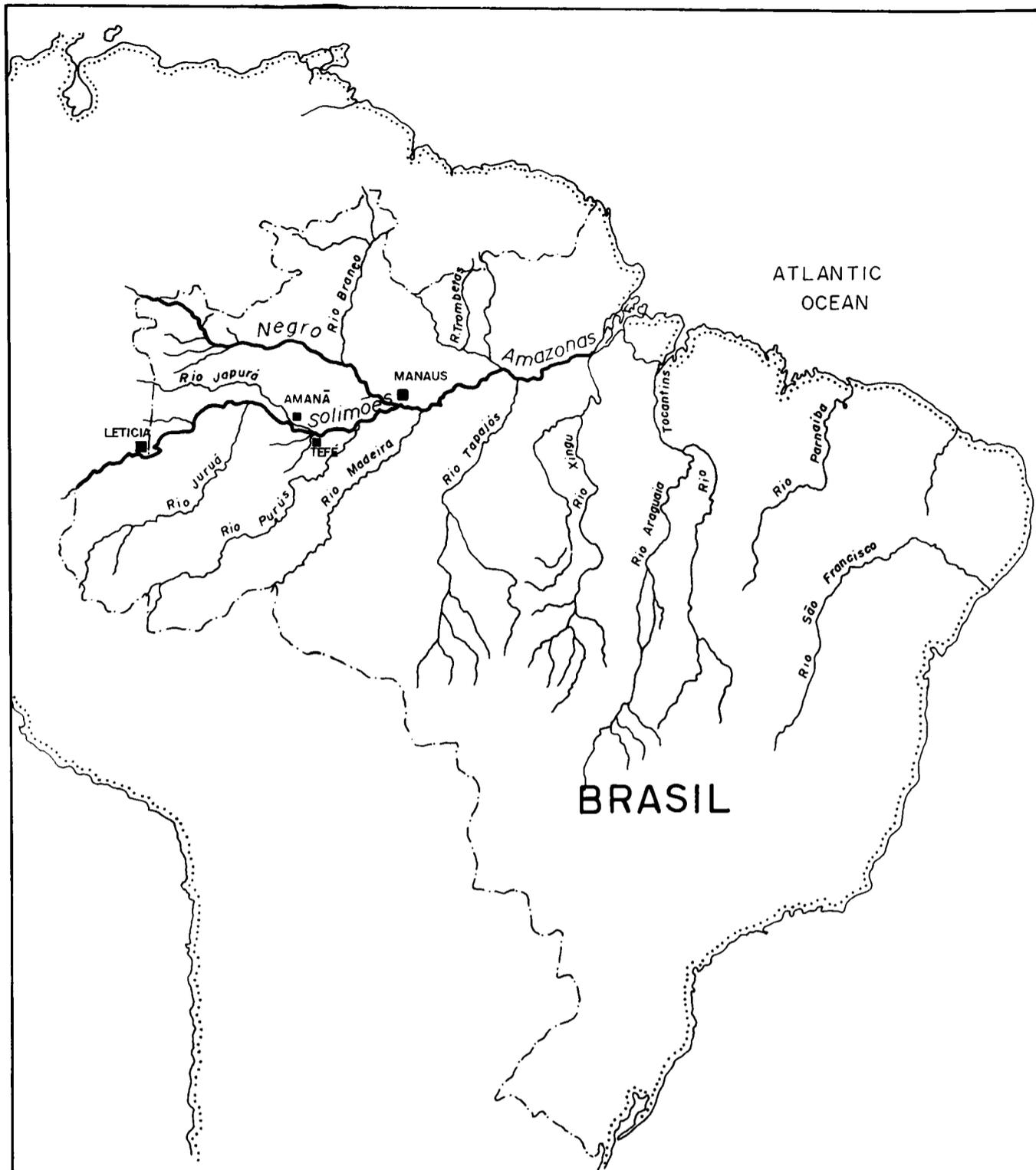


Fig. 1. Map of the study region.

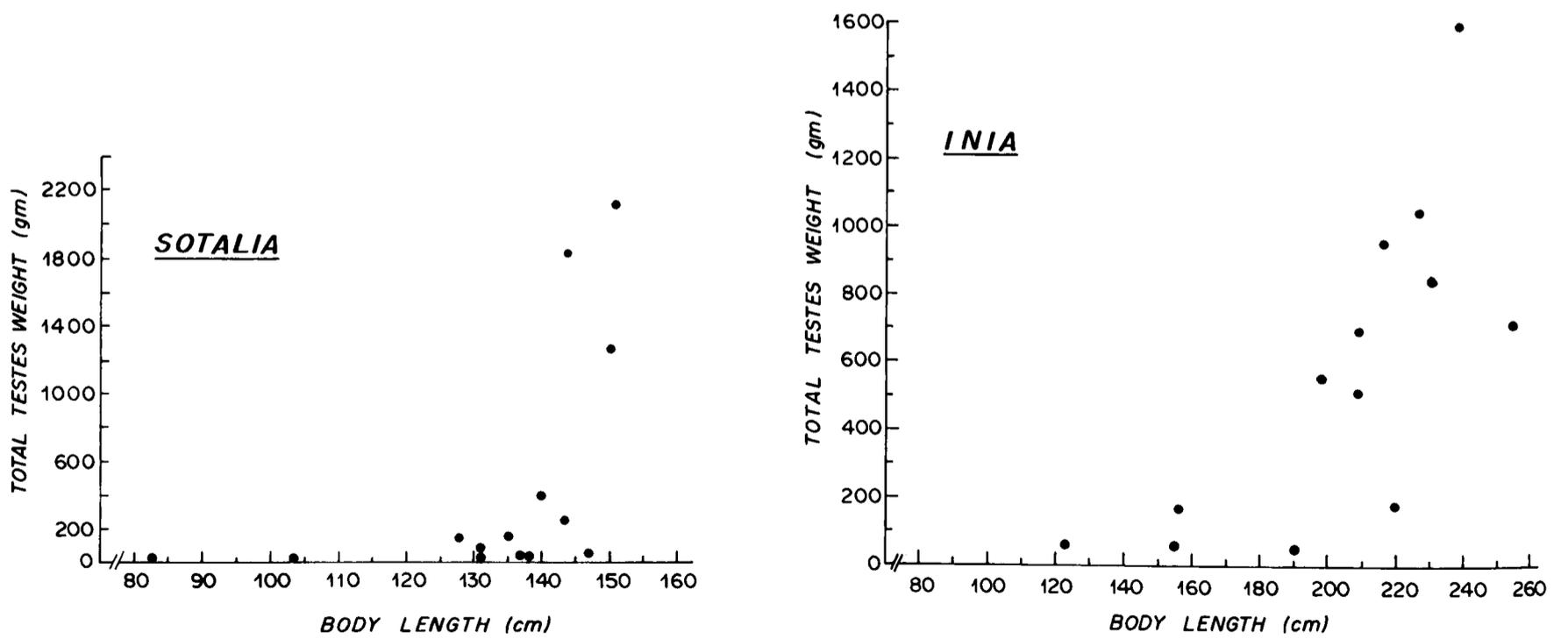


Fig. 2. Testes weight (combined) as a function of body length for (a) *Sotalia fluviatilis* and (b) *Inia geoffrensis*.

Table 1  
Collection data, length, weight and reproductive condition of specimens

No.	Locality	Date of death	Length (cm)	Weight (kg)	Gonad weight (g)		Reproductive status
					Left	Right	
<i>Females: Inia geoffrensis</i>							
35	L. Tefé	25/05/80	81.0	8.2	—	—	Newborn
23	L. Amanã	10/09/79	108.5	21.3	2.0	2.0	Immature – young of 22
19	L. Amanã	05/09/79	133.0	53.0	4.0	6.0	Immature – young of 17
22	L. Amanã	10/09/79	183.0	67.4	10.0	9.0	Lactating. 1 <i>C. albicans</i> + 1 <i>C. lutea</i> – left ovary; 1 <i>C. albicans</i> – right ovary
34	L. Tefé	25/05/80	188.0	83.0	—	11.0	Pregnant. 1 <i>CL+CA</i> – left, 2 <i>CAs</i> – right
07	L. Tefé	26/05/79	195.0	70.5	8.5	7.5	Resting. 6 <i>C. albicans</i> in left ovary, 4 <i>C. albicans</i> – right ovary
17	L. Amanã	05/09/79	196.0	96.5	10.0	6.0	Lactating. 4 <i>C. albicans</i> in left ovary, 3 <i>C. albicans</i> – right ovary
<i>Sotalia fluviatilis</i>							
24	L. Amanã	05/11/79	101.5	—	—	—	Immature
27	L. Amanã	12/12/79	105.5	19.3	< 1.0	1.0	Immature
05	L. Tefé	24/05/79	122.0	26.0	2.0	2.0	Immature
15	L. Amanã	29/08/79	128.5	28.0	—	—	Immature
47	R. Amazonas	31/08/80	138.5	40.0	5.3	1.6	Resting 10 <i>C. albicans</i> – left ovary
06	L. Tefé	24/05/79	139.0	45.0	9.0	2.0	Pregnant. 1 <i>C. lutea</i> and 4 <i>C. albicans</i> – left ovary
41	R. Negro	09/80	144.0	—	—	—	Pregnant. (?) 1 <i>C. lutea</i> – left ovary
45	R. Amazonas	31/08/80	148.0	47.0	—	—	Resting. 1 <i>C. albicans</i> – left ovary
26	L. Amanã	24/11/79	148.5	—	4.0	1.0	Pregnant. 1 <i>C. lutea</i> and 1 <i>C. albicans</i> – left ovary
32	L. Amanã	17/05/80	149.0	40.0	20.0	10.0	Lactating. 2 <i>C. albicans</i> – left ovary
48	R. Amazonas	31/08/80	149.0	53.0	5.0	2.5	Lactating. 5 <i>C. albicans</i> – left ovary
<i>Males: Inia geoffrensis</i>							
37	R. Negro	28/04/80	114.5	15.5	—	—	Immature
14	L. Amanã	27/08/79	123.0	30.1	35.0	30.0	Immature
18	L. Amanã	05/09/79	154.5	84.3	40.0	30.0	Immature
29	R. Negro	05/05/80	156.5	83.2	85.0	81.0	Immature
03	L. Tefé	22/05/79	190.5	70.0	26.0	24.0	Immature
02	L. Tefé	21/05/79	198.5	103.5	300.0	260.0	Active (?)
04	L. Tefé	23/05/79	209.0	110.0	280.0	240.0	Active
30	L. Amanã	14/05/80	204.0	118.0	340.0	360.0	Active
08	L. Tefé	25/05/79	216.5	112.5	540.0	420.0	Active
01	L. Tefé	08/05/79	220.0	~ 120.0	102.0	88.0	Inactive (?)
33	L. Tefé	21/05/80	225.0	127.0	420.0	430.0	Active
49	R. Solimões	11/80	227.0	—	540.0	510.0	Active
21	L. Amanã	07/09/79	238.5	159.5	800.0	800.0	Active
20	L. Amanã	07/09/79	255.0	128.7	370.0	350.0	Active
<i>Sotalia fluviatilis</i>							
44	R. Amazonas	31/08/80	83.0	10.0	4.0	4.0	Immature – young of 48
42	R. Amazonas	30/08/80	103.5	15.5	5.9	5.9	Immature
SN	L. Amanã	09/11/80	111.0	—	—	—	Immature
43	R. Amazonas	30/08/80	128.0	35.3	73.2	73.2	Immature
46	R. Amazonas	08/80	131.0	31.5	16.0	16.5	Immature
40	R. Purus	04/08/80	131.0	29.0	40.0	35.0	Immature
36	R. Negro	23/04/80	132.0	34.7	—	—	—
28	R. Negro	19/03/80	135.0	30.0	74.2	73.5	Immature
52	R. Solimões	31/08/81	137.0	37.0	20.0	19.2	Immature
31	L. Amanã	16/05/80	138.0	35.5	18.0	20.0	Immature
50	R. Madeira	13/01/81	140.0	36.0	186.0	207.0	Inactive
25	L. Amanã	22/11/79	143.5	—	132.0	126.0	Inactive
39	R. Juruá	23/06/80	144.0	40.0	900.0	920.0	Active
51	R. Solimões	31/08/81	147.0	42.0	26.9	28.9	Inactive
38	R. Juruá	23/06/80	150.0	47.0	598.3	677.0	Active
16	L. Amanã	29/08/79	152.0	42.0	1,050.0	1,060.0	Active

Combined testes weights for immature and inactive males ranged from 8 g to 393 g, whereas those of active males were between 1,275 g and 2,110 g. The testes/body weight ratio of young or inactive males is usually less than 1% and that of active males is from 2.5 to 5.0% (Fig. 3a). Our data are too few to define any obvious seasonal sexual rhythm even though the active males ( $n = 3$ ) were only

encountered in the months of June to August, occurring simultaneously with inactive adult males.

#### *The female*

The length of the adult female tucuxi is between 128.5 and 138.5 cm; a more precise definition awaits examination of females of intermediate sizes. The maximum number

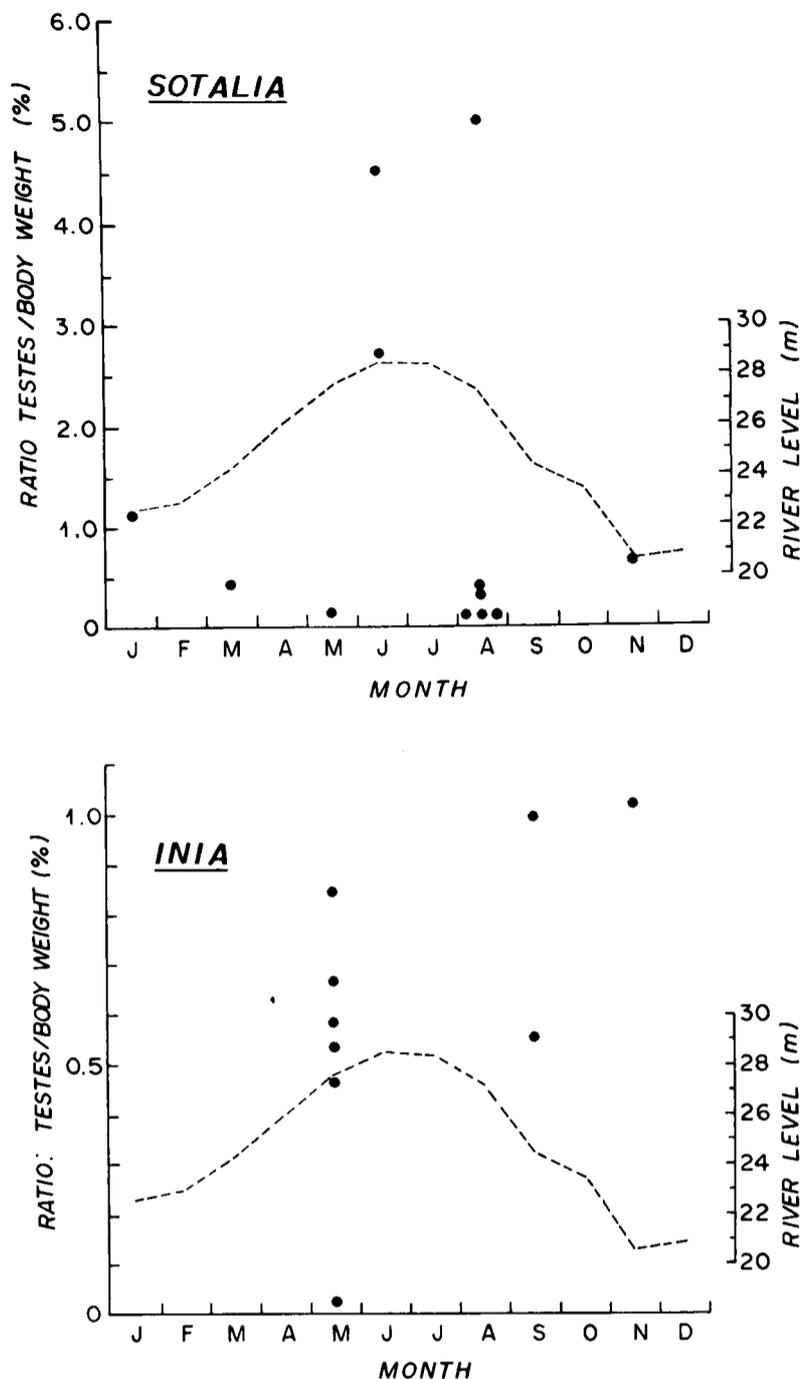


Fig. 3. Ratio of testes weight to body weight for (a) adult specimens of *Sotalia* and (b) *Inia* males on a seasonal basis and compared to annual river levels.

of macroscopically visible corpora was 10 in animal No. 47. All ovarian scars observed were in the left ovary. The 7 adult females for which we have gross reproductive data may be separated into the following reproductive states; 'resting' (non-pregnant and not lactating), 42%; pregnant, 29%; and lactating, 29%. These ranged in size between 138.5 and 149 cm.

#### Length at birth, gestation, and foetal and postnatal growth

The largest foetus was 71 cm long, and the smallest neonate was 83 cm long. We suggest that the probable length at birth is about 75 cm.

Using the method of Huggett and Widas (1951) with the modifications proposed by Laws (1959), Kasuya (1977) and Perrin, Coe and Zweifel (1976), the length of gestation for *Sotalia* was calculated to be approximately 10.2 months using a  $t_0$  (the intercept where the linear growth line transects the time axis) of 0.135 for the initial stage of geometric growth. In varying the value of  $t_0$  from 0.12 to 0.15 (see Perrin *et al.*, 1976), the minimum and maximum estimates of gestation in *Sotalia* are 10.0 months and 10.3 months, respectively.

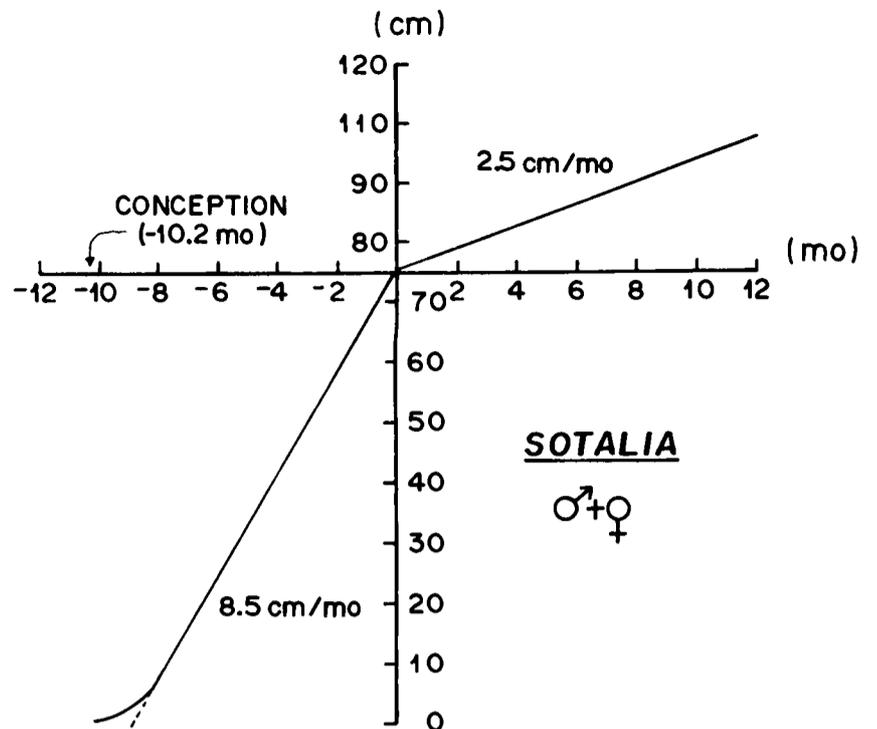


Fig. 4. Prenatal and neonatal growth rates for *Sotalia*, with deduced gestation period of 10.2 months.

Although the sample sizes are minimal, preliminary regressions of pre- and postnatal growth rates may be made:

$$\begin{aligned} \text{prenatal (linear phase)} \\ Y = 8.532x + 11.516 \quad (\text{cm/month}) \quad (1) \\ (n = 3; r^2 = 0.99) \end{aligned}$$

$$\begin{aligned} \text{postnatal} \\ Y = 2.507x + 71.09 \quad (\text{cm/month}) \quad (2) \\ (n = 6; r^2 = 0.72) \end{aligned}$$

The relationship of foetal and postnatal growth during a period equal to the gestation period is shown in Fig. 4.

#### Seasonality of births

If the body length and month of capture of foetal and young specimens of *Sotalia* are plotted twice, 12 months apart, to give a continuous curve (Fig. 5), an apparent birth period occurs between the months of October and November. This period coincides with the lowest annual river levels. A 10.2-month gestation would imply that conception occurs during the months of December and January.

#### *Inia*

##### The male

In our sample, enlarged testes were found in males of 198 cm or larger, and a male of 190.5 cm still had small immature testes (Fig. 2b). The relationship between combined testes weight and body length above 198 cm appears to be almost a linear function, as only a single adult-sized animal with immature testes was found.

When expressed as a percentage of body weight, *Inia* testes weights are proportionately less than those in *Sotalia*, reaching a maximum of 1.2% in adult males and a minimum of 0.2% (Fig. 3b). With the exception of the single 220 cm male with unusually small testes, all males above 198.5 cm had combined testes weight/body weight ratios of 0.4% or greater and did not show any seasonal sexual rhythm.

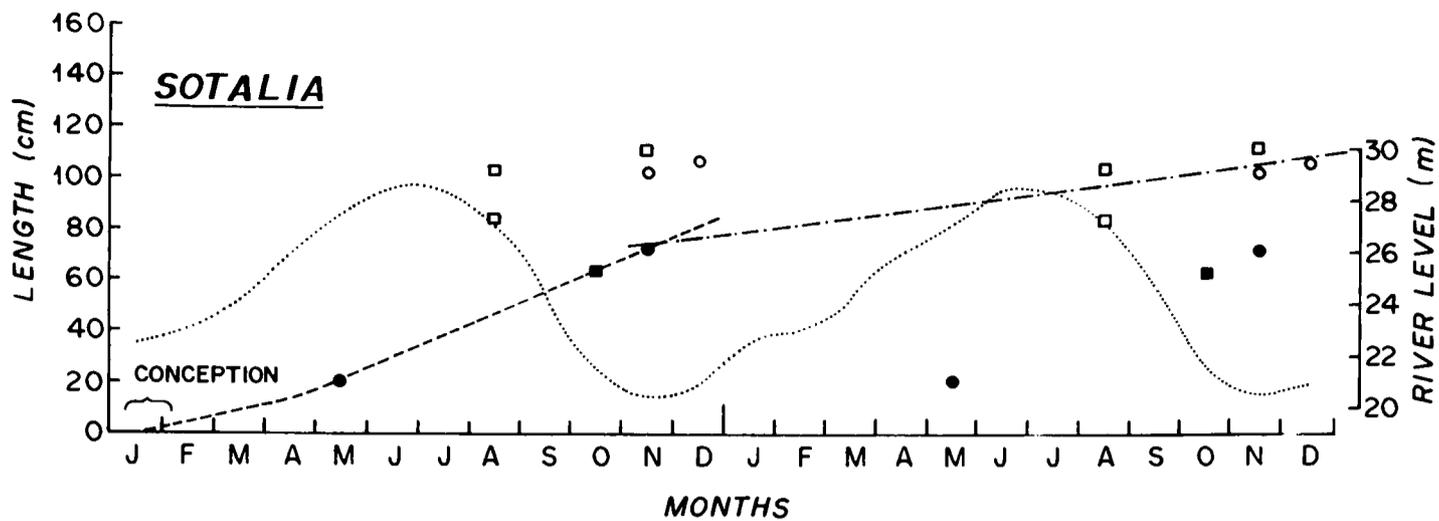


Fig. 5. Lengths and dates of capture of foetal (solid symbols) and immature specimens of *Sotalia* plotted twice to allow the sequence of development to be shown. Females are indicated by round symbols, males by squares. Dotted line is river level. Dashed line is inferred growth.

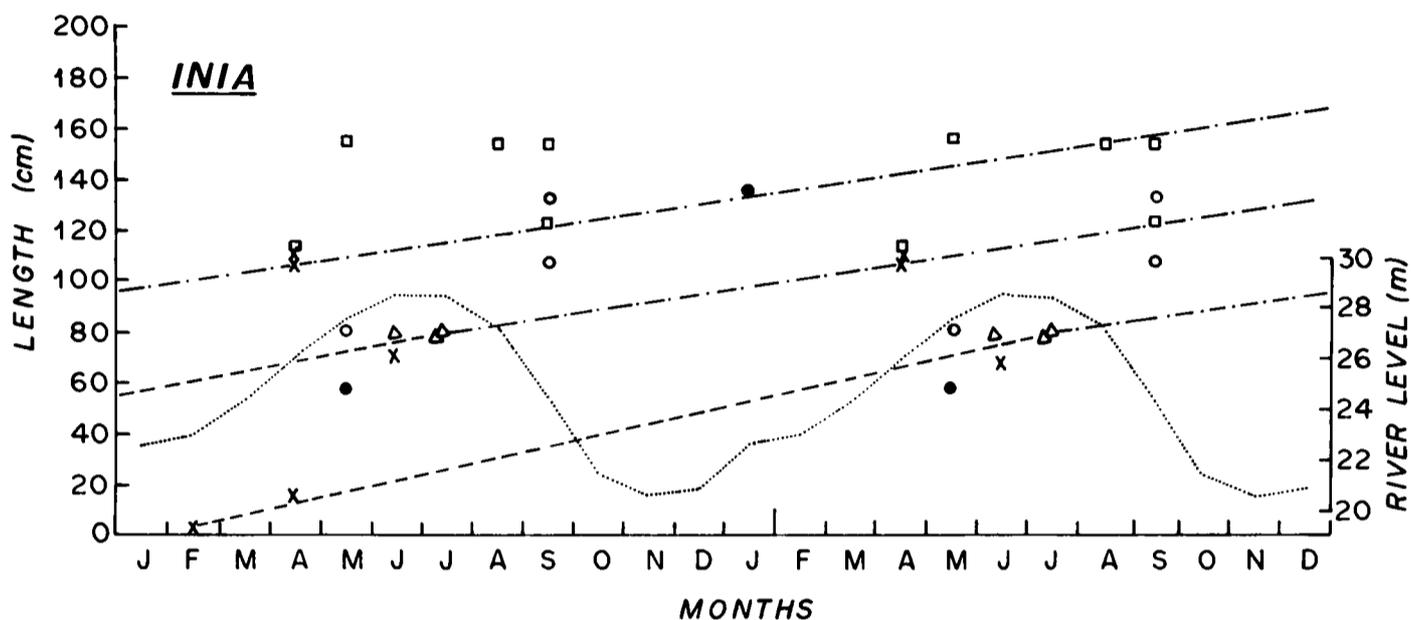


Fig. 6. Lengths/dates of capture for *Inia*. Symbols are as in Fig. 4; x's represent foetal data taken from Harrison and Brownell 1972 and R. L. Jenkins *in litt.* Dashed lines represent three possible cohorts.

*The female*

Females of over 183 cm may be considered adult, because at that size they may be lactating and have ovarian scars indicating previous reproductive events. We suggest that the actual size at attainment of maturity may be less than the value given here, as our sample lacks data for the size classes between 133 cm and 183 cm.

Ovarian scars were present in both ovaries of all the females and there was no significant difference between the numbers of scars in the left and right ovaries ( $X^2 = 0.125; P < 0.05$ ). Of the four adult females analyzed here, two were lactating, one resting and one pregnant.

*Length at birth, gestation and foetal/postnatal growth*

The smallest neonatal boutu in our sample was 81 cm long. Obvious foetal folds indicated that this animal had been recently born. We did not examine any near-term foetuses (the largest was 66 cm long).

Our sample is too small to allow us to draw any conclusions on the length of gestation, foetal or neonatal growth rates. We have tried to remedy this weakness in our data by including data from animals caught in Leticia, Colombia (Harrison and Brownell, 1971; R. L. Jenkins *in litt.*) as shown in Fig. 6. Foetal growth

would thus be about 4.5 cm/month and neonatal growth about 2.5 cm/month. The gestation period, calculated in a similar manner to that for *Sotalia*, would give an improbable 17+ month pregnancy, suggesting that there may be notable differences in breeding populations for different regions in the Amazon. Unfortunately, although there have been three captive births of *Inia*, the actual gestation has only been estimated, as about 8.5 months (Caldwell and Caldwell, 1972).

*Seasonality of births*

There may be a considerable spread in calving period, as we recorded in 81-cm neonate and a 66-cm foetus in the same month, May, from areas relatively close to each other. However, it appears that calving occurs during the months May to July, coincident with the peak river levels and their initial decline (Fig. 6).

**DISCUSSION**

**The males**

Our estimate of attainment of sexual maturity in the male tucuxi at 139 cm is considerably lower than that of Harrison and Brownell (1971). Grafton (1968) reported that a 133.4 cm male that had been in captivity for two

years had testes that were 6 cm by 4 cm and that the germinal epithelium was apparently active. This size-class (130–140 cm) was well represented in our sample and although some individuals may have had slightly larger testes (~ 200 g) than others (Fig. 2a), we do not consider these animals sexually active. Conversely, for the boutu, our value for adult males of 198 cm or larger is lower than the 228 cm cited by Harrison and Brownell (1971) and is more in line with the finding of a 208 cm adult male in the Orinoco River (Trebbau and van Bree, 1974).

We have too few data to allow us to determine whether *Sotalia* and/or *Inia* males show seasonal sexual rhythms as has been shown for other delphinids (Ridgway and Green, 1967). However, the presence of a reproductively inactive adult (Figs 2a, 3a) is suggestive of some sort of differential effect of season on the reproductive status of the males. In contrast, the data for *Inia* shows a much greater correlation between testes and adult size (Figs 2b, 3b). The male boutu appears to remain sexually active on a continuous basis after attaining adulthood, as may be deduced from our finding of active males in the months of May, September and November. The male 'investment' in reproduction in *Inia* is relatively modest, as the total testes weight in an active adult attains a maximum of slightly over 1% of the total body weight. *Sotalia* males, when reproductively active, 'invest' up to 5% of their body weight (a 42-kg animal may have a combined testes weight of over 2 kg not including the proportionately enlarged epididymis (0.3 kg)). In our admittedly small sample, only 50% of the males were active, indicating that not only body size governs reproductive status. It has been shown that the dugong (*Dugong dugon*) is also a discontinuous breeder in that only a certain proportion of the adult males of a population are reproductively active at any time (Marsh, Heinsohn and Glover, in press) although the critical factor has not yet been defined. Other tropical dolphins also exhibit seasonal variation in testis weight, e.g. *Stenella longirostris* (Perrin and Henderson, 1984).

Possibly the most notable difference between *Sotalia* and *Inia*, apart from disparate body sizes, is the fact that *Sotalia* is more social than *Inia*, generally occurring in small groups of 2–5 individuals, whereas *Inia* is generally solitary or occasionally may be seen in pairs (Layne, 1958; Magnusson, Best and da Silva, 1980). We suggest that the large testes may reflect a polyandrous system in which several males mate with a single oestrous female. Reproductive advantage in this sort of system is gained by the male that inseminates with sufficient ejaculate to compete with that of other males (Dewsbury and Baumgardner, 1981). This would require greater sperm production and hence larger testes. *Inia* could be a representative of a monogamous breeding system in which the male need only ejaculate enough sperm to ensure fertilization. Such a relationship between testes weight, body weight and breeding systems has recently been described for primates (Harcourt, Harvey, Larson and Short, 1981). What factors, such as nutrition, social, endogenous or others (Sadler, 1969) may influence the switching on and off of testicular function in *Sotalia* is not known.

### The females

*Sotalia* females attain maturity between 132 and 137 cm; Harrison and Brownell (1971) and R. L. Jenkins (*in litt.*) report on an immature female and a pregnant female that are within the size-ranges of our sample. Ovulations as indicated by ovarian scars were exclusively in the left ovary in *Sotalia* (this study, Harrison and Brownell, 1971) as is characteristic of the Delphinidae (Ohsumi, 1964, Harrison, Boice and Brownell, 1969).

*Inia* females are reproductively active at body lengths of over 180 cm (this study, Harrison and Brownell, 1971; Trebbau and van Bree, 1974) and may be simultaneously gravid and lactating (Harrison and Brownell, 1971). In contrast to the ovarian polarity of *Sotalia*, *Inia* has almost equal numbers of ovarian scars in the right and left ovary (this study), a characteristic shared with the closely related *Plantanista gangetica* (Harrison, Brownell and Boice, 1972). Another plantanistid, *Pontoporia blainvillei* shows a distinct lefthand polarity (Harrison, Bryden, McBrearty and Brownell, 1981). Using the ovary-based classification scheme of Ohsumi (1964), *Inia* and *Platanista* may be considered Type I (maturity and ovulation occurs in both ovaries equally), whereas *Sotalia* and *Pontoporia* apparently have a Type III system (ovulation occurs initially in the left ovary and only later in the right).

Sexual dimorphism is not present in *Inia* ( $t_{62} = 2.0$ ;  $P < 0.05$ ) but is possibly present in *Sotalia* ( $t_{25} = 0.5$ ;  $P < 0.05$ ) with the female being slightly larger in the latter species (Fig. 6). *Inia* is exceptional in that the other plantanistids are sexually dimorphic (Brownell, 1984). However, this lack of dimorphism is compatible with the proposed monogamous mating system for this species as monogamous species tend to have a low degree of dimorphism (Ralls, 1977; Eisenberg, 1981).

The apparent tendency for females of *Sotalia* to be slightly larger may be an artifact of our small data set, or it may in fact be related to pressures of reproductive specialization. *Sotalia* is one of the smallest dolphins, and a slight increase in size over that of the male may allow the production of a larger (more viable?) foetus and allow the female to better sustain the demands of lactation.

The estimated size of the boutu at birth should be relatively accurate, as in addition to our 81 cm neonate there are an additional five reports of neonates (Huffman, 1970; McCuster, 1973; Caldwell and Caldwell, 1972; Harrison and Brownell, 1971; R. L. Jenkins, pers. comm.) ranging from 76 cm to 83.6 cm ( $\bar{X} = 79.4 \pm 3.5$  m). The size at birth for *Sotalia* is between 71 and 83 cm; we have arbitrarily chosen 75 cm as an approximation until further data are available.

Relationships between gestation times, prenatal growth rate, and neonatal body length have been modeled by Kasuya (1977) and Perrin, Holts and Miller (1977). For *Sotalia*, the predicted gestation period after Perrin *et al.* (1977) would be between 10.4 and 11.1 months, which is relatively close to our estimated gestation of 10.0 to 10.3 months. Foetal growth rate according to the model of Kasuya (1977) for *Sotalia* would be 8.16 cm/month, very close to our calculated value of 8.5 cm/month (Fig. 4). The predicted gestation period for *Inia* would be from 10.7 to 11.2 months (mean 10.9 months), which seems much more probable than

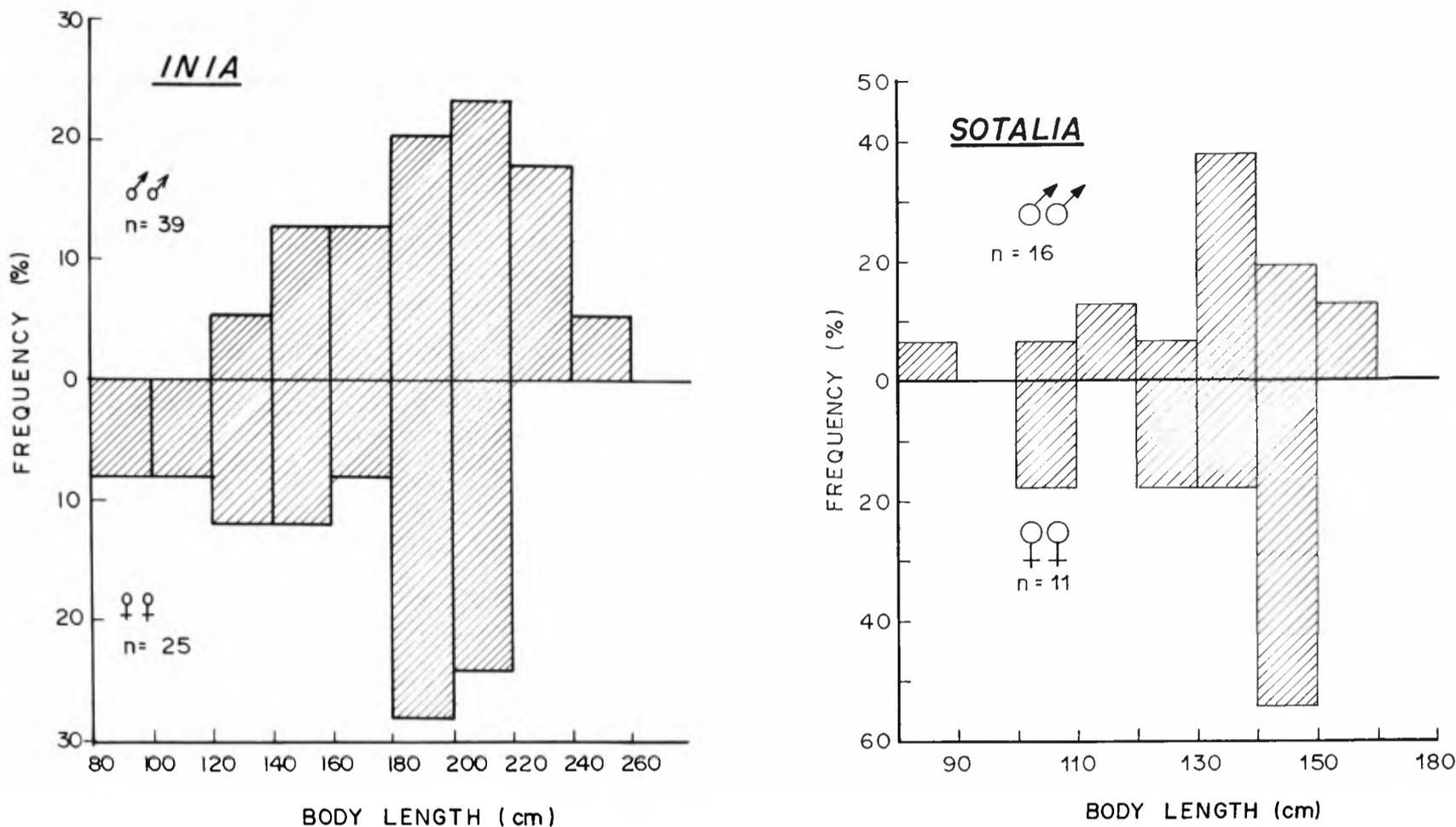


Fig. 7. Size frequencies for *Inia* and *Sotalia*.

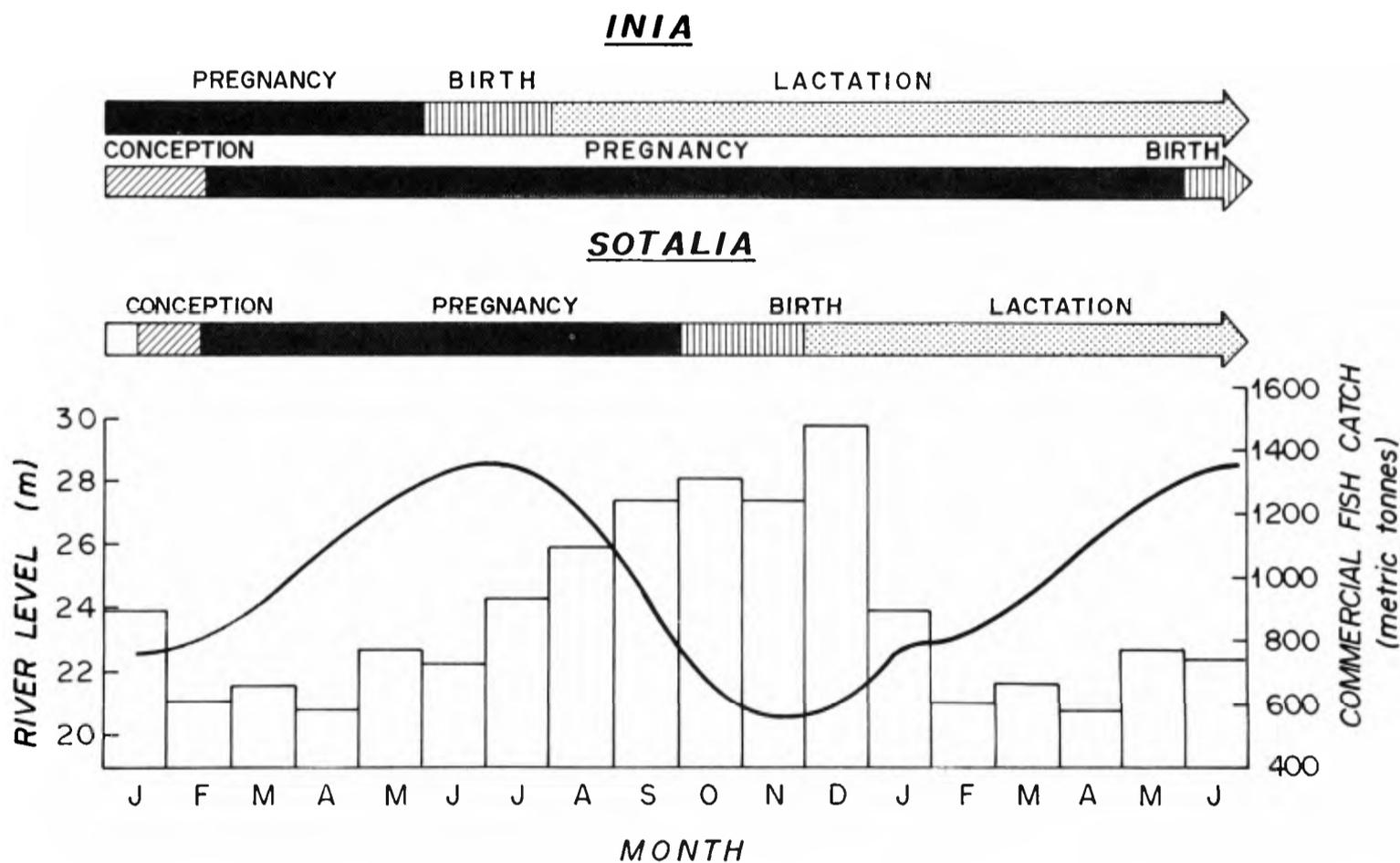


Fig. 8. Summary of proposed seasonal reproductive schedules of *Inia* and *Sotalia*.

our calculated value of 17 months. The estimated foetal growth rate would thus be about 8.35 cm/months.

**Reproductive seasonality in Amazon River dolphins**

Most mammals tend to show seasonality of reproduction when in a seasonally fluctuating environment where the survival of the progeny and even the female may be

greatly increased by synchronizing the reproductive cycle to the most favorable environmental epoch (Low, 1978; Sadlier, 1969). In cetaceans the obvious examples are those arctic species such as *Delphinapterus leucas* and *Monodon monoceros* which give birth during the relatively warmer summer (Best and Fisher, 1974; Sergeant, 1973). Although temperature differences are slight in the equatorial central Amazon region, the

extreme environmental variability imposed by the annual flooding cycles of the Amazon River is sufficient to modify the reproductive rhythms of most aquatic organisms, including the dolphins. In Fig. 7 we have shown the approximate reproductive events of both *Inia* and *Sotalia* in relation to the annual river flooding cycle during 1.5 years. It is clear that *Inia* calves are born at peak or declining river levels and *Sotalia* calving is at almost the lowest river levels. As both are predators, this would be the most opportune time of year for increased feeding. The fish that are dispersed throughout the vast floodplain areas during the high water are gradually concentrated in the permanent water bodies and river channels during the dry season and are thus much more susceptible to predation (see Goulding, 1980 and 1981 for further discussion). A histogram of the mean monthly commercial fish catch in Manaus (Honda, Correa, Castelo and Zapelini, 1975) superimposed on the river level graph (Fig. 7) shows the inverse cycle of fish availability and river level. Herbivorous aquatic mammals such as the Amazonian manatee (*Trichechus inunguis*) are also seasonal in calving. However, they are completely out of phase with the dolphins because this species depends on aquatic plant production, which is highest during the rising river levels (Best, 1982).

The difference in breeding season between *Sotalia* and *Inia* may only be an artifact of our small sample size. It is consistent, however, with the different feeding habits of the two species and the fact that there is a slight temporal difference in the greatest availability of preferred food fish. It has been previously shown (Layne, 1958; Magnusson, Best and da Silva, 1980; Pilleri and Gehr, 1977) that the habitat usage of the boto is wider in that it enters the flooded forest and grassland areas in search of food in addition to sharing the more pelagic niche of *Sotalia* in the larger lakes and river channels. One of us (da Silva, 1983) has found that the diets of these species differ in line with this habitat difference; *Inia* feeds predominantly on solitary, benthic-type fish, while *Sotalia* specializes in schooling, pelagic fish. Thus, as the river levels commence to fall, the fish species that invade the floodplains are the first to become vulnerable to predation as they initiate the annual migration into deeper water. Pelagic schooling fishes, the typical prey species for *Sotalia*, will show the concentration effect only after the floodplains have essentially dried up and the lakes and river channels are reduced to their seasonal minima.

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## **Session IV**

# **Are Cetacean Reproductive Rates Density-Dependent?**



# Density Dependence in Cetacean Populations

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## ABSTRACT

Cetacean populations, along with the populations of other large mammals (and animals in general) are regulated through density-dependent changes in reproduction and survival. These changes seem to be expressed most commonly in the processes associated with recruitment (i.e. birth and juvenile survival) and to involve causes associated with food resources. Growing evidence indicates that social and behavioral factors are also important causal elements.

Evolution, however, seems to have resulted in certain features of the dynamics of animal populations being somewhat independent of both the casual factors involved in density dependence and its modes of expression. There is an observed pattern in which the level of populations which produce maximum net growth in numbers is more closely related to the maximum rate of increase per generation time than to other factors. Spanning a broad spectrum of species types (fishes, insects, mammals, protozoans and bacteria), this pattern involves maximum growth rates at high population levels for species with low rates of increase per generation time. Conversely, species with high rates of increase per generation time exhibit maximum growth rates at lower levels (often less than 50% of their carrying capacity).

## INTRODUCTION

Research on the population dynamics of large mammals has resulted in a considerable collection of information supporting the view that the populations of such species are regulated through density-dependent changes in reproduction and survival. A preliminary review of this literature is presented in Fowler, Bunderson, Cherry, Ryel and Steele (1980); summaries are found in Fowler (1981a, 1981b).

The purpose of this paper is to (1) briefly review the empirical information concerning density dependence in

large mammals with special reference to the cetaceans, and (2) place the density-dependent aspects of the dynamics of cetacean populations in a general perspective as provided by comparisons with a broad range of other types of species. The two following, somewhat independent, sections deal with these objectives in order.

## SUMMARY OF EVIDENCE FOR DENSITY DEPENDENCE IN CETACEAN POPULATIONS

As shown in Table 1, there are at least 16 species of marine mammals for which there is evidence of density

Table 1

A list of marine mammals for which there is evidence of density dependence (see text for sources of information)

Species	Common name	Birthrate	Age at first reproduction	Juvenile survival	Adult survival	Recruitment
<i>Dugong dugon</i>	Dugong		+			
<i>Halichoerus grypus</i>	Gray seal			+		
<i>Phoca groenlandicus</i>	Harp seal	+	+	+		
<i>Callorhinus ursinus</i>	Northern fur seal		+	+		+
<i>Leptonychotes weddelli</i>	Weddell seal		+			
<i>Mirounga angustirostris</i>	Northern elephant seal			+		
<i>M. lionina</i>	Southern elephant seal		+			
<i>Stenella attenuata</i>	Spotted dolphin	+	+			
<i>S. coeruleoalba</i>	Striped dolphin	+	+			+
<i>S. longirostris</i>	Spinner dolphin	+				
<i>Balaenoptera musculus</i>	Blue whale	+	+			+
<i>B. physalus</i>	Fin whale	+	+			+
<i>B. borealis</i>	Sei whale	+	+			
<i>Physeter macrocephalus</i>	Sperm whale	+				
<i>Eschrichtius robustus</i>	Gray whale					+
<i>Orcinus orca</i>	Killer whale	+		+	+	

dependence (the majority of which are reviewed in Fowler *et al.*, 1980). The more recent published information concerning density dependence in cetacean populations is reviewed below.

Previous work on *Stenella* spp. has indicated that density-dependent regulation occurs in populations of these species (see Fowler *et al.*, 1980). Further work on *Stenella* is presented by Smith (1984) who compares information from three populations of *S. longirostris* in an analysis to determine the extent and form of density-dependent responses for this species. Data on gross reproductive rates are used to show that such comparisons of separate populations may be useful in determining estimates of population levels which exhibit maximum net productivity.

A second species for which recent evidence for density dependence has been found is the killer whale (*Orcinus orca*). Bigg (1982) has described a comparison of harvested pods of killer whales in the vicinity of Vancouver Island, British Columbia, with unharvested pods in the same region. Prior to 1977, young animals were taken from some pods for the purposes of exhibition. In comparing these harvested pods with the unharvested pods, the birth rate of adult females and the survival of both juveniles and adults were higher in the harvested pods. It is difficult to visualize how density within the study area as a whole could have resulted in the differences in survival. Such changes seem to have been more a result of local changes (i.e. at the level of the area occupied by a pod). Bigg (1982) indicates that the differences may have been created by social or behavioral changes within the pods, especially in the case of renewed reproductive activity among older females.

Additional information concerning evidence of density dependence in cetaceans involves reproductive rates in sperm whales, (*Physeter macrocephalus*) as published by Best (1980). This information concerns a population in the vicinity of Durban, South Africa, examined from 1962 to 1975. During this period the population was subjected to intensified harvest of the female population. From 1962 to 1967, 5–7% of the females in excess of 15 years of age were pregnant. This increased to 10.5% in the years 1973–75. The total mean pregnancy rate for 1962 to 1967 was 17.1% and increased to 21.4% in the period 1973 to 1975. The largest changes occur in the older age classes, which is similar to Bigg's (1982) observations concerning the change in observed pregnancy rate of killer whales. Both species exhibit highly organized social systems.

Reilly (1981) conducted a study of the population dynamics of gray whales (*Eschrichtius robustus*) using information concerning the population off the west coast of North America. As estimated for 1967 and 1980, the levels of this population, in combination with an estimated carrying capacity, were combined with estimates of reproductive rates and the estimated commercial harvest over time to construct a series of population models. The basic objective was to simulate the population's dynamics in order to mimic the changes indicated by the estimated populations for 1967 and 1980. The model which most nearly met this objective indicated that some form of density dependence is necessary to explain the observed dynamics. A general lack of more detailed information prohibits any conclusions regarding how this density dependence may have been expressed.

Table 2  
Comparison of expression of density dependence in terrestrial and marine large mammals

	Marine mammals	Terrestrial mammals	Total
No. species	16	22	38
Density dependence in (mode of expression):			
1. Birth rate	7	13	20
2. Age at first birth	10	9	19
3. Juvenile survival	5	13	18
4. Adult survival	1	5	6
5. Recruitment only	4	4	8
Causes involve:			
1. Social factors	3	5	8
2. Resource levels	7	18	25
3. Predation		1	1
4. Disease	1		1

An overview of the factors causing density dependence to occur in cetacean populations is presented in Table 2. Of the 38 species for which there is evidence of density dependence, most cases involve changes in the abundance of resource levels (especially food resources, Fowler *et al.*, 1980).

It is important to note, however, that the exhibition of density dependence based on factors internal to the population (labeled social factors in Table 2) shows signs of being very important. The incidence of density-dependent regulation of populations through social factors is probably greater for the species which exhibit higher social organization. Social factors are known to be of importance in density-dependent population regulation among lions (*Panthera leo*; Starfield, Furniss and Smuts, 1981) and grizzly bears (*Ursus arctos*; McCullough, 1981), and it now appears that similar evidence exists for the sperm whale and the killer whale.

The reproductive process is probably the most important point for expression of regulatory changes in the life cycle of large mammals. An examination of the data in Tables 1 and 2 shows that the bulk of evidence for density dependence involves age at first reproduction and birth rates. Both of these are expressions of age-specific birth rates, and the age groups which would be expected to show most variability in expressed reproductive rates are the younger age classes. Closely associated with reproduction is juvenile survival, which also shows evidence of density-dependent variability. Both birth and juvenile survival are, in large part, products of the ability of females to produce young and provide parental care. Thus, it appears that the larger-scale process of producing young recruits (i.e. the combination of birth and juvenile survival) may be the single most important component of population regulation in large mammals in general and specifically for cetaceans.

Adult survival undoubtedly plays an important role as a regulatory mechanism for large mammals, even though there are few species for which there is evidence of its being density dependent. Within the life history strategy of large mammals, very small changes in adult survival result in rather large changes in the population growth rate (e.g. see Fowler and Smith, 1973). Finding evidence of density-dependent adult survival is difficult, however,

because of the difficulty in estimating the survival of adult large mammals with sufficient precision and accuracy to detect changes.

In general, it appears that the mechanisms through which density dependence is expressed are quite similar for marine and large terrestrial mammals. One difference between these two groups, seen in the limited amount of evidence in support of density-dependent adult survival in marine mammals, is most likely a reflection of our inability to produce good measurements rather than a real difference between the terrestrial and marine species.

The general types of dynamics reviewed above, however, can be contrasted with those observed for other types of distinctly different species. The populations of many insects and fishes, for example, seem to exhibit a greater tendency to be regulated through the direct influence of predation and diseases. Diseases do play a role in the population dynamics of large mammals (as reviewed in Fowler *et al.*, 1980), but less directly than for other species. Diseases in large mammal populations are often considered to be a means through which the effects of reduced resources are indirectly expressed (i.e. through weakened condition), resulting in higher mortality rates or lower reproductive rates. Diseases in large mammals also seem to result in less severe population fluctuation than often seen in other species. The degree to which predation acts as an important factor in the regulatory process for large mammals is poorly understood (see, however, Walters, Stocker and Haber, 1981).

#### NON-LINEARITY IN DENSITY DEPENDENCE

We now turn to the second objective of this paper, that of looking at density dependence of cetacean populations in an overall perspective. In considering this objective we will be dealing with populations on a numerical basis rather than in units of biomass.

An overview of the literature concerning the population dynamics and density dependence of animals in general indicates that there is a general pattern to the relationship between density-dependent variables and population size (Fowler, 1981a). Large-mammal populations tend to exhibit their greatest level of productivity (rate of population change) at population levels which are close to the mean naturally occurring population levels (or the carrying capacity of their natural environments). So far, all such populations appear to grow most rapidly (in numbers per unit time) at levels greater than 50% of the carrying capacity, some at 80% or higher. For this to happen, the density-dependent process must be one in which the majority of density-dependent change occurs at high population levels. In addition to the information summarized in Fowler (1981a, 1981b) evidence in support of this pattern exists for gray whales (Reilly, 1981), moose (Crete *et al.*, 1981), and *Stenella* spp. (Smith, 1984).

This pattern can be more precisely described if it is expressed in more quantitative form. To do so, we assign the symbol  $K$  to the carrying capacity (mean number of animals in a population undergoing natural fluctuations about the level supportable by the environment). If the number of animals in the population at which, on the average, the most rapid growth occurs is represented by the symbol  $N^*$  (sometimes called MNPL for maximum

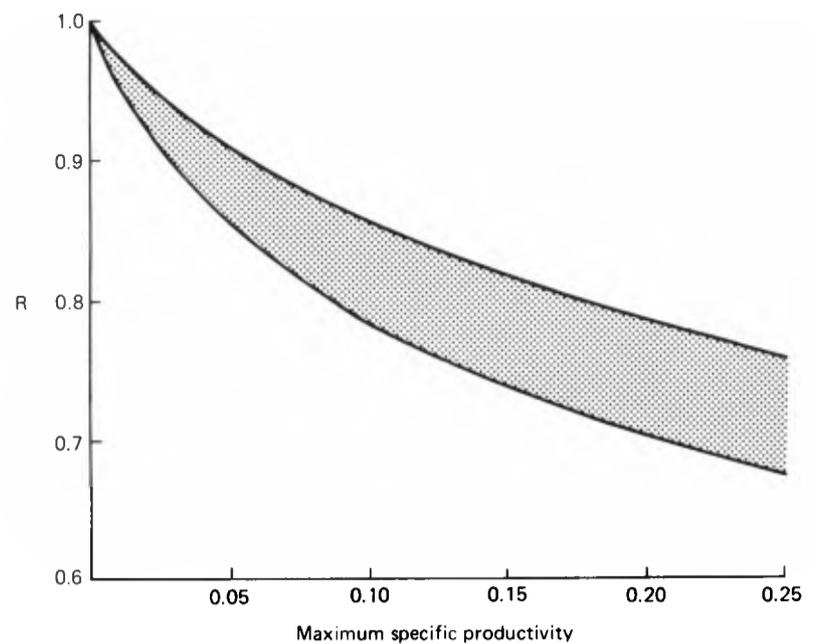


Fig. 1. Theoretically derived relationship between the population level at which the maximum population growth is observed (expressed as a fraction of the carrying capacity,  $N^*/K = R$ ) and the maximum intrinsic rate of change.

net productivity level), then the ratio  $N^*/K$  is the fraction of the carrying capacity at which maximum production (population growth) is realized. This ratio will be represented by the symbol  $R$ . The maximum rate of increase per generation is  $rT$ , where  $r$  is the maximum instantaneous rate of change and  $T$  is the corresponding generation time (the unit of time being the same in each case). The maximum net replacement rate is approximately equal to  $e^{rT}$ . (These terms are defined in Mertz, 1971; Murray, 1979; and Goodman, 1981.)

As reviewed in Fowler (1981a, 1981b) there are two bases for the expression of the pattern described above. One involves trophic dynamics and the other involves evolutionary processes. Fig. 1 shows one relationship between  $R = N^*/K$  and  $r$  as expected from evolutionary arguments and a resulting stability analysis based on one particular mathematical model (Fowler *et al.*, 1980). Thus both theory (as represented in Fig. 1 and described in Fowler, 1981a) and empirical information (as reviewed in Fowler, 1981a) support and explain the existence of the pattern. So far, however, a clear quantitative description of this relationship has not been produced.

In view of the necessity of managing marine mammal populations and the provisions of the US Marine Mammal Protection Act, it would be useful to have some relatively simple means of determining the level at which a population exhibits its maximum net rate of increase relative to its carrying capacity ( $N^*/K = R$ ). This point has been the subject of considerable attention in the management of the dolphin species involved in the eastern tropical Pacific tuna fishery (Smith, 1979).

To provide a preliminary basis for estimating  $R$ , we may examine the relationship between  $R$  and  $r$ . There are several relationships of this type published in the literature; each supports the existence of the general pattern. One is that of Bellows (1981), whose analysis of 14 different species of insects covers a wide range of species-specific reproductive rates. Fig. 2 is a representation of the relationship reported by Bellows between the population level at which maximum net productivity is exhibited (expressed as a fraction,  $R$ , of its carrying capacity) as a function of the 'intrinsic rate of increase'

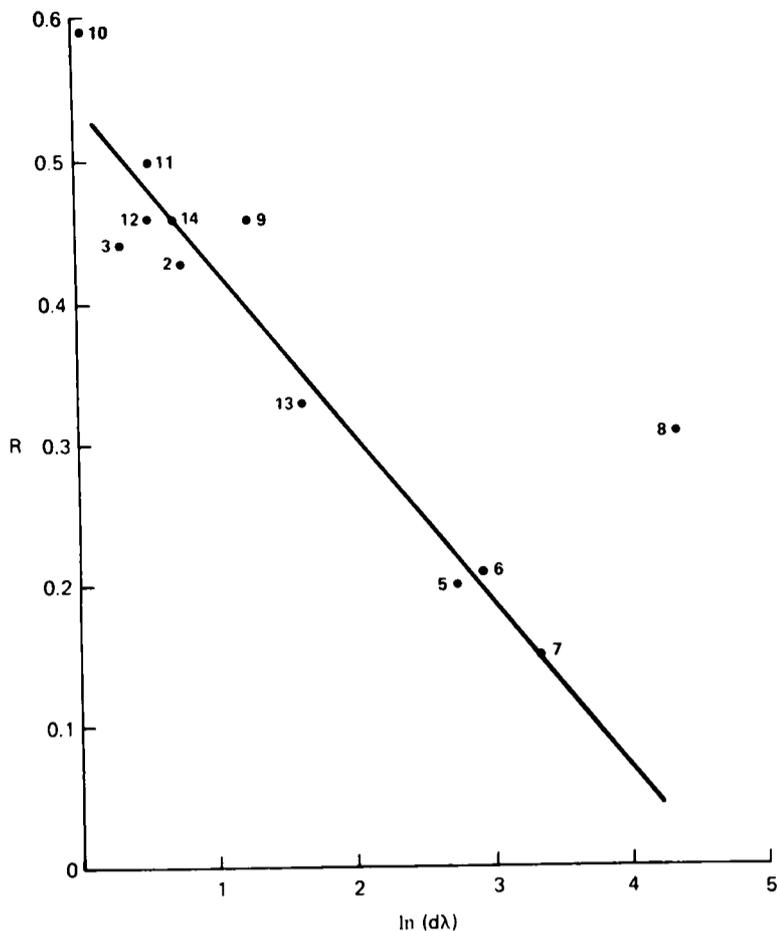


Fig. 2. The relationship found between  $R$  and Bellows' (1981) intrinsic rate of change for 12 species of insects. The numbers correspond to those used by Bellows (1981).

( $d\lambda$ , in his notation, and closely related to  $r$  as used here). The line in Fig. 2 is a relationship formed by all of the points (except Point 8) with respect to changes in the logarithm of the 'intrinsic rate of increase'. (Point 8 was ignored in determining the regression line shown because of the peculiar nature of this species as described by Bellows. However, this point does not change the conclusions reached here.) The relationship shown in Fig. 2 supports the conclusion reached by Fowler *et al.* (1980) and Fowler (1981a) that the largest population growth rates will occur at high population levels for species with low maximum specific reproductive rates (and vice versa). It also represents a first step toward quantitatively defining the relationship suggested by Fig. 1.

Similar work has been conducted by Cushing (1971) and Garrod and Knights (1979) on fish populations. The results of these studies again support the pattern expected from the theory (developed in Fowler *et al.*, 1980 and Fowler, 1981a) behind Fig. 1. Collectively, this work shows that  $R$  is negatively correlated with factors which contribute to population growth (such as specific rates of production or fecundity). And, as mentioned in Fowler (1981a), the estimated values for  $R = N^*/K$  tend to be clustered below 0.5 for both the fish of these studies and the insects of Bellows' work.

The relationship in Fig. 1 is based on an analysis conducted within an evolutionary paradigm. As described in Fowler (1981a) and Fowler *et al.* (1980), these arguments involve the assumption that there is an evolutionary impact of the production of young on the survival and reproduction of parental stock in the succeeding generation. Species with different generation times would be expected to behave differently when compared on a common unit of real time. For example, the impact of new recruits felt by a population of insects

one month after reproduction will be quite different from that of a whale population. It is logical, then, to look for the pattern in Fig. 1 scaled to the rate of increase over one generation rather than chronological time. The generation time is the unit of time of most evolutionary significance (e.g. see Fowler and MacMahon, 1982).

We therefore hypothesize that the shape of density-dependent curves and productivity curves (and more specifically the value of  $N^*/K = R$ ) bears some general relationship to the rate of increase per generation time. If such a relationship exists, it would encompass the data reviewed above, because generation time varies more

Table 3

List of species shown in Fig. 3 for which there is information on  $R$  and the net replacement rate (see text for details)

1. African elephant (*Loxodonta africana*)  
 $R$ : From Smith (1979)  
 $\ln rT$ : Based on Fowler and Smith (1973)
2. Sheep (*Ovis spp.*)  
 $R$ : From Schoener (1973)  
 $\ln rT$ : Based on Murray (1979)<sup>1</sup> and Ricklefs (1973)
3. Fin whale (*Balaenoptera physalus*)  
 $R$ : From Chapman (1981)  
 $\ln rT$ : Based on Chapman (1981), Gambell (1975)
4. Spinner dolphin (*Stenella longirostris*)  
 $R$ : From Smith (1984)  
 $\ln rT$ : Based on Smith (1979)
5. *Escherichia coli* (bacteria)  
 $R$ : Analysis of data shown in Hutchinson (1978)  
 $\ln rT$ : Based on doubling each generation
6. *Paramecium caudatum* (protozoan)  
 $R$ : From Schoener (1973)  
 $\ln rT$ : From Murray (1979)<sup>1</sup>
7. Fur seal (*Callorhinus ursinus*)  
 $R$ : From Eberhardt (1981) and Smith (1973)  
 $\ln rT$ : Based on Smith (1973) and Eberhardt (1981)
9. Gray whale (*Eschrichtius robustus*)  
 $R$ : From Reilly (1981)  
 $\ln rT$ : Based on Reilly (1981) (assuming a generation time of 14 years)
9. Bighorn sheep (*Ovis canadensis*)  
 $R$ : From Smith (1979)  
 $\ln rT$ : From Murray (1979)<sup>1</sup>
10. Grizzly bear (*Ursus arctos*)  
 $R$ : From McCullough (1981)  
 $\ln rT$ : Based on Bunnell & Tait (1981) and McCullough (1981)
11. White-tailed deer (*Odocoileus virginianus*)  
 $R$ : From Smith (1979) and McCullough (1979)  
 $\ln rT$ : From Murray (1979)<sup>1</sup> and McCullough (1981)
12. Blue whale (*B. musculus*)  
 $R$ : From Chapman (1981)  
 $\ln rT$ : Based on Chapman (1981) and Gulland (1981)
13. Striped bass (*Roccus saxatilis*)  
 $R$ : Based on Smith (1973)  
 $\ln rT$ : Based on Smith (1973)
14. Mouse (*Mus musculus*)  
 $R$ : From Harris and Kochel (1981)  
 $\ln rT$ : Based on Murray (1979) and Harris and Kochel (1981)
15. Water flea (*Daphnia spp.*)  
 $R$ : Based on Smith (1963), Schoener (1973)  
 $\ln rT$ : From Murray (1979)<sup>1</sup> and Smith (1963)
16. Fruit fly (*Drosophila spp.*)  
 $R$ : From Mueller and Ayala (1981)  
 $\ln rT$ : From Murray (1979)<sup>1</sup>
17. Flour beetle (*Tribolium spp.*)  
 $R$ : From mean of values reported by Schoener (1973) and fit of data in Desharnais and Costantino (1982)  
 $\ln rT$ : From Murray (1979)<sup>1</sup>

<sup>1</sup> Taken from a presentation of the relationship between  $r$  and the net replacement rate as based on Heron (1972) and Smith (1954).

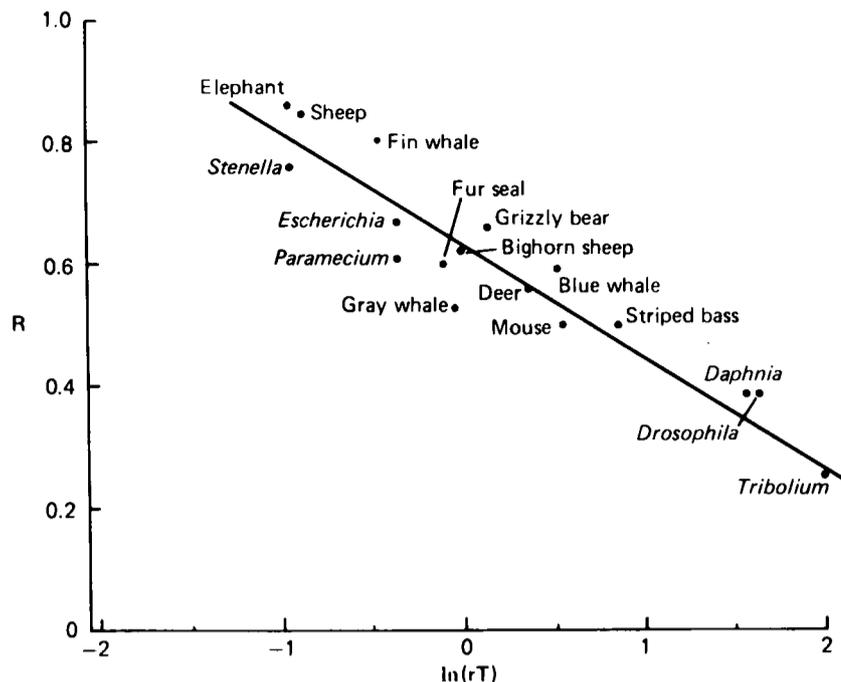


Fig. 3. The relationship between  $R$  and the rate of increase per generation time ( $rT$ ) for 17 species of animals.

between groups of species (such as insects and large mammals) than it does within such groups.

Table 3 contains a list of species (not to be considered exhaustive) for which it was possible to determine first approximations for the maximum rate of increase per generation time ( $rT$ ) and the level of the population (in numbers) at which maximum rates of increase were observed, expressed as a fraction of final equilibrium mean population levels ( $R$ ). Unfortunately, the insect species in Bellows' (1981) work and the fish species of Cushing (1971) and Garrod and Knights (1979) cannot be included because of lack of information on generation time. The values in Table 3 were determined for each species, either as a value reported directly in the literature or as estimates based on determinations using reported data. Reported data were used for determining  $R$  by fitting the generalized production model (Richards, 1959; Chapman, 1960). The results are shown graphically in Fig. 3. As can be seen, the list includes a wide variety of species. Included are bacteria, such as *Escherichia*, and large-mammal species of various types. Also included are two insects and *Daphnia* (a cladoceran) along with *Paramecium* (a protozoan). The relationship between  $R$  and  $rT$  is non-linear as expected from Fig. 1. The linear relationship shown in Fig. 3 is produced by using the logarithm of the rate of increase per generation time as the independent variable.

Fig. 3, then, represents the results of an attempt to define a quantitative relationship expected on the basis of the theoretical arguments used to develop Fig. 1. The regression line fitted to the data shown in Fig. 3 is closely approximated by the equation:

$$R = 1 - \frac{1}{e} - \frac{\ln(rT)}{2e}.$$

Although preliminary, the parameter values of this equation may be useful in determining the nature of the process which produces the observed relationship. Through the refinement and collection of additional empirical information in combination with population genetic studies related to the dynamics resulting in this

relationship, we should gain a better understanding of animal population dynamics.

It is possible, using the line in Fig. 3, to produce preliminary estimates of the levels at which populations will exhibit their maximum net productivity. For example, if we assume that *Stenella* populations have a generation time of 13 years and a maximum specific rate of increase per year of 3% per year (both hypothetical but realistic values), the level of the population at which maximum net productivity will occur is about 0.81 of the carrying capacity. This is consistent with the estimate of 0.76 produced by Smith (1984) and shown in Fig. 3. Similarly, if we assume that Dall's porpoise (*Phocoenoides dalli*) exhibits a maximum increase per year of 12% and has a generation time of approximately eight years, the level at which maximum net productivity would be expected to occur is approximately 0.65 of the equilibrium population level ( $K$ ).

In view of the statistical variability about the relationship shown in Fig. 3, there is a note of caution to be expressed in using the approach presented above for purposes of management. Because of variance in the values of  $rT$  and  $R$  the precise nature of the relationship needs further study; such variance includes the measurement error for both variables, which is potentially quite high in view of the ways in which the values for each point were determined. A second component of the variance for each variable is that due to species-specific deviation from any such relationship. Further work should be conducted to verify the pattern represented by this relationship and determine its statistical properties with sufficient clarity to offer clearer statements concerning reliability.

## DISCUSSION

This preliminary comparative analysis of the population dynamics of various species of animals reveals a pattern. There is a tendency for species with low maximal rates of increase per generation time (low  $rT$ ) to exhibit most density-dependent changes at high population levels (high  $R$ ); and species with high  $rT$  tend to show most changes at low levels (low  $R$ ). Even small-bodied species such as bacteria and protozoans which reproduce through binary fission fit this pattern. Although they have a very short generation time, the number of offspring produced through fission is limited to one per original organism. Other species, such as many insects, which produce large numbers of offspring per generation exhibit a different type of population dynamics; most density-dependent change for such species occurs at lower population levels.

This general pattern is consistent with the more specific patterns described in earlier work by Bellows (1981), Cushing (1971) and Garrod and Knights (1979). In each case the generation times of the species involved in the groups being studied were sufficiently similar to allow for detection of the relationship as based on fecundity or rates of change over chronological time alone. This tendency is also exhibited within large-mammal species as is seen by the scatter of points along the line in Fig. 3. Deer, for example, tend to exhibit their greatest production at intermediate population levels (McCullough, 1979). Other large mammal species whose populations grow more slowly but with similar generation times

exhibit most density dependence at higher population levels.

There is a difference in the quality of the relationship between  $R$  and  $rT$  on the one hand and those between  $R$  and such factors as listed in Table 2 on the other. In the case of  $R$  and  $rT$ , the relationship is apparently clear and shows the potential of meaningful quantitative formulation (Fig. 3). In the case of  $R$  and other factors, the relationships are vague and qualitative. For example, there is a tendency for species categorized as 'K-selected' species to show high  $R$  and 'r-selected' species to show low  $R$  (Fowler, 1981a); however, this relationship, even though it may be valuable to understand, is imprecise and qualitative. Exceptions are cause for concern. For example, among the species with complex behavioral and social systems (traits often attributed to 'K-selected' species) there is a tendency to show high  $R$ ; yet simple organisms such as bacteria and protozoa are also represented by species with  $R$  greater than 0.5 (Fig. 3).

By contrast, the relative clarity of the relationship between  $R$  and  $rT$  is indicative of a more direct involvement of  $rT$  in the natural selection through which  $R$  is determined. This is not unexpected since the arguments used to develop the relationship shown in Fig. 1 (as a prediction of such a relationship) provide an evolutionary explanation for the relationship. Therefore, the other factors (such as those listed in Table 2), as obvious components of population dynamics, may not contribute directly to the determination of  $R$ . They may be related to  $R$  indirectly, however, insofar as they contribute to life-history strategies (Fowler, 1981a), especially the components of life-history strategies involved in  $rT$ .

These insights into population dynamics have important implications at both theoretical and practical levels of population work. It is especially important to note the possibility that  $R$  is more of an inherent characteristic of species than it is a property of the short term interactions between species and their environments. This would explain the difficulty experienced in attempts to relate  $R$  to such factors as predator-prey relationships and competition.

Having identified the pattern, it must be noted that there are implications concerning the opportunity and ability to observe density-dependent change in population dynamics. Because most density-dependent change appears to occur at population levels close to the carrying capacity for species with low rates of change per generation time (such as may be the case for some of the great whales), it is expected that, except during the initial reduction of such populations, there will be little observable change. Thus, in the history of the exploitation of some of the large whales, it is likely that most of the changes probably occurred early in the history of exploitation prior to the more intensive monitoring in modern times. A large part of the data collected concerning populations of such species have been collected following such change, and it is not expected that these data will indicate much density-dependent change.

### SUMMARY

Data from a variety of sources indicate that populations of cetaceans and other large mammals are regulated

through detectable density-dependent mechanisms. The reproductive process (involving the fecundity of adults, the age at first reproduction of females, and juvenile survival) seems to be the most important component of density-dependent change for large mammals. The expression of density dependence for such species seems commonly to involve resource levels as a cause. There is growing evidence, however, that some density-dependent change is brought about by social or behavioral factors.

These causes and modes of expression of density dependence have, so far, shown no clear relationship to the levels of populations at which maximum rates of increase are observed ( $N^*/K = R$ ). Previous studies of this characteristic ( $R$ ) of populations have shown that it seems to be related to life-history strategy (Fowler, 1981a). This relationship is refined in this paper through a preliminary analysis of published data on a number of widely divergent types of populations. This analysis indicates that the most important variable behind the relationship is the rate of increase per generation time. This is a relationship which evolutionary arguments predict.

Through further refinement of this relationship, it is possible that a measure of the maximum rate of increase per generation time may be useful in estimating the population level which would be expected to produce the greatest growth. Specifically, as based on the apparent general nature of this pattern, it is expected that  $R$  for cetacean populations can be predicted from  $r$  and  $T$ , as can the  $R$  for other species.

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# Levels of Maximum Net Productivity in Populations of Large Terrestrial Mammals

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## ABSTRACT

It has been argued that the maximum net productivity level for dolphin stocks involved in the tuna purse seine fishery in the eastern tropical Pacific Ocean is likely in the range of 65–80% of their pre-exploitation abundance, i.e. carrying capacity of their ecosystem. The argument is based, in part, on examples of nonlinear relationships between certain indicators of productivity and population density for several terrestrial populations of large mammals. It is against this background that changes in net productivity as related to population density are examined for three terrestrial populations of large mammals: bison, longhorn cattle and Soay sheep. In each instance, the data indicate that maximum net productivity is achieved at a population level corresponding to 50% of carrying capacity, and hence do not support the argument that has been made regarding the MNP level for dolphin stocks.

## INTRODUCTION

A workshop on the status of dolphin stocks involved in the tuna purse seine fishery in the eastern tropical Pacific Ocean (ETP) was held at the Southwest Fisheries Center, National Marine Fisheries Service, in August 1979. Among the matters considered at the workshop were maximum net productivity (MNP) levels for the dolphin populations. As mentioned in the report of the workshop (Smith, 1979),<sup>1</sup> direct evidence on MNP levels for these populations was lacking. Nevertheless, the argument was made that the MNPL for each dolphin stock involved in the fishery is likely in the range of 65–80% of its estimated pre-exploitation population size.<sup>2</sup> The argument was based, in part, on examples of nonlinear relationships between certain indicators of productivity and population density for several terrestrial populations of large mammals that are given in Fowler (1978).<sup>3</sup>

Because of the importance attached to specification of MNP levels for dolphin stocks in management decisions pertaining to the ETP tuna purse seine fishery, any evidence on MNPLs which might be considered as being applicable to dolphins should be carefully scrutinized. What follows is a review of productivity and density data for three terrestrial populations of large mammals – bison, longhorn cattle and Soay sheep – specifically cited by Fowler as cases where the upper limits of nonlinearity in the relation between productivity and density may have been observed, that is, cases where maximum population growth is achieved at population levels near the carrying capacity. Additionally, Fowler indicates that the data from the three populations are relatively free of statistical problems so commonly associated with population measurements. It is for these reasons that they have been chosen for examination in this study.

<sup>1</sup> The report of the workshop is referred to as the SOPS Workshop Report.

<sup>2</sup> Pre-exploitation population size in the SOPS Workshop Report is variously referred to as 'initial population level', 'equilibrium unharvested population level' or 'equilibrium abundance'. Workshop participants considered the estimated pre-exploitation population level for each stock to be the carrying capacity of its ecosystem.

<sup>3</sup> Fowler's paper is identified as (Document) SOPS 79/15 in the SOPS Workshop Report.

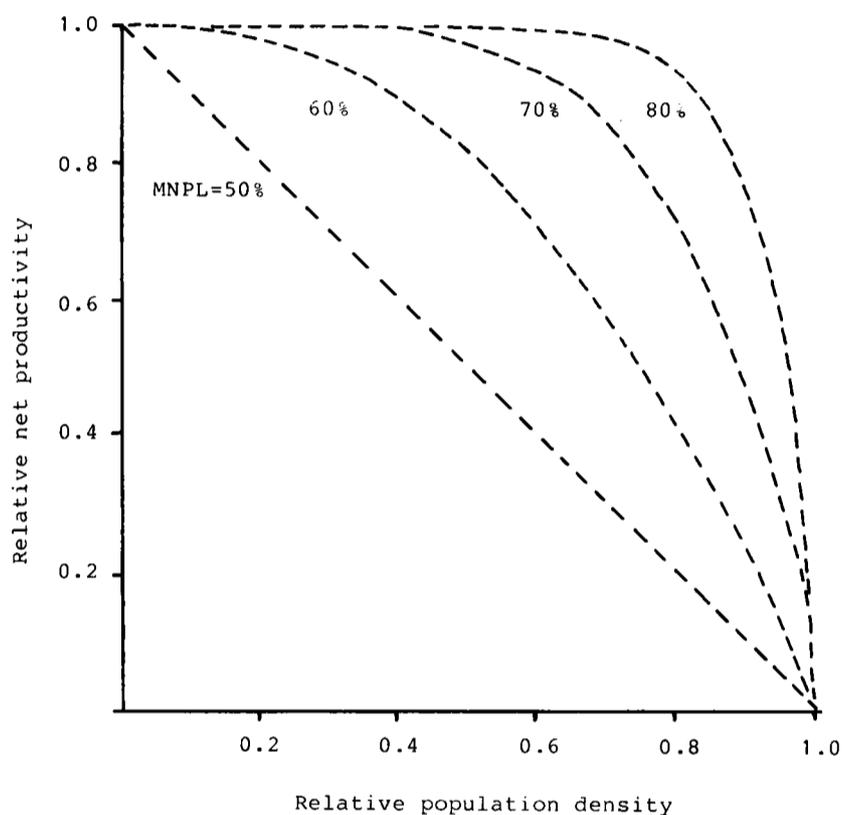
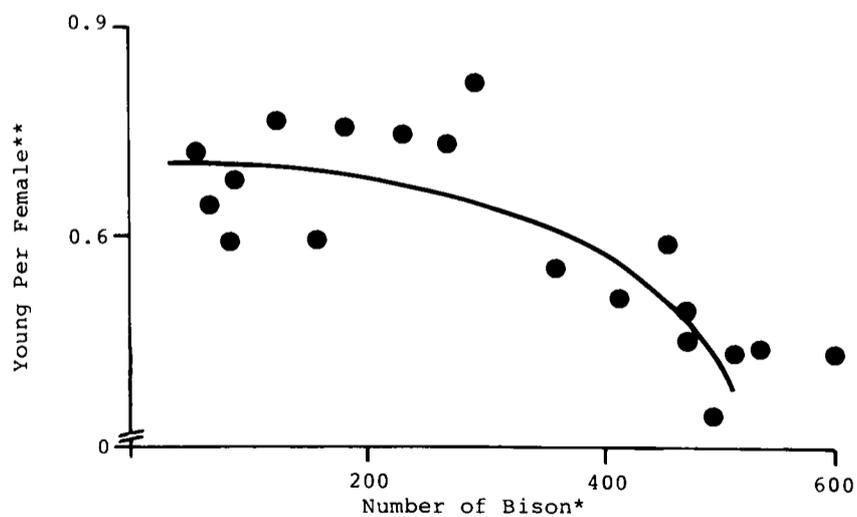


Fig. 1. Productivity in relation to population density for various MNP levels.



\* On January 1 preceding calving in May and June

\*\* Three-year-old females at time of calving.

Fig. 2. Relation between birth rate and size of the bison population on the National Bison Range during 1911–1928, as shown in Fowler (1978) from Gross, Roelle and Williams (1973).

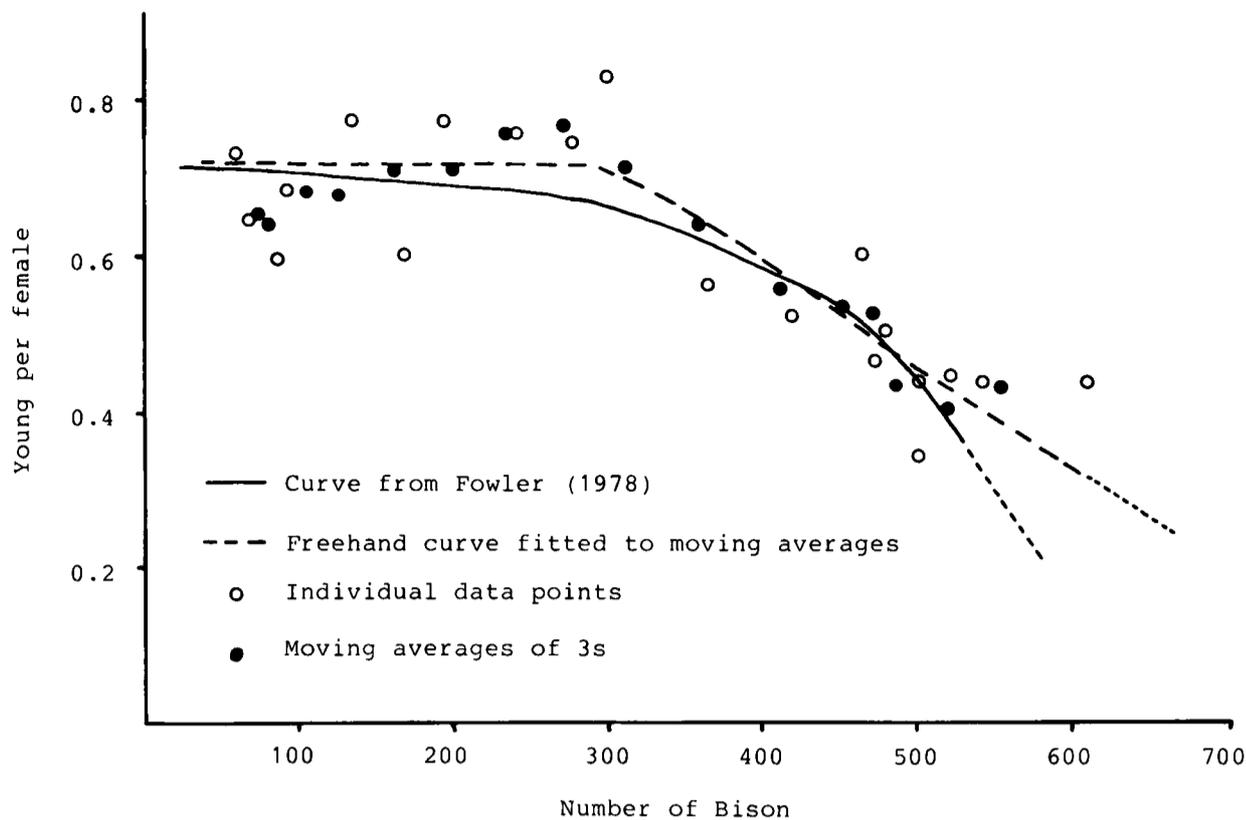


Fig. 3. Relation between birth rate and size of the bison population on the National Bison Range during 1911–1928 as depicted in Fowler (1978) and by a curve fitted to moving averages. (From data points shown in Fig. 2.)

Table 1

Annual changes in the size of the bison population on the National Bison Range, 1909–10 to 1927–28. (From Roelle, 1977)

Year (1 Oct. to 30 Sep.)	Number bison at start of year (1 Oct.) <sup>a</sup>	Population change during year				Number bison at end of year (30 Sep.)	Number bison harvested
		Calves born	Natural deaths <sup>b</sup>	Net increase			
				No. bison	Rate		
1909–10	37	11	0	11	0.30	48	0
1910–11	51 <sup>c</sup>	19	0	19	0.37	70	0
1911–12	70	16	1	15	0.21	85	0
1912–13	85	19	0	19	0.22	104	0
1913–14	104	26	0	26	0.25	130	0
1914–15	130	34	0	34	0.26	164	0
1915–16	164	32	2	30	0.18	194	0
1916–17	194	47	1	46	0.24	240	0
1917–18	240	56	1	55	0.23	295	0
1918–19	295	73	1	72	0.24	367	0
1919–20	367	58	5	53	0.14	420	0
1920–21	420	68	9	59	0.14	479	0
1921–22	479	82	7	75	0.16	554	0
1922–23	554	85	4	81	0.15	635	29
1923–24	606	96	5	91	0.15	697	197
1924–25	500	77	10	67	0.13	567	93
1925–26	474	140	17	123	0.26	597	50
1926–27	547	118	12	106	0.19	653	178
1927–28	475	79	20	59	0.12	534	190

<sup>a</sup> After harvesting (if any), which is assumed to take place on 1 October.

<sup>b</sup> Losses given by Roelle for 1 June–31 May are divided as follows: One-third during 1 June–30 September, and two-thirds during 1 Oct.–31 May.

<sup>c</sup> Includes 3 bison brought to the refuge in the fall of 1910.

Background for this study is provided in Fig. 1, which shows the relation of population productivity to stock density for MNP levels of 50, 60, 70 and 80%.

### BISON

Fig. 2 shows the relation between birth rate and population size for bison on the National Bison Range during 1911–1928 as given in Fowler (1978). Fowler does not specify an MNPL for the population. Neither does

the SOPS Workshop Report, which indicates only that the bison data were considered as supporting evidence for MNP occurring at high population levels – presumably meaning, in the context of the SOPS Workshop Report, an MNPL within or near the range of 65–80% of carrying capacity. Whatever the MNPL that Fowler's curve was intended to suggest, it is greater than the MNPL suggested by a curve fitted to moving averages of birth rates and population sizes (Fig. 3) or the straight lines that Gross, Roelle and Williams (1973) and

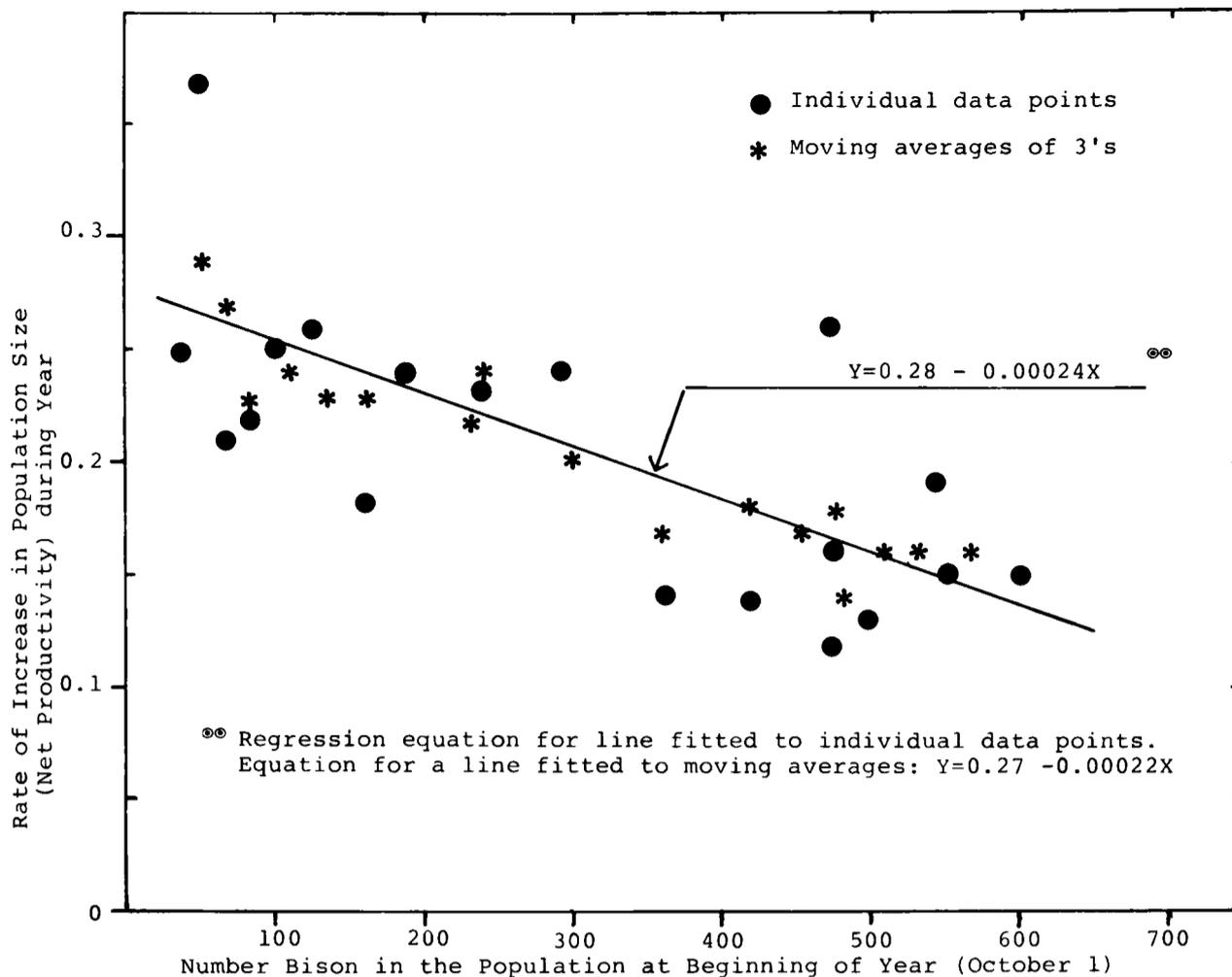


Fig. 4. Rate of annual increase in the bison population on the National Bison Range in relation to population size at beginning of year, 1909–1910 to 1927–1928. (From Table 1.)

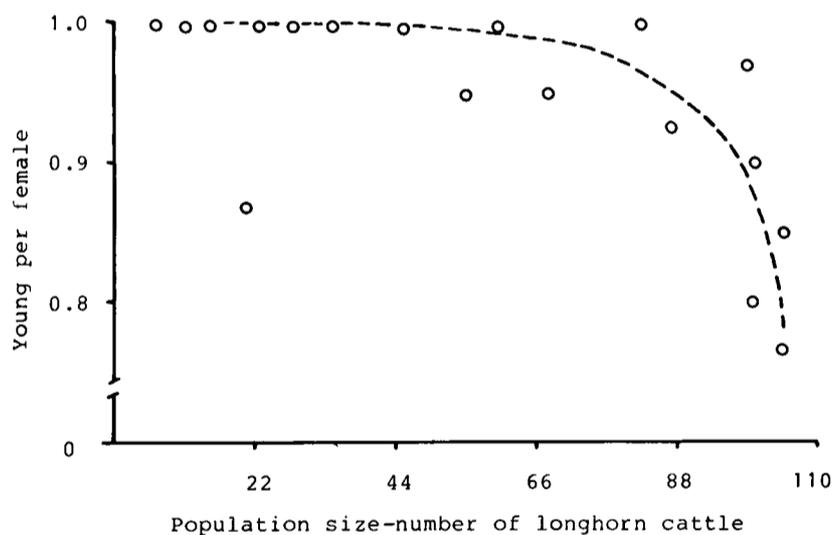


Fig. 5. Relation between birth rate and size of the longhorn cattle population on the Fort Niobrara National Wildlife Refuge during 1936–1960, as shown in Fowler (1978) from Gross, Roelle and Williams, (1973).

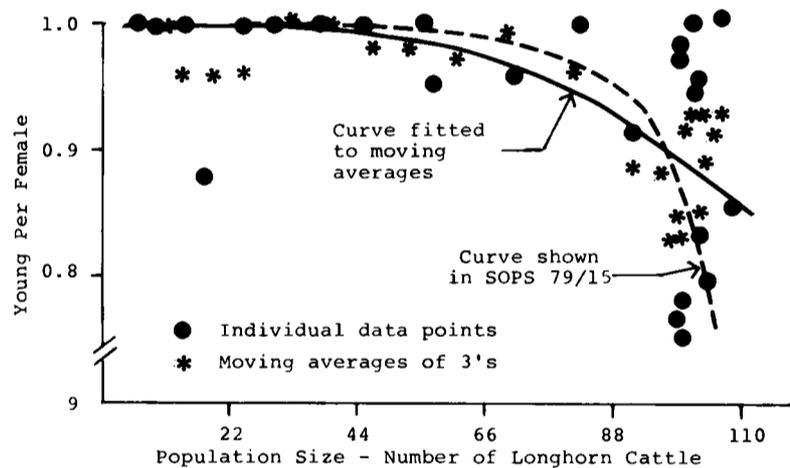


Fig. 6. Relation between birth rate and size of the longhorn cattle population on the Fort Niobrara National Wildlife Refuge during 1936–1960, incorporating data from Bartholow (1977).

Roelle (1977) used to describe the relation between young per breeding female and population size on certain dates preceding calving (1 January in Gross *et al.*, 1973 and 1 June in Roelle, 1977). Both of the curves shown in Fig. 3 as well as the straight lines of Gross *et al.* and Roelle might be quite misleading as to MNPL, however, because natural mortality has not been taken into consideration. All four relationships reflect density-dependent changes in gross productivity, not net productivity.

Information on net productivity for the bison population from 1909–1910 to 1927–1928, the period encompassed in Fowler's study, is given in Table 1, which shows the annual changes in population size due to

recruitment, natural deaths and harvests. The relation between the rate of annual increase in population size (net productivity) and the number of bison in the population at the beginning of the year is shown in Fig. 4. An MNPL of 50% is indicated.

### LONGHORN CATTLE

Fig. 5 shows the relation between birth rate and population size for longhorn cattle on the Fort Niobrara National Wildlife Refuge during 1936–1960 as depicted in Fowler (1978). Data for the figure originally came from Gross *et al.* (1973) who evidently used postharvest

Table 2

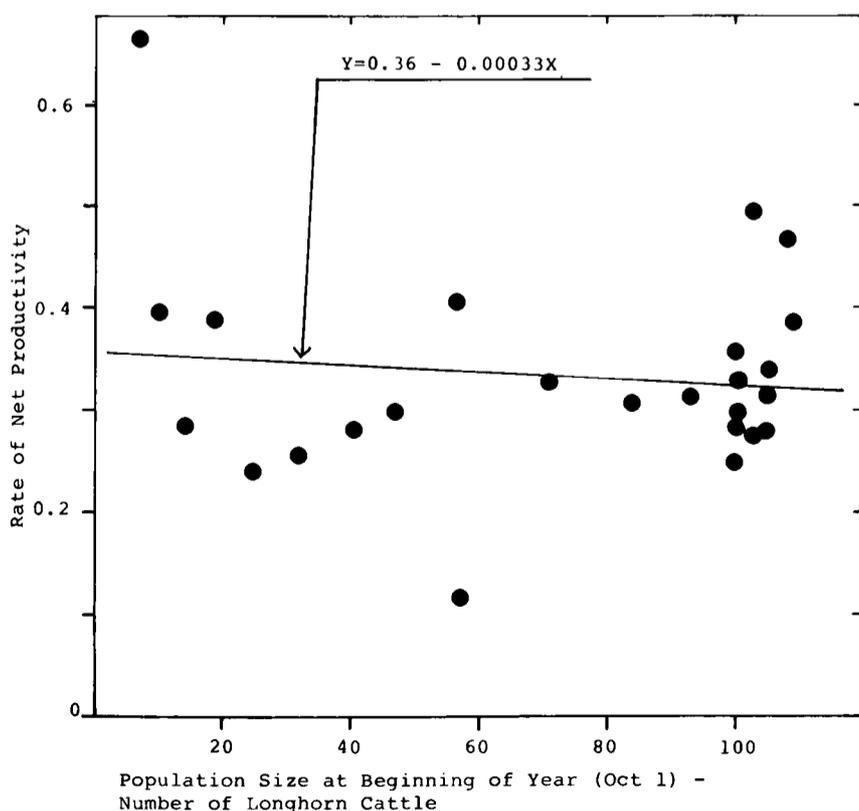
Annual changes in the size of the longhorn cattle population on the Fort Niobrara National Wildlife Refuge, 1936-37 to 1971-72.  
(From Bartholow, 1977)

Year (1 Oct. to 30 Sep.)	Number cattle at start of year (1 Oct.) <sup>a</sup>	Population change during year				Number cattle at end of year (30 Sep.)	Number cattle harvested
		Calves born	Natural deaths <sup>b</sup>	Net increase			
				No. cattle	Rate		
1936-37	6	4	0	4	0.67	10	0
1937-38	10	4	0	4	0.40	14	0
1938-39	14	4	0	4	0.29	18	0
1939-40	18	7	0	7	0.39	25	0
1940-41	25	7	1	6	0.24	31	0
1941-42	31	8	0	8	0.26	39	0
1942-43	39	11	0	11	0.28	50	4
1943-44	46	16	2	14	0.30	60	3
1944-45	57	19	12	7	0.12	64	8
1945-46	56	24	1	23	0.41	79	9
1946-47	70	24	1	23	0.33	93	10
1947-48	83	26	0	26	0.31	109	17
1948-49	92	30	1	29	0.32	121	21
1949-50	100	37	4	33	0.33	133	33
1950-51	100	31	1	30	0.30	130	30
1951-52	100	30	1	29	0.29	129	30
1952-53	99	39	3	36	0.36	135	33
1953-54	102	51	0	51	0.50	153	46
1954-55	107	53	3	50	0.47	157	48
1955-56	109	45	2	43	0.39	152	49
1956-57	103	30	1	29	0.28	132	33
1957-58	99	29	4	25	0.25	124	21
1958-59	103	30	1	29	0.28	132	28
1959-60	104	34	1	33	0.32	137	33
1960-61	104	36	1	35	0.34	139	30
1961-62	109	36	2	34	0.31	143	30
1962-63	113	35	0	35	0.31	148	18
1963-64	130	42	1	41	0.32	171	20
1964-65	151	48	1	47	0.31	198	18
1965-66	180	55	3	52	0.29	232	6
1966-67	226	63	2 <sup>c</sup>	61	0.27	287	49
1967-68	238	71	1	70	0.29	308	44
1968-69	264	73	4	69	0.26	333	71
1969-70	262	72	2	70	0.27	332	99
1970-71	233	55	6 <sup>c</sup>	49	0.21	282	53
1971-72	229	63	7	56	0.24	285	59

<sup>a</sup> After harvesting (assumed to take place on 1 October).

<sup>c</sup> Includes unexplained loss of one animal.

<sup>b</sup> Winter deaths (1 Oct.-31 May) plus summer deaths (1 June-30 Sep.).



population size as a measure of density and did not have birth rate information for several of the years between 1936 and 1960. A more recent paper (Bartholow, 1977) gives birth rate data for all years during that period and 1961-1971, plus information on natural mortality and harvests.

As in the case of bison, neither Fowler nor the SOPS Workshop Report specify an MNPL for the longhorn cattle population, but it appears that Fig. 5 was intended to convey the impression that MNP is achieved at a population level near carrying capacity. An alternative curve, one which incorporates data from Bartholow for all years during 1936-1960 and is fitted to moving averages of birth rates and population size, leaves a different impression, namely, that MNP occurs at a much lower population level (Fig. 6).<sup>4</sup> Both curves, of course, reflect gross productivity rather than net productivity, hence might be misleading with respect to MNPL.

[Text continues on p. 386]

Fig. 7. Rate of annual increase in the longhorn cattle population on the Fort Niobrara National Wildlife Refuge in relation to population size at beginning of year, 1936-37 to 1960-61 (from Table 2).

<sup>4</sup> Bartholow gives 1.28 and 1.33 as the number of young per female for populations of 102 and 107 animals, respectively. Since twins rarely occur, these are shown as truncated values of 1.0 in Fig. 6.

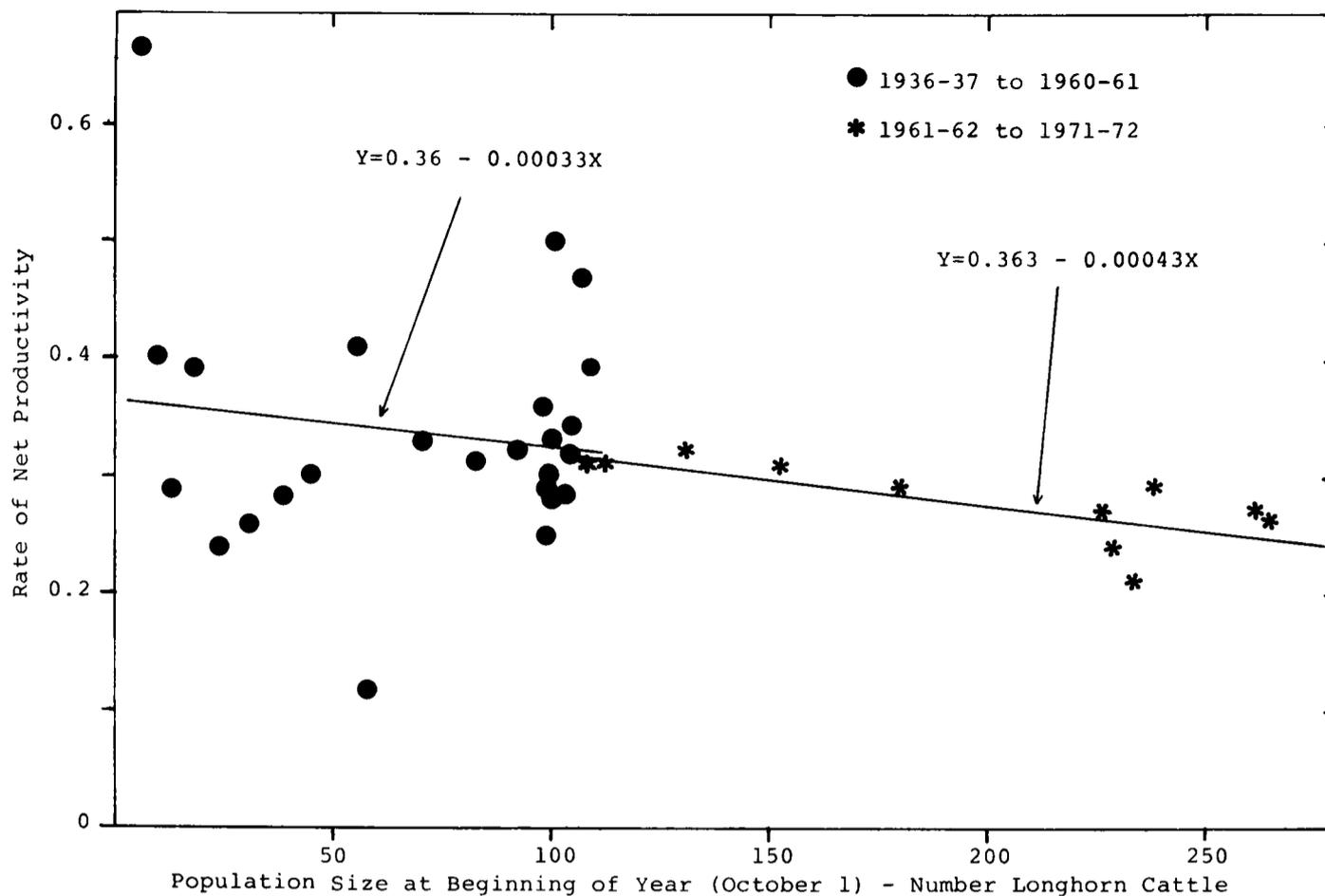


Fig. 8. Rate of annual increase in the longhorn cattle population on the Fort Niobrara National Wildlife Refuge in relation to population size at the beginning of year, 1936-37 to 1960-61 and 1961-62 to 1971-72 (from Table 2).

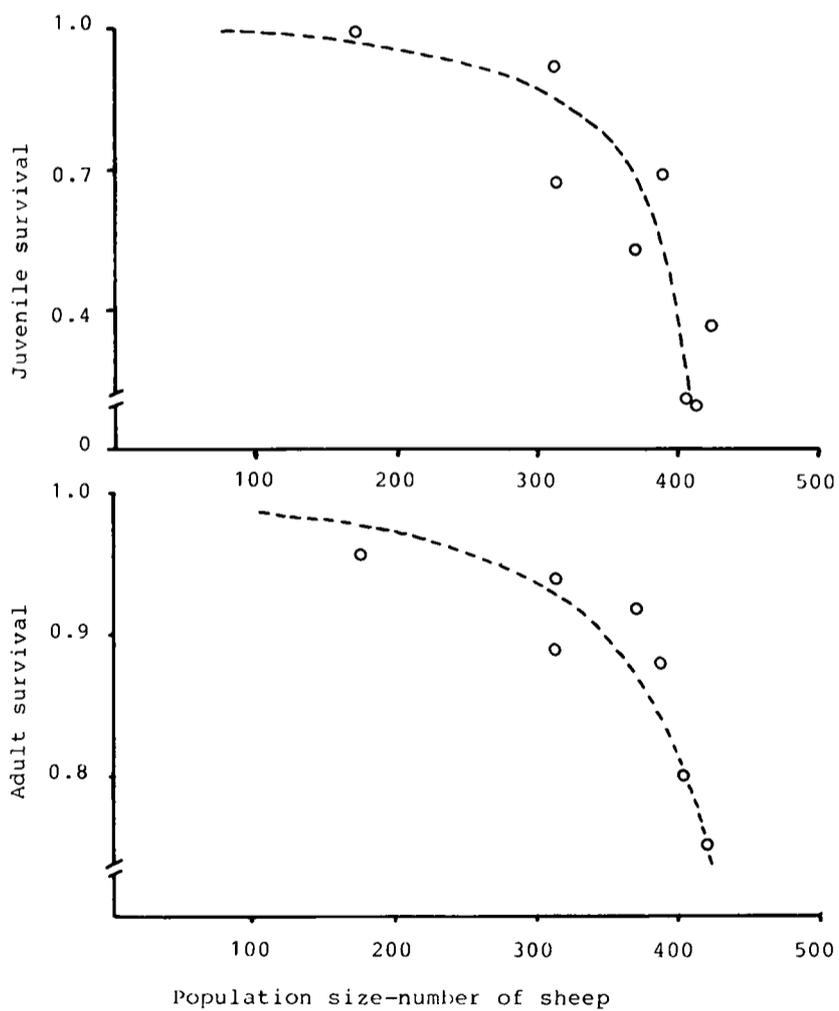


Fig. 9. Survival of juvenile (lambs) and adult (two years old and over) female Soay sheep in relation to population size as shown in Fowler (1978) from Grubb (1974).

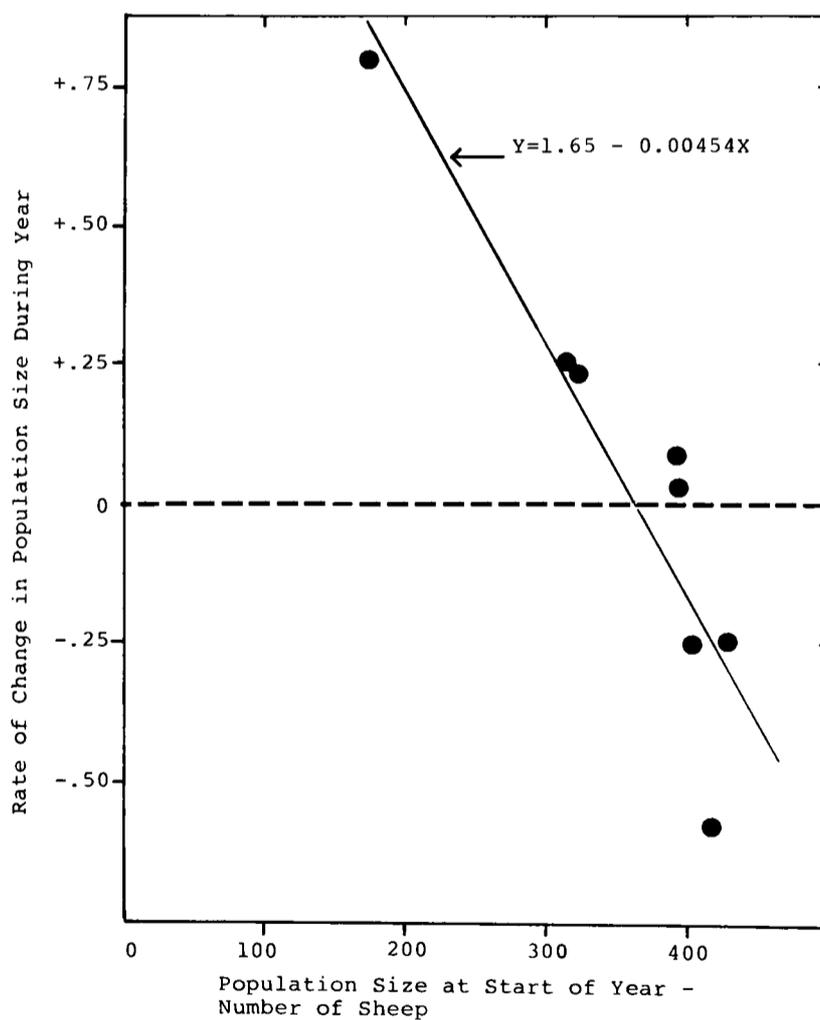


Fig. 10. Rate of annual increase or decrease in the Village Glen population of Soay sheep on Hirta Island in relation to population size at beginning of the year, 1959-60 to 1966-67 (from Table 3).

Table 3

Annual changes in the size of the Village Glen population of Soay sheep on Hirta Island, 1959-67. (From Grubb, 1974)

Year (1 May to 30 Apr.)	Number sheep at start of year (1 May)	Population change during year				Number sheep at end of year (30 Apr.)
		Lambs born <sup>a</sup>	Natural deaths	Net change		
				No. sheep	Rate	
1959-60	415	44	285	-241	-0.58	174
1960-61	174	148	9	139	0.80	313
1961-62	313	116	37	79	0.25	392
1962-63	392	127	96	31	0.08	423
1963-64	423	84	190	-106	-0.25	317
1964-65	317	151	76	75	0.24	392
1965-66	392	129	117	12	0.03	404
1966-67	404	96	196	-100	-0.25	304

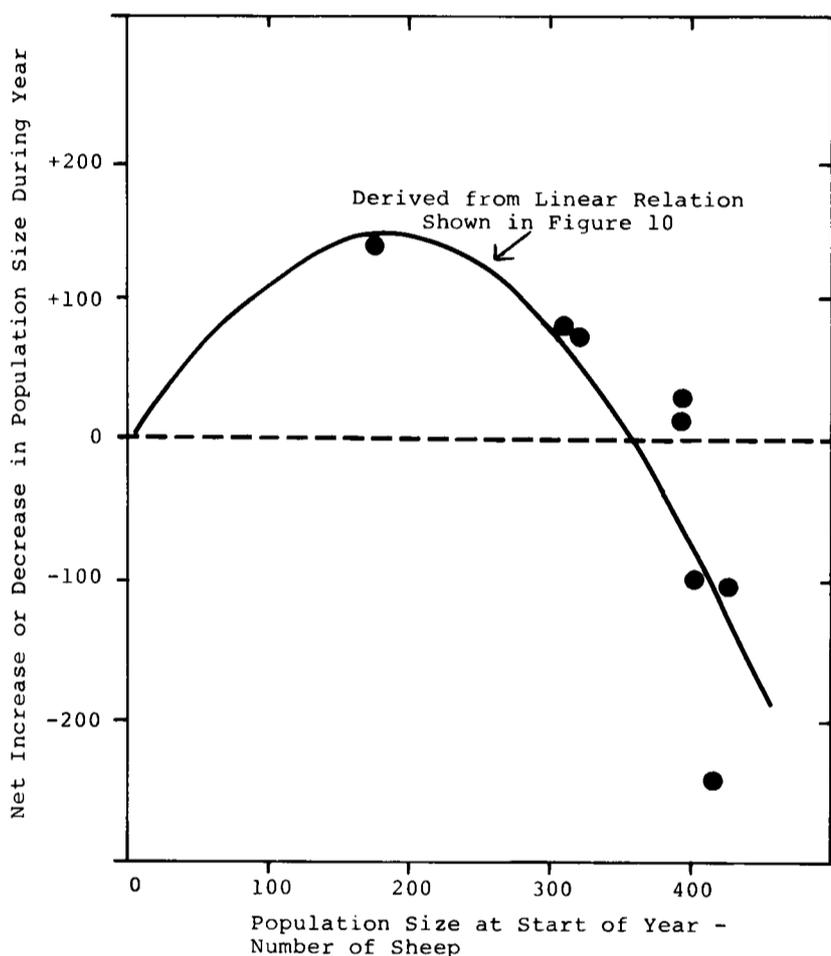
<sup>a</sup> Number of animals surviving neonatal mortality.

Fig. 11. Net change in the number of animals in the Village Glen population of Soay sheep in relation to population size at beginning of year, 1959-60 to 1966-67 (from Table 3).

Statistics on annual changes in the size of the longhorn cattle population due to recruitment, natural mortality and harvests during 1936-1972 are given in Table 2. The relation between net productivity and population size during 1936-1960, the period encompassed in Fowler (1978), is shown in Fig. 7. A straight line is used to describe the relationship. Although several of the data points deviate considerably from the line, it provides a far better description of the relationship than would be offered by a curve of the sort shown in Fig. 5.

The data for 1961-1972 also indicate that net productivity is linearly related to population size (Fig. 8), with the straight line being, in effect, an extension of the line fitted to the data for 1936-1960. Based on the productivity vs. density data for all years as a whole, an MNPL of 50% is indicated.

## SOAY SHEEP

Fig. 9 shows two relationships between survival rate and size of a Soay sheep population (the Village Glen population) on Hirta Island during 1959-1967 as they appear in Fowler (1978), one for juvenile females (lambs that had survived neonatal mortality) and the other for adult females (2 years of age and older). Although the relationships leave one aspect of productivity to be taken into account, namely recruitment, the SOPS Workshop Report indicates that they were considered as supporting evidence for the argument that MNPL is achieved at a population level significantly higher than 50% of carrying capacity.

Table 3 gives data on annual changes in the size of the Village Glen population of Soay sheep during 1959-1967 (Grubb, 1974). Fig. 10 shows the relation between net productivity and population size as represented by a straight line, and Fig. 11 the net increases or decreases in numbers of sheep during the year in relation to population size at the beginning of the year. An MNPL of 50% is indicated.

## SUMMARY

Changes in net productivity as related to population density indicate that maximum net productivity in the bison population on the National Bison Range, the longhorn cattle population on the Fort Niobrara National Wildlife Refuge, and a Soay sheep population on Hirta Island is achieved at a population level corresponding to 50% of carrying capacity. The findings with respect to MNPL for these populations do not support the argument that the MNP level for porpoise stocks involved in the tuna purse seine fishery in the eastern tropical Pacific is likely to be in the range of 65-80% of their pre-exploitation abundance.

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# Observed and Maximum Rates of Increase in Gray Whales, *Eschrichtius robustus*

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## ABSTRACT

Shore station censuses indicate that the California stock of gray whales increased at an annual rate of 2.5% during 1967–1980, concurrent with an annual exploitation of approximately 1.2%, i.e. net reproduction was near 3.7% per year. In light of this net reproduction, vital-rate estimates for the *circa* 1967 population were re-evaluated. The most likely values during that period were: pregnancy rate of 0.467, mean age at sexual maturity of 8 years, adult survival of 0.945 and juvenile survival of 0.899. To estimate maximum net rate of increase, biologically defined limits of pregnancy rate, age at sexual maturation and juvenile survival were used to generate a Leslie matrix, with adult survival held constant at the 1967 level. The dominant eigenvalue of the matrix was calculated as 1.069. If a stable age structure can be assumed in populations at a very low level, this indicates a possible maximum net rate of increase approaching 6.7% per year.

## INTRODUCTION

In the study of animal population biology the rate of increase exhibited by a reproductive stock is of interest in both applied and theoretical contexts. The maximum possible, or intrinsic rate of increase, and the realized rate under a set of definable and measurable conditions have relevance both for the study of population dynamics in general and for the management of exploited mammal populations.

In this study I have estimated the maximum rate of increase for the California stock of gray whales from what is known or can be inferred of the stock's vital rates, utilizing a population projection matrix. The observed rate of increase was calculated directly from data collected during annual shore station censuses. In the course of estimating the rates of increase, our state of knowledge of much of the reproductive biology of the stock has been reviewed, with new estimates made for some vital rates. Dependence of the rate of increase on population density or some related factor is tacitly assumed here. Data do not presently exist to test this assumption for gray whales.

Observed rate of increase, as measured through sighting censuses, is addressed here first. All available time series of sighting censuses were reviewed for applicability as indices of change in population size. Results from this section are then utilized in the following sections, in the estimation of vital rates and finally of maximum rate of increase. These results have potential interest in interpreting the assumed 'recovery' of the stock from severe depletion, in evaluating the effects of contemporary exploitation by the Soviet subsistence fishery, and in estimating the potential impact of major perturbations resulting from natural or man-induced changes on the calving and feeding grounds.

As part of their monographic study, Rice and Wolman (1971) reviewed information available up to 1970 on rate of increase. From Point Loma censuses of the 1950s they estimated an annual increase of 12.2%. This is re-estimated below. Rice and Wolman (1971) also estimated an annual rate of increase of 0.8% from the 1954–1964

Baja lagoon censuses. These data are also reviewed here.

Chapman (1981) estimated observed rate of increase from two of the time series examined here: early Pt Loma shore counts (10.4%) and Baja lagoon aerial counts (8.0%).

Previous studies which treated gray whale vital rates include Blokhin (1979; 1982), Ohsumi (1976), Rice and Wolman (1971), Zenkovich (1934; 1937), Zimushko (1969a; 1969b; 1970; 1971; 1973) and Zimushko and Ivashin (1980). Findings from these studies are reviewed below, with new estimates produced in some cases.

## DATA SOURCES

### Sighting time series

Data exist from four series of censuses of gray whale population size: three from shore-based counts of southbound migrating whales and one from aerial censuses of whales on their winter grounds along Baja California. For two of the four with interpretable data, rate of increase was estimated using exponential regression techniques.

### Vital rates

Two data sources exist for the estimation of gray whale vital rates: from a series of whales examined by Rice and Wolman (1971) during the 1960s and from animals examined in the Soviet subsistence fishery during the 1960s, early 1970s and 1978–1980.

During 1959 through 1969 Rice and Wolman (1971) examined 316 gray whales collected off the coast of central California, between Half Moon Bay (37° 30' N) and Point Reyes (39° 00' N). Whales were captured *en route* both north and south (Table 1). The majority of collections were made during 1964 through 1969, with a mean collection date of 1967. For vital rate estimation, in both Rice and Wolman's analysis and here, the entire series was pooled over collection years in order to maximize sample sizes. It is possible that one or all vital

Table 1

Dates of capture for 316 gray whales collected off the central coast of California for Rice and Wolman (1971), used here for estimation of vital rates

Dates	Number of whales taken	Direction of migration
23-26 Feb. 1959	2	North
23-30 Mar. 1962	4	North
14-25 Mar. 1964	20	North
22-29 Mar. 1966	26	North
14 Dec. 1966-19 Jan. 1967	95	South
21 Feb.-9 Mar. 1967	30	North
14-25 Jan. 1968	35	South
26 Feb.-11 Mar. 1968	24	North
2-11 Apr. 1968	7	North
20 Dec. 1968-9 Jan. 1969	50	South
2-16 Mar. 1969	23	North

rates changed during the 10 years sampled (1959-69). If so, statistics estimated from the pooled data are at best representative of the mean rates and may also be biased.

Ohsumi (1976) utilized the Rice and Wolman (1971) estimates of pregnancy rate, age at sexual maturity and adult mortality in a simulation study. He estimated juvenile mortality from their data using a simple balance equation. An alternative method to estimate juvenile mortality is proposed below.

Soviet scientists have examined a sample of animals taken in the subsistence fishery in the Bering and Chukchi Seas. A limited amount of information has been reported in a number of short communications. For the years since 1948, total Soviet landings have been reported (Ivashin and Mineev, 1981; Blokhin, 1979; 1982). For 1965 through 1980, sex ratio and proportion mature of landed animals have been reported (Zimushko and Ivashin, 1980; Blokhin, 1982) (Table 2). Frequencies of pregnant females were reported for 1965-1970 (Zimushko, 1969a) and 1978-1980 (Blokhin, 1982). Zenkovich (1937) listed some information on pregnancies from a 1933-1936 series of Bering/Chukchi Sea specimens. For growth and related parameters, analyses and conclusions with varying and limited amounts of supporting data have been published (Zimushko, 1969a; 1969b; 1970; 1971; 1973; Zimushko and Ivashin, 1980; Blokhin, 1979; 1982).

The 1965-70 series of vital-rate estimates from the Soviet data represent roughly the same time period as the Rice and Wolman series and should be comparable from that standpoint. For 1978-1980 the proportion of mature females which were pregnant in catch sub-samples was reported (Blokhin, 1982). Sample sizes were given only for the 1980 data.

Below I review comparative estimates for pregnancy rate, age at sexual maturation, adult and juvenile survival (mortality) rates. New estimates are made here for all but age at sexual maturation.

## METHODS

### Age determination

As with other baleen whales, earplug laminae have been the primary measure of age in gray whales (Rice and Wolman, 1971; Zimushko, 1973). For adult females, ovarian corpora have also been used. Both time scales are subject to assumptions that are partially or totally untested, including regularity in time of deposition of marks and persistence of marks throughout life. Rice and Wolman estimated that one earplug layer was deposited per year, except for the first year of life, when two layers were deposited. Their interpretation is followed here.

The one-year pattern is in agreement with Roe's (1967) conclusions for fin whales. Zimushko (1969a 1969b; 1971; 1973), however, suggested that two layers per year were deposited in gray whales. This interpretation implied a halved life span (about 30 years at most), sexual maturation at 4.5 years with a minimum of 3 years, and a doubled ovulation rate (in relation to Rice and Wolman's interpretation). In later Soviet papers (Zimushko and Ivashin, 1980; Blokhin, 1979; 1982) the two-layers-per-year interpretation is no longer cited. Lacking new information, the interpretation of Rice and Wolman appears to be the most reasonable.

Notable problems with earplug ageing of gray whales are that the plugs are 'readable' in only about half of the individuals and that there may be fading of juvenile-deposited layers in later life (Rice and Wolman, 1971). Because of these problems, Rice and Wolman used the frequency of corpora in the ovaries of adult females as an alternate scale (discussed below).

### Vital rates

Adult survival was estimated in this study and by Rice and Wolman (1971) using the methods of Chapman and Robson (1960). Alternate estimates with older whales truncated were made here in response to Rice and Wolman's (1971) concern that age determination of these 'older' whales was relatively imprecise.

Indirect methods must be employed to estimate juvenile survival. This is because in both the Soviet fishery (Zimushko and Ivashin, 1980) and probably to a lesser extent in the California scientific collections (Rice and Wolman, 1971) juvenile whales were selected against.

Table 2

Gray whales captured in the Soviet subsistence fishery from the Bering and Chukchi Seas, which were sampled for (at least) measurement and sex identification. From Zimushko and Ivashin (1980) and Blokhin (1982)

		1965	66	67	68	69	70	71	72	73	74	75	76	77	78	79 <sup>1</sup>	80
Adult	F	47	16	16	31	11	56	1	21	73	74	73	84	4	8	?	44
Juvenile	F	41	2	8	1	2	10	1	1	4	14	40	11	6	7	?	26
Adult	M	39	19	30	10	4	69	2	3	89	80	30	57	?	?	?	19
Juvenile	M	17	4	10	6	1	6	0	0	6	11	28	11	?	?	?	9
Total no.		144	41	64	48	18	141	4	25	172	179	171	163	19	31	?	98

<sup>1</sup> For 1979 the sample size examined for age/sex status was not reported.

Prior to conducting his simulation of population trends, Ohsumi (1976, Equation 4) estimated juvenile mortality (where mortality is the negative logarithm of survival) using a two-age-class balance equation (also occasionally used by the International Whaling Commission's Scientific Committee):

$$1 - e^{-(M+F)} = (P/2) e^{-(M'+F) X_m}$$

where  $M'$  = juvenile mortality,  $M$  = adult mortality,  $P$  = pregnancy rate,  $F$  = fishing mortality and  $X_m$  = age at sexual maturation. This model assumes no net recruitment, equal vulnerability of juveniles and adults to fishing death, and population lumped into two age classes. Since we have estimates of gray-whale population growth and the range of ages during which sexual maturity is attained, it is possible to estimate juvenile survival more accurately, using this additional information.

As an alternative balance model to estimate juvenile survival, I have used a Leslie (1945) population-projection matrix,<sup>1</sup>

$$L = \begin{pmatrix} f_0 & f_1 & \dots & f_k \\ S_0 & 0 & \dots & 0 \\ 0 & S_1 & \dots & 0 \\ 0 & 0 & \dots & S_{k-1} & 0 \end{pmatrix}$$

where the elements of the top row are age-specific fecundities, the elements of the subdiagonal are age-specific survivals, and  $k+1$  specifies the number of age classes. Here  $k+1$  was set at 40, since approximately 98% of the population is 40 or younger (Rice and Wolman, 1971). Rate of increase can be dealt with implicitly when using a Leslie matrix, since the dominant eigenvalue  $\lambda$  (see Leslie, 1945) is the antilog of rate increase:  $\lambda = e^r$ .

With values set for  $\lambda$ ,  $f$  (fecundity vector) and adult survival, the characteristic equation for the Leslie matrix can be solved iteratively for  $S_0$ , the juvenile survival rate.

Even when only estimates of 'juvenile' and 'adult' rates exist, if a distribution of transition proportions between juvenile and adult stages can be approximated, recruitment to sexual maturity can be reflected as a gradual process. This introduces some of the advantages of a fully age-structured model.

In employing this age-structured technique, rates were assumed constant over large series of ages, i.e. 0-4 years for juveniles, 12+ years for adults. For the apparent transition period of 5-11 years of age, both fecundity and survival rates were changed gradually. The cut-points were defined by the age-at-sexual-maturation data, described in Vital Rates. To accomplish this, a function approximating the proportion of each age class sexually mature was defined, for  $a$  = age and  $x_m$  = median age at maturity, as

$$f(a) = \begin{cases} 0 & a = 0, 4 \\ (a-5) \cdot (0.5/X_m - 5) & a = 5, X_m \\ 0.5 + (11-a) \cdot (0.5/11 - X_m) & a = X_m + 1, 11 \\ 1.0 & a > 11 \end{cases}$$

The result is a vector  $r$  with elements on the interval (0, 1) which are the proportions of each age group sexually mature, and  $f(a)$  set at 0.5 at the defined age at sexual

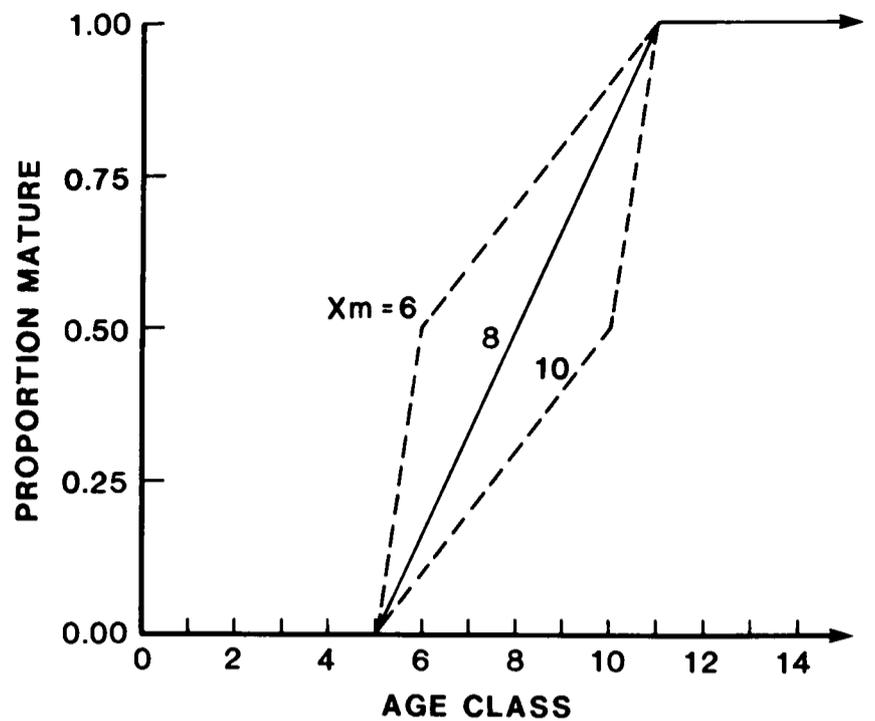


Fig. 1. Examples of vectors of proportions of each age class mature, for mean ages at sexual maturity of 6, 8 and 10 years.

maturation  $X_m$ . Fig. 1 illustrates the vector  $r$  for three values of age at maturation ( $X_m$ ). The vector of age-specific fecundities was then generated by multiplying  $r$  by half the pregnancy rate and by juvenile survival, to estimate female young surviving through their birth year:

$$f = r \cdot (P/2) \cdot S_j$$

The vector of age-specific survivals ( $s$ ) was generated by defining a transition between juvenile ( $S_j$ ) and adult survival ( $S_a$ ) as

$$s = (S_a \cdot r) + [S_j \cdot (1 - r)].$$

(In the current use, we are attempting to estimate  $S_j$ ).

The gradual recruitment of age classes to the mature population during the transition years 5 through 11 is a closer representation of variability to be expected in the process of maturation in a mammalian population than simple knife-edged recruitment. To complete the procedure, a Leslie matrix (2) was defined using  $s$  and  $f$ .

Juvenile survival ( $S_j$ ) was estimated by setting  $S_a$ ,  $P$ ,  $X_m$  and  $\lambda$ , and iteratively changing  $S_j$  until the characteristic equation for (2) was solved for  $\lambda$  to within a minimum tolerance of 0.001.

### Rate of increase

Maximum rate of increase was also estimated using the Leslie matrix. To accomplish this,  $S_j$ ,  $P$ , and  $X_m$  were set at values which were identified here as biological limits that would be approached as population density approached zero, assuming that these vital rates are variable in a density-dependent manner. Adult survival ( $S_a$ ) was assumed not to be density-dependent here, following the arguments of Fowler (1981) and Eberhardt and Siniff (1977). The maximum rate of increase was then calculated from the dominant eigenvalue of the resulting matrix.

<sup>1</sup> Other, simpler methods could be used to estimate juvenile survival here, e.g. a Leslie matrix with all fully adult age classes collapsed into one term. The full matrix approach was used for consistency with a larger, complementary study (Reilly, 1981) in which population projection was done.

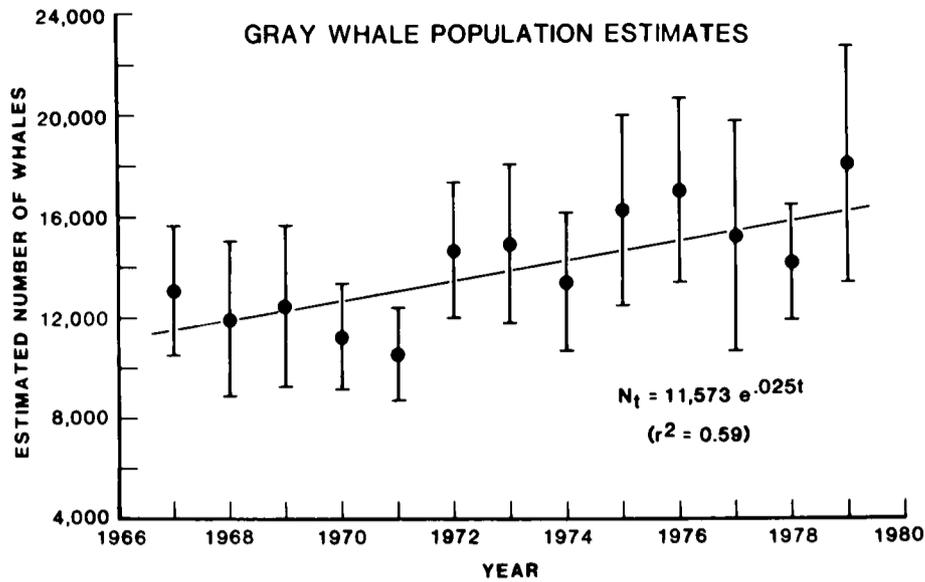


Fig. 2. Gray-whale population estimates and 95% confidence limits from Monterey shore censuses, 1967-68 through 1979-80.

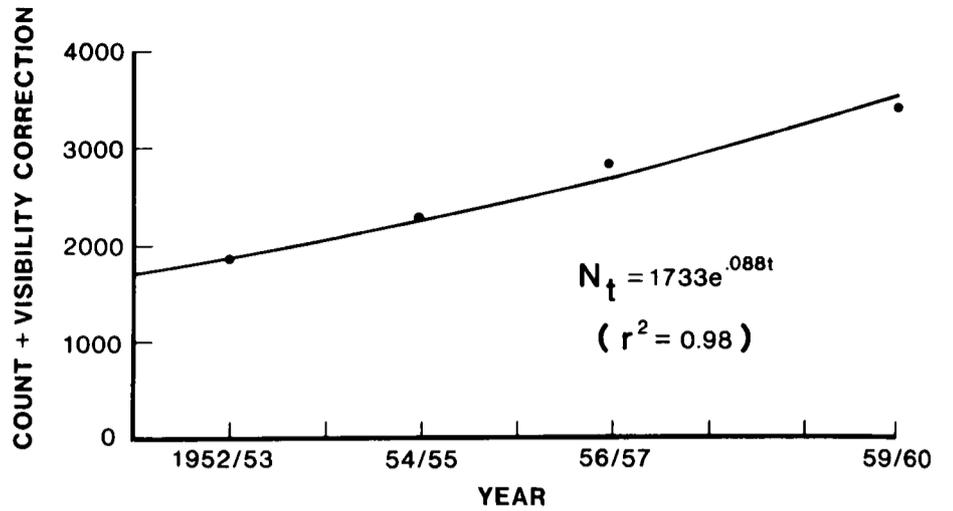


Fig. 3. Gray-whale population estimates from four Point Loma shore censuses during the 1950s.

## SIGHTING TIME SERIES: OBSERVED RATES OF INCREASE

### Monterey shore censuses

Of the four time series of sighting-census data, the Monterey shore censuses appear to be the best for measuring the rate of change in population size. This is because it is a series of 13 consecutive censuses (1967-68 through 1979-80) of southbound migrants, during which consistent and well documented counting and data recording methods were used. Also, annual variability, due to changing weather and visibility conditions, and intra- and interobserver biases were addressed at least in part (Reilly, Rice and Wolman, 1980; 1983). A potential limitation of this series as an index of change in population size is that the census site was moved a few miles south from the original location after the seventh year. However, the two sites were very similar in seaward sighting perspective, and the data showed no significant differences between locations; group size distributions recorded at the two stations were not different, and the offshore distance distributions showed much less variation between locations than between years at either location (Reilly *et al.*, 1980; 1983).

The rate of change in population size during the 13 years censused was 2.5% per year (S.E. = 0.96) (Fig. 2). When the approximately 1.2% annual harvest in the Soviet subsistence fishery during these same years is also considered, an annual net reproduction of near 3.7% is indicated. (The term 'net reproduction' is used here to describe net rate of increase plus removals by humans).

### Hubbs/Scripps shore censuses

Beginning in 1946-47 at the Scripps Institution of Oceanography (near San Diego, California) students under the direction of Carl L. Hubbs were stationed on top of a classroom building. The amount of effort and the methods applied are not clear from the secondhand accounts available (Walker, 1949; Gilmore, 1960). The recorded counts in 1946-47 through 1951-52 (omitting 1950-51) were 250, 500, 600 and 800. An increase is clear. If the methods and efforts were fairly constant (which is doubtful, given the 100% increase in the 2nd year) and

if the migration corridor was unchanged during this time, an exponential rate of increase of 20% per year was occurring. This seems unlikely. I consider these data unreliable, having so little accompanying information on effort expended and methods used.

### Early Point Loma shore censuses

Beginning in 1952-53 a census of southbound migrants was conducted from Point Loma (San Diego, California) intermittently until 1959-60. Gilmore (1960), who supervised the efforts, eliminated two of the first five annual counts from consideration, due to irregularity of methods and/or effort. Rice (1961) reported the results of the final (1959-60) count for the series. The value of these data as an index is contingent upon the validity of Gilmore's (1960) and Rice's (1961) schemes to correct for whales missed due to poor visibility. Gilmore (1960) subjectively estimated the percent reduction in visibility each day to upwardly adjust his counts, while Rice (1961) drew a smooth curve on a figure connecting the higher count days. Consequently, the data from 1959-60 are not strictly comparable to those from previous years.

Another problem with the Point Loma data, perhaps the most serious, is the likelihood that the proportion of the population passing close enough to shore to be seen changed throughout the years covered, due to increasing nearshore boat traffic (Rice, 1965; Reeves, 1977; Gilmore, 1978). If one were to disregard the above inconsistencies and use the four 'good' censuses from the 1950s to estimate the rate of change during the decade, an exponential rate of 8.8% per year is indicated (Fig. 3). This is lower than Chapman's (1981) estimate (10.4%) because he used the authors' final population estimates (which include further unstandardized corrections) rather than just the raw data corrected for visibility as used here. Rice and Wolman's (1971) estimate of 12.2% annual increase from the same data probably represents a miscalculation.

There were five further censuses conducted at Point Loma intermittently between 1967-68 and 1978-79. These were not analyzed in detail by Reilly *et al.* (1980; 1983) due to the above unaddressed questions regarding the distribution of, and changes in, the migratory

corridor. Further, the methods used during the later Point Loma series differed somewhat from the early efforts there and are therefore not reasonably considered as part of a single time series.

#### Baja lagoon aerial censuses

There have been a number of aerial counts conducted on the winter grounds during the past 30 years. These were begun in 1952 by Carl L. and Laura Hubbs, and repeated by them and others during most years through 1964 (Hubbs and Hubbs, 1967; Gilmore, 1960). Gard (1974; 1978) conducted similar counts during 1970, '73, '74, '75, and '76. Recently, Rice, Wolman, Withrow and Fleischer (1981) and Rice, Wolman and Withrow (manuscript) conducted aerial counts on the winter grounds in 1980 and 1981, respectively.

As with the early shore censuses, the aerial counts were not conducted in a consistent manner. As discussed by Rice *et al.* (manuscript), reliable estimates from aerial counts in and outside the calving lagoons can be obtained only if many replicate surveys are made within a short time period, at the same time each year, along standardized census tracks at standardized altitude and speed, under good visibility conditions. With the exception of the very latest, none of the annual aerial surveys meet any of the requirements, except that most were conducted sometime during February. Rice *et al.* (manuscript) feel that these early efforts are consequently, 'worthless for estimating population sizes and trends'. Consequently, no rate of increase estimates are produced here from the lagoon aerial counts. Previously published estimates from this series include 0.8% per year (1954-64,  $n = 4$ , Rice and Wolman, 1971), and 8.0% (1952-59,  $n = 4$ , Chapman, 1981).

In summary, of four available time series of gray whale sighting surveys, only one is reliable enough to allow estimation of rate of change in population size: the Monterey 13-year series. The early Scripps series are not interpretable given present information. The 1950s Point Loma counts are of questionable value as an index of change due to unstandardized methodology. The Baja Lagoon aerial counts have even more severe methodological inconsistencies. The Point Loma series from the 1950s, perhaps the most reliable of the three sources other than Monterey, indicates a rate of increase of 8.8% per year. The possibility of the population achieving an 8.8% per year rate of increase is considered below in relation to vital rate estimates.

### VITAL RATES AND MAXIMUM RATE OF INCREASE

In this section I review available information pertinent to gray whale vital rates, present slightly different estimates for the *circa*-1967 pregnancy rate and adult and juvenile mortality and use the existing estimate for age at sexual maturation. Then, the maximum rate of increase is inferred from the vital-rate values assumed for the near-zero population level, by use of a Leslie matrix. This rate is an estimate of the asymptotic or potential for the population, equivalent to  $r_s$  of Caughley (1977).

#### Age at sexual maturity

Both Rice and Wolman (1971) and Zimushko (1969a; 1971) used evidence of ovulation or pregnancy as evidence of maturity in females. Rice and Wolman found immature females with as many as 12 earplug layers and mature ones with as few as six. The median number of layers at maturity was nine. Zimushko also concluded that nine layers was the approximate time of attainment of maturity for females. The minimum number of layers in a mature female was eight in the Soviet sample, and the maximum in an immature individual was 12. The disparity in minimum layers for maturity was most likely due to sampling error. Only 34 females were examined by Zimushko (1969a), while Rice and Wolman (1971) examined a total of 140 females (not counting fetuses), of which 68 had readable ear plugs.

For the detection of maturity in males, Rice and Wolman relied solely on histological examination of the testes for evidence of spermatogenesis. Zimushko (1969a; 1971) examined a sub-sample histologically (apparently nine of 23, but this is not clear), using percent of seminal ducts open as a criterion of maturity. He combined this with an analysis of growth rate of testes weight to conclude that males reach maturity at approximately 11.1 m in length (Zimushko, 1971). Ranges in numbers of earplug laminae at maturity are not clearly stated for males from these studies. Rice and Wolman found essentially the same timing in males as in females. The median number of earplug layers at maturity was 9, the minimum 6 and the maximum 12.

Following this approach, then, gray whales became sexually mature at a median age of 8 years, a minimum age of 5 years, and a maximum of 11 years.

#### Population pregnancy rate

The independent data sets available on life history should allow two independent estimates of pregnancy rate for the *circa*-1967 population: one from the summer feeding grounds and one from the migration past central California. There are problems with the estimates produced from both, however. A revised estimate for this time period has been calculated here. Blokhin (1982) reported pregnancy rate statistics from the 1978, 1979, and 1980 harvests. These results are compared below to the pregnancy rate information for the late 1960s. A number of issues relative to an accurate determination of current and maximum pregnancy rate are problematic. These include ovulation rate, accurate ageing (discussed above), length of and possible overlap in gestation and lactation, and sampling biases.

In the sampling of migrating gray whales conducted by Rice and Wolman (1971) one important component of the population was missed due to the timing of the captures (e.g. Poole, 1984): post-partum females with calves of the year. There also appeared to be biases toward late pregnant females captured during the southward migration. Consequently, direct estimation of population pregnancy rate from their data is not possible.

Rice and Wolman (1971) examined a total of 116 mature females (Table 3). Late pregnant females headed south and post-partum females headed north were excluded from their computations of pregnancy rate

Table 3

Reproductive state of sexually mature female gray whales examined by Rice and Wolman (1971), classified by direction of migration

South		North	
Condition	Number	Condition	Number
Late pregnant	56	Post-partum (non-lactating)	2
Recently ovulated	28	Early pregnancy	22
		Resting	8

Table 4

Percent of mature females which were pregnant from Soviet gray-whale catches for four consecutive years ( $P$ ), 1965–1968 from Zimushko (1969), with sample sizes for each year ( $n$ ) inferred from Zimushko and Ivashin (1980; Table 3), and a chi-squared test of differences in proportion pregnant between years

	Year				Total
	1965	1966	1967	1968	
$P$	46.3%	56.3	33.3	53.1	46.7%
$n(P)$	22	9	9	17	57
$n(\text{not } P)$	25	7	18	15	65

$\chi^2 = 3.055$ , d.f. = 3,  $P = 0.617$  (not significant).

because of the apparent biases mentioned above. They assumed that all 28 recently-ovulated animals headed south had conceived and that the number of females impregnated the previous year (giving birth in the current 'year' and absent from the samples) was approximately equal to the number assumed pregnant in the 'current' year. Consequently, 50 were in effect added to the denominator of the ratio of pregnant to total from the sub-sample (50/58), to produce  $P_1 = 50/58 + 50 = 0.463$ .

There are two aspects of Rice and Wolman's pregnancy rate estimation that may be in error. First, the assumption of one pregnant (post-partum) female missed for each 'pregnant' (recently ovulated or early pregnancy) whale in the sample appears valid for northbound captures but not for southbound. Second, it is probably unreasonable to assume that all corpora lutea observed represented pregnancies. Alternative interpretations are possible, but these also require conjecture.

Data from the Soviet fishery may help to clarify the issue of the *circa*-1967 pregnancy rate. Zimushko (1969b) reported percent pregnant by year for four years (1965 through 1968). From Zimushko and Ivashin (1980, Table 3) the sample sizes can be inferred (Table 4). Zimushko (1969b) speculated from this four year series that the proportion pregnant oscillates on a two-year cycle: one year above 50%, one year below. From this he further speculated that only a proportion of the population was on a two-year breeding cycle and that other females gave birth two, three or even four years in a row before resting for a year. Contributing to this picture was Zimushko's early (1969a; 1969b; 1971; 1973) interpretation of ageing, i.e. two layers accumulated per year.

I conducted a chi-squared test of differences in proportions pregnant between years in the Soviet data (Table 4). An hypothesis of equal proportions between

years cannot be rejected. Pooling the data over years, then, gives:

$$p_2 = 57/122 = 0.467$$

with variance

$$\text{var}(p_2) = (0.467)(1 - 0.467)/121 = 0.00205.$$

This is quite close to Rice and Wolman's (1971) original estimate (0.463) from the California series. If the sampling was unbiased, this estimate should be a valid representation of the pregnancy rate, being based upon 122 captures of adult females. The 95% confidence limits are (0.376, 0.558).

The variation between years in proportion pregnant in the 1965–1968 data from the summer grounds is possibly due to temporal sampling differences. This is suggested by the data and analyses of Blokhin (1982) for the years 1978–1980. He found a strong decreasing trend in proportion of mature females which were pregnant, by month from July through October, in the Soviet subsistence-fishery captures. The July proportion was near 0.90, declining to near 0.10 in October (Blokhin, 1982; Fig. 2). The overall pregnancy rate during the 3 years is not directly calculable, since the raw data were reported only for 1980. In that year the pregnancy rate was 0.52. For 1978 and 1979 only proportions were reported, without sample sizes: 0.30 for 1978 and 0.84 for 1979. Blokhin mentioned that seasonality was probably responsible for the wide distance between these estimates, sampling for 1978 having been predominantly late in the summer while sampling for 1979 was predominantly early in the summer. The mean of the three proportions is 0.55. It is possible that this is an accurate estimate, but an examination of the components of the calving interval (below) suggests that a rate greater than 0.5 is unlikely. Sampling bias toward pregnant females is suggested here. This also casts some doubt on the accuracy of the earlier summer-range data as well.

It is interesting to note that the proportion pregnant appears to be positively corrected with the proportion sexually mature in the three annual samples reported by Blokhin (1982): 1978 had 46% mature and 30% pregnant; 1979 had 87% and 84%, while 1980 had 63% and 52%. This also suggests that much of the inter-year variation in pregnancy rates is due to sampling problems.

For maximum pregnancy rate (or minimum calving interval), Rice and Wolman (1971) estimated 0.5 (2 years), while Zimushko (1969a; 1969b; 1971) estimated that it is greater than 0.5 (less than 2 years). Apparently these authors had differing interpretations of the components of the calving interval, i.e. length of gestation, and the possibility of overlapping lactation and/or gestation with ovulation. The minimum calving interval biologically possible is an important factor in the estimation of maximum rate of increase. Consequently the separate components of the calving interval are reviewed below.

### Lactation period

The lactation period is indicated to be approximately 7 months, from collection dates of weaned calves reported from the summer feeding grounds (Zenkovich, 1937; Tomilin, 1957). Nearly all calves collected during August

and later, by the above sources, were weaned, having solid food but no milk in their stomachs. No data exist to examine possible trends in lactation period with time or changing population size.

### Gestation period

Rice and Wolman estimated the gestation period to be 13 months, using the curve-fitting method of Hugget and Widdas (1951). This method assumes fetal growth to fall into two phases: an initial slow period followed by a longer, much faster period of growth. The later part of the gestation period is estimated from empirical data on fetal sizes and calendar date. Estimation of the initial phase is not as straightforward. Based upon an analysis of the state of development of two embryos, Rice and Wolman (p. 79) estimated the initial phase to last 75 days. The empirically estimated phase was 325 days, so their estimate of the total period was 400 days, or about 13 months.

Zimushko and Ivashin (1980) approached this situation in a different, slightly more qualitative manner. On a 'circular graph' of months of the year they plotted the sizes of fetuses by month. They concluded that the period is less than 12 months, not 13. Their figure shows the mean conception date to be in mid-February. This is about 11 months from the mean birth date of 20 January (Rice *et al.*, 1981). It appears, however, that Zimushko's technique does not take the initial, slow phase of fetal growth (Laws, 1959) into account. Zimushko's extrapolated conception date (February) is in fact near the date at which the line from the 'linear' growth phase in Rice and Wolman's (1971; Fig. 29) analysis meets the origin. Also, all adult females taken by Rice and Wolman on the southward migration (except those with near-term fetuses) had fresh large corpora lutea. This indicates that they had at least ovulated, if not conceived. No embryos were found in these females. This could have been due to the small size of a new conceptus. Alternatively, all of these individuals could have ovulated again during the same season. This second alternative is not supported by the available data on ovulation rate (see below).

For gestation period, then, available data are not entirely conclusive. More work is desirable on estimation of the early phase of fetal growth. A period somewhat greater than 12 months appears most likely at this time.

### Frequency and timing of ovulation

A simple linear regression of number of corpora lutea and c. albicantia vs. number of ear-plug laminae for 49 female gray whales results in the following equation (Table 5; data from Rice and Wolman, 1971):

$$\text{No. corpora} = (0.518) \cdot (\text{no. layers}) - 0.891$$

$$(r^2 = 0.614)$$

The slope of 0.518 is not significantly different from 0.5 ( $t = 0.334$   $p = 0.65$ ) (Fig. 4). If multiple sequential ovulations were a common phenomena, a higher rate of ovulation would be expected. These data appear to support the concept of a 2-year minimum breeding cycle. Certainly not all ovulations would result in pregnancies.

Another factor to be considered in determining the

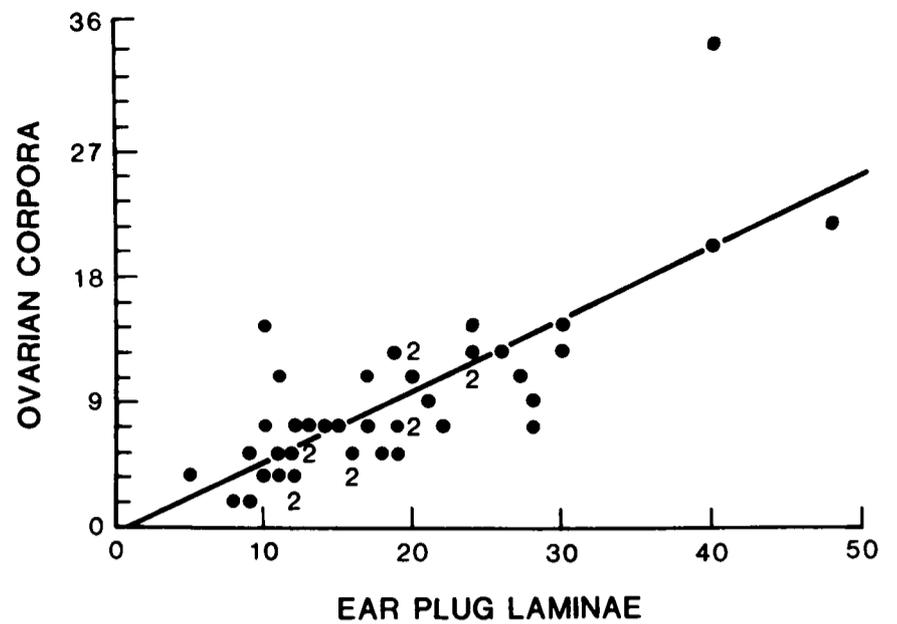


Fig. 4. Relationship between frequencies of ear-plug laminae and ovarian corpora for 49 gray whales. The slope = 0.518 ( $r^2 = 0.614$ ).

length of the female reproductive cycle is the occurrence of either a post-lactation or post-partum ovulation/conception. A post-lactation ovulation/conception appears unlikely, given the relative uniformity in size of fetuses with time of year (Rice and Wolman, 1971; Zimushko and Ivashin, 1980) and the overall fairly precise, annual timing of the gray whale migration schedule. Given that Rice and Wolman (1971) observed no enlarged follicles in ovaries from 56 southbound females with near-term fetuses, a common post-partum ovulation also appears unlikely. It apparently does occur on some occasions, though, since Zimushko (1969a) reported the capture of seven simultaneously lactating and pregnant females from the Soviet fishery. The total sample size from which these seven were drawn was not stated and is difficult to infer from the text. As no near-term females were found to exhibit signs of imminent ovulation from the California specimen series, however, I consider this a relatively uncommon event.

When discussing life history characteristics in relation to ovarian scars, it is important to remember that there are still uncertainties involved: (a) ovulation may not be a regular, semi-annual event, (b) ovulation rate may change with age, and (c) it is unknown if all corpora persist throughout life (Perrin and Donovan, 1984).

### Age-specific pregnancy rates

Zimushko (1970) examined the ovaries of 70 mature female gray whales. He distinguished two types of corpora albicantia: those of ovulations which had resulted in pregnancy, and those which had not.<sup>2</sup> From this he inferred a declining fecundity with age, as represented by a decreasing ratio of the corpora of pregnancy to those of non-pregnancy in older whales (Zimushko, 1973). No sample size was given for testing this hypothesis. A ratio of 1:1 for whales 12.0–12.5 m long, and 1:2.5 for females of 13.1–13.5 m was reported. A figure was presented by Zimushko (1973) with data for nine points (reproduced in Zimushko and Ivashin, 1980) to illustrate this concept. Unfortunately, the points cannot be read from the figure without conjecture, and

<sup>2</sup> Ivashin (1984) describes methods used by Soviet scientists for classifying corpora.

no means of substantiating the changing ratio is available. Regarding the basic premise, that two types of corpora albicantia can be distinguished for gray whales, Rice (pers. comm. 1981) states that Zimushko's method is faulty and that no clear consistent difference exists (see also Perrin and Donovan, 1984; Ivashin, 1984).

Laws (1961) could distinguish no such differences in fin whale corpora. Mizroch (1981) found no decline in proportion pregnant with age in an analysis of a large series of Southern Hemisphere baleen whale reproductive data. I have assumed fecundity constant for adult (beyond 11 years of age) gray whales, lacking conclusive evidence to the contrary. This controversy is not likely to be settled without substantial histological research on gray whale corpora.

In summary, neither the pregnancy rates for *circa*-1967 and 1978–80 nor maximum pregnancy rates can be unambiguously determined from available information. The data on ovulation rate and ovarian condition of southbound migrating females point to a two-year minimum cycle. It is not entirely clear what the gestation period is, but the best available data point to a period greater than 12 months, also supporting a two-year minimum cycle. The report of seven simultaneously pregnant and lactating females captured from the feeding grounds (Zimushko, 1969a) bears further verification, including accessory data on the size of the sample from which these were drawn. They point to an inconsistency in our understanding of gray whale reproductive biology as yet unresolved.

#### Adult survival rate

The Rice and Wolman (1971) samples provided the only information available on adult survival rate ( $S_a$ ). From their data (Table 5), apparent adult survival rate ( $A$ ) can be estimated from the frequencies of individuals per age class. If the population is stable in age structure, stationary in size and has not been subject to exploitation, this should be an unbiased estimate of adult survival. The California stock of gray whales had most likely been under exploitation continually since pre-history (Mitchell, 1979). There is no way of knowing if the age structure was stable in the mid 1960s, but the population was probably increasing in size. Consequently, while apparent survival ( $A$ ) has been estimated with some degree of certainty here, the proportions of this estimate ascribable to growth ( $G$ ) and exploitation ( $F$ ) are less certain.

Rice and Wolman preferred the use of ovarian corpora to estimate apparent adult female survival and reported a Chapman–Robson ( $C-R$ ) estimate of 0.921 ( $M = 0.082$ ). Using earplug laminae and the entire adult series (8 years and older), their  $C-R$  estimates were 0.909 for females and 0.922 for males.

Earplug laminae are the reference time scale for ovarian corpora; the relation is linear and significant (see above) but not remarkably so, with  $r^2 = 0.614$ . Both time scales are questionable but of interest, because only about one half of the earplugs were readable and because readings for older animals may not be accurate (Rice and Wolman, 1971).

To obtain variances to facilitate comparisons (not presented in Rice and Wolman, 1971), I have recalculated  $C-R$  survival rates from age-class frequencies for four

Table 5  
Age composition of gray whales from Rice and Wolman (1971)  
based upon ovarian corpora and earplug laminae as time scales

Estimated age (years)	Ovarian corpora		Ear-plug laminae		
	No. corpora	No. individuals	No. laminae	No. females	No. males
1			2	5	3
2			3	2	5
3			4	1	2
4			5	2	4
5			6	4	3
6			7		5
7			8	5	7
8			9	3	3
9	1	8	10	3	5
10			11	3	6
11	2	15	12	5	3
12			13	4	6
13	3	12	14	1	6
14			15	1	2
15	4	11	16	3	
16			17	2	4
17	5	9	18	1	3
18			19	3	3
19	6	11	20	5	3
20			21	1	6
21	7	11	22	1	4
22			23		2
23	8	6	24	4	1
24			25		1
25	9	8	26	1	
26			27	1	
27	10	5	28	2	1
28			29		2
29	11	3	30	2	
30					
31	12	5			
32			33		1
33	13	4			
34			35		1
35	14	2			
36					
37	15	2	38		1
39			40	1	4
40			41	1	
46			47		1
47	20	1	48	1	
50					
51	22	1			
57			58		1
69			70		1
76					
77	35	1			

cases: males and females separately, using laminae and all data; females using laminae but truncating 'older' (30 years and older) whales; and females using corpora (Table 6). Adult male survival (0.920, S.E. = 0.012,  $n = 49$ , not in Table 6) is significantly different from adult female survival ( $Z^2 = 5.0$ ,  $P < 0.01$ ). Since only female survival is of interest for the rate-of-increase calculations, the sexes were treated separately and males not considered further here.

Following Robson and Chapman (1961), a comparison of  $C-R$  and Heincke estimates at ages 8–12 showed no under-representation of those age classes ( $Z^2 = 0.55$ , 0.47, 0.38, 0.15, respectively; none significant at  $\alpha = 0.05$ ). Consequently 8 years is a valid starting point for  $C-R$  computations.

Table 6

Estimates and standard errors of apparent adult female survival from frequency per age class using ear-plug laminae and ovarian corpora counts as age indicators, with and without truncation of age-30 and older individuals (original data from Rice and Wolman, 1971).  $A$  is the mean apparent survival rate and  $Z$  the corresponding apparent mortality coefficient

Data	Ageing technique	
	Ovarian corpora	Ear plug laminae
All 8+ years females	0.918 ± 0.007	0.910 ± 0.012
8-30-years females		0.908 ± 0.012
	$\bar{A} = 0.912$ ( $Z = 0.092$ )	

There is no well defined criterion with which to select one of the three available estimates of female survival as the best estimate (Table 6). All are quite close, however, and overlap in 95% confidence intervals. A simple average of the three was calculated:  $\bar{A} = 0.912$  ( $Z = 0.092$ ) where  $A$  is apparent survival ( $Z$  is total instantaneous mortality), including effects of population growth ( $G$ ) and fishing mortality ( $F$ ). The female data are fitted well by a geometric series with  $A = 0.912$  ( $X^2 = 34.27$ ,  $d.f. = 29$ ,  $P = 0.77$ ), validating the use of the  $C-R$  statistics.

Following Ohsumi (1976) I have estimated natural mortality ( $M$ ) by subtracting population growth ( $G$ ) and fishing mortality ( $F$ ) from apparent total mortality ( $Z$ ):  $M = Z - (F + G)$ . However, determining  $F$  and  $G$  during the time period of interest (about 40 years prior to 1967, since about 98% of the population was 40 or less in 1967 - Table 5) is at best a gross approximation.

Reported catches for 1927-1967 (summarized in Reilly, 1981) averaged only about 80/year, but they are reported to have increased to over 100/year during the 20 years immediately preceding 1967. There is no direct estimate of the population size or the precise nature of its changes during this period. An estimate does exist of  $F + G$  for the 13 years following 1967. For lack of better information, I tentatively assumed  $F + G$  constant at the same rate prior to 1967 as that measured for 1967-1980, or about 0.037. From  $Z = -\ln(0.912) = 0.092$  and from (1),  $M$  was approximated as  $M = 0.092 - 0.037 = 0.055$  ( $S = 0.946$ ).

### Juvenile survival rate

With other vital rates set at their presumed *circa*-1967 values ( $P = 0.469$ ,  $S_a = 0.946$ ,  $X_m = 8$ ,  $\lambda = 1.037$ ) juvenile survival  $S_j$  was estimated to be 0.893 (Table 7). This corresponds to a mortality coefficient of 0.113. Using the two-compartment model (1) and slightly different values for vital rates, Ohsumi (1976) estimated the juvenile mortality coefficient to be 0.167, notably higher than my estimate of 0.113. This latter estimate is hopefully more accurate, because (1) Ohsumi's (1976) estimate of pregnancy rate was probably too low; (2) his

<sup>3</sup>  $F$  was set at  $0.0175 = 179/10,242$  from the average kill 1955-1966 (Zimushko and Ivashin, 1980) and from the average population size during those years as extrapolated from the exponential model estimated for the years covered by the Monterey census by Reilly *et al.* (1983).

Table 7

The ranges of pregnancy rate ( $P$ ), juvenile survival ( $S_j$ ), adult survival ( $S_a$ ) and age at sexual maturation ( $X_m$ ) determined here for two different population levels, with dominant eigenvalues ( $\lambda$ ) for each set.  $S_j$  was adjusted to yield  $\lambda = 1.037$  for *circa* 1967. For near zero,<sup>2</sup>  $P$  was adjusted to yield  $\lambda = 1.09$ , holding  $S_a$ , and  $X_m$  at near-zero<sup>1</sup> levels

Population level	$P$	$X_m$	$S_j$	$S_a$	$\lambda$
Near zero <sup>2</sup>	0.642	5	0.940	0.945	1.090
Near zero <sup>1</sup>	0.500	5	0.940	0.945	1.069
<i>Circa</i> 1967 <sup>3</sup>	0.469	8	0.893	0.945	1.037

<sup>1</sup> For maximum  $P$  of 0.50.

<sup>2</sup> For maximum  $P$  of 0.642.

<sup>3</sup> Approximately 12,500.

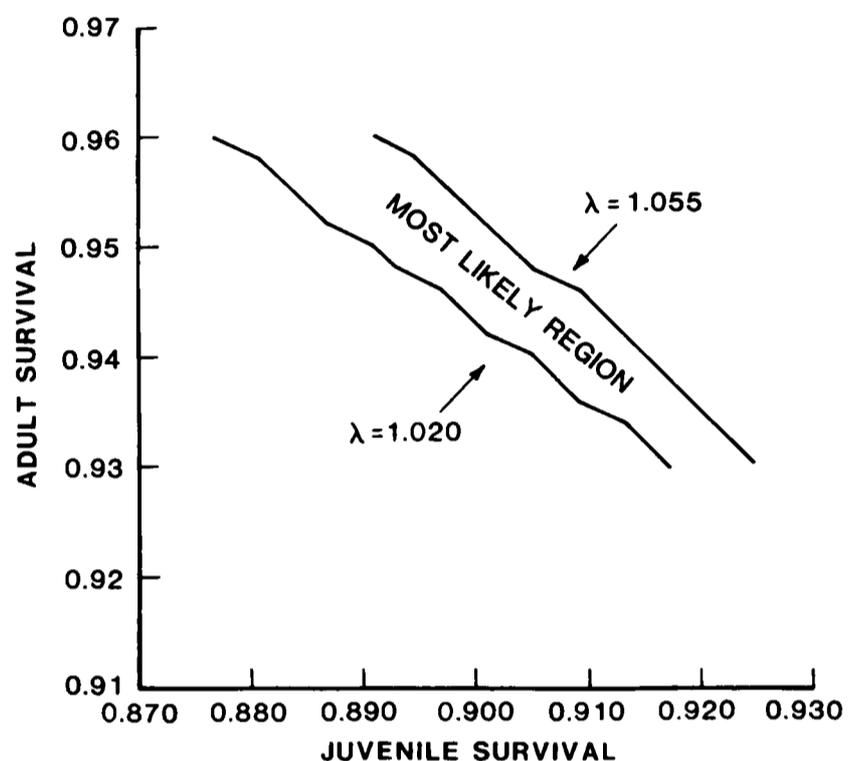


Fig. 5. Relationship between juvenile survival, adult survival and *per capita* rate of increase for the *circa*-1967 gray-whale population. A best estimate of 0.893 for juvenile survival corresponds to adult survival of 0.945 and  $\lambda = 1.037$ .

estimate of adult mortality rate was probably too high; and (3) population growth was not accounted for in his estimation procedures.<sup>3</sup>

The estimate of juvenile survival produced here is dependent on the accuracy of my estimates of other vital rates. In Fig. 5 the sensitivity of estimates of  $S_j$  to values of adult survival and rate of increase is examined. The figure shows a region defined by  $S_a = 0.945 \pm 0.015$  and  $\lambda = 1.037 \pm 0.018$ . Within these boundaries juvenile survival varies from about 0.878 to about 0.924. The central value of this 'most likely region' is, by definition, 0.893.

### Maximum rate of increase

The maximum rate of increase which could be achieved by gray whales is dependent on the extremes approached by other vital rates as density nears zero. For pregnancy rate, if a two-year minimum calving interval is assumed, the maximum rate will be 0.5. Given the range in

observed ages at sexual maturation from 5 to 11 years, it seems reasonable to assume that the population median or mean age at sexual maturation would approach 5 years at minimum. Since adult survival (assumed density-independent here) was estimated to be 0.946, it is assumed that juvenile survival would approach but probably not equal or surpass this rate. Consequently a value of 0.940 was assumed for this exercise. Given this set of vital rates (Table 7) and a Leslie matrix constructed as in (2), a dominant eigenvalue of 1.069 was calculated. This equals a maximum rate of increase of approximately 6.7% per year for the California stock of gray whales, if a stable age structure can be assumed in populations at very low levels.

Considering the uncertainty encountered here in defining maximum pregnancy rate, and the possible rate of increase of 8.8% per year implied by early Pt Loma censuses, it is of interest to determine what the pregnancy rate must be to result in an 8.8% rate of increase. Holding the other vital rates at their previous extremes, pregnancy rate must be 0.64 for  $\lambda = 1.09$ . It does not seem likely that the population pregnancy rate could exceed the ovulation rate, calculated at 0.518. However, sufficient information does not exist on maximum pregnancy rate to dismiss the higher  $P$  and  $\lambda$  values considered here.

### CRITIQUE AND SUMMARY

This study reviewed all available information on realized rate of increase from four series of sighting censuses and on vital rates and related biological topics from two specimen series and a number of previous analyses. It then utilized information from both topics to estimate the maximum rate of increase that gray whales might achieve.

Although gray whales are perhaps the best studied of all baleen whales, much research is still needed to satisfactorily describe their life history and population dynamics. The length of gestation, verification of ageing, flexibility in ovulation and conception, and (ultimately) the minimum calving interval are among the major topics requiring further research. Estimates of juvenile survival and maximum rate of increase produced here are contingent on the validity of estimates and assumptions made regarding other aspects of the life history. Future findings from direct observation may indicate a reassessment of juvenile survival and maximum rate of increase. The following outline summarizes the information reviewed and (in some instances) the parameters re-estimated here.

#### Observed rates of increase

1. The Monterey shore censuses conducted annually from 1967–68 through 1979–80 indicate a net rate of increase of 2.5% per year. If the removals from the Soviet subsistence fishery are considered as well, the mean net productivity was approximately 3.7% per year.
2. Census series from Scripps in the late 1940s, Point Loma in the 1950s through 1970s and from the calving grounds are not reliable as indices of population change.

#### Vital rates

3. Life-history data for the estimation of vital rates are available from two sources: a series collected by Rice and Wolman (1971) off the central California coast, and a limited sample from the Soviet subsistence fishery. All available data appear to apply roughly to the 1967 population.
4. The mean age at sexual maturation was 8 years, with a range of ages from 5–11 years for both sexes.
5. The population pregnancy rate *circa* 1967 was estimated here to be 0.467 with a standard error of 0.045.
6. There is some uncertainty regarding the gestation period, but available data suggest a minimum period somewhat greater than 12 months.
7. The *circa*-1967 ovulation rate was 0.518/year (S.E. = 0.059).
8. Lactation appears to have been near 7 months in duration.
9. The minimum calving interval is probably near 2 years. A report of seven simultaneously pregnant and lactating females on the summer grounds needs further investigation.
10. Female adult survival rate was estimated to be 0.945, corresponding to a mortality coefficient of 0.056. Juvenile survival was estimated to be within the range 0.878–0.924, with a best estimate being 0.893, corresponding to a mortality coefficient of 0.113.
11. Adult male survival is significantly higher than adult female survival, as calculated using ear-plug laminae as indicators of age.

#### Maximum rate of increase

12. The asymptotic maximum or intrinsic rate of increase for the stock is estimated to approach 6.7% per year as population density approaches zero.

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# Have Pregnancy Rates of Southern Hemisphere Fin Whales, *Balaenoptera physalus*, Increased?

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## ABSTRACT

A study of pregnancy rates of Southern Hemisphere fin whales (*Balaenoptera physalus*) was conducted using generalized linear modelling, orthogonal polynomial fitting techniques, and correlation analysis.

Apparent pregnancy rates were analyzed separately for catches by Norway, the United Kingdom and Japan in International Whaling Commission Statistical Areas II, III and IV. Using generalized linear modelling, we examined pregnancy rate as a function of average length, season, Series (latitude) and month, and found the data to be highly variable, with different models appropriate for the various Area-nation groups.

The seasonal component of the modelled pregnancy rates was examined for trend, because, for management purposes, it is important to know if pregnancy rates had increased as exploitation increased and the population declined. No trends were apparent.

One might expect similarities of patterns of the seasonal components within a given Area when comparing data by nation. We compared the Norwegian seasonal components with the United Kingdom seasonal components and found no significant correlations for any of the data sets in any Area.

In addition, we examined the correlation between the seasonal components and cumulative biomass removals of fin and blue whales by season. Only two of ten correlations were significant at the  $\alpha = 0.05$  level.

The fin whale data set contains records from over 250,000 female whales. Yet in spite of the large sample sizes used in these analyses, we found very high variability in pregnancy rates across all factors examined. Thus, it is impossible to assert that the population responded to heavy harvesting with increasing pregnancy rates or a shortened breeding cycle. We see significant differences and much variability by season, but no apparent trend. The variation we see could be due to environmental factors, the cyclic nature of the reproductive cycle, segregation among females by age or pregnancy condition, improper collection or reporting of data, or other unknown factors. If there is a trend at all, the variability masks it. If there is no trend (and there is no evidence for one) then assuming increases in reproductive rates, and consequently basing harvesting strategies upon such an assumed increase, could have severe, negative effects on the population.

## INTRODUCTION

It has been assumed generally that the reproductive rates of Southern Hemisphere baleen whales have acted in a density-dependent fashion. Some researchers, most notably Mackintosh (1942), Laws (1961), and Gambell (1973), have reported increases in pregnancy rates of Southern Hemisphere baleen whales as the whale biomass declined due to exploitation. This manifestation of the classic density-dependent response appears now to be spurious, however, perhaps caused by injudicious pooling of disparate data sets or improper consideration of the factors (other than density) which affect apparent pregnancy rates.

Because the baleen whale catch data collected by the Bureau of International Whaling Statistics (BIWS) have been made available on a computer tape, it is now possible to examine the pregnancy data from this vast data set (e.g. 256,760 female fin whales with recorded pregnancy data) easily, without resorting to pooling or subsampling.

The first (and to date only) statistical rather than descriptive analyses of baleen whale pregnancy rates were studies of sei whale (*Balaenoptera borealis*) rates (Mizroch, 1980), and blue (*B. musculus*) and fin (*B. physalus*) whale rates (Mizroch, 1981), using the BIWS data. These studies found no evidence of trends in baleen whale pregnancy rates. Because of the controversial nature of this subject, however, it was decided to continue and improve upon these early studies. This study will concentrate on the fin whale, which has had the longest time series of catches and the highest overall catch total.

In addition, a more sophisticated statistical approach will be used. Therefore, this study will present analyses in which fewer *a priori* selections of data were needed.

## HISTORY OF EXPLOITATION

According to Mackintosh (1965), whaling was first undertaken in the Antarctic in 1904 and at first was conducted mostly by Norwegian and British companies. The initial target species was the humpback whale (*Megaptera novaeangliae*), but as the humpback population dwindled due to exploitation, the whalers turned to the blue and fin whales. By 1912/13, the blue and fin whale catches outnumbered humpback whale catches. Until the onset of pelagic whaling in 1925/26, catches of all whales in the Antarctic averaged about 9,000 per year. With pelagic whaling, the industry was no longer limited to harvesting within a certain radius from a land station or moored processing ship and therefore could process the whales wherever they were to be found. Total catches in the Antarctic climbed to 20,341 in 1928/29 (mainly blue and fin whales), 30,655 in 1929/30, and 40,201 in 1930/31 (Fig. 1) (Bureau of International Whaling Statistics, 1931).

Catches of whales dropped to 9,572 in 1931/32, due in part to the world-wide economic depression and also because all the Norwegian fleets stayed home that year (Tønnessen and Johnsen, 1982). Catches began to rise again in 1932/33 and averaged about 33,000 through 1939/40 (Bureau of International Whaling Statistics, 1958), when most whaling was interrupted by World War II. Japan had begun whaling in 1934/35, and Germany,

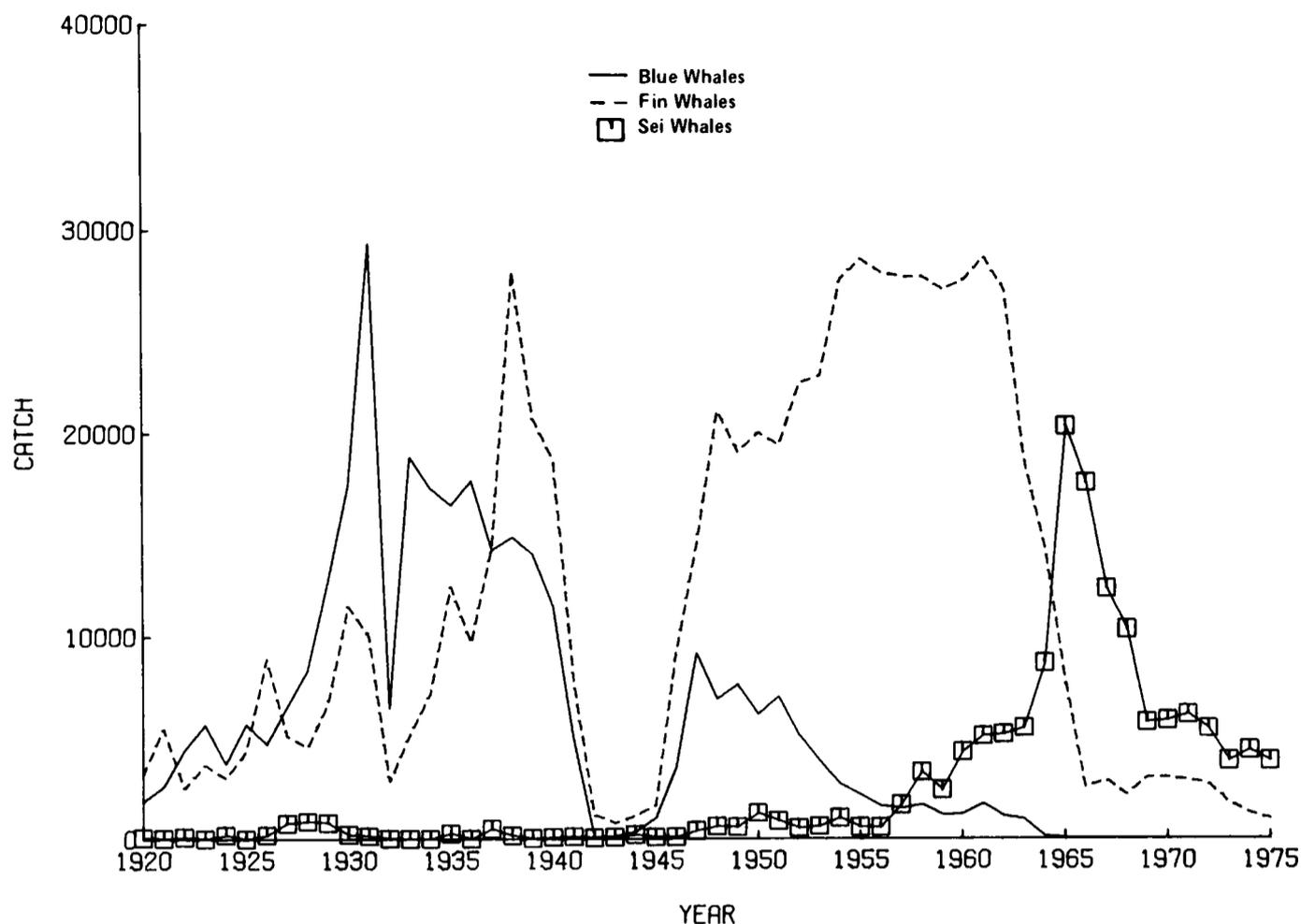


Fig. 1. Catch of blue, fin, and sei whales in the Antarctic 1920–75 (from the Bureau of International Whaling Statistics).

Table 1

Catch of female fin whales (with pregnancy data recorded) by nation, Series, and month

Nation, Series, and month	Area		
	II	III	IV
Nation			
Japan	6,235	18,763	14,836
Norway	31,792	48,122	12,878
UK	20,702	13,121	5,707
Series			
D (40–49° S)	1,008	7,051	1,116
A (50–59° S)	26,679	38,002	9,928
B (60–69° S)	44,373	54,360	29,199
C (70–79° S)	128	849	2
Month			
December	5,399	8,805	4,247
January	26,364	36,174	17,529
February	25,647	35,208	11,761
March	13,857	19,094	6,566
April	819	852	67

Panama and Denmark began operations in 1936/37. These latter nations operated outside the various production agreements and conventions adhered to by the British and Norwegians, and most, with the exception of Japan, did not engage in substantial Antarctic whaling after the war.

In the post-war years, the Soviet Union, the Netherlands, the Republic of South Africa, and briefly, Panama, joined Japan, Norway and the United Kingdom (UK) as Antarctic whaling nations. By this time, the International Whaling Conference of 1946 had established the International Whaling Commission (IWC) to oversee and regulate Antarctic whaling. The

Norwegian Bureau of International Whaling Statistics, which had been established in 1929 by the Norwegian government, was asked to collect data on behalf of the IWC (Tønnessen and Johnsen, 1982).

As the blue whale declined in abundance, catches of fin whales rose, dominating in the catches from 1936/37 to 1964/65 (Fig. 1). In the late 1950s, as fin whales were becoming scarce, catches of sei whales began to increase. Catches of fin whales had averaged about 26,000 during the 1950s. By 1964/65, the catch of fin whales dropped below 10,000 and the catch of sei whales peaked at over 20,000.

The Antarctic had been divided into five, and later six, Statistical Areas by the IWC (Tønnessen and Johnsen, 1982; IWC, 1958), but only Areas II, III and IV had both long histories of exploitation and large catches (Table 1). These Areas were subdivided into 10° latitude blocks known as Series; and as the target species changed, so did the latitude of operation, since the whale species tended to segregate by broad blocks of latitude. For example, most pre-war catches, more blue than fin whales, were concentrated in Series B (60–69° S), the immediate post-war catches, comprising more fin than blue whales, were in Series B and Series A (50–59° S). By the mid-1960s, the catches were predominantly in Series D (40–49° S), as sei whales were preferred.

As many as 10 different nations had been involved in Antarctic whaling over the years. Some were involved for a few years during the pre-World War II era, when Norway and the United Kingdom were the main participants in the regulatory schemes. Others, such as the Soviet Union, started extensive operations only in the post-war years. Because the data used in this study are commercial data collected by the BIWS, and because our goal is to look for trends over time, we analyzed data from

only those nations with large pre- and post-war catches.

Norway has the longest continuous catch history over all Areas, with BIWS data beginning in 1932/33 and ending about 1958/59 in Area IV, 1965/66 in Area II, and 1966/67 in Area III. The BIWS data from the United Kingdom catches begin in 1931/32 and end in 1962/63 in Area II, 1961/62 in Area III, and 1959/60 in Area IV. Japan began Antarctic whaling in Areas III and IV in 1934/35, continued in Area IV through 1940/41 (Tillman and Ohsumi, 1981) and resumed in the post-war years 1950/51 in Area IV, 1955/56 in Area II, and 1962/63 in Area III. The Japanese data on the BIWS data file are incomplete, however, as we had no data for the war years 1939/40–1940/41.

**SELECTION OF FACTORS**

One of the more striking aspects of baleen whale life history is the long-distance migration each whale undertakes each year. Most species of baleen whales, including blue, fin and sei whales, migrate from breeding areas in the low latitudes to feeding areas in the high latitudes. Female whales generally follow a two year breeding cycle, mating at low latitudes in the winter, migrating to high latitudes to feed in the summer, returning to low latitudes about a year after conception

to give birth, and thereafter bringing a soon-to-be-weaned calf to the feeding grounds.

Antarctic pelagic whaling occurs on the feeding grounds during the austral summer, while whales are migrating in and out of the harvesting area by sexual classes. Pregnant females lead the wave of migration, arriving on the grounds early in the season, and also leave to return to the breeding areas earlier than males, lactating females with calves, and juveniles (Mackintosh, 1965).

Our data are from commercially caught whales in which presence or absence of a foetus was noted for females. Since 1937, it has been prohibited to catch fin whales accompanied by a calf, and therefore our samples do not represent the entire female population. Pregnancy rates reported herein are apparent pregnancy rates only (i.e. a female with a foetus is considered pregnant) and represent an index of the true pregnancy rate for the population. As the females wean their calves on the feeding grounds, apparent pregnancy rate is expected to drop, since these resting whales have now become available for harvest. Also, as the pregnant females move northward to the breeding grounds, apparent pregnancy rate is expected to drop, since resting females remain behind for some time. Therefore, an analysis must consider monthly trend, since pregnancy

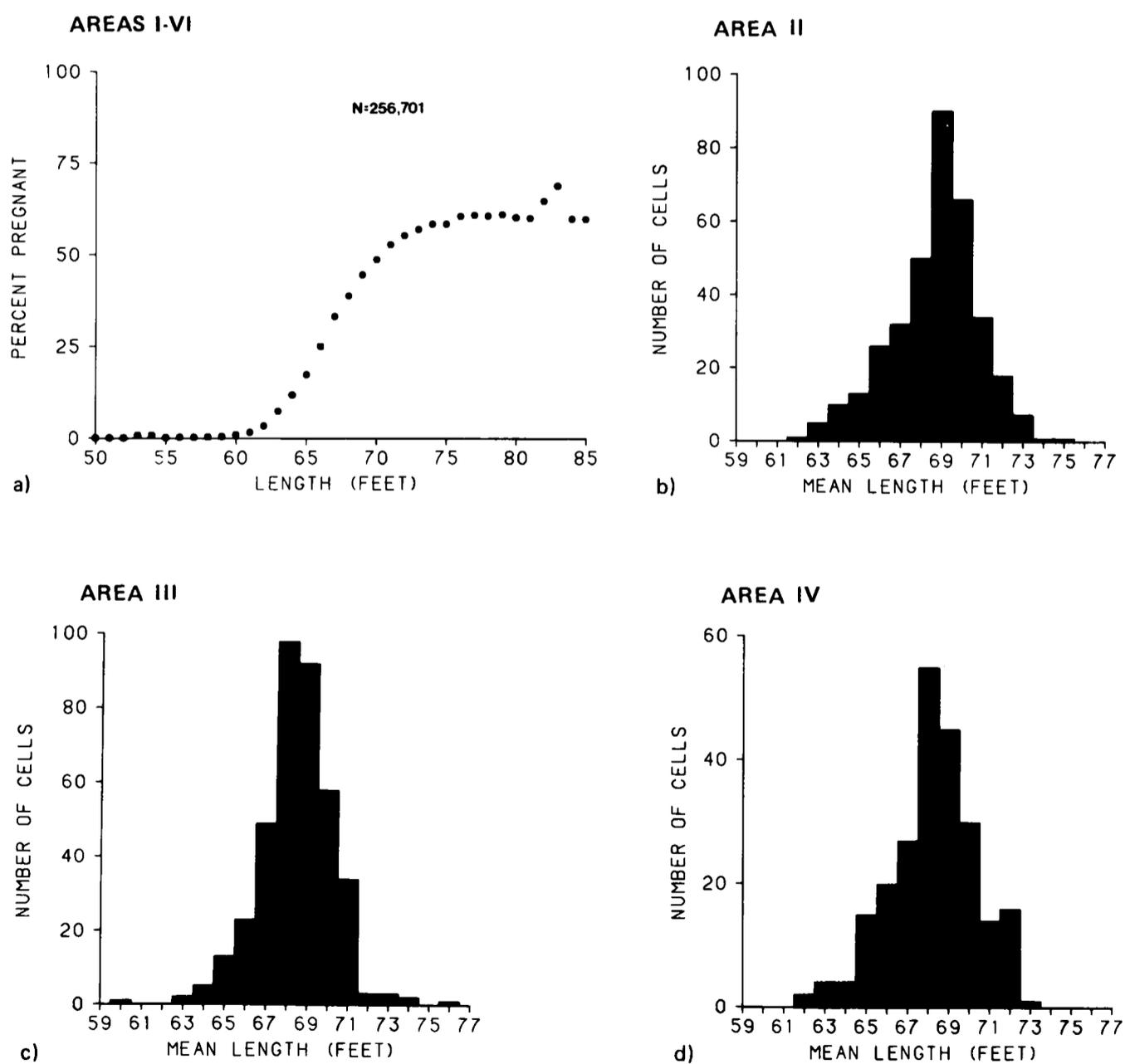


Fig. 2. (a) Pregnancy rate versus length of Antarctic fin whales, Areas I–VI, lengths 50–85 feet. Sample size is 256,701. (b)–(d) Frequencies of mean length of females in each nation/season/Series/month cell, Area II, III and IV.

rate is expected to vary both due to migration and regulatory factors. The whaling season generally ran from December through March or April, with peak catches in January and February (Table 1).

Since migration occurs from north to south (and vice versa), latitude of catch must also be considered as a factor. By convention, we analyzed by 10° latitude blocks, Series A–D (Table 1).

Because the IWC Statistical Areas had different histories of exploitation, we analyzed separately by Statistical Area, choosing Areas II, III and IV because of their extensive pre- and post-war catches (Table 1).

In addition, we analyzed separately by nation, choosing the national fleets with the longest catch histories (Norway, the United Kingdom, and Japan) and omitting the catches by other national fleets, since they occurred over much shorter periods (Table 1).

In a study of pregnancy rates, it is necessary to adjust somehow for the likelihood of a given female being mature. Since maturity, and by inference pregnancy rate, is a function of length (Fig. 2), we chose to use length as a covariate in this analysis. Earlier analyses by Mizroch (1980, 1981) had selected only 'mature' females (that is, only females at least as long as the mean length at maturity). By using length as a covariate in this analysis, we have eliminated the need for *a priori* selection and maintained an adequate sample size.

Due to migration patterns, regulations, and differences in both operating techniques and areas of operation, the factors mentioned above (Area, nation, season, Series and month) can influence observed pregnancy rates in the catch. In addition, pooling across factors would obscure interactions among the factors. Therefore, we reduced our data to Area/nation/season/Series/month cells, and used mean length of all females in each cell as a covariate. The range of mean lengths in the cells is presented in Fig. 2 for Areas II, III and IV. The mean lengths fall well within the region of approximate linearity of the pregnancy rate versus length curve (Fig. 2).

Years in which catch by nation totaled less than 100 were omitted, as well as any Area/nation/season/Series/month cell with catches less than 15. The entire fin-whale data set contains data from over 250,000 female whales, and, consequently, sample sizes within the cells were large. Over 71% of the cells represented 50 or more females, and over 52% represented 100 or more females. In addition, we omitted the post-war years, 1945/46 and 1946/47, because of the possibility that data collection had been less than complete in those years due to the temporary 'special relaxation' of the 1937 International Whaling Agreement regulations (Bureau of International Whaling Statistics, 1949, p. 7). There was indication at the time that some companies did not report the required biological information to the BIWS (Bureau of International Whaling Statistics, 1948, p. 19).

## STATISTICAL METHODS

Our principal interest was to describe how apparent pregnancy rate varied among the several Areas of collection, nations and time of year and to assess trends over season. Pregnancy condition is considered a binomial response variable (i.e., a female is either pregnant or not), and the factors Area, nation, season, Series and

month are categorical explanatory variables (to be called factors hereafter). Mean length of the females within each cell is used as a covariate, and is assumed to be linear, since the computed mean lengths fall within the region of approximate linearity of the pregnancy rate versus length curve (Fig. 2).

Before the genesis of certain statistical techniques and computer programs designed to handle such large analyses, most researchers handled multidimensional contingency tables by examining the two-dimensional contingency tables within the larger table, and then performing appropriate chi-square tests. This approach has several drawbacks, among them that it "does not allow for the simultaneous examination of... pairwise relationships", and it "ignores the possibility of three-factor and higher-order interactions among the variables" (Fienberg, 1980).

The technique chosen for this study, analysis of deviance, was developed by Nelder and Wedderburn (1972) in a presentation of a class of generalized linear models including a generalization for the binomial distribution. A package of computer programs, GLIM (Generalized Linear Interactive Modelling), was developed to fit these models and was used in the analysis (Baker and Nelder, 1978).

Analysis of deviance can be viewed as an extension of analysis of variance both because it can accommodate non-orthogonal terms, and because it is a generalized technique, and thus can be used with non-Normal data (McCullagh and Nelder, 1983). In addition, the model selection procedure is akin to step-wise regression, in that terms are added to or subtracted from the model based upon their conditioned likelihood (conditioned on previous additions to the model). As each term is added to the model, its contribution to explaining the variation in the data is expressed as a reduction in the overall discrepancy (or an increase in goodness of fit) (McCullagh and Nelder, 1983). These reductions in discrepancy are inevitably accompanied by reductions in degrees of freedom (= number of data points – number of free parameters estimated). The decision as to whether a term is significant or not is based on the significance of the deviance (i.e., the reduction in discrepancy) given the degrees of freedom. For the binomial distribution, the deviances have a distribution that is asymptotically chi-square.

Nelder and Wedderburn (1972), among others, point out the extremes in selecting appropriate models: the "minimal model, which contains the smallest set of terms the problem allows, and the complete model", in which the data can be fit exactly. With the addition of each term, goodness-of-fit improves, but so does complexity. In general, a simpler model is preferred over a more complicated one that may give a slightly better fit (Fienberg, 1980).

The data, in the form of  $r$  pregnant females out of  $n$  sampled in each Area/nation/season/Series/month cell, were transformed using the logit transformation [ $L = \log(r/n - r)$ ] (Cox, 1970). The range of the logit transformation ( $-\infty, \infty$ ) gives rise to models that are (usually) easy to interpret when transformed.

In the current analysis, terms were added to the model if their conditional likelihood was less than the 10% point of the chi-square distribution with the same number of

Table 2

Deviance of single-effect models, likelihood and mean likelihood of single effects for the entire data set (Areas II-IV, nations Japan, Norway and UK)

Factor	Deviance	df	Likelihood	df	Mean likelihood
Total	10,580	1,177			
Length	8,200	1,176	2,380	1	2,380
Nation	8,585	1,174	1,995	3	665
Series	10,310	1,174	270	3	90
Month	10,300	1,173	280	4	70
Season	8,932	1,140	1,648	37	45
Area	10,530	1,175	50	2	25

degrees of freedom. The first term added was that with the largest likelihood, and other variables were added in order of percentile of their conditioned likelihood. A particular model was considered a candidate for acceptance if the residual component was less than the 0.9975 percentile of the appropriate chi-square distribution. This procedure, outlined by Goodman (1971) and illustrated by Fienberg (1980), simplifies model selection somewhat, but often one must choose among two or three models. In these cases, the simplest model was chosen, aiming for a compromise between complexity of the model and interpretation of results.

When a particular factor had a very large likelihood value, the recommendation of Goodman (1971) was followed and separate analyses were done for each level of the factor. In the present paper, this recommendation applies to the factor nation.

**RESULTS AND DISCUSSION**

Using combined data for Norway, United Kingdom, and Japan, we investigated the effects of the factors nation, Area, season, Series, month, and the covariate mean length on transformed pregnancy rate (Table 2). Although mean length is the strongest of these effects, most of the factors were significant – that is, the pregnancy rate across most factors was not the same. However, the results indicate that differences among nations were very pronounced while differences among Areas were not nearly so. The strong nation effect may be due to operational differences or merely differences in experience among those collecting the biological data. In any case, the nation effect was quite strong, so we analyzed each nation separately.

Further analyses of the Norwegian and United Kingdom samples indicated substantial Area differences and Area × season interactions which required separate analyses by Area. This was not the case for the Japanese samples. Thus, separate models were fitted to Areas II, III and IV for the Norwegian and United Kingdom samples and one model incorporating Areas II-IV was fitted to the Japanese data. These models are summarized in Tables 3-5.

**Description of fitted models**

*Norway*

Three models were fitted to the Norwegian data – one for each of the IWC Statistical Areas (Table 3). The simplest model fitted was to Area IV and contains only a slope for mean length and a seasonal correction term

Table 3

Analysis of deviance of selected models for data from Norwegian catches\*

Source	Likelihood	df	Mean likelihood	Percentile (1 - p)
<b>Area II</b>				
Corrected total	874.0	133		
Length	514.7	1	514.70	> 0.999
Season   length	193.5	24	8.06	> 0.999
Month   length, season	12.8	4	3.20	0.988
Length × month   length, season, month	12.1	4	3.03	0.983
Deviance	140.9	100	1.41	0.996
<b>Area III</b>				
Corrected total	1,402.0	149		
Length	328.0	1	328.00	> 0.999
Season   length	750.5	26	28.87	> 0.999
Month   season, length	23.1	4	5.78	> 0.999
Series   length, season, month	10.0	2	5.00	0.993
Length × season   length, season, month, Series	155.4	24	6.48	> 0.999
Season × Series   length, season, month, Series, length × season	62.1	27	2.30	> 0.999
Deviance	73.0	65	1.12	0.768
<b>Area IV</b>				
Corrected total	305.6	58		
Length	99.6	1	99.60	> 0.999
Season   length	139.7	18	7.76	> 0.999
Deviance	66.3	40	1.66	0.994

\* Explanation of notation: Length × month | length, season, month translates as length, month interaction, conditioned on length, season and month.

Table 4  
Analysis of deviance of selected models for data from United Kingdom catches

Source	Likelihood	df	Mean likelihood	Percentile
<b>Area II</b>				
Corrected total	461.2	115		
Length	167.9	1	167.90	> 0.999
Season   length	137.2	23	5.96	> 0.999
Month   length, season	28.8	4	7.20	> 0.999
Series   length, season, month	5.8	2	2.80	0.945
Deviance	121.5	85	1.43	0.994
<b>Area III</b>				
Corrected total	1,032.0	74		
Length	361.1	1	361.00	> 0.999
Season   length	545.4	18	30.30	> 0.999
Month   length, season	16.0	4	4.00	0.999
Series   length, season, month	0.3	1	0.30	0.416
Season × Series   length, season, Series, month	45.5	10	4.55	> 0.999
Deviance	63.7	40	1.59	0.990
<b>Area IV</b>				
Corrected total	216.2	47		
Length	61.6	1	61.60	> 0.999
Season   length	77.8	16	4.86	> 0.999
Month   length, season	20.5	3	6.83	0.999
Length × month   length, season	19.5	3	6.50	0.999
Deviance	36.9	25	1.48	0.941

Table 5  
Analysis of deviance of selected models for data from Japanese catches, Areas II–IV

Source	Likelihood	df	Mean likelihood	Percentile
Corrected total (excl. 1962/63)	1,506.0	145		
Length	326.0	1	326.00	> 0.999
Season   length	911.3	24	37.97	> 0.999
Series   length, season	23.7	2	11.85	> 0.999
Month   length, season, Series	49.5	4	12.38	> 0.999
Length × season   length, season, Series, month	60.3	24	2.51	> 0.999
Area   length, season, Series, month, length × season	OA	2	0.2	0.1810
Length × area   length, season, Series, month, length × season, area	13.1	2	6.55	0.999
Deviance	121.7	86	1.42	0.993
Corrected total (1962/63 only)	140.1	15		
Month	71.3	3	23.77	> 0.999
Series   month	22.6	2	11.30	> 0.999
Month × Series   month, Series	37.9	3	12.63	> 0.999
Deviance	8.3	7	1.19	0.693
Total deviance	130.0	93	1.39	0.993

(deviance = 66.3, 40 df,  $p = 0.006$ ). Details of this model are presented in the Appendix. Thus, the pregnancy rate in Area IV has been modelled as a linear function of the mean length of the female catch, with adjustments in the intercept for each season.

The models for Areas II and III were more complex. The model for Area II (deviance = 140.9, 100 df,  $p = 0.004$ ) contains, in addition to the mean length and season terms, a correction for month and a length × month interaction term. Pregnancy rate has been modelled as a linear function of mean length of the female catch with

separate slopes and intercepts required for each month and season. The model for Area II (deviance = 72.9, 65 df,  $p = 0.232$ ) is even more complicated. Besides requiring length, season and month parameters, it also has Series, and season × Series and length × season interaction terms.

#### *United Kingdom*

Models were fitted to IWC Statistical Areas II, III and IV for UK data (Table 4). The simplest model fitted was for Area II (deviance = 121.5, 85 df,  $p = 0.006$ ). This

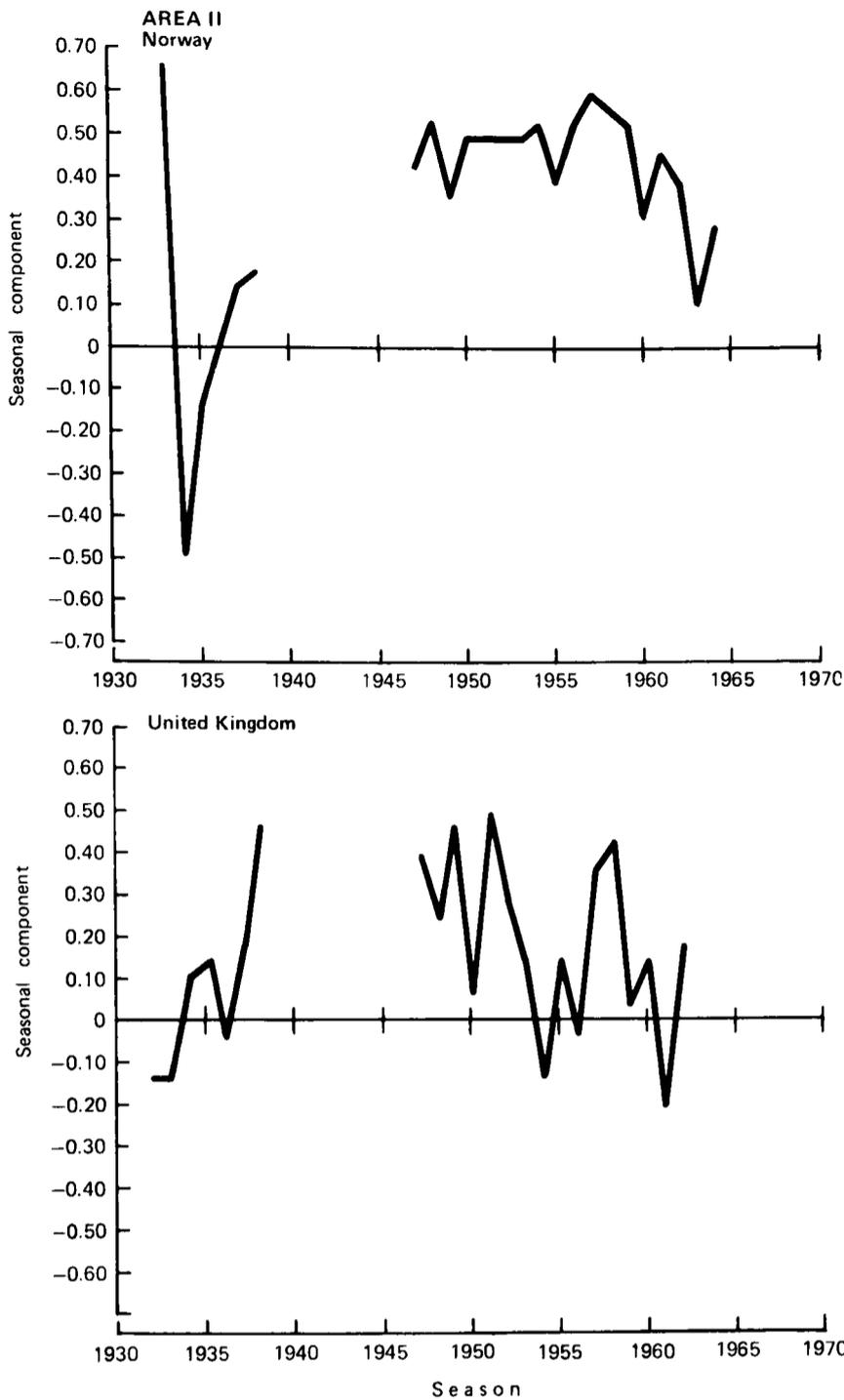


Fig. 3. The seasonal components of the transformed pregnancy rates over seasons for IWC Area II models, Norway and United Kingdom.

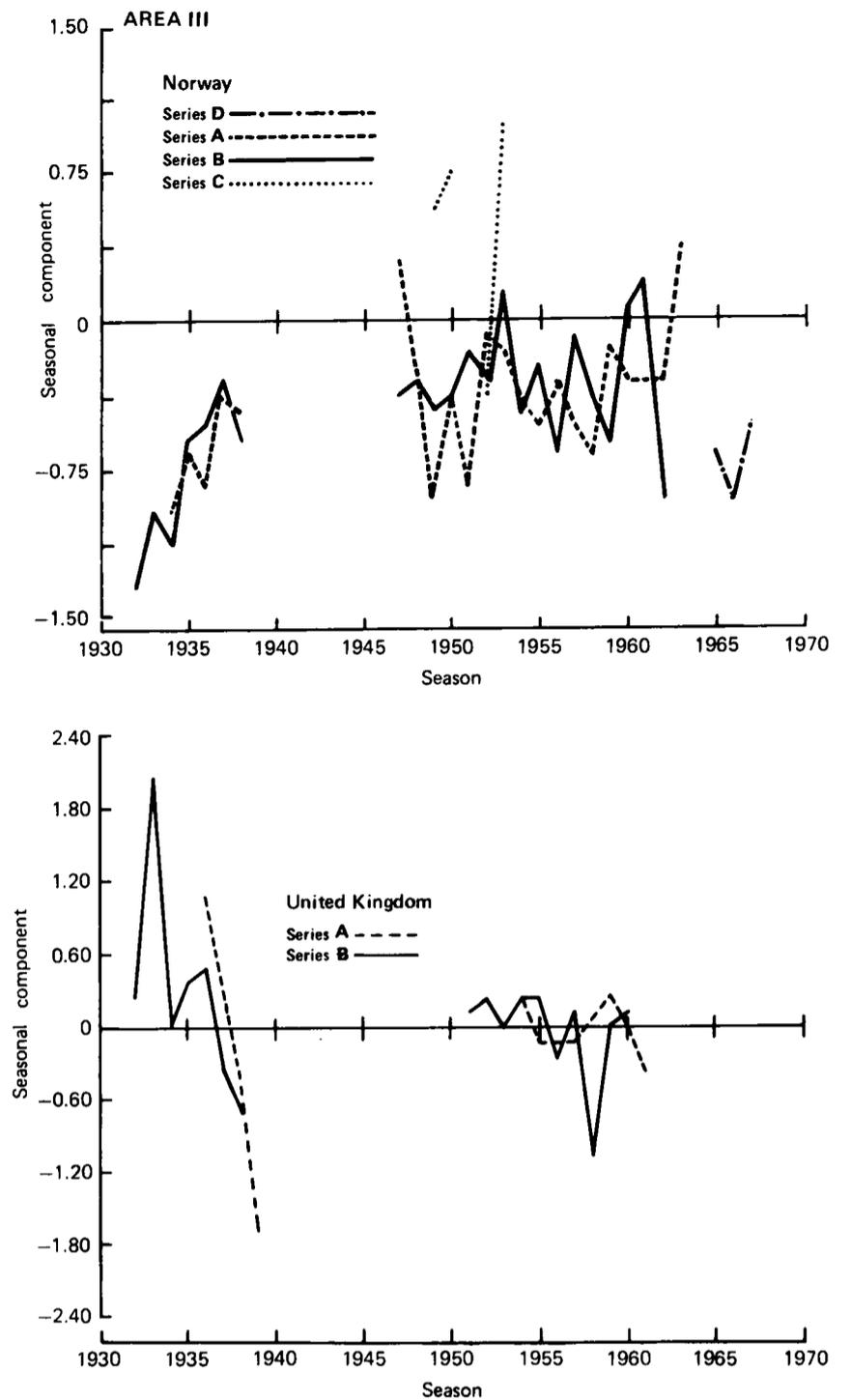


Fig. 4. The seasonal components of the transformed pregnancy rates over seasons for IWC Area III models, Norway and United Kingdom.

model contained a slope for mean length plus terms for the main effects of season, month, and Series. Therefore, pregnancy rate can be modelled as a linear function of mean length of females in each cell with the intercept adjusted by season, month, and Series.

The model for Area III (deviance = 63.7, 40 df,  $p = 0.010$ ) required the same main effects (season, month, Series, and mean length) plus a season  $\times$  Series interaction (that is, additional adjustment to the intercept for each season/Series combination). The model for Area IV (deviance = 36.9, 25 df,  $p = 0.059$ ) was somewhat simpler. It contained the main effects season, length, month and a length  $\times$  month interaction term.

#### Japan

To describe pregnancy rates for the Japanese data, models were fitted separately to two subsamples – all data except 1962/63 and 1962/63 data only – and then the results were combined into a single model (Table 5). This was done because of the very high variability of the transformed pregnancy rates within the 1962/63 samples

(mean deviance = 9.34 as opposed to about 4.13 within all other years).

For the 1962/63 sample only, a model with a month  $\times$  Series interaction term adequately accounted for the variability within this sample (deviance = 8.3, 7 df,  $p = 0.307$ ). For the remainder of the years, the data required correction terms for season, Series, and month. The main effect, Area, was not significant in itself but appears in the model through a length  $\times$  Area interaction term. A length  $\times$  season interaction term also appears. Thus separate slopes were required for each Area and each season with adjustments to the intercept by season, Series and month. The deviance of the fitted model for non-1962/63 data is 121.7, 86 df,  $p = 0.007$ . This results in a deviance of 130.0, 93 df,  $p = 0.007$  for the model as a whole.

#### Description of the seasonal components

General linear modelling has allowed us to assess in a formal way the effects of the factors which affect apparent

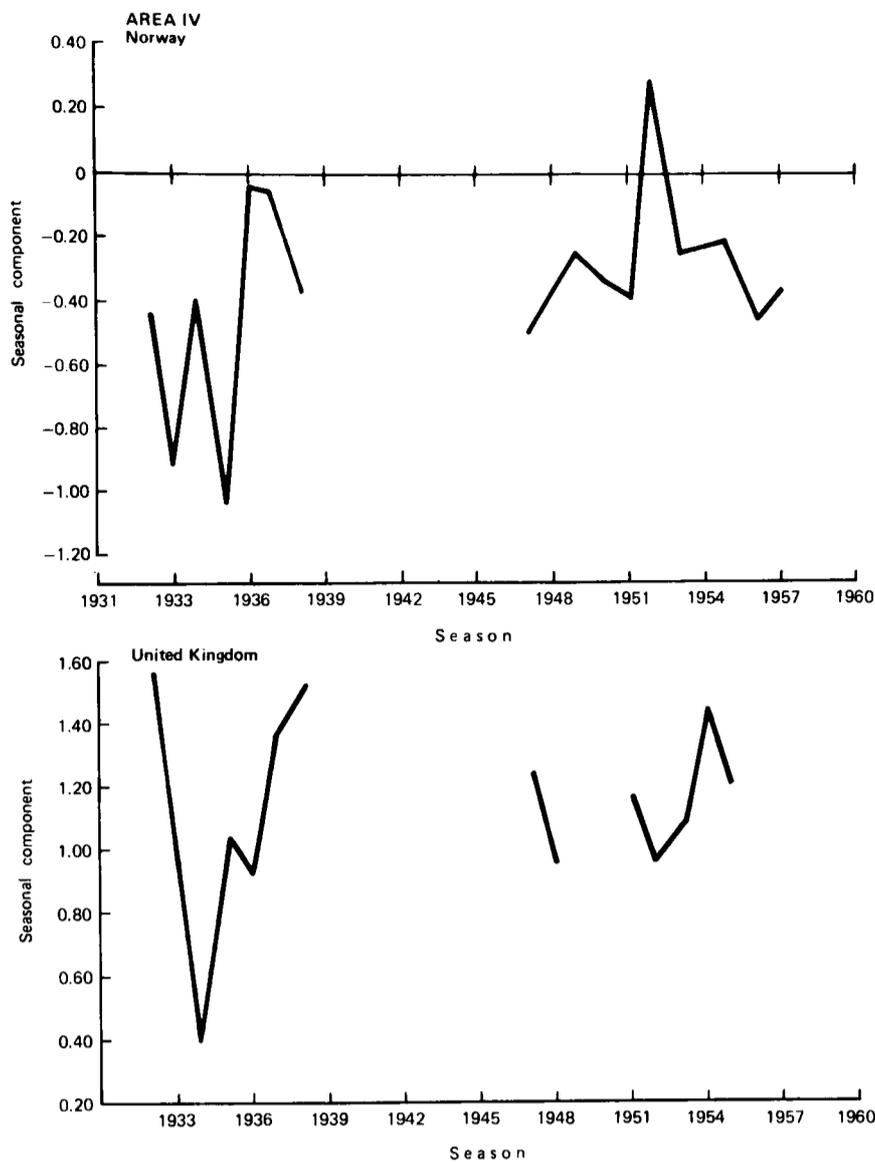


Fig. 5. The seasonal components of the transformed pregnancy rates over seasons for IWC Area IV models, Norway and United Kingdom.

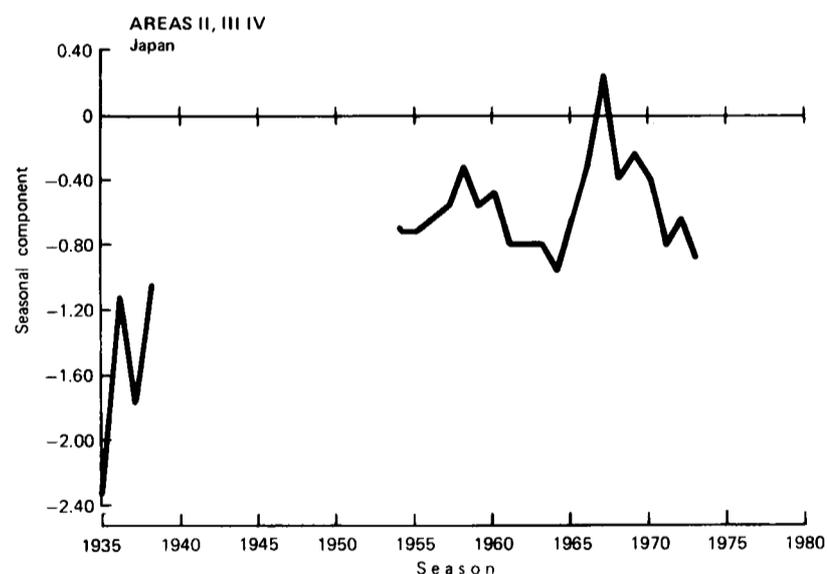


Fig. 6. The seasonal components of the transformed pregnancy rates over seasons for models using Japanese data, Areas II-IV, all seasons except 1962/63.

Table 6

Correlations ( $r$ ), sample sizes ( $n$ ) and  $p$ -values ( $p$ ) Norwegian and British seasonal components within Area

Area	$r$	$n$	$p$
II	0.023	22	0.9191
III			
Series A	-0.450	13	0.1228
Series B	-0.257	17	0.3193
IV	0.039	13	0.8994

Table 7

Catch and estimated weight of blue and fin whales in IWC Area II

Season	Catch		Weight (in tons)		Cumulative <sup>1</sup> weight
	Blue	Fin	Blue	Fin	
1931/32	668	482	61,301	25,493	86,795
1932/33	1,728	1,772	151,098	90,509	328,401
1933/34	1,601	1,092	145,458	57,469	531,329
1934/35	2,183	2,260	188,094	114,950	834,372
1935/36	3,791	3,379	318,007	169,929	1,322,308
1936/37	4,064	6,002	340,426	300,574	1,963,307
1937/38	2,561	10,762	218,293	537,750	2,719,351
1938/39	3,450	6,183	294,421	306,944	3,320,716
1945/46	599	4,901	50,040	245,224	3,615,980
1946/47	1,857	4,655	156,187	224,874	3,997,041
1947/48	1,536	6,128	119,799	311,674	4,428,514
1948/49	2,031	5,013	170,868	248,375	4,847,757
1949/50	1,051	7,157	88,361	356,634	5,292,752
1950/51	1,516	5,096	122,118	243,801	5,658,671
1951/52	447	5,959	37,121	300,764	5,996,556
1952/53	727	4,552	62,142	232,067	6,290,765
1953/54	540	7,435	44,805	369,382	6,704,952
1954/55	470	4,963	40,368	245,373	6,990,693
1955/56	439	6,597	34,866	313,245	7,338,804
1956/57	330	10,643	26,080	529,119	7,894,003
1957/58	236	5,211	19,265	258,351	8,171,620
1958/59	57	4,298	5,214	211,303	8,388,138
1959/60	58	4,718	5,047	231,518	8,624,703
1960/61	128	5,195	11,326	251,696	8,887,725
1961/62	189	6,538	15,414	327,973	9,231,111
1962/63	14	5,546	1,437	272,281	9,504,829
1963/64	0	7,318	0	365,106	9,869,936
1964/65	0	4,484	0	209,499	10,079,434
1965/66	0	612	0	27,516	10,106,951
1966/67	0	81	0	3,772	10,110,723
1967/68	0	173	0	7,948	10,118,671
1968/69	0	32	0	1,455	10,120,125
1969/70	0	32	0	1,497	10,121,622
1970/71	0	307	0	14,326	10,135,948
1971/72	0	263	0	12,445	10,148,393
1972/73	0	124	0	6,011	10,154,405
1973/74	0	199	0	9,465	10,163,870
1974/75	0	53	0	2,712	10,166,582
	32,271	150,215			

<sup>1</sup> Small differences between the sum of blue and fin whale weight and 'cumulative weight' are due to rounding.

pregnancy rates. In addition, we can isolate just the seasonal (i.e. yearly) component while adjusting for the other important factors such as Series and month. The seasonal component of an observation is the adjustment to the estimate of the logit of the pregnancy rate due to season only. For example, if pregnancy rate is modelled as a linear function of season only, then the seasonal component is the seasonal deviation from the grand mean. If pregnancy rate is modelled as a linear function of season, Series, and month with no interactions involving season, the seasonal component is the term added for each season. When interactions with season are present, then several components exist – one for each level of the interacting factor. In this case, the components are calculated for each level as in the case where no interaction is present. Once calculated, seasonal components can then be examined for trends over the years of exploitation.

For the models without an interaction term including season (i.e. Areas II and IV, Norway and UK), the

Table 8

Catch and estimated weight of blue and fin whales in IWC Area III<sup>1</sup>

Season	Catch		Weight (in tons)		Cumulative weight
	Blue	Fin	Blue	Fin	
1931/32	1,276	38	123,864	2,170	126,033
1932/33	9,992	1,692	880,147	86,303	1,092,483
1933/34	7,254	2,145	648,480	110,186	1,851,149
1934/35	8,299	8,005	665,849	392,232	2,909,230
1935/36	9,541	5,232	752,510	260,087	3,921,827
1936/37	5,031	5,005	403,328	254,581	4,579,736
1937/38	6,461	8,997	539,434	455,227	5,574,397
1938/39	4,452	5,484	354,825	263,301	6,192,523
1945/46	2,917	2,800	241,177	137,221	6,570,921
1946/47	2,963	4,382	247,296	225,960	7,044,177
1947/48	1,886	6,412	159,089	323,237	7,526,503
1948/49	2,972	6,457	258,033	333,550	8,118,086
1949/50	1,518	5,065	127,516	253,185	8,498,787
1950/51	1,419	4,079	116,396	193,532	8,808,715
1951/52	1,847	7,091	159,566	360,360	9,328,642
1952/53	1,452	11,229	118,482	550,039	9,997,163
1953/54	1,569	11,367	130,506	555,289	10,682,958
1954/55	685	13,568	57,006	649,717	11,389,681
1955/56	299	7,075	25,575	344,280	11,759,536
1956/57	275	3,780	23,026	186,771	11,969,334
1957/58	619	9,198	49,693	444,945	12,463,972
1958/59	373	9,168	32,150	439,965	12,936,088
1959/60	221	9,297	18,092	450,641	13,404,820
1960/61	1,112	13,242	72,599	660,428	14,137,847
1961/62	455	11,818	30,405	574,858	14,743,110
1962/63	715	8,977	43,791	422,661	15,095,562
1963/64	80	4,540	4,810	214,734	15,429,105
1964/65	11	1,209	622	56,499	15,486,226
1965/66	0	1,008	0	48,407	15,534,633
1966/67	2	1,534	72	73,582	15,608,287
1967/68	0	776	0	36,553	15,644,840
1968/69	0	527	0	26,089	15,670,929
1969/70	0	1,533	0	73,559	15,744,488
1970/71	0	1,696	0	79,992	15,824,481
1971/72	0	1,528	0	73,585	15,898,065
1972/73	0	875	0	42,526	15,940,592
1973/74	0	422	0	20,355	15,960,947
1974/75	0	168	0	7,833	15,968,780
75,696		197,419			

<sup>1</sup> Small differences between the sum of blue and fin whale weight and 'cumulative weight' are due to rounding.

seasonal component is simply the season term of the model plus the grand mean. However, both Area III models had a season × Series interaction term, and therefore the seasonal components were calculated separately for each Series. The seasonal components for Area II data (Norway and UK) are shown in Fig. 3; Area III (Norway and UK) in Fig. 4; Area IV (Norway and UK) in Fig. 5; and Areas II–IV combined (Japan) in Fig. 6. The high variability and lack of pattern of these graphs are easily seen.

We attempted to describe the seasonal components quantitatively by fitting orthogonal polynomials to them and found that linear and quadratic models inadequately described the patterns in all cases but two. Two sets had significant 5th degree (or greater) terms; three had significant 3rd or 4th degree terms; while for five, a constant fitted the components as well as any polynomial up to degree 6.

Although the seasonal components appear to have no explicable patterns, one might expect similarities of

Table 9

Catch and estimated weight of blue and fin whales in IWC Area IV

Season	Catch		Weight (in tons)		Cumulative <sup>1</sup> weight
	Blue	Fin	Blue	Fin	
1931/32	3,497	423	377,404	23,873	401,277
1932/33	6,728	969	633,612	54,072	1,088,961
1933/34	7,883	2,209	717,379	118,530	1,924,870
1934/35	5,476	1,429	490,931	76,650	2,492,451
1935/36	3,014	548	260,126	29,252	2,781,829
1936/37	5,082	2,284	403,574	112,905	3,298,308
1937/38	5,779	6,651	479,353	338,743	4,116,404
1938/39	4,901	5,718	402,987	283,980	4,803,371
1946/47	3,352	3,355	276,006	165,275	5,244,651
1947/48	1,947	4,686	169,940	237,143	5,651,735
1948/49	1,312	3,038	112,182	150,265	5,914,182
1949/50	929	2,917	79,292	140,720	6,134,195
1950/51	1,076	4,140	87,559	198,708	6,420,462
1951/52	1,188	2,190	96,840	108,431	6,625,733
1952/53	839	1,589	66,351	75,659	6,767,743
1953/54	356	2,287	28,461	111,587	6,907,790
1954/55	309	2,829	25,103	135,131	7,068,024
1955/56	323	3,158	26,372	151,588	7,245,983
1956/57	80	323	6,685	14,439	7,267,107
1957/58	186	3,521	14,564	163,539	7,445,210
1958/59	335	7,425	27,518	357,133	7,829,861
1959/60	413	6,510	27,805	310,526	8,168,192
1960/61	191	2,113	12,030	98,787	8,279,009
1961/62	119	3,157	8,186	142,333	8,429,527
1962/63	66	1,725	4,391	79,654	8,513,572
1963/64	32	777	1,858	34,631	8,550,062
1964/65	9	745	548	33,271	8,583,881
1965/66	0	64	0	2,866	8,586,748
1966/67	2	388	74	18,862	8,605,684
1967/68	0	753	0	38,546	8,644,230
1968/69	0	1,652	0	80,153	8,724,383
1969/70	0	1,080	0	51,184	8,775,567
1970/71	0	670	0	30,038	8,805,606
1971/72	0	727	0	31,584	8,837,190
1972/73	0	290	0	13,751	8,850,941
1973/74	0	90	0	3,589	8,854,530
1974/75	0	248	0	10,973	8,865,503
55,424		82,678			

<sup>1</sup> Small differences between the sum of blue and fin whale weight and 'cumulative weight' are due to rounding.

Table 10

Correlations (*r*) sample sizes (*n*), and *p*-values (*p*) of seasonal factors with biomass removals within Area. See text for details

Area	<i>r</i>	<i>n</i>	<i>p</i>
II			
Norway	0.477	24	0.0205
UK	0.116	23	0.5995
III			
Norway			
Series D	0.513	3	0.6571
Series A	0.420	22	0.0516
Series B	0.607	23	0.0021
Series C	0.561	10	0.0916
UK			
Series A	-0.022	13	0.9431
Series B	-0.425	17	0.0890
IV			
Norway	0.430	17	0.0849
UK	0.101	15	0.7203

patterns within a given Area when comparing data by nation. We compared the Norwegian seasonal factors with the UK seasonal factors, however, and found no significant correlations for any of the data sets (Table 6). There are no correlations between nations' seasonal patterns within any Area. This is unexpected, but it further strengthens the argument that data from different nations should not be pooled.

As a final check, we examined the correlation between the seasonal components and cumulative biomass removals of fin and blue whales. Biomass (i.e. weight) was calculated using the equation  $W = a(L/0.33)^b$ ,  $W$  = weight,  $L$  = length (in feet, as on the BIWS data tape), using the parameters calculated by Lockyer (1976) for blue whales ( $a = 0.0046, b = 3.09$ ) and for fin whales ( $a = 0.0238, b = 2.53$ ). Results are tabulated in Tables 7-9. Only 2 of 10 correlations (Table 10) were significant at the  $\alpha = 0.05$  level (Norway Area II; Norway Area III, Series B). If biomass removals have a real effect on pregnancy rates due to density dependence, one would expect more sets to be correlated, especially in the same Area or Series, or for whales taken by the same national fleet.

### CONCLUSIONS

In spite of the large sample sizes used in these analyses, we found very high variability in pregnancy rates across all factors examined. Thus, it is impossible to show that the population responded to heavy harvesting with increasing pregnancy rates or a shortened breeding cycle. We see significant differences and much variability by season, but no apparent trend. The variation we see could be due to environmental factors, the cyclic nature of the reproductive cycle, segregation among females by age or pregnancy condition, improper collection or reporting of data, or other unknown factors. If there is a trend at all, the variability masks it. If there is no trend (and there is no evidence for one) then assuming increases in reproductive rates, and consequently basing harvesting strategies upon such an assumed increase, could have severe, negative effects on a population.

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### APPENDIX

The data in our models (expressed as  $r$  pregnant females out of  $n$  females caught) are considered to be binomial random variables whose means are related in some way to the underlying variates describing the catch. Each observation  $r(i, j, k, l, m)$  is the number of pregnant females in season  $i$ , Area  $j$ , Series  $k$ , nation  $l$ , and month  $m$ , and  $n(i, j, k, l, m)$  is the total number of females in the same cell, and  $r(i, j, k, l, m)/n(i, j, k, l, m)$  is the pregnancy rate in that cell.

As explained in the text, the logit of the pregnancy rate is linearly modelled as a function of the concomitant variables. We describe here for the simplest example (Area IV, Norway) how to derive estimated pregnancy rates from the terms of the linear model. That model required only a slope for length and a seasonal intercept.

Thus if

- $r(i, j)$  is the number of pregnant females observed in cell  $j$  of season  $i$ ,
- $n(i, j)$  is the catch size in the  $j$ th cell of season  $i$ ,
- $l(i, j)$  is the mean length in the  $j$ th cell of season  $i$ ,
- $y(i, j) = \log [r(i, j)/(n(i, j) - r(i, j))]$ ,
- and  $\text{logit}^{-1} [y(i, j)] = \exp(y(i, j))/(1 + \exp(y(i, j)))$

The GLIM program fitted the model

$$y(i, j) = \text{leng} \cdot l(i, j) + \text{season}(i) + \text{GM},$$

where  $\text{leng}$  is a common slope for length,  $\text{season}(i)$  is an adjustment to the intercept for the  $i$ th season, and  $\text{GM}$  is the grand mean.  $\text{Logit}^{-1} [\hat{y}(i, j)]$  is the estimated pregnancy rate for cell  $j$  of season  $j$ .

# Recruitment Rates of Antarctic Fin Whales, *Balaenoptera physalus*, Inferred from Cohort Analysis

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## ABSTRACT

Several previous studies have attempted to make direct estimates of the change in recruitment rates that attended the exploitation of Antarctic fin whale stocks. In every one, the results were questionable owing to uncertainty concerning the estimated age compositions of early catches. This paper attempts to remove two sources of that uncertainty: the effects of an increase in growth rates that may or may not have occurred, and the effects of operational differences among countries in measuring whales. Its conclusion, like that of earlier studies, is that despite the apparent increase in pregnancy rates and the apparent decrease in the age at sexual maturity, recruitment rates fell rather than rose during the 1930s.

## INTRODUCTION

There are two quite distinct steps in an assessment of an exploited whale stock: first, estimating the original size of the stock and the amount by which fishing has reduced it; and second, determining the sustainable yield as a function of stock size. As in other fisheries, these two aims tend to be mutually exclusive. To estimate initial and present absolute stock sizes, either from change in catch-per-effort or change in catch composition, what is needed is a short period of intense exploitation that removes most of the stock. In this respect the Antarctic whale fisheries have been nearly ideal. But to estimate sustainable yield, what is needed is a number of years in which the rates of fishing mortality and net recruitment are of comparable size, and records of this sort are lacking.

As a result, while the sizes of Antarctic baleen stocks during their respective periods of exploitation are known reasonably well, their dynamics are hardly known at all, and scientific advice about sustainable yields has necessarily been based on one or the other of two assumptions:

- (i) In most early assessments (i.e. of blue and fin whales) it was supposed that the gross recruitment rate would increase with declining stock size to a maximum of two to three times the natural mortality rate.
- (ii) In most recent assessments (i.e. of sei and minke whales), an increase in recruitment rates has been calculated from observed changes in pregnancy rates and mean ages of sexual maturity. While it does seem plausible that these changes in reproductive parameters would produce more recruits, it has never been verified empirically. Moreover, this approach does not allow for possible changes in juvenile mortality, which could have a large effect on recruitment rates.

Owing to their relatively long period of exploitation, Antarctic fin whale stocks offer perhaps the best opportunity to obtain direct estimates of the actual change in recruitment rates as stock sizes were reduced by fishing. Allen (1970, 1971, 1972, 1973) has done this

by one method, estimating relative recruitment to the fishery year by year from changes in age composition of the catch and then determining absolute numbers from the effect of catches on catch per effort. But as explained by Allen (1973), the early age compositions required by this method were obtained by applying recent (i.e. *circa* 1960) age-length keys to early length distributions (i.e. back to 1931) and therefore are likely biased. Clark (1982) has attempted to do the same thing by a different method, viz by decomposing the early length compositions into age compositions by finite mixture methods and then back-calculating historical breeding stock sizes and subsequent recruitments by cohort analysis. Theoretical details of this method are given in Clark (1981).

Like Allen's, Clark's results showed a decrease rather than an increase in gross recruitment rates during the period of exploitation, but also like Allen's, Clark's results were questionable owing to doubts about the estimated age composition of the early catches. In Clark's case, the doubts arose from differences between Japanese and British age-length sampling data from Antarctic Areas II and III in the early 1960s. While the two data sets agreed as to the mean length of physically mature whales, they disagreed as to the lengths of adolescent animals: the British data showed females reaching the invariant mean length at sexual maturity around age 6, and therefore indicated an increase in growth rate during the period of exploitation, while the Japanese data showed animals reaching the mean length at sexual maturity around age 10, and therefore indicated no change in growth rate during the period of exploitation. Since the Japanese data were by far the most numerous, Clark decomposed all fin whale catches before about 1964 according to Japanese length-at-age distributions from the early 1960s.

With respect to Clark's reconstruction, there remains the question of whether the growth rate increased while stocks were being reduced. Another question is whether or not the length measurements from different countries are really comparable. In age-length sampling data from the 1950s, for example, the mean length of physically mature animals in Japanese records is 2–3 feet less than the corresponding British figure, and the length at which

50% of females are mature is also 2–3 feet less in Japanese than in British or Norwegian records. It is possible, therefore, that at least part of the discrepancy between Japanese and British age-length data from the early 1960s resulted simply from differences in operational procedures for measuring whales.

The purpose of this paper is to investigate how a change in growth rate, or differences among national length measurements, would affect Clark's results. Basically, the procedure will be to repeat the decompositions of length distributions and the cohort analyses with a range of assumptions about a change in growth rate and possible differences among national length measurements. It will be seen that the results are practically the same in every case.

### ALLOWANCE FOR A CHANGE IN GROWTH

In order to estimate the relative age distribution underlying a total relative length distribution, it is necessary to know the relative length distributions of all the age groups present. As explained by Clark (1981), these age-specific distributions become the columns of the regression matrix used to decompose overall length distributions.

Now if there was no change in the growth rate of Antarctic fin whales, then only one matrix of age-specific length distributions is needed to decompose all the historical length distributions of each stock, and an empirical estimate of that matrix can be obtained directly from recent joint age-length distributions. This was the plan followed by Clark (1982).

Earplug readings, however, indicate that the mean age at sexual maturity has declined, while the corresponding mean length at sexual maturity, like the mean length at physical maturity, has remained constant. Lockyer (1978) reported these lengths for females as 65.3 and 73.0 ft, respectively, and further supposed that the length at one year of age had also remained constant at 52.6 ft. With these three points fixed, the age at sexual maturity determines a von Bertalanffy growth curve. (A lower age at maturity of course requires a higher growth rate, since the fixed length at sexual maturity must be reached sooner.) These lengths in fact refer only to the stocks in Areas II, III and IV. In other Areas growth is different, and since all kinds of biological data are relatively scarce for those stocks, only the stocks in Areas II–IV will be considered here.

Table 1 shows the estimated changes in mean age at sexual maturity by Area, treated in each case as a linear decline over a period of 30 years or so. For the purposes of this paper, the growth curves implied by the end points

Table 1

Approximate end points of a linear trend in mean age at sexual maturity with year-class as read from figures in Lockyer (1979)

Area	Start of trend		End of trend	
	Year-class	Age	Year-class	Age
II	1920	10.5	1950	6.5
III	1920	11.5	1950	8.0
IV	1920	11.5	1950	8.5

in each Area were calculated, and the growth rates so obtained (i.e. the values of the von Bertalanffy parameter  $K$ ) were taken to define a corresponding linear increase over the same period.

Given the initial growth schedule implied by the starting values, and the sequence of year-specific values of  $K$ , it was then a fairly straightforward computational problem to update the length-at-age schedule each year according to the prevailing growth rate. In this scheme, of course, the mean length of a particular year-class at a particular age depended on the history of  $K$ -values it had experienced.

To flesh out the distribution of length around each mean, it was assumed that the distributions were normal. In accordance with empirical joint age-length distributions, the standard deviation was made to decrease linearly from 4 ft at age 1 to 3 ft at age 20 and beyond.

While the matrices of relative length distributions constructed in this way are about the best that can be done, they disagree in some respects with empirical data:

- (i) The form of empirical relative length distributions is not very close to normal. The Japanese distributions of length at age reported by Clark (1982) tend to have long flat tails and spikes in the middle.
- (ii) Except for rather low ages at sexual maturity, the calculated von Bertalanffy lengths are too low around the age at physical maturity – 25 years or so (Table 2). Whales in nature stop growing then, but when  $K$  is low the von Bertalanffy curve at age 25 is still some way from the asymptote.

Table 2

Female fin growth schedules calculated from the von Bertalanffy equation

Age at maturity Corresponding $K$	12 0.09	9 0.12	6 0.19
Length at age:			
3	55.9	57.0	59.2
6	59.9	61.9	65.3
9	63.0	65.3	68.7
12	65.3	67.7	70.6
15	67.1	69.3	71.7
18	68.5	70.4	72.2
21	69.5	71.2	72.6
24	70.3	71.8	72.8
27	71.0	72.1	72.9
30	71.4	72.4	72.9
33	71.8	72.6	73.0
36	72.1	72.7	73.0

- (iii) Finally, and particularly for Area II where the growth rate is supposed to have increased most, the calculated matrix disagrees with the largest and best set of age-length sampling data available, namely, the Japanese collections from around 1960, which indicate no increase in growth rate. Since there is no way to resolve this conflict, the length decompositions below will be performed both with and without the change in growth rate implied by the values in Table 1.

### ALLOWANCE FOR DIFFERENCES AMONG NATIONAL MEASUREMENTS

As mentioned above, the mean lengths reported by various countries for the same groups of fin whales sometimes agree but usually do not. In particular:

- (i) Japanese and British data from the early 1960s agree as to the mean length of physically mature animals, but disagree as to the mean lengths of adolescents.
- (ii) Japanese data from the late 1960s agree with British data from the early 1960s for all age groups.
- (iii) Japanese data from the late 1950s show a mean length of physically mature animals some 2–3 feet less than British data from the same period.
- (iv) Graphs of pregnancy rates as a function of length are similar in shape for all countries, but in Japanese data are shifted downward by 2–3 feet.

What all these data suggest is the possibility of some differences among countries in the method of measuring whales, so that the scales were not really the same, or at least not always the same. This question is discussed more fully by Clark (1983).

Probably there was no consistent relationship among national measurements, but for the purposes of this paper some average differences will be estimated and employed. Of all comparisons, the most consistent differences appear among the various national records of pregnancy rate as a function of length. Since some countries were evidently much more conscientious than others in looking for foetuses, the absolute values are in fact quite variable, but they can all be put on a common standard by scaling each set of national pregnancy-at-length proportions by the value obtained for large whales (here 73 feet and above), which were certainly almost all mature.

When this is done, each country's results are set on a scale from zero to one as a function of length, but set off from one another as a result of the supposed differences among length measurements. To estimate those differences, what was done was to find the amount by which one schedule would have to be shifted to make it coincide as closely as possible with another. Specifically, in Areas II–V where Norwegian catches were the most numerous, the scaled Norwegian schedule was taken as the standard, and the scaled schedules of other countries were shifted one way or the other to make them coincide as well as possible, according to a weighted sum-of-squares criterion.

The minimizing shifts were located in each case by means of an interactive computer routine that mapped the sum of squares over a prescribed range of trial shifts, and by this means enabled the user to focus in on the minimum, in cases where there was a minimum. For the minor whaling countries there often was no minimum, but for the major countries a minimum almost always appeared, and its value was quite consistent among Areas (Table 3).

When these minimizing shifts are weighted by the goodness-of-fit in each Area and referred to the UK rather than Norway (since the fixed lengths referred to above are UK lengths), the upshot is that with respect to UK length measurements on animals of equal size, Nor-

Table 3

Shifts (in ft) required to minimize the weighted sum of squared differences between the indicated and the Norwegian scaled pregnancy-at-length schedules, 1931–64 catches

Area	II	III	IV	V
<i>Country</i>				
USSR	-0.22	0.27	0.47	0.50
Japan	2.36	2.08	2.32	1.74
Netherlands	0.34	0.81	- <sup>1</sup>	- <sup>1</sup>
UK	-0.07	-0.62	-0.26	-0.64

<sup>1</sup> Negligible catches.

wegian measurements are 0.42 ft less, Soviet measurements 0.69 ft less, Dutch measurements 1.00 ft less, and Japanese measurements 2.57 ft less. For other countries no estimates were obtained.

Since the consistency, and even the occurrence, of differences among national length measurements are in doubt, all decompositions were performed both with and without the shifts set out above.

### CALCULATIONS AND RESULTS

For each Area, stock histories were reconstructed by the procedure detailed by Clark (1982), viz.:

- (i) The starting point was a stock equal in size to the commonly accepted estimates obtained by the DeLury technique, and equal in age composition to the well-sampled Japanese catches from around 1960. No allowance was made for partial recruitment, so the abundance of the youngest age groups was likely underestimated.
- (ii) The length compositions of all female catches back to 1931 were decomposed into age groups by the regression method.
- (iii) The size and composition of the stock in each year was back-calculated from the starting point to 1931 by cohort analysis (i.e. by adding to each year-class the estimated catches taken from it and calculated natural mortality). From 1931 back to 1915 or so, when lengths were not reported, catches in Areas II and III were allocated to age groups according to their abundance in the back-calculated stock.

The final result of these calculations in each case was a series of estimates of the size of each year-class at age 3 and the number of mature females that produced it. (For simplicity and comparability mature females were defined throughout as those 10 years and older.) A happy property of these results is that while the absolute numbers are sensitive to the starting stock size and natural mortality rate used in the cohort analysis, the gross recruitment rates calculated from them are nearly identical under all reasonable assumptions.

As explained above, the entire procedure was carried out in four ways for each Area: with and without a change in growth rate; and with and without shifting national length compositions to account for possible differences in length measurements. When a national length composition was shifted, the operative size limit and consequently the regression matrix were adjusted accordingly. In effect, each country's catches in each season were translated to

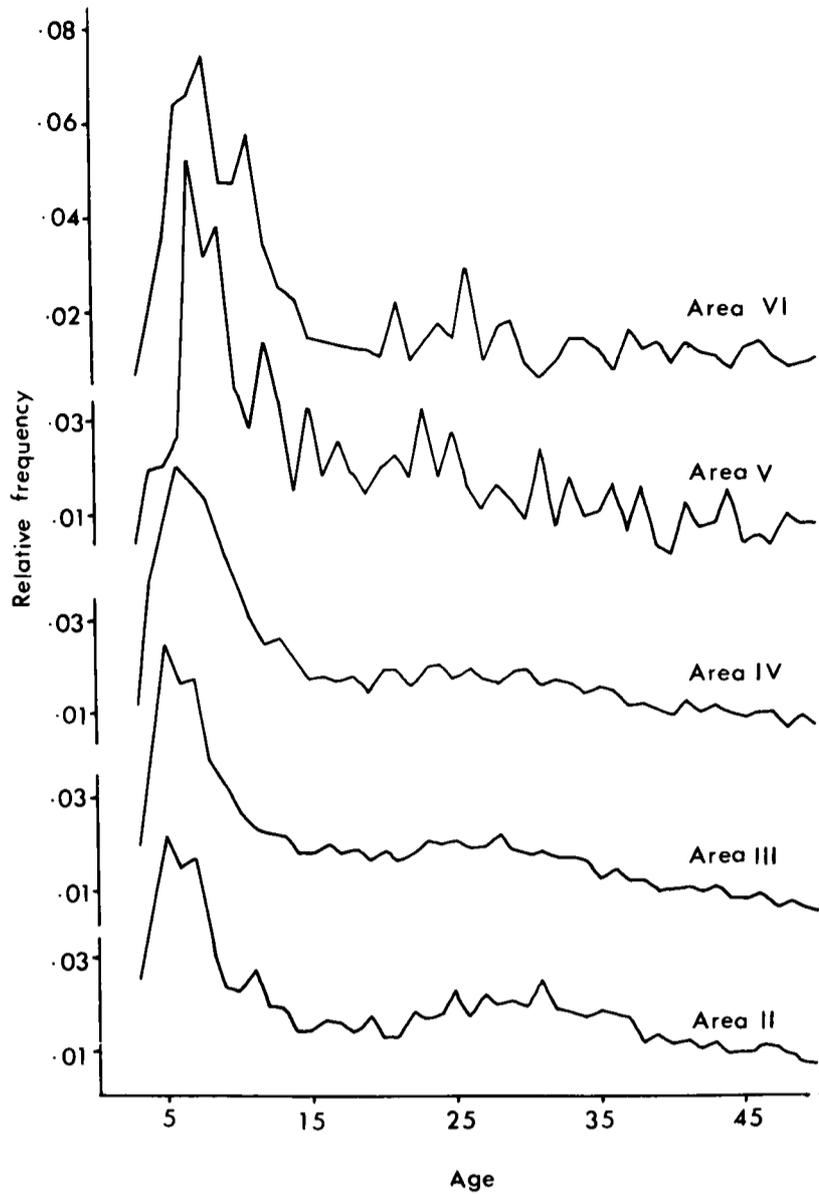


Fig. 1. Age distributions of Japanese catches of female fin whales around 1960. (Reproduced from Clark, 1982.)

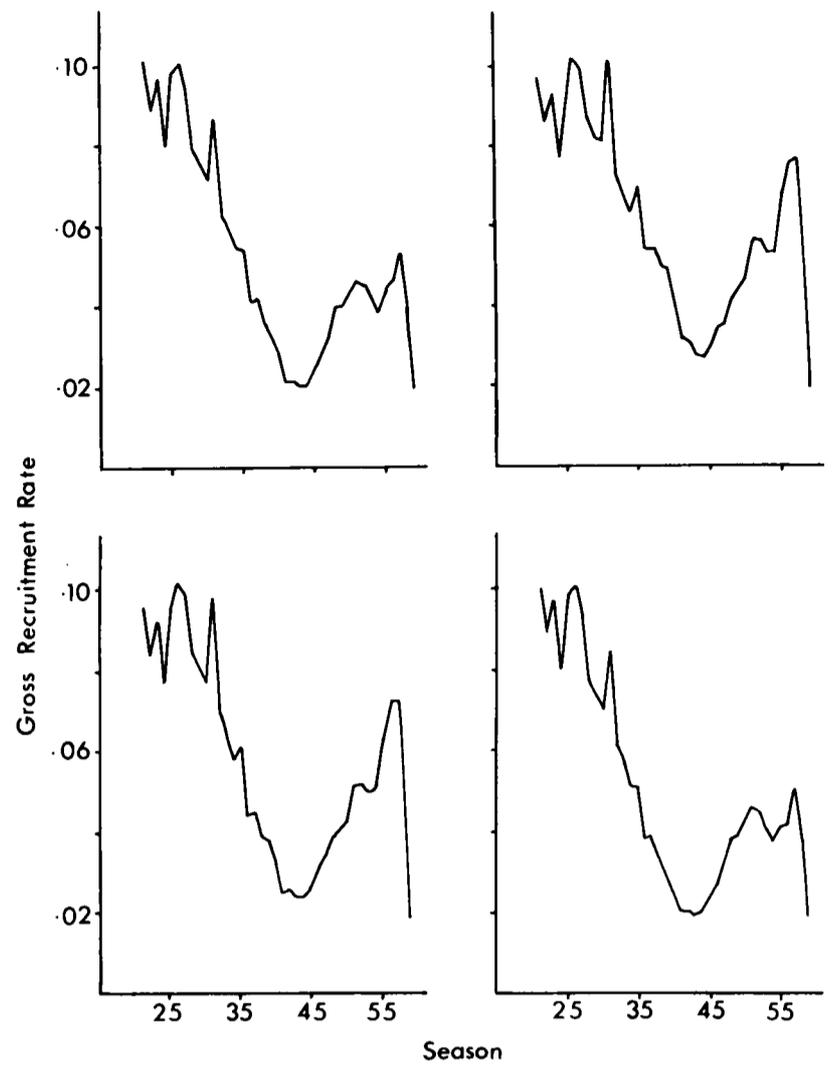


Fig. 2. Recruitment rates in Area II by season (where 25 = 1925/26 etc.) estimated according to various treatments of national length distributions and growth, as follows:

- (a) Lengths not shifted, growth constant.
- (b) Lengths not shifted, growth accelerated.
- (c) Lengths shifted, growth constant.
- (d) Lengths shifted, growth accelerated.

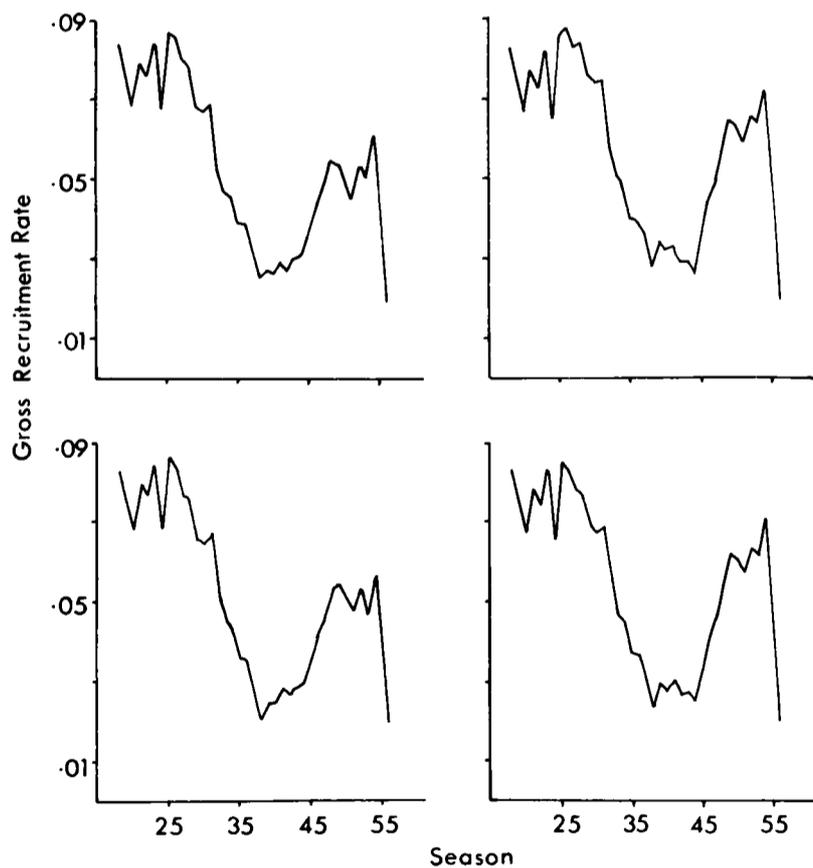


Fig. 3. Recruitment rates in Area III by season (where 25 = 1925/26 etc.) estimated according to various treatments of national length distributions and growth, as follows:

- (a) Lengths not shifted, growth constant.
- (b) Lengths not shifted, growth accelerated.
- (c) Lengths shifted, growth constant.
- (d) Lengths shifted, growth accelerated.

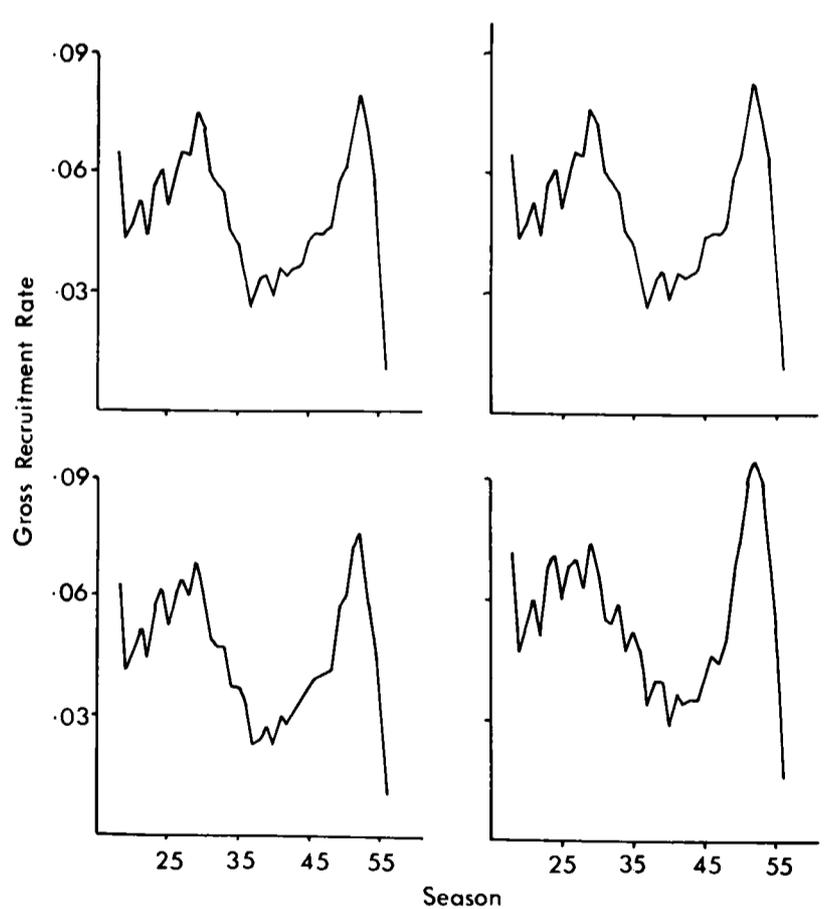


Fig. 4. Recruitment rates in Area IV by season (where 25 = 1925/26 etc.) estimated according to various treatments of national length distributions and growth, as follows:

- (a) Lengths not shifted, growth constant.
- (b) Lengths not shifted, growth accelerated.
- (c) Lengths shifted, growth constant.
- (d) Lengths shifted, growth accelerated.

British feet and then decomposed according to a regression matrix scaled in British feet but trimmed to the size limit appropriate to that country.

The resulting sequences of estimated gross recruitment rates (Figs 2–4) are very similar under all assumptions. They are also very similar to the results previously reported by Clark (1982). They show a large decline in the 1930s, followed by an increase in the 1940s. Only in Area IV, however, does the post-war increase reach the level of 1930, which was presumably close to the replacement level. The very sharp drop-off at the very end of each graph is certainly the result of partial recruitment of the few youngest age groups in the starting stock of each cohort analysis. That feature is of course not meaningful, but its very abruptness does suggest that the effect of partial recruitment does not extend back more than a few years from the end of each series.

In addition to the series plotted in Figs 2–4, a few sets of results were obtained with the standard deviation of length at age fixed at 3 ft throughout (rather than declining linearly from 4 ft at age 1 to 3 ft at age 20 and beyond). These results are not reported because the change had virtually no effect.

### DISCUSSION

Within wide limits, the results obtained here do not depend on the assumed starting stock sizes, natural mortality rates, growth changes, or differences among national length measurements. Since the length-at-age distributions used for the decompositions, and the various national catch-at-length distributions, can be shifted substantially without much effect, it is also unlikely that the results could be much affected by length selection, which in theory would be expected to produce some bias in the estimated catch-at-age distributions.

With all those possible causes of error accounted for, the only one remaining is the age composition of adult animals in Japanese samples from around 1960 (Fig. 1). As explained by Clark (1982), it is the relatively flat section of those distributions between ages 15 and 30 that translates into decreasing estimated recruitment rates between 1930 and 1945. Allen (pers. comm.) has suggested that owing to length selection, recruitment to the fishery may not have been complete until the age of physical maturity (i.e. around age 25), in which case the estimated recruitment rates could be biased all the way back to 1935 or so – virtually the whole series. It seems unlikely, however, that length selection could have this effect, since at least by age 20 the mean length is

within two feet of the asymptotic length, and the sharp decline in estimated recruitment in the 1930s depends on the relative abundance of animals 20–30 years old in Japanese catches around 1960.

If the Japanese data do not accurately represent the age composition of adults in 1960, it may be because of latitudinal segregation by age rather than length selection. Japanese catches were taken mostly at lower latitudes than British and Norwegian catches (e.g. 50° S rather than 60° S), so if younger adults were more likely to summer in high latitudes than older adults the Japanese catches would not accurately show their relative abundance. This possibility needs to be checked against British, Norwegian and Soviet age compositions, which is to say that those countries' data should be made available for study, as the Japanese data have.

But latitudinal segregation by age seems far-fetched. It would certainly not be considered as a possible source of error if the results had shown the assumed increase in recruitment rates under exploitation rather than a decrease.

After finding a similar decline in recruitment rates by his methods, Allen (1972) wrote: 'Thus, although there appears to be evidence, both of an increase in the pregnancy rate and of an advance in the age at maturity, direct measurement of the recruitment rate so far presents no evidence of any compensatory rise accompanying the decline of the population.' The conclusion of the work reported here is the same.

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# Growth and Reproductive Rates in Two Populations of Spinner Dolphins, *Stenella longirostris*, with Different Histories of Exploitation<sup>1</sup>

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## ABSTRACT

A model of density-dependent change in net reproductive rate (births minus deaths) has been used in assessing status of dolphin stocks in the eastern tropical Pacific. The eastern spinner population has been estimated to be at a lower fraction of original size (17–25%) than is the population of whitebelly spinners (58–72%). Higher reproductive rates would be expected in the former than in the latter on the basis of the density-dependent model, provided the latter is above its level of maximum net production. Based on analyses of over 4,000 specimens collected through 1978: (1) there is a relative paucity of fully adult males in the eastern spinner population (possibly resulting in lower average fertility), (2) the eastern spinner female attains sexual maturity about one tooth-layer unit (probably one year) earlier than does the whitebelly spinner, (3) ovulation rate in young females is lower in the eastern spinner population, and (4) the proportion of all females which are sexually mature is lower in the eastern spinner population. Gross annual reproductive rates (proportion female  $\times$  proportion of females mature  $\times$  pregnancy rate) are not different in the two populations (about 8–10% in both cases). This comparison does not confirm the hypothesis that a density-dependent increase in gross reproduction occurs in the spinner dolphin.

## INTRODUCTION

Tuna seiners operating in the eastern tropical Pacific (ETP) kill dolphins incidentally during fishing operations (Perrin, 1969; Fox, 1978). The incidental kill has reduced the abundance of some geographical forms, by as much as 83% (Smith, 1983). The basic model used in assessing the status of stocks and estimating net production has been based on density-dependent change in gross production, i.e. that reproductive rates go up as density goes down (*loc. cit.*). Such a change has not been observed in a dolphin population; its use in dolphin assessment and management has been based on observations of populations of terrestrial mammals, pinnipeds and two baleen whales (Fowler, 1981). This paper presents the results of a comparative study of two populations estimated to be at different proportions of their initial sizes, in an attempt to validate the assumption of density-dependent change in reproductive rates.

At least four morphologically differentiated stocks of spinner dolphins, *Stenella longirostris* (Gray, 1828), exist in the eastern tropical Pacific (Perrin, 1975a and b; Perrin, Sloan and Henderson, 1979; and Au, Perryman and Perrin, 1979). The two forms treated in this paper are the 'eastern spinner dolphin', which occurs from close to the coast of Mexico and Central America to several hundred kilometers offshore, and the 'northern whitebelly spinner dolphin', which is a more high-seas form, found north of the equator and ranging west to about 150° W long. In 1979, the population of eastern spinners was estimated to be 17–25% (central estimate 20%) of its initial size, whereas the population of northern whitebelly spinners was estimated to be 58–72% (central estimate 65%) of initial size (Smith, 1983). In assessment and management

of the ETP dolphin stocks, maximum net productivity level (MNPL, in numbers of individuals) has been assumed to occur at population size somewhere between 50 and 80% of initial size (Smith, 1983). If it is assumed that the two rather similar populations had similar reproductive rates prior to exploitation, then from the population-dynamics theory outlined above, the current reproductive rates should be higher in the eastern spinner population than in the whitebelly spinner population, providing that MNPL is below 65% and that the form of the density-dependent response is not strongly curvilinear (see Fowler, 1984, for discussion of the form of the density-dependent response). Alternatively, no detectable difference in the reproductive rates could mean that both populations are below (or above) MNPL, that the form of the response is strongly curvilinear, that the two populations had different rates initially, or that density-dependence may exist but act on some other life history parameter. The purposes of this paper are to present estimates of growth and reproductive parameters for the northern whitebelly spinner, as was done for the eastern spinner (Perrin, Holts and Miller, 1977), and to compare the estimates for the two populations.

## MATERIALS AND METHODS

### The field program

Most of the data and specimens were collected by NMFS scientific technicians aboard commercial tuna seiners. The collection procedures were the same as previously described for the spotted dolphin, *Stenella attenuata* (Perrin, Coe and Zweifel, 1976). Data were collected on 1 cruise in 1968, 4 in 1971, 12 in 1972, 21 in 1973, 33 in 1974, 30 in 1975, 48 in 1976, 72 in 1977 and 74 in 1978. Some specimens were also collected by personnel of the Inter-American Tropical Tuna Commission aboard chartered purse seiners.

In 1971 and early 1972, when the field program was

<sup>1</sup> An earlier version of this paper was working Document SOPS/79/30 prepared for the Status of Porpoise Stocks Workshop, 27–31 August 1979 at the Southwest Fisheries Center, La Jolla, California, and SWFC Admin. Rep. LJ-79-29 (1979).

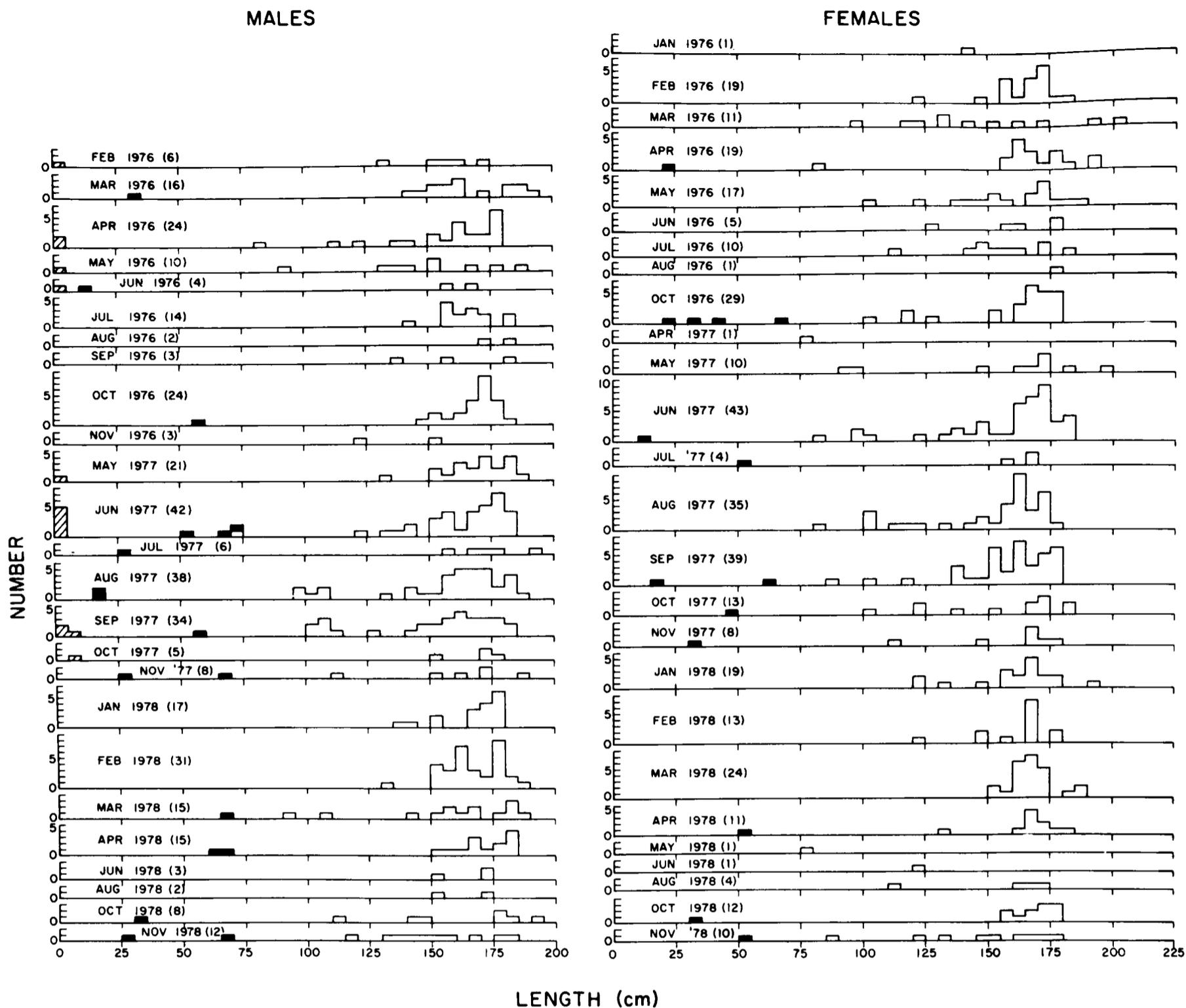


Fig. 1. Length frequency distributions by month and year of eastern spinner dolphins collected 1976-78 and included in the present study. (Sample sizes in parentheses.) Solid squares represent foetuses; hatched squares represent foetuses of undetermined sex (plotted with males).

very limited, adult female specimens were preferentially selected for dissection when available, and the samples for those periods are therefore biased with respect to the age and sex structures of the kill. In 1968 and on cruises from October 1972 on, no selection was done in determining which animals were to be examined (the attempt was made to examine all the animals in small-kill sets - less than about 30 - and the first 30 or so that came to hand in large-kill sets), and those samples are assumed to be cross-sectional with respect to the kill. Foetuses were not collected in 1968.

The sample of animals for which life history data including, but not limited to, sex and body length were collected includes over 4,000 specimens. Length-frequency data by month and sex were presented for eastern spinner specimens collected before 1976 in Perrin *et al.* (1977); length-frequency data for the balance of the eastern spinner material (1976-78) and the whitebelly spinner specimens are presented in Figs 1 and 2. Charts showing collection localities are presented in Henderson, Perrin and Miller (1980).

The morphological differences between the two races of spinner dolphins are average differences, with considerable overlap, and their geographical ranges overlap, so schools and single-school groups of specimens are identified at sea based on their model characteristics. In case of single specimens or small series of specimens coming from the area of geographical overlap and for which information on the nature of the entire school is minimal, the danger exists of erroneous identification. Such error would tend to obscure any differences between the two populations in reproductive parameters. We were conservative in reviewing identification of such specimens to race, and designated many as 'unidentified spinner dolphins' (excluded from the present study).

Laboratory procedures were the same as reported for the studies of the eastern form of *S. longirostris* (Perrin *et al.*, 1977) and of the spotted dolphin (Perrin *et al.*, 1976).

The NORMSEP computer program was used to define modes in the length-frequency distributions for eastern calves. The program was written by Hasselblad (1966)

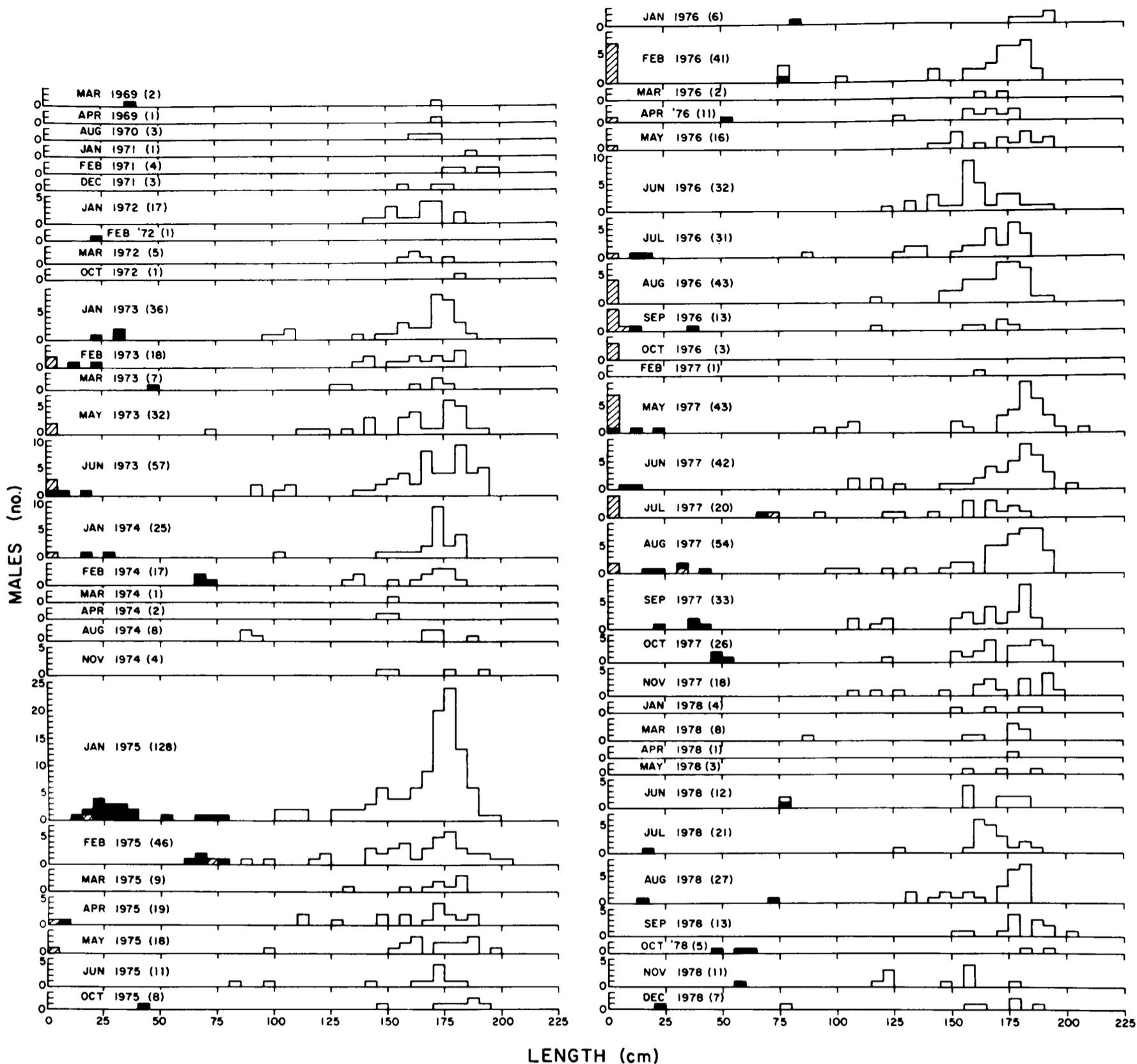


Fig. 2A. Length-frequency distributions by month and year of male northern whitebelly spinner dolphins collected 1969-78 and included in the present study. (Sample sizes in parentheses.)

and modified by Patrick K. Tomlinson, Inter-American Tropical Tuna Commission. The program separates a mixture of normal length distributions into its components, assuming that the length of individuals within age groups are normally distributed and that an unbiased sample of the length distribution was obtained that would allow estimation of growth rates in juveniles. The computer programs BMDPAR and BMDP3R (Dixon, 1981) were used in fitting nonlinear models.

**RESULTS**

**Growth**

*Length at Birth*

The average length at birth in the eastern spinner was estimated by Perrin *et al.* (1977) at 76.9 cm based on a sample of 101 fetuses and calves, including 23 specimens

of the whitebelly spinner and 23 unidentified to race. We estimated average length at birth in the whitebelly spinner based on a sample of 51 fetuses and calves to be 75.9 cm, based on a fit to the logistic model (Fig. 3). We rounded the estimate off to 76 cm in analyses below. The estimate is subject to the same potential biases as that for the eastern spinner (elaborated in Perrin *et al.*, 1977).

*Length of gestation and foetal growth rates*

We assumed these parameters to be the same in both forms, i.e. 10.6 months and 8.37 cm/month (linear phase), as estimated for the eastern spinner (Perrin *et al.*, 1977).

*Postnatal growth*

Perrin *et al.* (1977) examined length frequency data for the eastern spinner (data from 1975 and earlier) and found no pattern of length mode progression over time. Growth rates were therefore estimated by more deductive

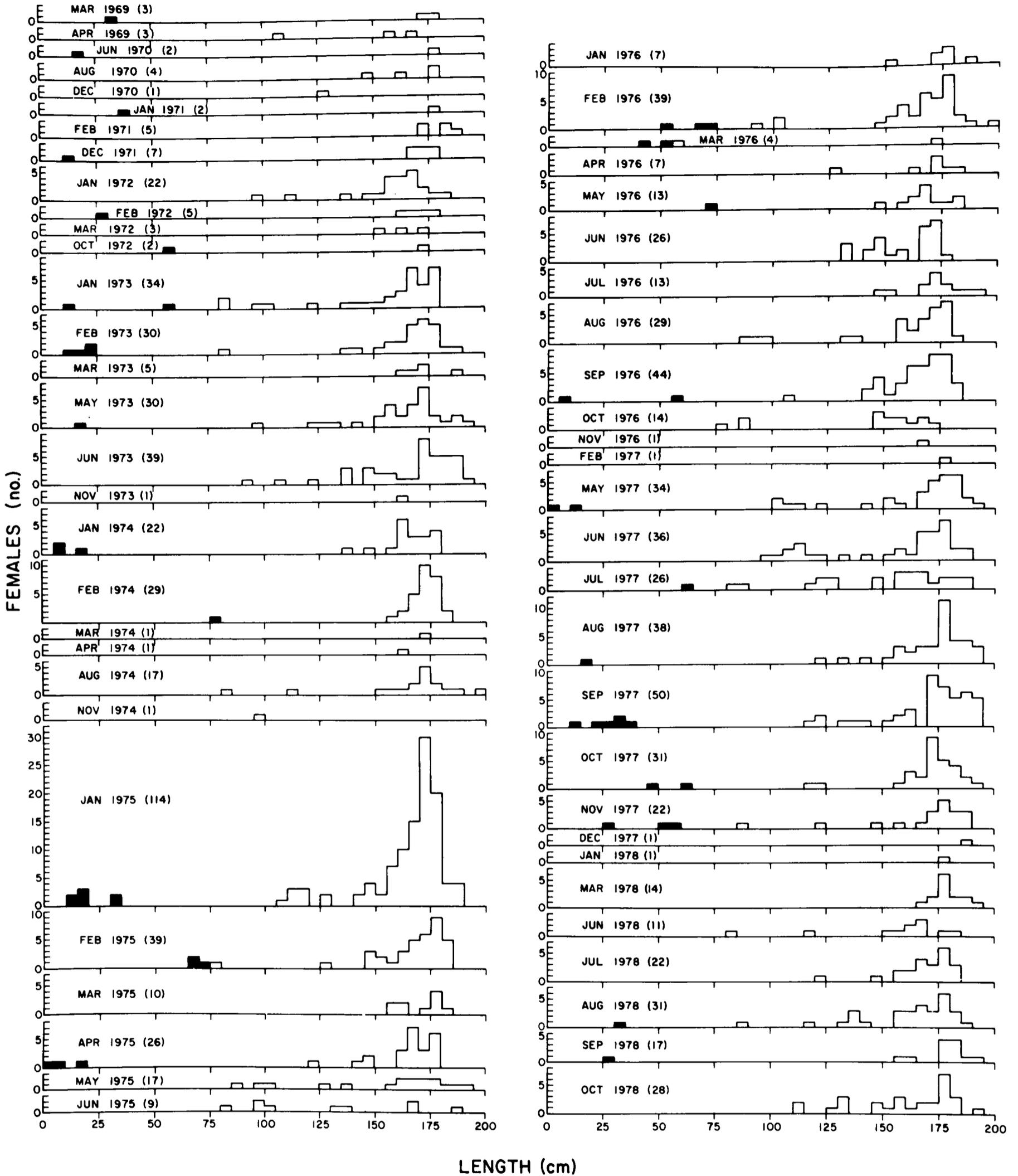


Fig. 2B. Length-frequency distributions by month and year of female northern whitebelly spinner dolphins collected 1969-78 and included in the present study. (Sample sizes in parentheses.)

means. We examined the length frequency data for the whitebelly spinner and encountered a similar situation, i.e. no clear pattern of modal progression with season, this in spite of the finding of seasonal patterns in the birth dates by Barlow (1984). However, re-examination of growth rates in the eastern spinner based on a larger

sample than was available for the first study (including data from 1976, 77 and 78) did yield a pattern of modal progression (Fig. 4) covering a span of at least 12 months after birth.

We fit the NORMSEP-estimated modes to the linear model, the logarithmic model and the Gompertz model.

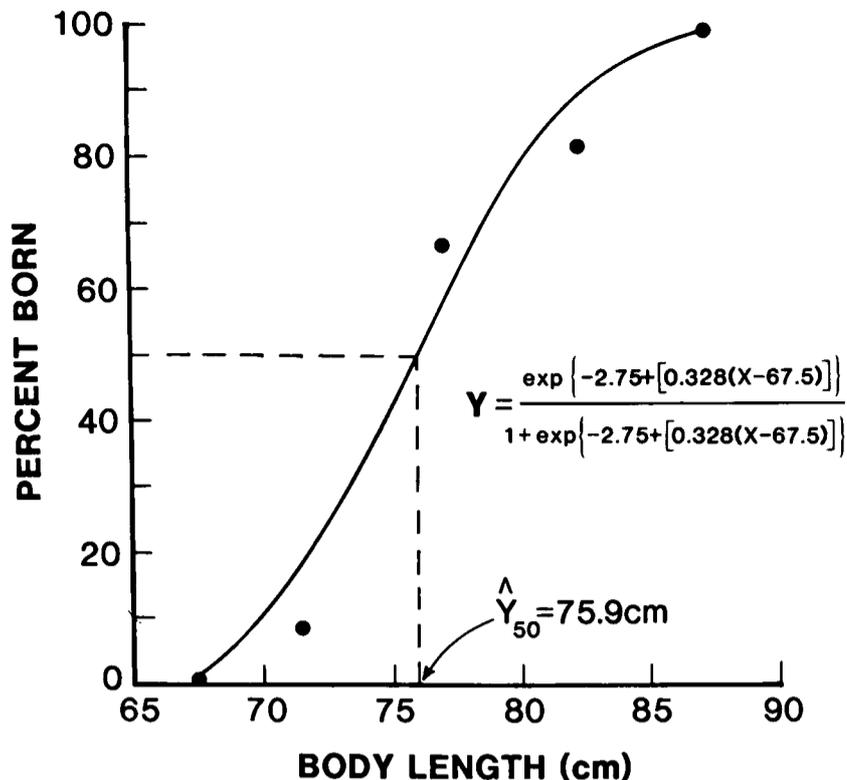


Fig. 3. Estimation of average length at birth, based on least-squares fit of per cent postnatal (percentage that are calves and not foetuses) on body length, in 5-cm increments, to the logistic model for 51 specimens of the northern whitebelly spinner dolphin (24 foetuses and 27 calves) between 65 and 89 cm long.

The Gompertz model provided the best fit (Fig. 3), yielding an estimated average growth rate for the first year of 4.3 cm/month and an average length at one year of 127.5 cm.

*Length relative to tooth layering*

Perrin *et al.* (1977) presented growth curves and equations for the eastern spinner in terms of length relative to number of postnatal dentinal growth layer groups (GLGs, terminology of Perrin and Myrick, 1980, = 'dentinal layers' in terminology of Perrin *et al.*, 1977). We examined relationships between GLGs and length for 170 male and 232 female northern whitebelly spinners (Fig. 6). The sub-samples for age determination were selected as for the eastern spinner (Perrin *et al.*, 1977).

We fitted curves to the single-GLG means using a two-cycle model<sup>2</sup> as was done for the eastern spinner (*loc. cit.*), with some differences. (1) The upper end of the second-phase curve (asymptotic length) estimated as it was for the eastern spinner, as the average length of the few very old ( $\geq 13$  GLGs) specimens in the samples for both sexes, was lower (by 16 mm in females) than the average length of adult animals, probably a statistical artifact. The procedure resulted in estimates of asymptotic length close to the average sizes of adults (for example 174.9 cm vs 175.2 cm in the females). (2) In the eastern-spinner analysis (Perrin *et al.*, 1977), animals with  $\geq 13$  GLGs were pooled into a single class. Whitebelly spinners with  $\geq 15$  GLGs were pooled in the final stratum because of a relatively larger number of older specimens – particularly in the male sample. (3) For the eastern spinner, male and female juveniles were considered jointly; the respective length and age means coincided almost exactly. For the northern whitebelly spinner, the

<sup>2</sup> See Perrin *et al.* (1976) for discussion of the rationale for a two-cycle model.

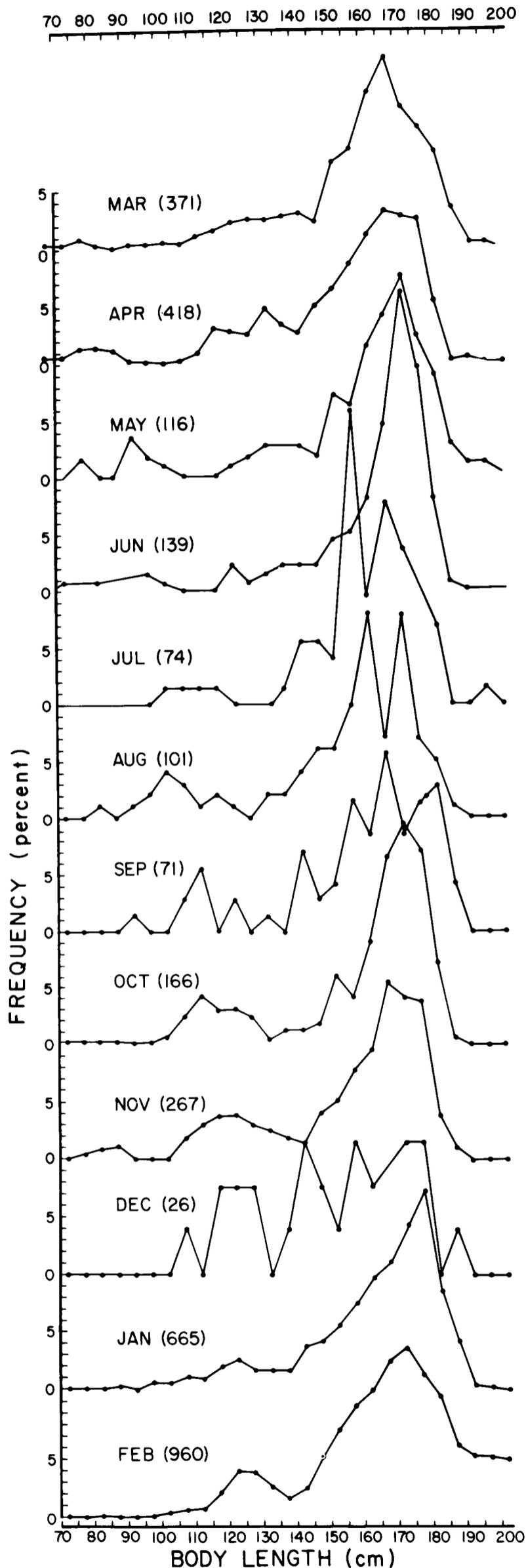


Fig. 4. Length-frequency distributions, by month for all years pooled, of body length in postnatal eastern spinner dolphins. (Sample sizes in parentheses.)

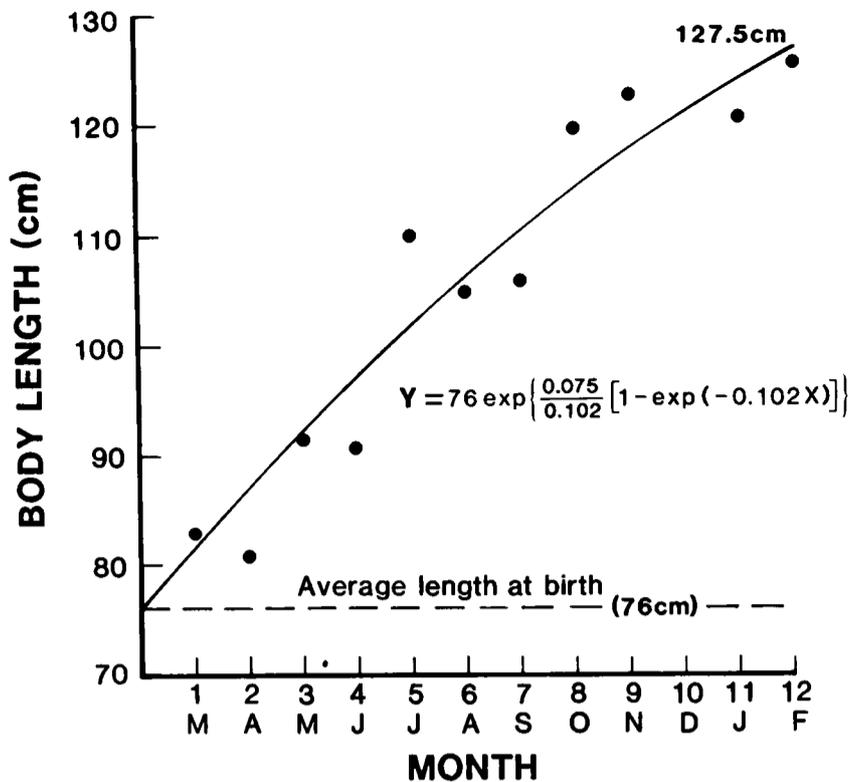


Fig. 5. Least-squares fit to the Gompertz model of mean body-length modes (NORMSEP-estimated from data in Fig. 4) on month of year. December was excluded because of small sample size.

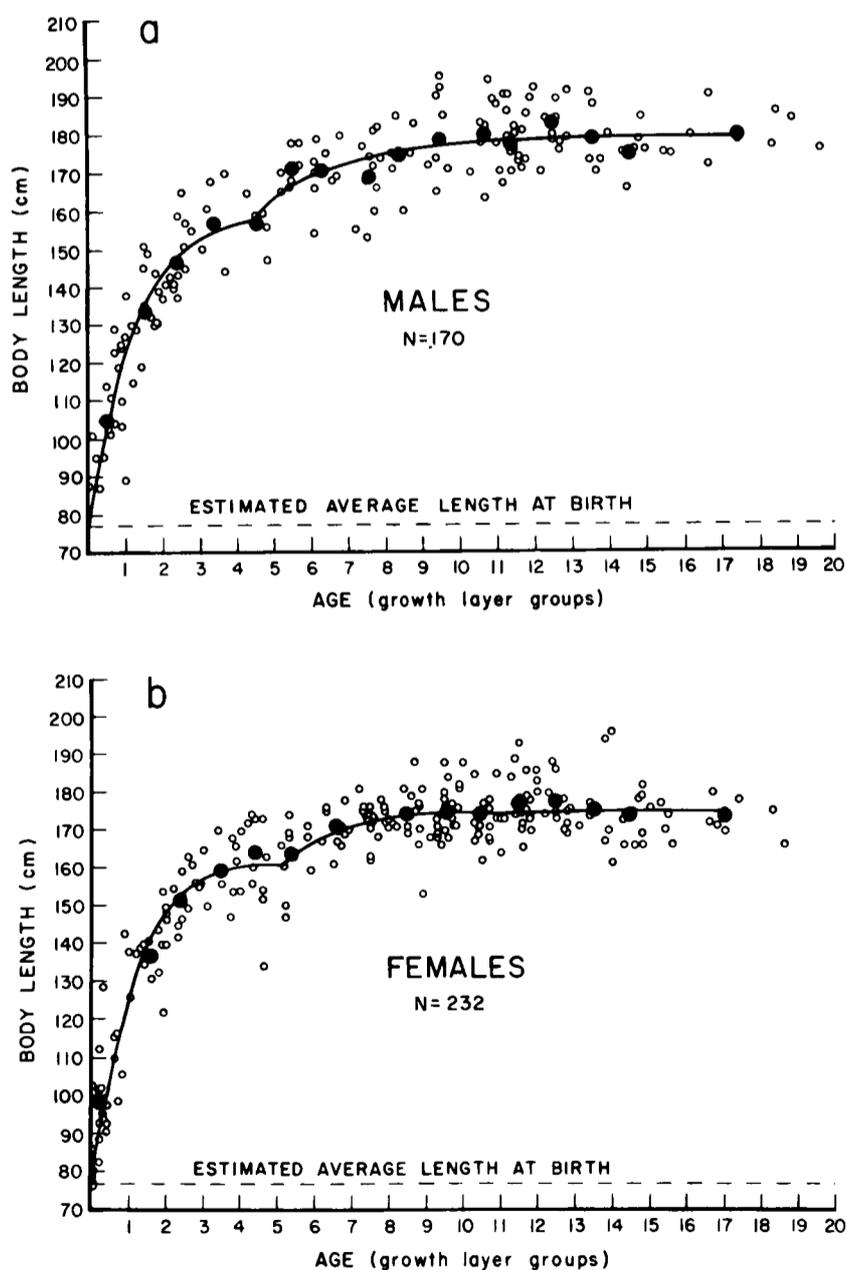


Fig. 6. Relationship between body length and age in northern whitebelly spinner dolphins. Lines are double-Laird-model fits to single-GLG means (solid symbols).

juvenile means differed between sexes, those for the females being higher than those for the males, and the data for juveniles of the two sexes were therefore fitted separately. Age at shift from the juvenile to 'adult' portions of the overall curve (age at onset of the adolescent growth spurt) differed between the sexes. It was 4.4 GLGs in males and 5.1 GLGs in females. Estimated lengths at these ages are 157.8 cm and 160.9 cm, respectively. The shift for the eastern spinner (sexes combined) came at 4.11 GLGs (rounded off to 4 GLGs).

The fitted growth equations for males are, for juveniles < 4.3 GLGs old,

$$L = 77 \exp\{0.730[1 - \exp(-0.946t)]\}$$

and, for  $\geq 4.3$  GLGs,

$$L = 157.8 \exp\{0.128[1 - \exp(-0.480(t - 4.339))]\}$$

where  $L$  = length in cm and  $t$  = age in GLGs.

For females the equations are, for juveniles with < 5.1 GLGs,

$$L = 77 \exp\{0.740[1 - \exp(-1.117t)]\}$$

and, for age  $\geq 5.1$  GLGs,

$$L = 160.9 \exp\{0.085[1 - \exp(-0.775(t - 5.145))]\}$$

The equations rearranged and reduced for estimating age from length are:

$\sigma < 158$  cm

$$t = -1.058 \ln(6.954 - 1.371 \ln L)$$

$\sigma \geq 158$  cm

$$t = 4.339 - 2.082 \ln(40.542 - 7.813 \ln L)$$

$\text{♀} < 161$  cm

$$t = -0.895 \ln(6.874 - 1.352 \ln L)$$

$\text{♀} \geq 161$  cm

$$t = 5.145 - 1.292 \ln(60.993 - 11.806 \ln L).$$

Length at 1 year of age in the eastern spinner was estimated above at 127.5 cm, based on progression of a length mode. That length is achieved at 1.29 GLGs, from the growth equation in Perrin *et al.* (1977). The previously used estimate of 134 cm (*loc. cit.*) was deductively derived; corresponding age is 1.57 GLGs, rounded off to the nearest half-GLG to 1.5 GLGs. The new estimate is also close to 1.5 GLGs, and that value is used below for both the eastern and the northern whitebelly spinners. Estimated average length at one year from the growth equations are then 132.5 cm for the eastern spinner and 137.2 cm (average of estimates for males and females) for the northern whitebelly spinner. Lacking a basis for calibrating the growth curve beyond the first year, we provisionally use below three alternative hypotheses for the rate of GLG disposition:

- I. One and one-half GLGs per year,
- II. One and one-half GLGs in the first year and one per year thereafter, or
- III. One and one-half GLGs per year until puberty and one per year thereafter.

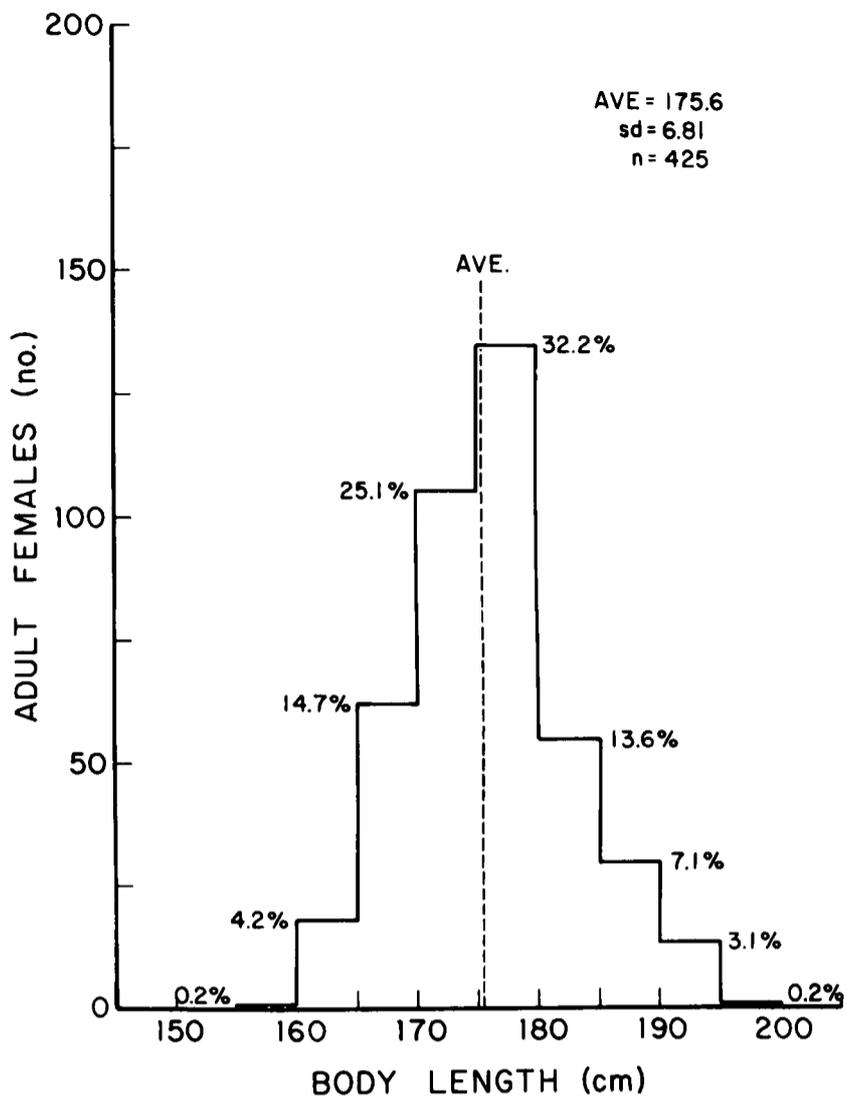


Fig. 7. Distributions of length of sexually adult female northern whitebelly spinner dolphins.

Table 1  
Comparison of juvenile growth rates in female eastern and northern whitebelly spinner dolphins

	Average length at 4 GLGs	Average length of adults
Eastern spinner	156.6 cm <sup>1</sup>	171.2 cm (n = 560)
Northern whitebelly spinner	159.9 cm	175.6 cm (n = 425)
Difference between races	3.3 cm	4.5 cm

<sup>1</sup> From new growth equation based on females included in pooled juvenile sample in Perrin *et al.*, 1977:

$$L = 77 \exp \left\{ \frac{0.6521}{0.8984} [-\exp(-0.894)t] \right\}$$

Adult female northern whitebelly spinners (those of which the ovaries contain at least one corpus of ovulation) average 175.6 cm in length (Fig. 7), compared to 171.2 cm for eastern spinners (Perrin *et al.*, 1977), a difference statistically significant at  $P < 0.0001$  (t-test). Length of adult males is more difficult to assess comparatively because of the absence of a clear criterion for attainment of sexual maturity (discussed below in section on male maturation). The difference in length of adult females is reflected in a difference in juvenile growth rates. Size at birth is the same or very nearly the same in the two populations, but juvenile northern whitebelly spinners grow faster than do juvenile eastern spinners, the difference being most pronounced in females (Table 1).

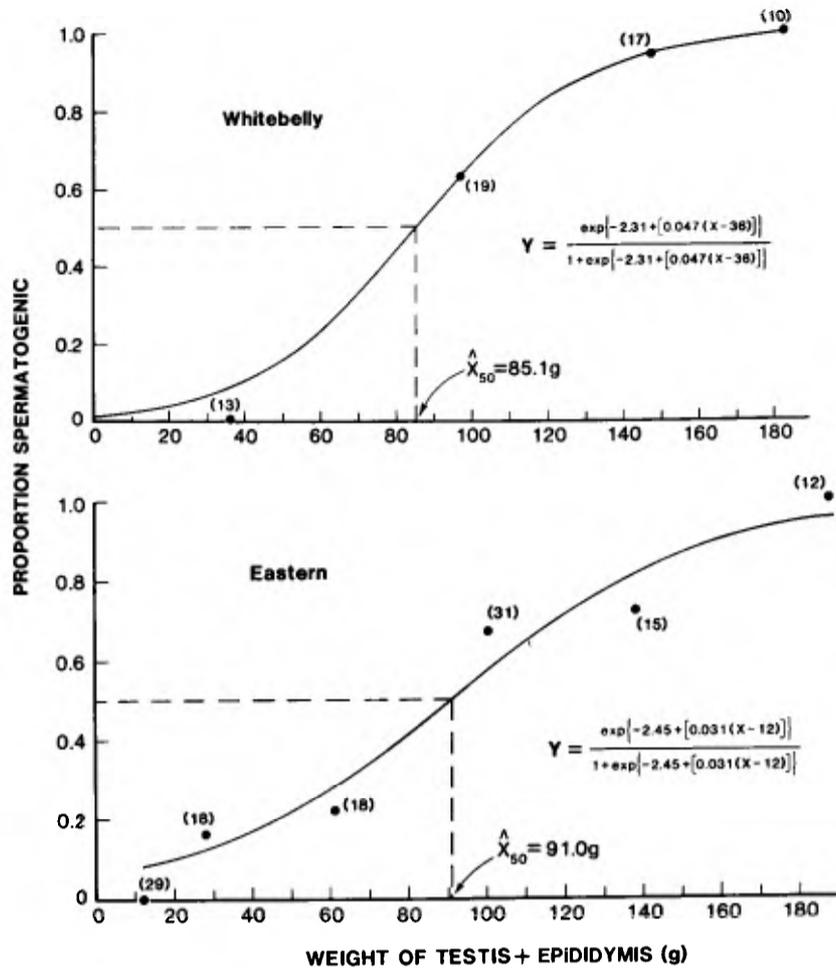


Fig. 8. Least-squares fit to the logistic model of testis-epididymis weight on proportion of males spermatogenic in the northern whitebelly and eastern spinner dolphins. Eastern data from Perrin *et al.*, 1977.

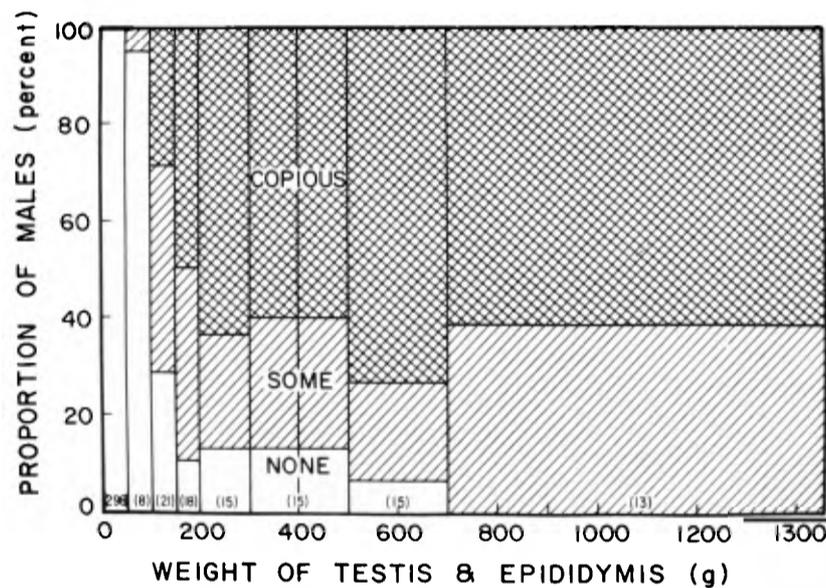


Fig. 9. Amount of sperm in epididymis in relation to combined testis-epididymis weight in northern whitebelly spinner dolphin. Terms defined in Perrin *et al.*, 1976. Sample sizes in parentheses. To be compared with Fig. 18 in Perrin *et al.*, 1977.

## Reproduction

### The male

There are marked differences between the two populations in morphological indices of reproductive maturity and function for males. Average weight of testis (with epididymis) at onset of spermatogenesis is 85.1 g, based on a logistic fit, in the whitebelly spinner. A similar fit of the data in Fig. 17 of Perrin *et al.*, 1977 for the eastern form yields a 50% value of 91.0 g (Fig. 8B). The two estimates of 91.0 g and 85.1 g are not statistically different from each other. The rounded-off average of 88 g is used below for both forms. The further course of average testicular development differs sharply between

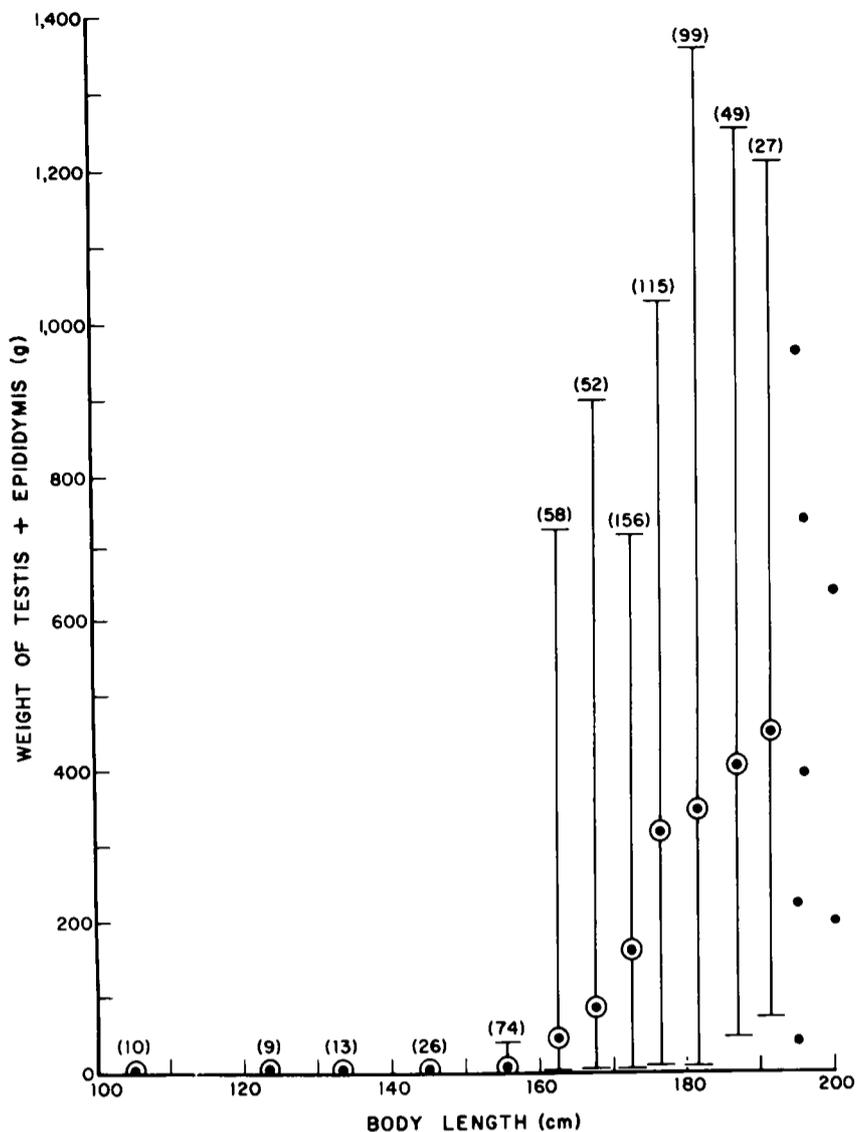


Fig. 10. Relationship between testis-epididymis weight and body length in the northern whitebelly spinner dolphin. Sample sizes in parentheses. Circled dots are sample means; vertical bars are ranges. Dashed circles are means for eastern spinner; sample sizes and ranges in Perrin *et al.* (1977).

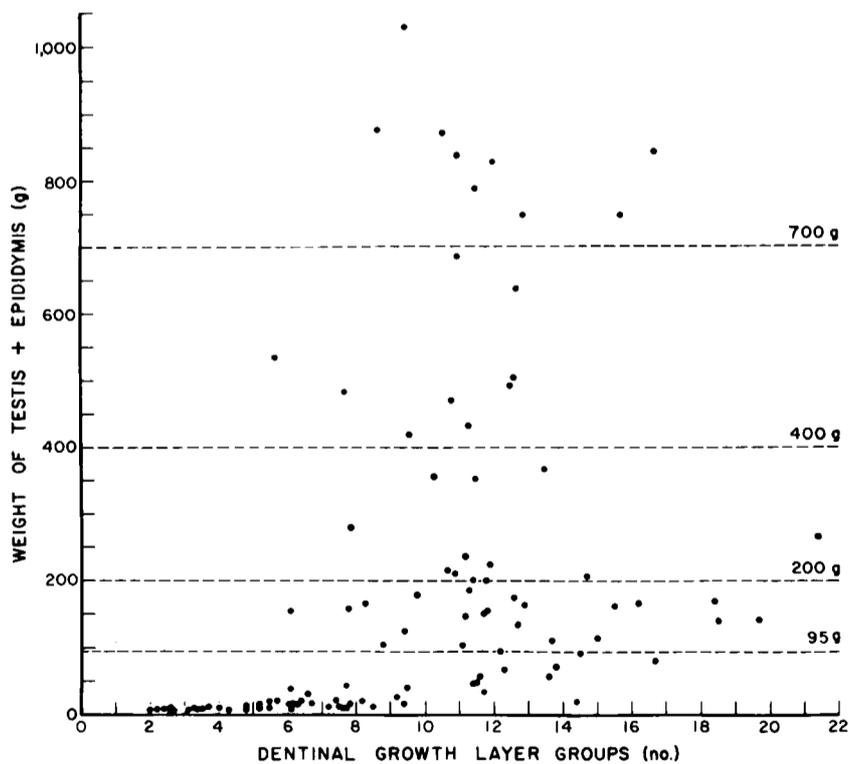


Fig. 11. Scatter plot of testis-epididymis weight on age (in GLGs) for 102 northern whitebelly spinner dolphins.

the two forms. In the eastern spinner, proportion of animals with 'copious' sperm in the epididymis increases to about 50% at testis-epididymis weight of about 400 g (*loc. cit.*) and levels out, whereas in the northern whitebelly spinner it increases to about 35%, at about 200 g (Fig. 9). In the original eastern sample (Fig. 18 in

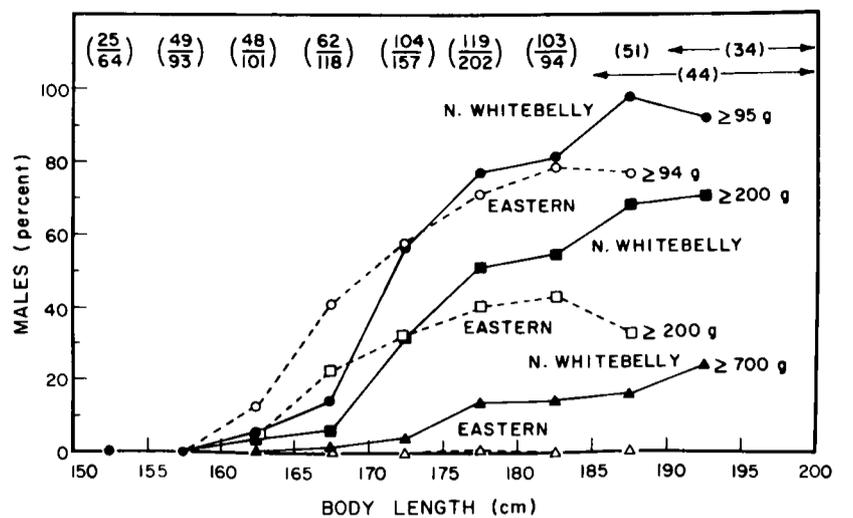


Fig. 12. Proportion of males of given length that have testis-epididymis weights  $\geq 95$  g,  $\geq 200$  g and  $\geq 700$  g in two populations of spinner dolphin: northern whitebelly spinner (solid lines) and eastern spinner (dashed lines). Sample sizes in parentheses (northern - bottom, whitebelly - top).

*loc. cit.*), no testis weighed more than 700 g, and only a very few of that size (but weighing less than 900 g) have been collected since (unpublished data). However, a sizeable proportion ( $> 20\%$  at the upper end of body-length size range) of northern whitebelly spinner testes weigh over 700 g (up to 1,354 g in the sample) and all of these examined histologically have had at least 'some' sperm in the epididymis. Amount of sperm in the epididymis would seem to be positively correlated with testis size, and adult eastern spinners have on the average smaller testes than do northern whitebelly spinners of the same length (Fig. 10) (even with a 5-cm adjustment for the racial difference in average length of adults) or age (compare Fig. 11 with Fig. 21 in *loc. cit.*). At any body length above about 170 cm for eastern spinners and 175 cm for whitebelly spinners, a greater proportion of northern whitebelly spinners attain any particular testis-weight criterion, even the criterion of average weight at first spermatogenesis, and very few eastern spinners attain the high testis weights ( $> 700$  g) associated with 100% incidence of sperm in the epididymis (Fig. 12). At least four alternative explanations suggest themselves: (1) there is seasonal fluctuation in testis size and the differences reflect seasonal biases in sampling, (2) there are inherent differences between the two populations in male reproductive development and morphology, (3) there are differential sampling biases *vis a vis* reproductively active males for the two populations, or (4) testis size (and possibly, male fertility) is depressed in the eastern population, possibly due to some aspect of exploitation.

To address the first of the above possibilities, we examined testis-weight distribution by month for the two populations (Fig. 13). The sample sizes are relatively small for some months, but a clear picture of pronounced seasonality emerges nonetheless. In the northern whitebelly spinner, a mode of large-testis-weight animals appears in February, centered around 700–800 g. The mode persists through May (although possibly retreating slightly), appears in June centered around 400–500 g; moves out to 600–700 g again in July–August; and all but disappears in September through January. The months of peak testis weight (and, presumably, peak fertility and breeding) are February and July–August. The eastern

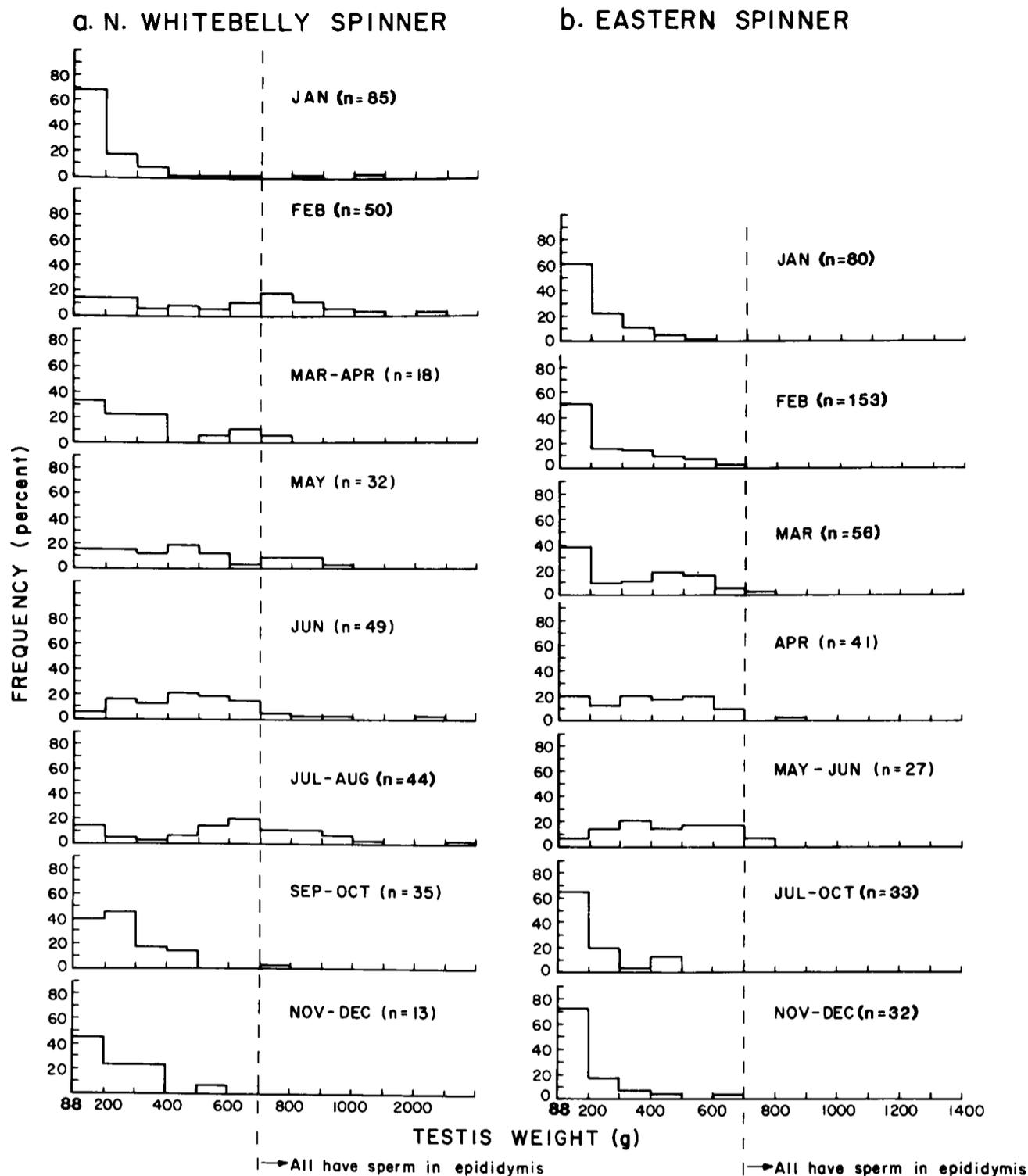


Fig. 13. Testis-epididymis weight distribution by month in two populations of spinner dolphins. Data from 1968-78 (most from 1973-78).

spinner also exhibits seasonality (Fig. 13b), but with important differences. A mode is present in March-June, centered around 400-500 g rather than around 700-800 g as in the northern whitebelly spinner. Only a very small proportion of the animals in the seasonally appearing mode in any month extend above the 700 g level, above which all individuals can be expected to have sperm in the epididymis. The apparent dearth of large-testis males, therefore, in the eastern samples is not an artifact of seasonally biased sampling.

<sup>3</sup> There is one other instance (based on adequate samples and comparable methods) of wide variation in maximum testis weight between populations of a single delphinid, that of *Delphinus delphis* in the Black Sea ( $n = 2,138$ , maximum weight = 1,000 g) and in the eastern North Pacific ( $n = 31$ , maximum weight = 1,672 g) (Perrin and Reilly, 1984). In this case also, the population with smaller testes is the more exploited one, in fact thought to have crashed because of over-exploitation (Smith, 1982). The difference between average lengths of adults in the two populations may be greater than for the two populations of *S. longirostris*, because the Black Sea form is relatively very small (Perrin, 1983).

The second alternative, that of inherent difference in testis weight, is unlikely because of the similar testis weight at first spermatogenesis and similar adult body length in the two populations.<sup>3</sup> The third alternative is also unlikely, because fishing practices do not differ with type of spinner dolphin involved. Of the four alternatives considered here, the most likely is that of depression of testis weight in the eastern spinner population, although inherent difference in testis size or differential sampling bias cannot be eliminated from consideration completely.

#### The female

*Attainment of sexual maturity.* The smallest sexually mature whitebelly spinner female (possessing at least one corpus of ovulation in the ovaries) encountered was 157 cm long, and the largest immature female was 188 cm long. This compares to 152 cm and 182 cm in the eastern spinner (Perrin *et al.*, 1977). The differences reflect the above-discussed approximately 5-cm difference in average length of adult females. Average length at attainment of

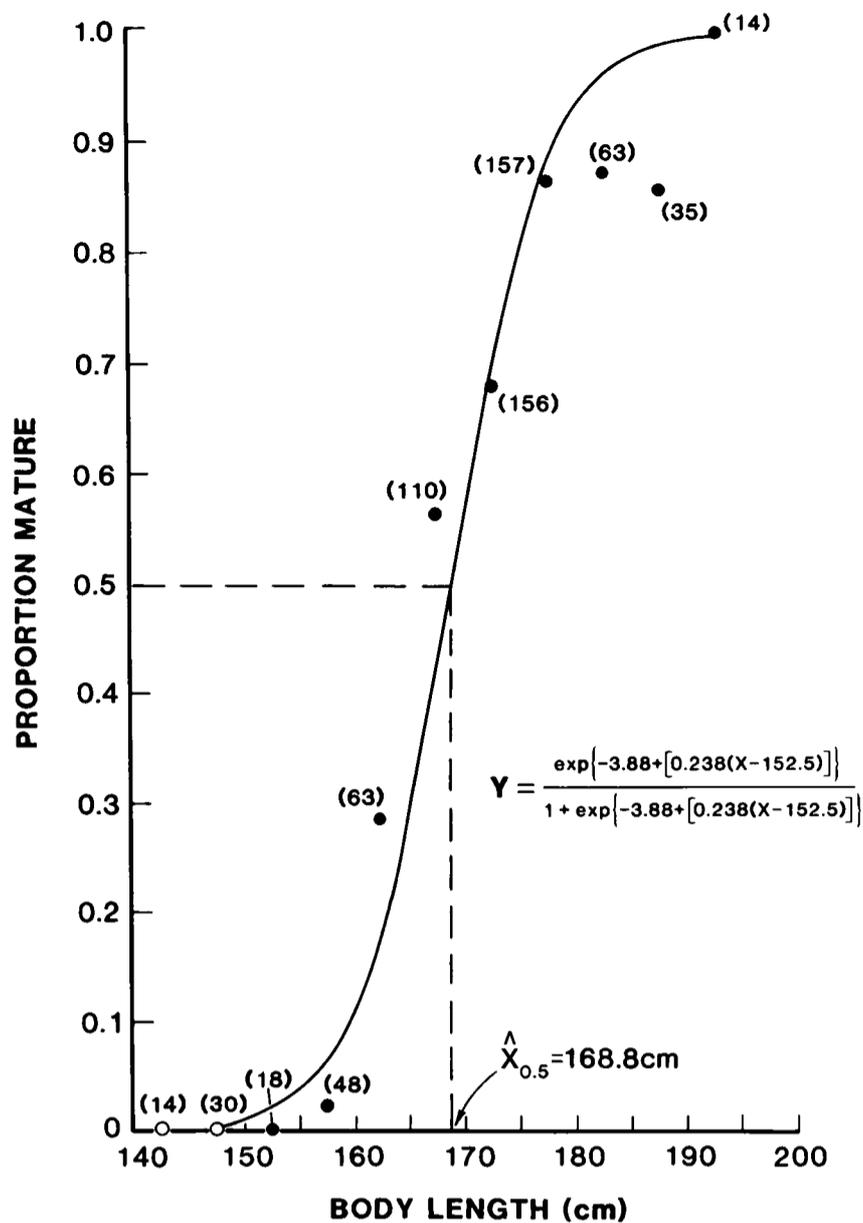


Fig. 14. Estimation of body length at which 50% of female northern spinner dolphins show ovarian evidence of sexual maturity, based on weighted least-squares fit to the logistic model. Sample sizes in parentheses. Open circles not included in regression.

sexual maturity differs between the two populations in the same direction (167.2 cm in the northern whitebelly spinner (Fig. 14) vs 164.1 cm in the eastern spinner (Fig. 22 in loc. cit.). The difference (4.7 cm) yields a younger predicted average maturation age (from the growth equations) in eastern spinners (5.2 GLGs) than in northern whitebelly spinners (7.1 GLGs).

Another estimate of average length at attainment of maturity is that length for which the number of longer immature animals is equal to the number of shorter mature animals. This point for the northern whitebelly spinner is 170 cm and for the eastern spinner is 165 cm, yielding estimates of age at maturation of 6.5 and 5.8 GLGs, respectively. These may be underestimates, because the method does not take mortality into account.

An estimate of length at first conception (not necessarily the same as age at first ovulation) can be made by calculating the average length of pregnant females with a corpus luteum only (indicating first pregnancy) and subtracting the growth that they can be assumed to have undergone during pregnancy. Sixteen primiparous northern whitebelly females averaged 171.6 cm in length. Predicted age at that length is 6.95 GLGs. The average length of their fetuses was 248 mm. This length is attained at about 4.3 months. Using the growth equations above to predict growth during 4.3 months for the various tooth-layering models and subtracting the growth increment from 171.6 cm yields estimates of length at first conception ranging from 169.7 cm (6.4 GLGs) to 170.4 cm (6.6 GLGs). The primiparous females in this sample, however, are only those that became pregnant at the first ovulation. This may cause the estimate to be an underestimate, because some females may ovulate several times, and presumably continue to grow, before becoming pregnant the first time. Also, this method

Table 2

Results of analyses of length and age at attainment of sexual maturity in two populations of spinner dolphins. Values calculated with the growth equations are in parentheses

Methods (and comments)	Length (cm)		GLGs (no.)		Age (years) under hypotheses					
	N.WB	EAST.	N.WB	EAST.	I		II		III	
					N.WB	EAST.	N.WB	EAST.	N.WB	EAST.
1. Length at which 50% have corpora (probable underestimate)	168.8	164.1 <sup>1</sup>	(7.1)	(5.2)	4.7	3.5	6.6	4.7	5.3	3.8 <sup>5</sup>
2. Length at which mature below equals immature above (possible underestimate)	170.0	160.0 <sup>2</sup>	(6.5)	(5.8)	4.3	3.9	6.0	5.3	4.8	4.4
3. Number of GLGs at which 50% have corpora (interpolation, but small sample sizes)	(170.8)	(164.2)	6.7	5.3 <sup>1</sup>	4.5	3.5	6.2	4.8	5.0	3.9
4. Length at first conception, <sup>3</sup> under hypothesis:	I	(169.7)	(6.4)	(—)	4.3	(—)	—	(—)	—	(—)
	II	(169.7)	(6.6)	(—)	—	—	6.1	(—)	—	—
	III	(170.4)	(6.6)	(—)	—	—	—	(—)	4.9 <sup>4</sup>	(—)

<sup>1</sup> From Perrin *et al.* (1977).

<sup>3</sup> No estimates for the eastern spinner by this method; see text.

<sup>4</sup> Switch from 1.5 to 1.0 GLG/year assumed to occur at 161 cm (5.41 GLGs).

<sup>2</sup> Includes data through 1978.

<sup>5</sup> Ditto, at 157 cm (4.13 GLGs).

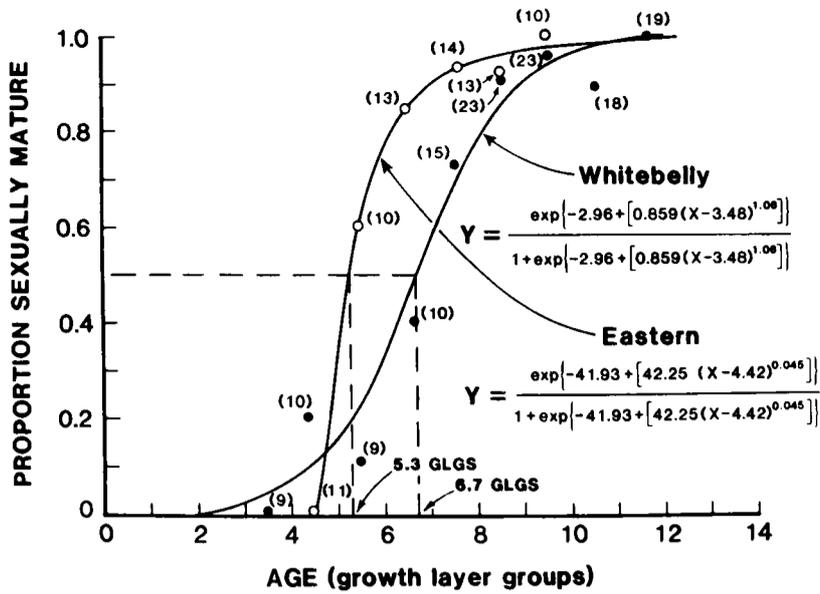


Fig. 15. Relationship between proportion of females sexually mature and age (in GLGs) in two populations of spinner dolphins, based on weighted least-squares fit to a generalized sigmoid model (described in text). Sample sizes in parentheses.

Table 3

Calculation of estimates of gross annual reproductive rates in two populations of spinner dolphins, based on pooled data for 1973-78. Approximate 95% confidence limits are  $\pm 2$  s.e. Sample sizes in parentheses. From Henderson *et al.*, 1980

	Northern whitebelly spinner	Eastern spinner
A. Percent female	50.9 $\pm$ 2.4 (1,778)	51.0 $\pm$ 1.8 (2,938)
B. Percentage of females reproductive	52.2 $\pm$ 3.6 (905)	43.2 $\pm$ 2.8 (1,492)
C. Annual pregnancy rate (percent)	35.6 $\pm$ 5.0 (366)	33.9 $\pm$ 4.2 (521)
A $\times$ B $\times$ C. Gross annual reproductive rate (percent)	9.4 $\pm$ 1.4 (1,631)	7.5 $\pm$ 1.2 (2,624)

assumes no effect of pregnancy on growth rate. Average length of 16 primiparous eastern spinners (171.4 cm) slightly exceeded the estimate of asymptotic size (170.9 cm) used in the growth curve fit; an estimate from the growth equation, therefore, was not possible for the eastern spinner.

Estimates of age at sexual maturity were also derived directly from the smaller samples for which age determinations (GLGs in dentine) were made (Fig. 15), based on a weighted (weight = inverse of variance estimated as  $\text{Var} = p(1-p)/n$ ) least-squares fit to a generalized sigmoid function:

$$Y = \frac{\exp(a + bX)^c}{1 + \exp(a + bX)^c}$$

where  $a$ ,  $b$  and  $c$  are fitted parameters. The estimates are 5.3 GLGs in the eastern spinner and 6.7 GLGs in the northern whitebelly spinner. The fitted curves, albeit based on few and small samples, are quite different in form.

The largely independent different estimates of age (in GLGs) at maturation are not widely disparate (Table 3). Averaging of the estimates for the northern whitebelly spinner by the various methods (using Option II in Table 3 of 1 GLG/year after the first year) yields a value of 6.7 GLGs, which value is used below. Averaging of the two

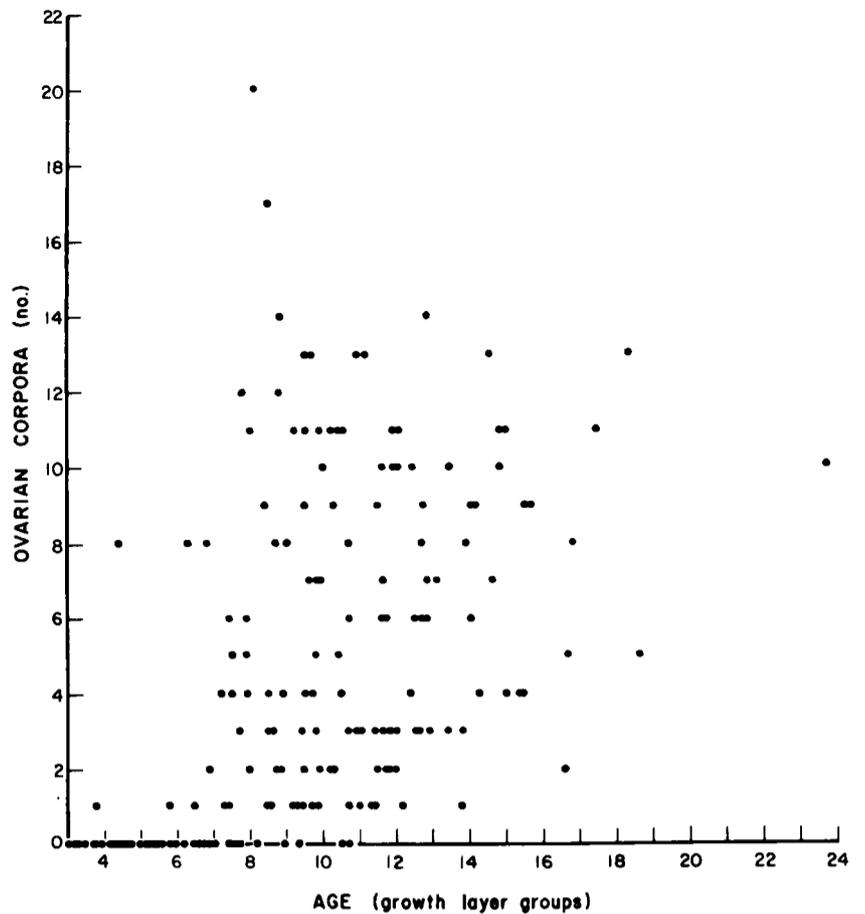


Fig. 16. Scatterplot of number of ovarian corpora on age in GLGs in the northern whitebelly spinner dolphin.

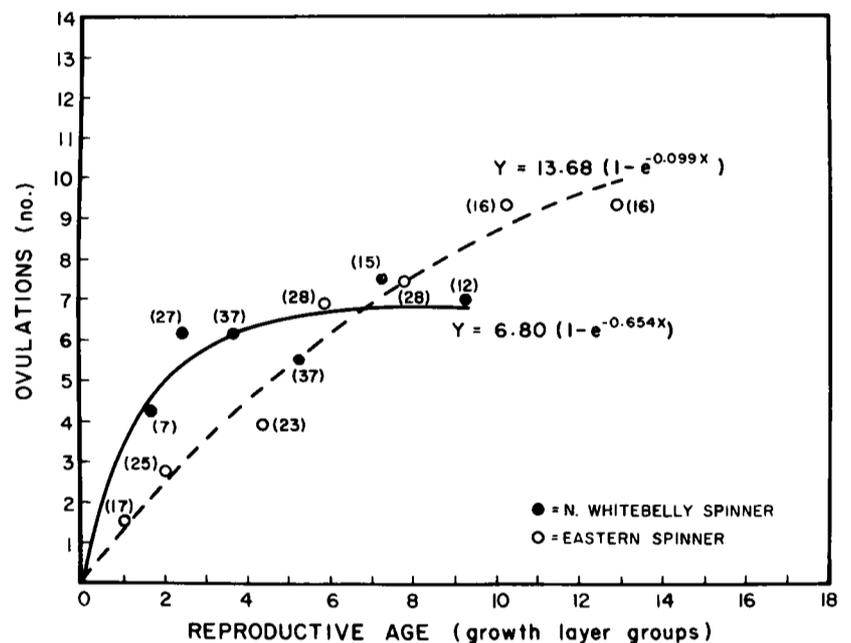


Fig. 17. Asymptotic fit of corpus count on average reproductive age in the northern whitebelly spinner dolphin. Dashed line is asymptotic fit to data for eastern spinner (Fig. 27 in Perrin *et al.*, 1977). Origin set at 0.001/0.001.

relatively most reliable estimates available for the eastern spinner yields an estimate of 5.6 GLGs.

If it is assumed that one GLG is deposited after the first year (Hypothesis II in Table 3), female northern whitebelly spinners on the average mature at about 6 years of age and eastern spinners at about 5 years.

**Ovulation Rate.** Number of corpora in the ovaries (an index of reproductive history of the individual female dolphin) increases sharply at about 6-7 GLGs in the northern whitebelly spinner (Fig. 16) and at about 5-6 GLGs and more rapidly in the eastern spinner (Fig. 6 in Perrin *et al.*, 1977). To estimate ovulation rate, the required estimates of average reproductive ages for 2-GLG intervals were calculated as in Perrin *et al.* (1977).

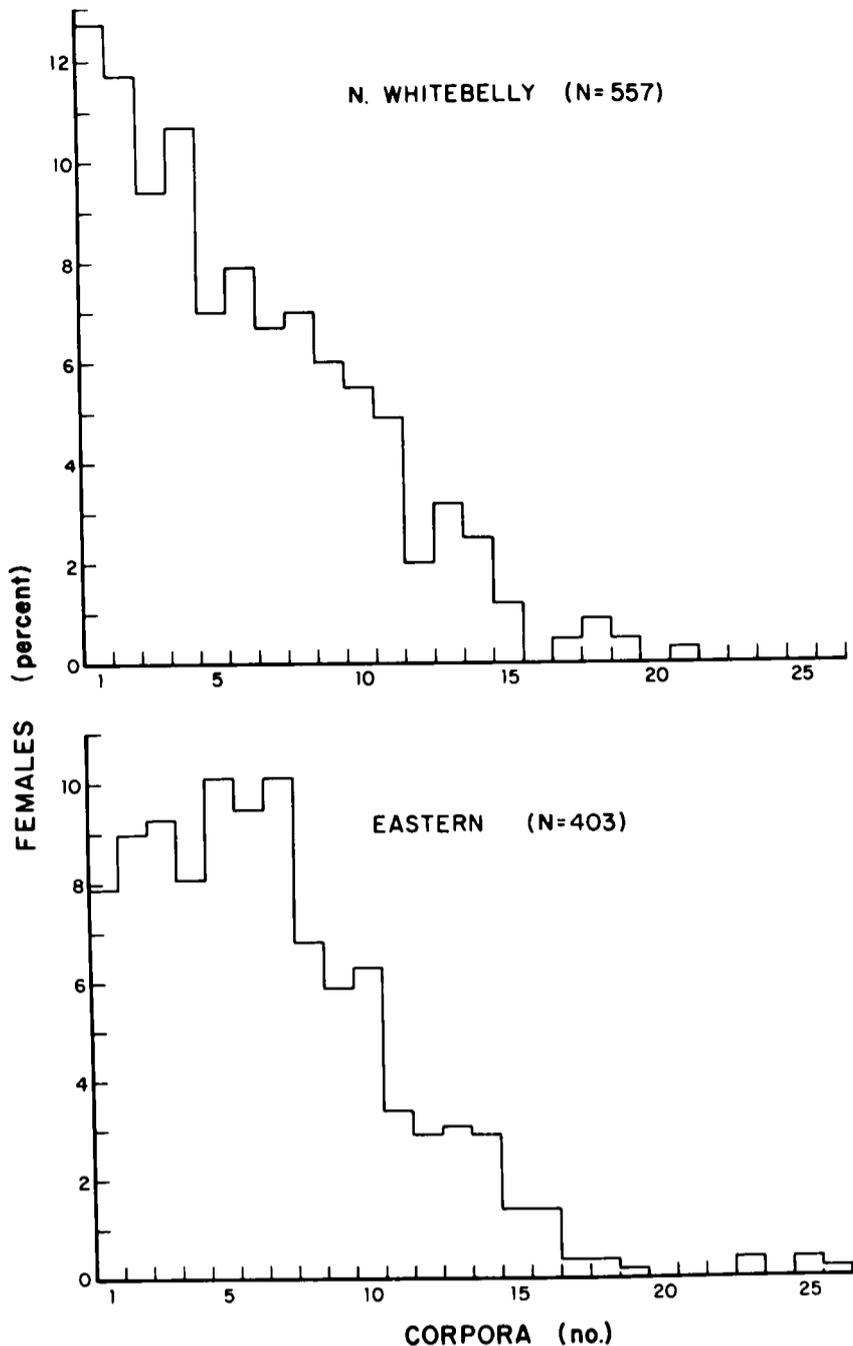


Fig. 18. Frequency distribution of corpus count in two populations of spinner dolphins. Includes samples from 1973-78.

Ovulation rates were estimated by fitting asymptotic curves to the 2-GLG-interval means of average reproductive age (Fig. 17) (assumes eventual cessation of ovulation in old females). Ovulation rate, as measured by these fits, in young females is higher in the northern whitebelly spinner than in the eastern spinner, but also levels off faster. The relative behavior of the two curves beyond about 8 GLGs of reproductive age may be greatly influenced by the small sample sizes involved at the higher ages, however, and all that can be said with some certainty is that during the first few years of reproductive life spinners in the eastern population ovulate less frequently than do those in the northern whitebelly population.

The shape of the corpora-count frequency distribution is an index of ovulation rate independent of the above fit to the corpora count on reproductive age. The distributions differ in the two populations (Fig. 18), most markedly so between 0 and about 7 corpora. The pattern of difference (higher frequency in the whitebelly population between one and four corpora and the reverse between four and seven corpora) can be explained by initial higher ovulation rate in the northern whitebelly population (although this does not take into account the possibility of differential mortality rates). The results of

Table 4

Percentage of females sexually immature in two populations of spinner dolphins, 1973-78. Sample sizes in parentheses. From Henderson *et al.*, 1980

Year	Northern whitebelly spinner	Eastern spinner
1973	48.9 (133)	54.4 (344)
1974	40.8 (49)	55.3 (396)
1975	45.5 (191)	57.0 (402)
1976	52.9 (191)	59.4 (106)
1977	48.2 (222)	59.7 (92)
1978	50.0 (118)	70 (92)

Table 5

Summary of parameters for two populations of *Stenella longirostris*. Sources in text and Tables 2-4

Parameters	Eastern spinner	Northern whitebelly spinner
1. Proportion of original population size	17-25%	58-72%
2. Length of gestation	10.6 months (0.88 year)	10.6 months (0.88 year)
3. Average length at birth	77 cm	76 cm
4. Average length at one year (1.5 GLGs, from growth curves)	132.5 cm	Ave. for M & F 137.2 cm
5. Average length of sexually mature female	171.2 cm	175.6 cm
6. Smallest adult female	152 cm	157 cm
7. Largest adult female	182 cm	188 cm
8. Average length of female at attainment of sexual maturity	164.1 cm	167.2 cm
9. Average age at attainment of sexual maturity in female (average of estimates by several methods)	5.6 GLGs (~ 5 years)	6.7 GLGs (~ 6 years)
10. Proportion of population female	0.510	0.509
11. Proportion of females reproductively adult	0.432	0.533
12. Annual pregnancy rate	0.339	0.356
13. Gross annual reproductive rate	0.075	0.094

the two analyses agree quantitatively as well; the asymptotic fits (Fig. 17) estimate that about seven corpora represents about the same reproductive span in the two populations, about seven GLGs (about 7 years, if a one-GLG/year deposition rate is assumed).

**Gross production.** Gross annual reproductive rate, estimated as proportion of the population female times proportion of females sexually mature (and not post-productive) times annual pregnancy rate (proportion of reproductive females divided by length of gestation - 0.883 year), did not differ between the two populations for the period 1973-78 (Table 4). Overall sex ratio was virtually identical in the two (very large) samples, about 0.96:1. The age structure of females, however, was quite different. Fifty-two percent of the northern whitebelly females were sexually mature, whereas only 43% of the eastern females were mature. The difference is statistically significant at  $\alpha$  0.05 (*t* test). (A larger proportion of

females were immature in the eastern than in the northern whitebelly samples for each year, 1973–78 (Table 5.) Pregnancy rate was about the same in the two populations, perhaps reflecting the above-discussed earlier age at maturity. The estimate of gross production was slightly higher for the northern whitebelly population than for the eastern population. The difference, however, is not statistically significant at  $\alpha = 0.05$ .<sup>4</sup>

## DISCUSSION

Although differences exist between the northern whitebelly spinner and eastern spinner populations in several growth and reproductive parameters (summarized in Table 5), there is no clear basis for inferring that historically greater exploitation of the eastern spinner has resulted in a higher gross reproductive rate for the population. As would be expected, age at attainment of sexual maturity is lower in the eastern spinner population, but the major difference between the two populations in terms of gross production is in the proportion of females that are sexually mature. Although eastern specimens mature earlier, the mortality rate in this population may be sufficiently greater to effect a reproductively significant downward shift in age structure. In addition, the dearth of mature males hardly seems an adaptive population response and conceivably is an effect on male maturation structure (and perhaps age structure) by the purse-seining operation, through age- and maturity-selective fishing mortality, disruption of maturity-inducing social structure, or some other mechanism. In short, density-dependent population response in reproductive rates induced by the fishery may be counteracted by a more direct effect of the same fishery.

The various parameter estimates used here may be subject to sampling bias of various sorts. The bias in favor of calves in small-kill samples found in the case of the offshore spotted dolphin (Henderson *et al.*, 1980) was not found to be significant in the spinner-dolphin samples, although that does not eliminate the possibility of systematic bias in sampling from kills of all sizes. In any case, it can reasonably be assumed that whatever sampling biases exist are operating similarly for samples from the two populations. A possible exception to this is seasonal bias, as both reproduction and sampling are differentially seasonal (Barlow, 1984), but the effect, if any, can be presumed to be very small because of the length of gestation (almost a year) and the relatively diffuse nature of the reproductive seasonality.

As noted above, one alternative hypothesis to that of non-response (in reproductive rates) to exploitation in the eastern spinner population is that response has occurred in both populations, i.e. that the northern whitebelly spinner population even at 58–72% of its original size is substantially below its level of maximum productivity. In this context it would be useful to examine reproductive rates in a third population, the southern whitebelly spinner population, which has been more lightly exploited than the other two (Smith, 1979, 1983). Sample sizes to date have not been large enough to allow

meaningful comparisons (Henderson *et al.*, 1980), although the trend in pregnancy rates with status for the three populations (higher rate with heavier exploitation) is consistent with the hypothesis that the northern whitebelly population has already responded to exploitation (Perrin and Reilly, 1984).

Although it has been assumed in assessment of the dolphin populations that there has been no effect of exploitation on survivorship (Smith, 1979, 1982), the possibility that such an effect exists cannot be ruled out. The possibility can be examined only through analysis of large representative samples of ages. The age analyses carried out in the study reported here were based on selected stratified samples that were aged to allow estimation of an age/growth curve; these aged samples were not adequate to allow estimation of populational age structure.

The results here point out the need for further research on the biology of the several populations, particularly on age structure and on male reproductive functional morphology and physiology.

## ACKNOWLEDGEMENTS

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R. B. Miller managed the data. A. A. Hohn and J. Barlow provided advice on analytical methods. D. G. Chapman, L. L. Eberhardt, R. J. Hofman, J. W. Horwood, J. G. Mead, G. T. Sakagawa and T. D. Smith read the manuscript and offered useful suggestions for its improvement.

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## **Session V**

# **Morphology, Behaviour and Physiology of Reproduction**



# Characteristics of Ovarian Corpora in Dolphins and Whales as Described by Soviet Scientists

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## ABSTRACT

The literature based on investigations conducted by Soviet specialists in the 1950s and 1960s on the identification of traces of pregnancy and ovulation (corpora lutea) in baleen whales (fin whale, humpback and gray whales), the common dolphin (*Delphinus delphis*) and the sperm whale is reviewed.

This review deals with differences in macroscopic and histologic structures of two types of scars.

## INTRODUCTION

Periodicity of births is important in studies of the biology of reproduction in whales. In practice there is little opportunity to conduct direct observations at sea. In recent years, underwater photography of whales has been carried out for identification of animals. This is possible when migration routes pass near a coast or the whales spend time in warm coastal waters during wintering and reproduction (gray and humpback whales). Such observations have allowed estimation of reproductive seasonality in humpback whales (Glockner-Ferrari and Ferrari, 1984) in the Hawaiian Islands area. This method has extremely restricted application; it cannot be used for most whale species. Therefore, the reproductive tract (mainly the ovaries) is an important and convenient source of data on the reproductive cycle.

A corpus luteum (CL) diminishes greatly in size and transforms into a corpus albicans (CA) after birth. If a corpus luteum of ovulation develops without pregnancy, it is soon resorbed into a CA of ovulation.

The differences between the two types of CAs being known, one can identify CAs of pregnancies and count them for an estimate of the total number of births. The whale's age being known, one can determine the time of first ovulation, times of pregnancies and births, the intervals between births, and duration of female reproductive activity. Thus, the reproductive ability of the whole population can be known.

To understand every type of ovarian scar, the characteristic macroscopic and microscopic appearance must be investigated thoroughly. Soviet specialists have performed investigations of this kind. The fullest studies have been of the Black Sea common dolphin (*Delphinus delphis*), fin whale (*Balaenoptera physalus*), humpback whale (*Megaptera novaeangliae*), gray whale (*Eschrichtius robustus*) and sperm whale (*Physeter macrocephalus*).

### 1. BLACK SEA COMMON DOLPHIN (*DELPHINUS DELPHIS*)

The ovaries of 92 females were examined; 18 had CLs but no embryos in their uteri; 10 had embryos from 1 cm to 82 cm long; 20 ovaries were from lactating females with CLs but no embryos in their uteri; 28 ovaries were from lactating females with no CLs and 16 were of immature and 'resting' females.

The ovaries were fixed in 10% Bouin's solution. The character and number of scars seen on the exterior surface of the ovaries, size of CLs and condition of blood vessels were noted. A series of sections were made perpendicular to the long axis of each ovary, yielding 8–10 sections connected at the base. To perform the microscopic investigations, the samples were paraffin-embedded and sectioned at 7–10 microns. The sections were stained with hemalum, Congo red, and hematoxylin. This work was performed by Popov (1951).

### Functioning corpus luteum of pregnancy

The process of follicle development and transformation into a CL of pregnancy is similar to that in other mammals and is closely connected to the local supply of blood.

Development of the CL in *Delphinus delphis* is as follows. The Graafian follicle is supplied with blood from the follicular artery, which is near the base of the follicle. Its branches cover the whole follicle on the surface, except at the top, i.e. the area of the future rupture.

As soon as ovulation has occurred, the growth rate of the Graafian follicle becomes very high. The developing CL becomes folded, and blood vessels and connective tissue are seen in the folds and are observed in the centre of the corpus.

The number of blood vessels increases greatly in the folds (Fig. 1b). Toward the end of pregnancy, the amount of connective tissue cells increases, and the folds of the CL become thinner (Fig. 1c); later they can be divided into different areas (Fig. 1d).

The CL is most intensively formed during the initial period of pregnancy, when transformation of the follicular cells into luteal cells is observed. Small numbers of histocytes are found in the lymph channels between luteal and follicular cells. The accumulation of large lipid vacuoles occurs.

The follicular cells diminish along with the formation of the CL, transforming into luteal cells with fine-grained cytoplasm and a small quantity of chromatin. Fibroblasts, histocytes and reticular cells are apparent between these cells. As the luteal cell propagation slows, phagocytosis increases. The blood vessel system is strongly developed.

In the second half of pregnancy one can observe a diminished number of luteal cells. They are subjected to

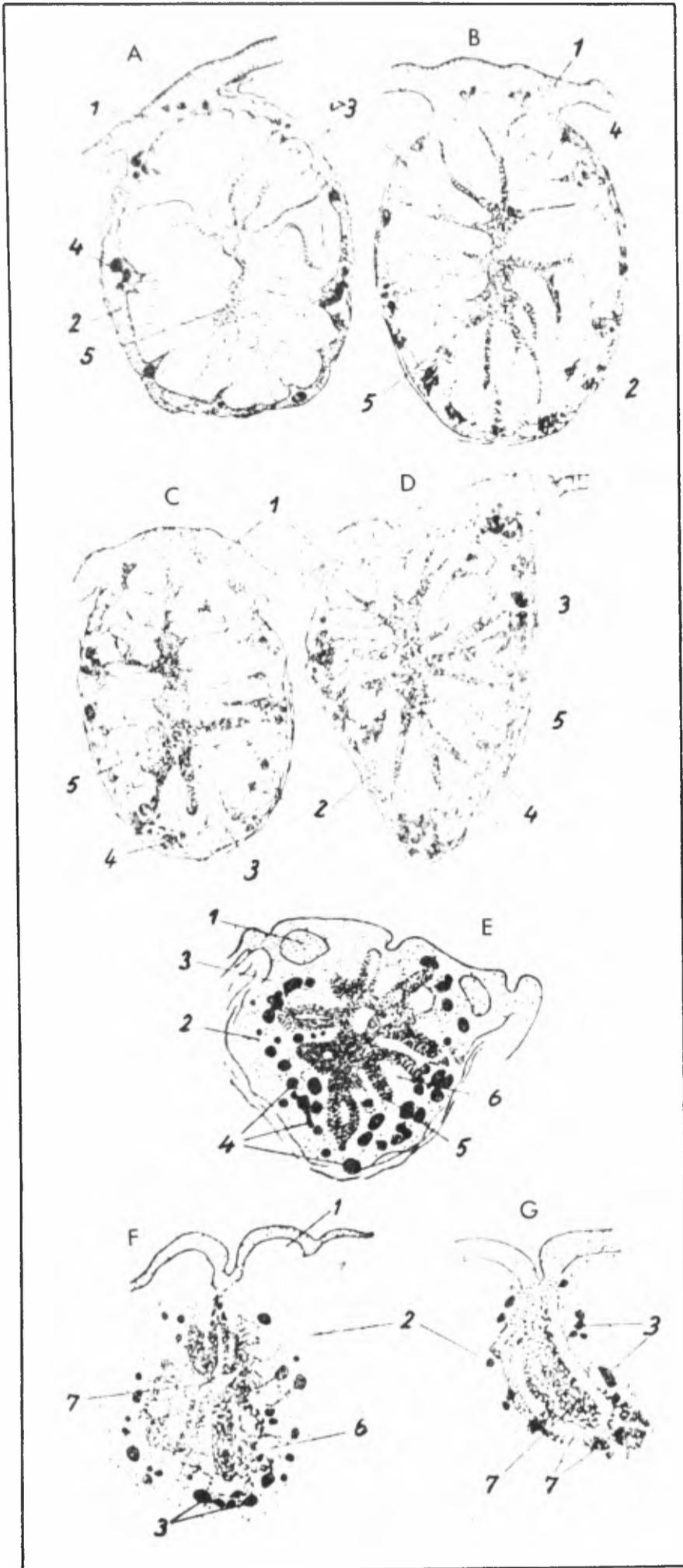


Fig. 1. Morphological changes of corpora albicantia during pregnancy (A, B, C and D  $\times 2$ , E-G  $\times 8-10$ ). A, B and C - changes during the first half of pregnancy; D and E - blood stagnation in the vessels; F - hyalinosis, G - atherosclerosis and sclerosis (from Popov, 1951). 1 - exterior surface of the ovary; 2 - surface; 3 - folds of the corpus luteum; 4 - blood vessels; 5 - central accumulation of connective tissue; 6 - xanthotrophic cells; 7 - central sclerosis.

vacuolization and then to phagocytosis. The blood vessels increase greatly, slightly enlarging, a feature not observed during the first months. Not long before birth,

the process of corpus luteum degeneration becomes more intense. Luteal cells form islets divided by developing connective tissue, with enlarged blood vessels. Round-celled infiltration of the connective tissue occurs and gelatinous tissue begins to form along the folds. The process of new blood-vessel formation continues. The yellow color of the corpus luteum of pregnancy becomes gradually pale and can disappear. The original size of 3-3.5 cm decreases to 1.5-2 cm in the second half of pregnancy, and sharply defined furrows appear on the surface.

These observations were made on ovaries of dolphins having neither embryos in their uterus nor milk in their mammary glands, as well as of females having embryos from 1 cm to 82 cm long.

#### Scar of corpus luteum of pregnancy<sup>1</sup>

After birth, the corpus luteum is transformed into a scar (CA) measuring initially 1-1.5 cm in *Delphinus delphis*. During the first half of the suckling period, the size is sharply reduced. It has the appearance of a distinct pale yellow protrusion on the surface of the ovary and is pierced with furrows having enlarged blood vessels.

Luteal cells are seen as small concentrations at this stage. The large cells often have two nuclei and are surrounded by histocytes and fibroblasts. An extremely characteristic feature of this stage is the marked enlargement of blood vessels with stasis and intensive development of connective tissue.

In the second half of the suckling period, the scar of the corpus luteum disappears from the surface and a 'folded type' of scar begins to develop (terminology of Popov, 1951). It lies deep in the ovary. Microscopic observations show that fibrous tissue is markedly developed, resulting in the closure of blood vessels (Fig. 1e). Hyalinosis is gradually increasing and passes from the periphery into the center of the scar.

As soon as the period of suckling is over, the scar diminishes to 3 mm and deep furrows occur instead of folds on the surface. Rich fibrous tissue growth (Fig. 1) takes place and the previously developed blood vessels atrophy gradually. In the last stage, no blood vessels are observed in the scar; earlier hyaline blood vessels disappear. The section surface is gelatinous. A small number of fibrocytes is observed.

#### Morphological changes in the scars of corpora lutea of pregnancy

A series of scars can be observed on the ovaries of mature females ranging from 3-5 mm up to the slightly elevated ones. The most distinctive remain pale yellow with thin blood vessels in the furrows. The scars lose their color while diminishing in size, blood vessels vanish and only a fold-type scar remains on the surface. This scar is most often round, with smooth folds separated from each other by shallow furrows. Such a scar lacks luteal cells, and

<sup>1</sup> The term 'scar of corpus luteum of pregnancy' covers all exterior signs found on the ovary (a crater, a protuberance, a scar) and the mass of a resorbed yellow body (CL) formed on the ovary surface or deep in the ovarian stroma (Zemskiy, 1956).

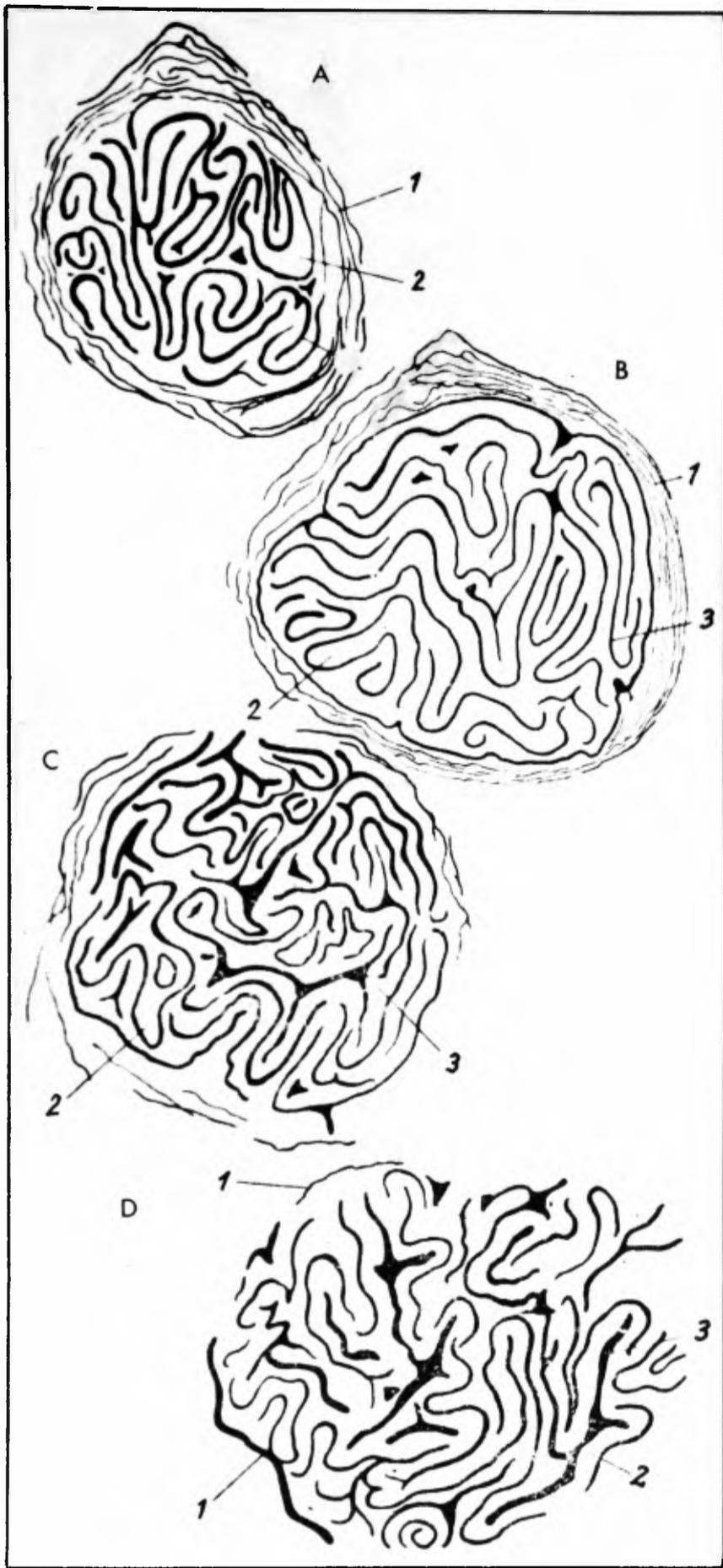


Fig. 2. Types of folded scars ( $\times 6-8$ ). 1 - wrinkled surface of the corpus luteum; 2 - folds; 3 - furrows (from Popov, 1951). Deeper furrows are drawn with thick lines.

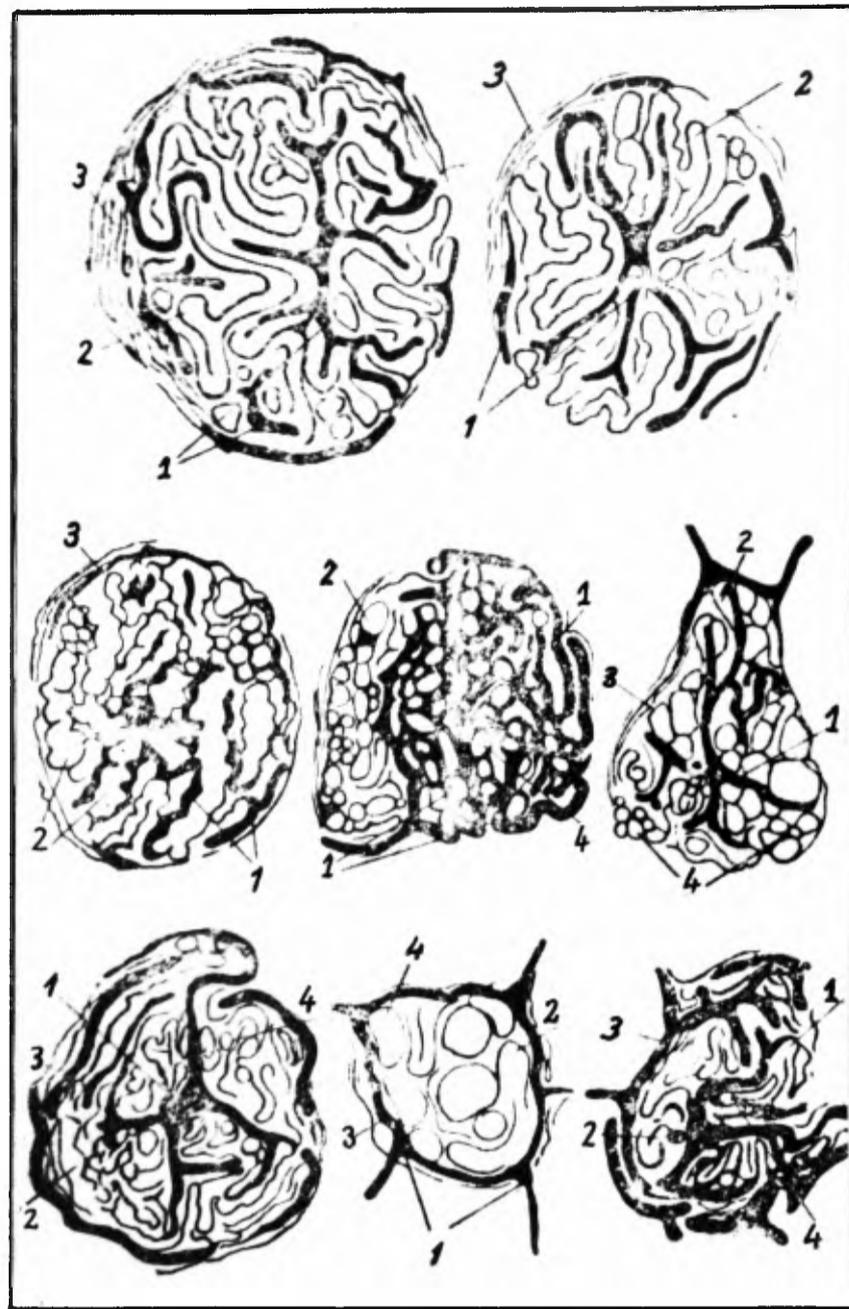


Fig. 3. Types of transitional (folded-ray) furrows from the surface (6-8 times increase) (from Popov, 1951).

- 1 - deep furrows;
- 2 - folds;
- 3 - corpus luteum surface;
- 4 - folds separated into protuberances.

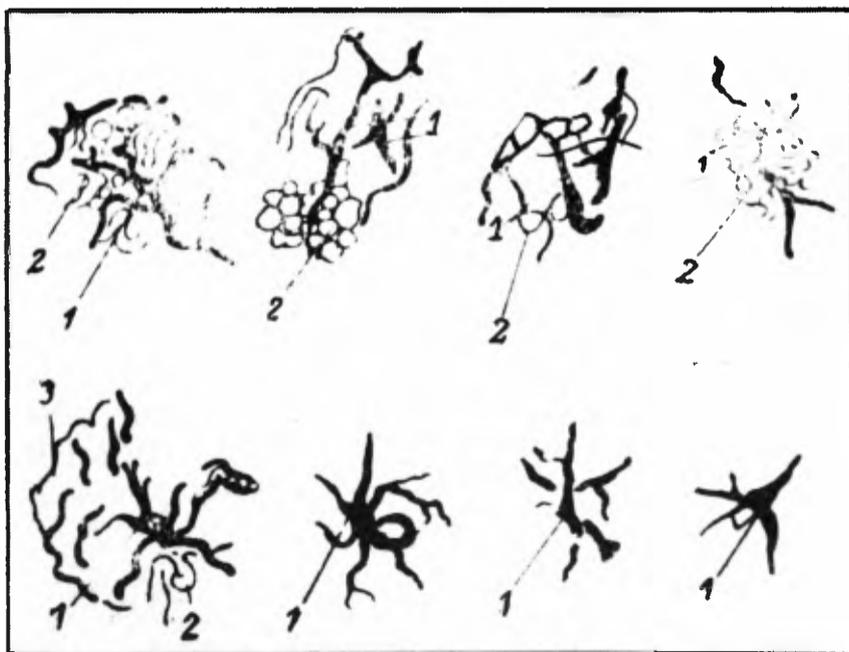


Fig. 4. Scars radiating from the surface ( $\times 8-10$ ) (from Popov, 1951).

- 1 - deep furrows and folds;
- 2 and 3 - the remainder of the folds and the former corpus luteum.

hyaline regeneration is observed in some. Four types of scars are distinguished (Fig. 2), which transform into folded scars of transitional type (Fig. 3). The diameter decreases from 0.5-1 cm to 2-3 mm. Deep furrows appear at first in the center and then cover the scar completely. The folds become much smaller, and cuts are noted on their borders. Small protuberances develop instead of folds. The number of such scars increases up to 30-35%, compared to 10-12% of the folded scars.

The transitional type of scar transforms into one of radial type; the folds and protuberances disappear, the

scar seems to be smoothed out, the central furrows become deeper, and later a small stellate scar remains (Fig. 4). This type of scar appears in the process of irreversible degeneration. In the opinion of Popov, it does not disappear during the life of a dolphin. It is encountered in 50–55% of all scars investigated.

#### Scar of corpus luteum of ovulation

Small, round, well-defined bodies 1–3 mm in diameter occur on the surface of the ovary in addition to those described. They have thickened edges. Hyaline degeneration of vessels and atheromatous connective tissue are seen in such scars; collagenous fibres are strongly developed, but only superficially.

Transitional phases between the radial scars and the bodies described above were not found. This allows the assumption that the bodies are scars of corpora lutea of ovulation. They do not reach the size of the corpus luteum of pregnancy, exist for a very short period, and, therefore, the extent of changes in the ovary is limited.

## 2. FIN WHALES OF THE SOUTHERN HEMISPHERE (*BALAENOPTERA PHYSALUS*)

During commercial operations by the Soviet fleet *Slava*, 354 pairs and 45 single ovaries were collected. They were fixed in 4–5% Formalin. The examination of ovaries was performed under laboratory conditions. The functioning corpora lutea of pregnancy were thoroughly examined, their diameter measured and inner structure noted. The number of different types of scars was estimated and a section was made through the center. The next sectioning was performed at 4–5 mm thickness. Separate areas of scars not more than 1 cm in size were taken for histology. Sections of the exterior area of the follicle rupture, the central part of the scar as well as the border to the ovarian stroma of 5–15 microns were prepared and stained with hematoxylin and fuchsin.

Investigations of the ovaries of fin-whales were performed by Zemskiy (1956, 1958).

#### Functioning corpus luteum

The corpus luteum of pregnancy in the fin whale is round and is at the periphery of the ovary. Its diameter varied from 11.5 to 18 cm. A crater, or a hollow surrounded by a raised border of luteal tissue, was observed most often on top of the corpus luteum (60%). The diameter of such a crater reached 8 cm. A protuberance of up to 5 mm was less often found at the site of the previous follicle. Sometimes, only a scar or a depression was seen externally (Fig. 5). A central cavity was usual in cases when no crater was observed, in 46% of the samples examined in this study. It was filled with hyaline matter; the diameter varying from 15 to 45 mm. The central cavity was absent in corpora lutea having a crater (11% of samples).

#### Scar of corpus luteum of pregnancy

The functioning corpus luteum in fin whales reaches a diameter of 14–18 cm and remains throughout pregnancy.

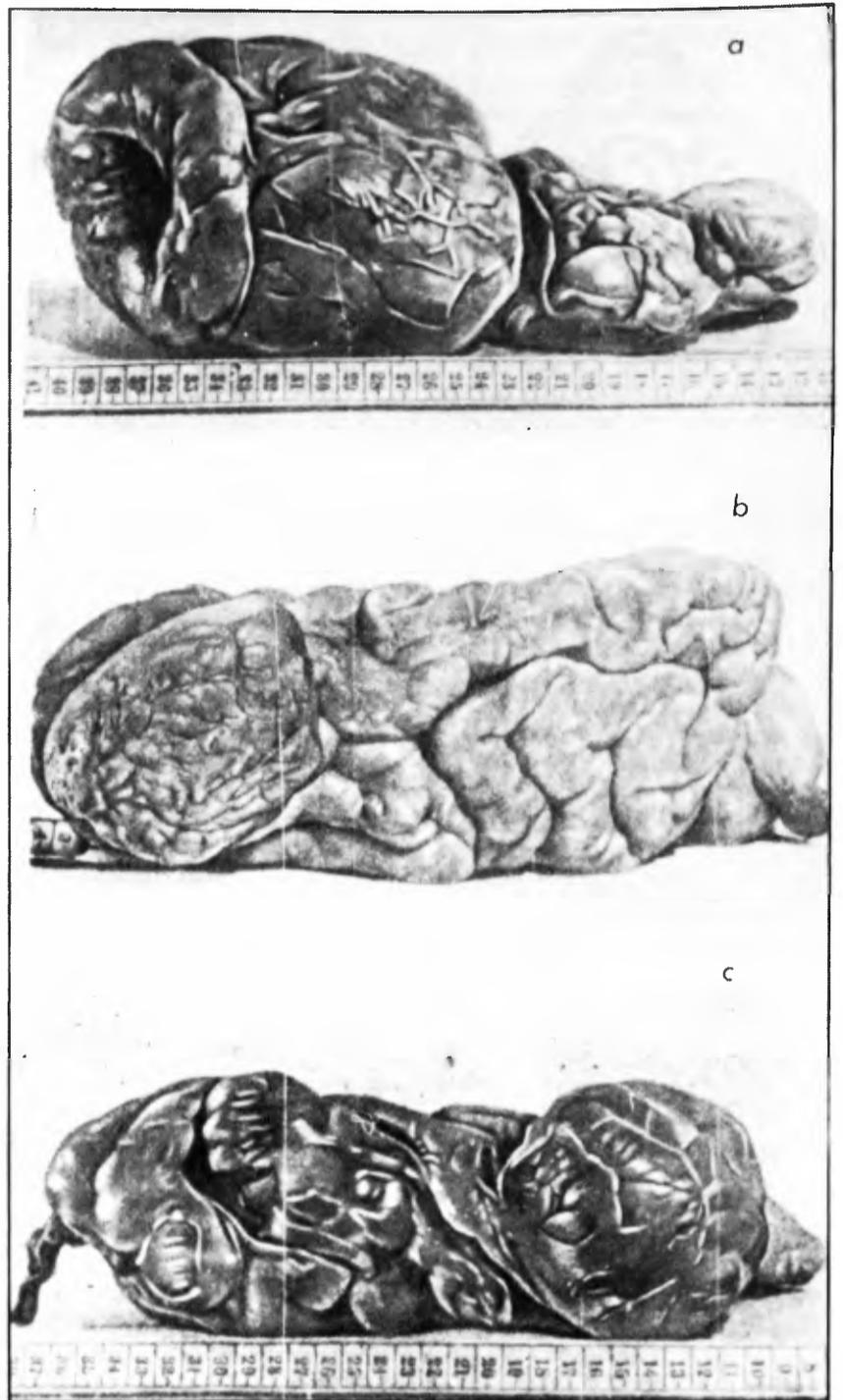


Fig. 5. Corpora lutea of pregnancy in fin whales (from Zemskiy, 1958).  
a – with crater; b – with protuberance; c – with scar.

After birth, the regression of the corpus luteum is slow and passes through two stages. It diminishes greatly in size during lactation and becomes firm. Thereafter the process of regression slows greatly, and the size of the scar is reduced to about 3–5 cm. Scars of this type were spread over the surface of the ovary; they were hard, had the form of a sphere or half-sphere and were separated from the surface of the ovary by a small stem. The diversity of the scar shapes reflects both the initial type of the corpus luteum and its age. The older scars differed greatly from the younger ones. The diameter varied from 2 to 10 cm. The scar was most often round and always had a clearly expressed demarcation near the base. A dense yellow-brown of varying hue was observed in sections. It was demarcated by connective-tissue fibres, which radiated from the central capsule and could be interrupted by numerous anastomoses. Blood vessels were seen mainly near the base of the scar.

Sclerosis was noticed in most blood vessels of the scar. Luteal cells were rare and deformed in most large scars. Histiocytes and fibroblasts were often observed in the dense connective tissue, and collagen fiber bundles were observed (Fig. 7).

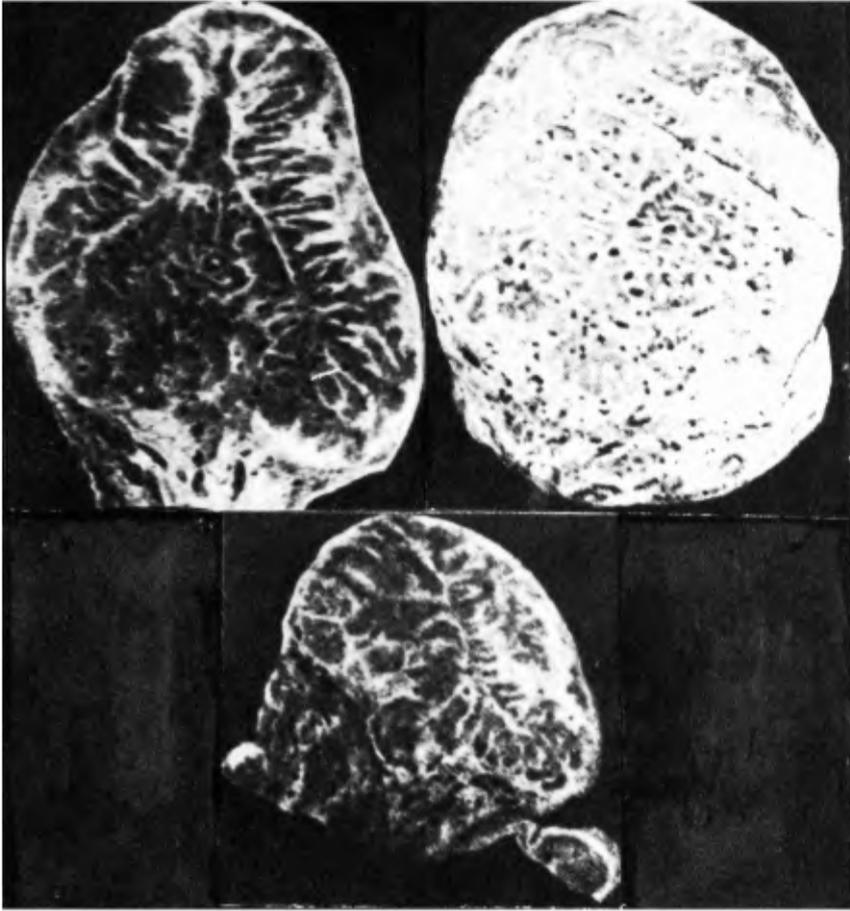


Fig. 6. Macroscopic sections of scars of corpora lutea of pregnancy (from Zemskiy, 1958).

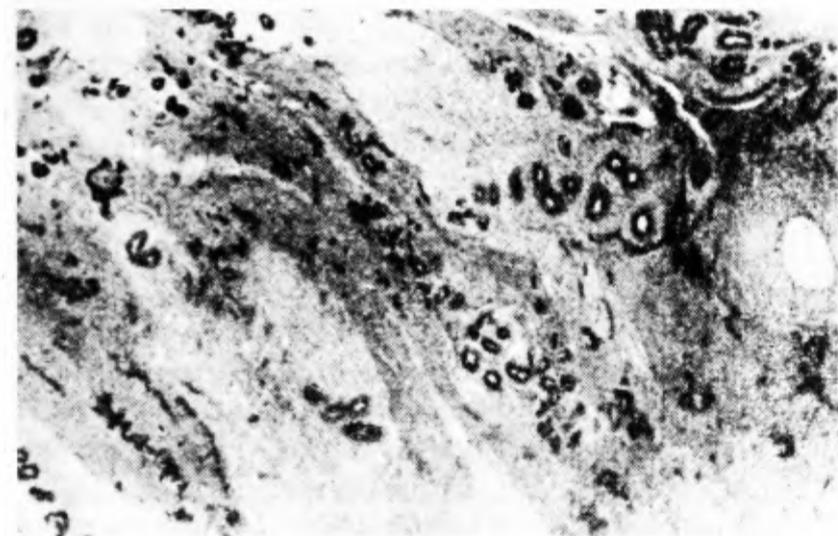


Fig. 7. Histological structure of the scar of corpus luteum of pregnancy (from Zemskiy, 1958).

#### Scar of corpus luteum of ovulation

A corpus luteum of ovulation exists for a short time and does not reach the size of a corpus luteum of pregnancy. Its regression is more rapid, with proliferation of many blood vessels. The scars of this type were not elevated above the ovarian surface; they formed only small swellings, and were softer than scars of corpora lutea of pregnancy. The cut surface was distinguished by a coagulated consistency (Fig. 8).

The scars consisted of light connective tissue around numerous blood vessels; they were sclerotic in most cases and partially filled with connective tissue. Engorged vessels were also encountered. Histiocytes and fibroblasts were not numerous. Collagen bundles were present only at the edge of the scar. Luteal cells were not observed (Fig. 9).



Fig. 8. Macroscopic sections of the scars of corpora lutea of ovulation (from Zemskiy, 1958).

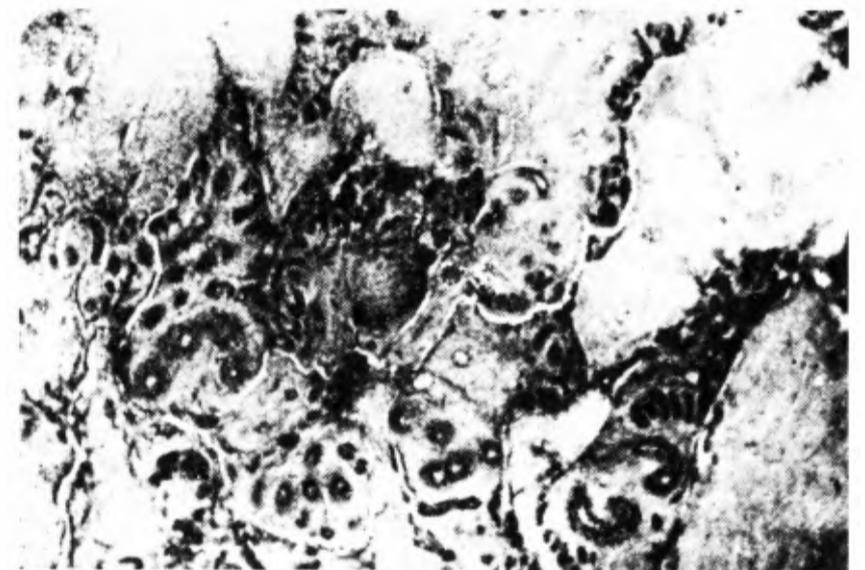


Fig. 9. Histological structure of the scar of corpus luteum of ovulation (from Zemskiy, 1958).

#### Follicular atresia

Examination of ovaries of mature whales showed that there were also some scars distinguished from both preceding types by the lack of evidence of ovulation. These scars were either small (not more than 4 cm<sup>2</sup>) without deep and short furrows, or spherical (up to 2 cm in diameter) and having a protuberant surface (Fig. 10).

Cut sections showed a small cavity filled with yellow luteal-like matter in 75% of the specimens. The cavity lacked follicular liquid. Connective tissue was absent. Such areas were rapidly resorbed and looked like small areas of fibrous tissue, only slightly differentiated from the ovarian stroma.



Fig. 10. Scars of atretic follicles on the ovaries of fin whales (from Zemskiy, 1958). a – spherical formation; b – shallow, short furrows.

Only a few atretic follicles were noted in the 200 ovaries.

Based on the material investigated, one can distinguish the macroscopic signs of scars from corpora lutea as follows:

(1) Scars of corpora lutea of pregnancy are usually located over the surface of the ovary and often have a clearly expressed boundary at the base. The scars range from 3 to 10 cm, are hard and consist of dense connective tissue with small areas of thin connective tissue. The cut surface is smooth and the connective tissue is of branched form, clearly expressed on the background of degenerated luteal cells of a yellow-brown colour. There is a central cavity. The blood vessels are mainly at the border between scar and ovarian stroma.

(2) The scars of corpora lutea of ovulation are most often found under the surface. The size is more stable and rarely exceeds 15–30 mm. They are smooth and consist mainly of light connective tissue. A coagulated structure is observed on a cut surface. A branched state of the connective tissue is rare. Blood vessels are numerous and partially sclerotic. The functioning corpus luteum affects the shape of the scars lying near it; they may become flat and elongated.

### 3. HUMPBACK WHALE (*MEGAPTERA NOVAEANGLIAE*) OF THE SOUTHERN HEMISPHERE

The humpback material was collected on board the Soviet fleet *Slava* during a trip into the South Atlantic area. Sixty-six pairs of ovaries were fixed in 4–5% Formalin. The condition of the ovaries was noted at the macroscopic level and all scars were described. Then the scars were cut perpendicular to the ovary. A series of sections was made 3–5 mm parallel to the first. The sizes were measured, and presence or absence of a central capsule was noted, as well as number and location of connective-tissue layers and surface character of the cut.

Pieces of the scars were sectioned at 10–15 microns by freezing microtome. These sections were stained with hematoxylin and eosin sudan III and then treated with 5% acetic acid.

These investigations were performed by Ivashin (1958).

#### Functioning corpus luteum of pregnancy

The corpora lutea of pregnancy were usually spherical, but elongated at times with a distinct boundary at the base (92.1% of 38 cases). They protruded 80–200 mm above the ovarian surface. They were from 86 to 164 mm

at the last stage of pregnancy (Chittleborough, 1954), smooth or at times wrinkled, and blood vessels were often visible. They could be easily distinguished from the scars of corpora lutea of pregnancy and ovulation by their appearance and size. A central cavity was found in 47%, a crater in 15.8%, and a protuberance in 26.3%.

#### Scar of corpus luteum of pregnancy

According to observations by Robins (1954) and Chittleborough (1954), the corpora lutea of ovulation in humpback whales measured from 32 to 88 mm. The corpus luteum of ovulation transforms into that of pregnancy after fertilization. The size of the scar depends both on the size of the initial corpus luteum and on the intensity and duration of regression. Soon after birth, the corpus luteum of pregnancy greatly decreases in volume. At different stages of suckling its size varied from 55 to 85 mm in three whales, two pregnant and one lactating. They were spherical and slightly flattened on the sides. Often they were narrower near the base.

Scars from previous pregnancies were spherical in most cases; sometimes they were enlarged at the apex or were slightly flattened. A noticeable separation occurred near the base (40.6% of all cases). Sometimes they protruded on the surface (55.4%) and were hard to the touch.

A crater or protuberance occurred in 12.9%. One hundred and one scars examined had neither crater nor protuberance (72.2%). Seventy-one per cent of scars varied from 36 to 55 mm (range from 30 to 85 mm).

The sections usually had round or somewhat elliptical form (Fig. 11). When scars were located inside the ovary, they differed sharply from the stroma. White connective-tissue fibres divided the luteal mass of the scar and areas of yellow color.

Blood vessels were seldom found on the surface of scars, their number was not stable near the base, and sometimes they were absent.

Microscopic studies (Fig. 12) showed that the scars consisted of centres of light connective tissue. Fibroblasts and histocytes were intensively developed, as was collagen. Most luteal cells had dispersed; occasionally they gathered into large, dense islets. Mitoses were not

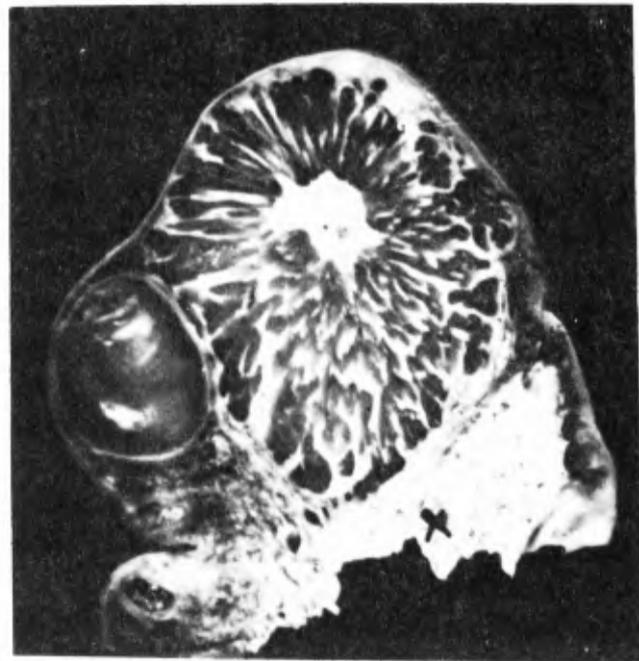


Fig. 11. Sections of scars of corpora lutea of pregnancy (from Ivashin, 1958). 1 – follicle; 2 – scar of corpus luteum of ovulation.

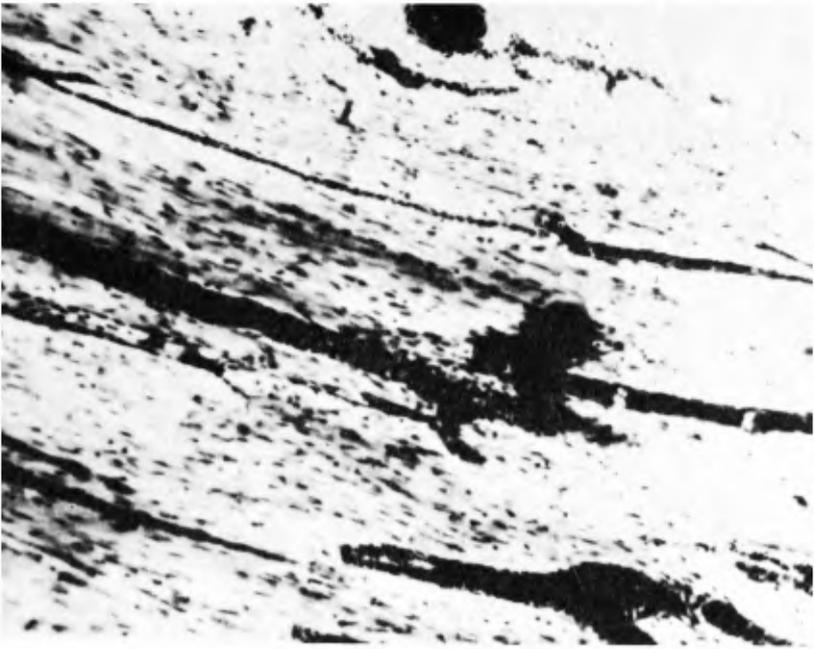


Fig. 12. Microscopic structure of corpus albicans of pregnancy (from Ivashin, 1958).

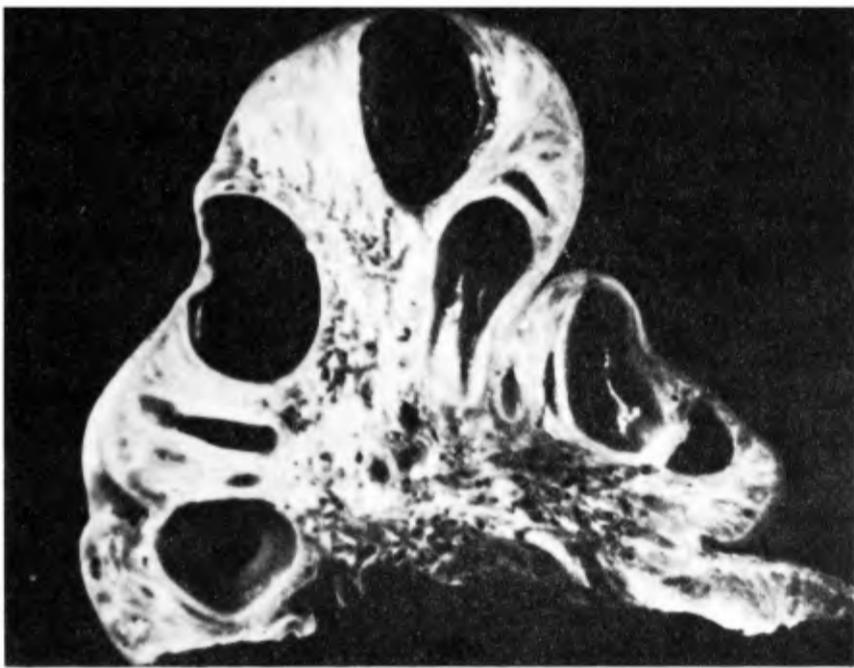


Fig. 13. Section of a corpus albicans of ovulation (from Ivashin, 1958).

observed, and many cells were vacuolated. Blood vessels were greatly enlarged (stasis), filled with decomposing erythrocytes, and had greatly thickened walls with hyalinization.

#### Scar of corpus luteum of ovulation

The corpora lutea of ovulation (32–88 mm) were smaller than those of pregnancy (86–164 mm). Their regression is more intensive, therefore they are smaller. The scars formed slight protrusions, some millimeters in height in 45.9%, or they were flat. Only a scar was seen on the surface 37.7% of the time. A crater was found in 9% of 22 scars. Most of the scars ranged from 16 to 30 mm (73.3%). Occasional scars were over 35 mm in size, but not more than 45 mm (6.2%). The sectioned surface was elongated, round or square (Fig. 13). Many connective-tissue fibres filled the mass so densely that the luteal cells of pale yellow color were hardly noticeable.

Histological analysis showed that the scars consisted of centres of a friable connective tissue with a great number of blood vessels, stasis and sclerosis of the walls

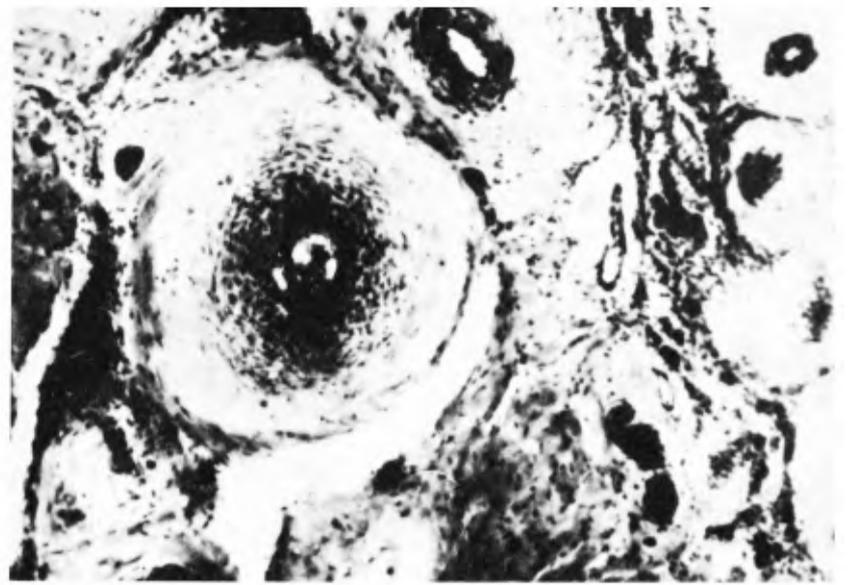


Fig. 14. Microscopic structure of a corpus albicans of ovulation (from Ivashin, 1958).

(Fig. 14). Luteal cells were vacuolated and scattered and surrounded by fibrocytes and histocytes.

The macroscopic signs of corpora albicantia are as follows:

(1) The scars of corpora lutea of pregnancy are usually large (30–35 mm); they are noticeably defined on the surface and hard. The cut surface is smooth and dense. The luteal tissue can be yellow or of different tints.

(2) The scars of corpora lutea of ovulation are usually small (16 to 30 mm); they are almost insignificant on the surface and soft to the touch. The cut surface is rough and friable and has much connective tissue that sometimes fills the whole scar. The cut surface can be almost smooth at an early stage of scar formation.

Regression of corpora lutea from pregnancy and ovulation are dissimilar. Luteal cells are considerably less numerous in the scars of the latter and begin to disappear much earlier. Blood-vessel hyalinosis and the phenomena connected to it (stasis or contraction of vacuolar lumina) take place as a local process, whereas this process covers the whole mass of blood vessels at once in scars of ovulation.

#### 4. GRAY WHALE (*ESCHRICHTIUS ROBUSTUS*)

The material was collected at the Chukotski Peninsula during the period of June–October, 1965–1968. The ovaries of 70 whales were fixed in 4–5% Formalin. A cut was made through the centre, and 3–4 mm sections were made parallel to the cut. A central slab was detached after its examination and measurement and used for microscopy. Sections of 10–15 microns were prepared with a freezing microtome and stained with Mayer's hematoxylin and eosin. In total, 150 preparations were made for histological analysis.

These studies were conducted by Zimushko (1970).

#### Functioning corpus luteum of pregnancy

The corpora lutea of pregnant females were round and had no clearly expressed boundary near the base. Their sizes ranged from 90 to 170 mm (mean diameter – 130 mm). A protuberance of 10 to 80 mm was noted on all corpora lutea of pregnancy. No craters were observed.

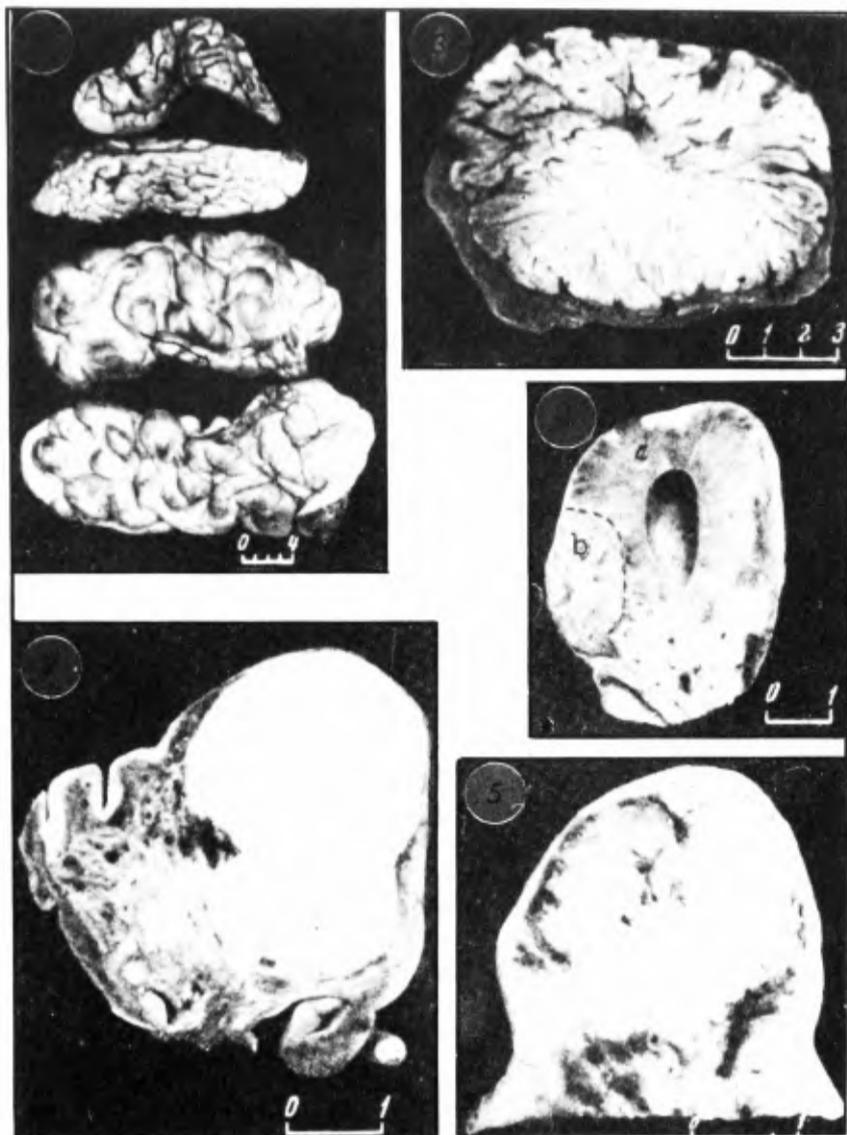


Fig. 15. Different formations in the ovaries of the grey whale (from Zimushko, 1970). 1 – above – ovaries of an immature female; below – ovaries of a mature female; 2 – atretic follicle (cut); 3 – corpus luteum of pregnancy (section); 4 – (a) trace of corpus luteum of pregnancy with capsule in the centre; (b) trace of the corpus luteum of ovulation; 5 – scar of ovulation (cut).

Capsules were found in 58%; they were covered by connective tissue and filled with gelatinous liquid. The connective-tissue bands often lay as rays in the background of a great volume of luteal tissue (Fig. 15(3)).

#### Scar of corpus luteum of pregnancy

Insignificant protrusions could be distinguished by their shape at the surface of the ovary. The surface cut was smooth; a great number of the connective-tissue strands radiated from the capsule (observed in 30%, Fig. 15-4) and, when a capsule was absent, these strands branched out in disorder from the main mass of the scar. The color varied from light-yellow to dark-brown.

The scars were dense to the touch. The mean size of 142 scars was  $33 \times 23$  mm (along great and small diameters of the ellipse). They were much larger in lactating females, reaching sizes from  $40 \times 25$  mm to  $65 \times 65$  mm.

Histological analysis showed that dense connective tissue prevailed in the scars (Fig. 16a). The number of blood vessels was small and they were small-sized. Sclerosis, hyalinosis and stasis were observed in the vessels. The connective tissue cells consisted of fibroblasts and histocytes; the luteal cells were degenerating.

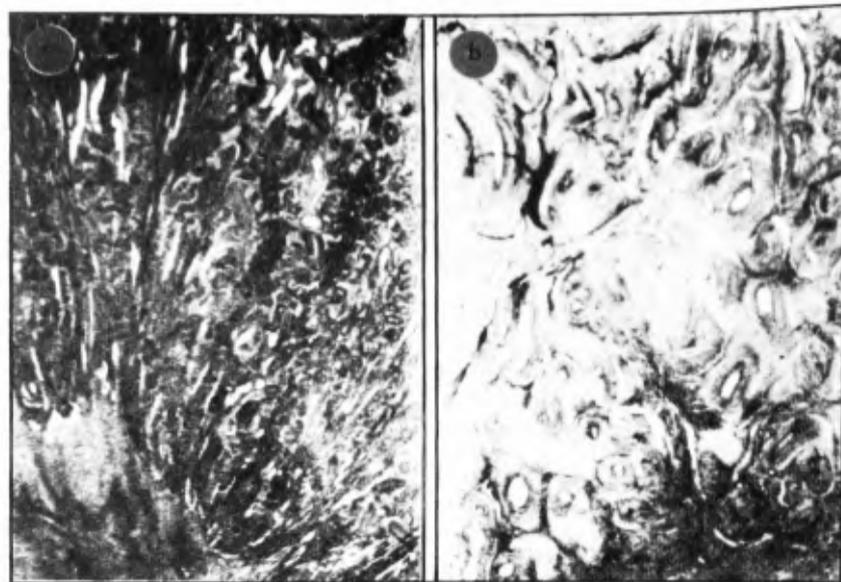


Fig. 16. Histological structure of the corpus albicans of pregnancy (a) and corpus albicans of ovulation (b) (from Zimushko, 1970).

#### Scar of corpus luteum of ovulation

Most often the scar had the shape of an insignificant protrusion; sometimes it was wrinkled. Its color was lighter than that of the ovary surrounding it, and it was covered with bluish spots. In some cases, a scar was found only after the ovary had been cut.

The surface of the cut was friable. A capsule was seldom observed and the number of connective-tissue bands were small, but dissemination of white connective tissue was clearly seen on the surface of sections. Sometimes bright strands of luteal tissue were seen on a yellowish or brown background (Fig. 15(4) and 15(5)). The 248 scars studied measured on the average  $29 \times 16$  mm and were soft.

Microscopic studies showed that friable connective tissue prevailed in the scars (Fig. 16). The porosity seen was due to many blood vessels, the majority being sclerotic, with stasis and hyalinosis.

#### Atresia of follicles

Atretic follicles without scars in the area of rupture measured from  $2 \times 6$  mm to  $12 \times 14$  mm. They were slightly detached from the ovarian stoma and had sometimes the appearance of small, branched yellow bands with orange or yellow tint. Twenty-one formations of this type were found. The largest atretic follicle measured 35 mm, was spherical and had a great number of blood vessels on its surface. A section showed its cavity was filled with a yellow coagulated mass (Fig. 15(2)).

The size of atretic bodies decreases with resorption; they transform into a 'fibrous body'. There were 18 formations of this type from 2 to 5 mm in size. Apparently, they persist for only a short time.

### 5. SPERM WHALE (*PHYSETER MACROCEPHALUS*)

During the period 1951–1956, 359 pairs of ovaries from pregnant, 'resting' and lactating females were collected at the coastal stations of the Kuril Islands (north-western Pacific).

Sections of 10–15 microns were prepared on freezing and ordinary microtomes for histological studies. They were dehydrated in alcohol, embedded in celloidin, and

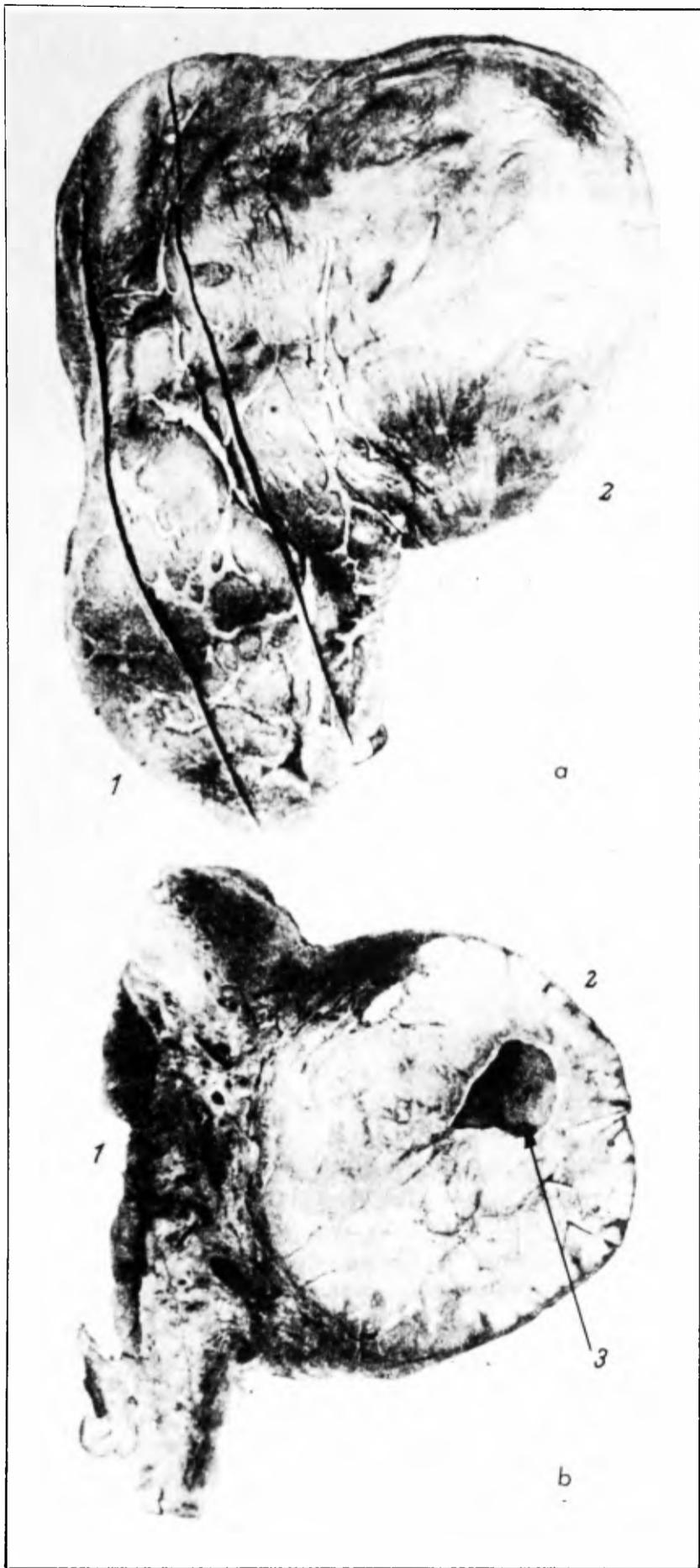


Fig. 17. Overall view (a) and a longitudinal section (b) of a sperm whale ovary (from Chuzhakina, 1961). 1 - ovary; 2 - corpus luteum of pregnancy; 3 - inner cavity of the corpus luteum of pregnancy.

stained with hematoxylin, eosin and sudan III. These studies were performed by Chuzhakina (1961; 1965).

**Functioning corpus luteum of pregnancy**

Contrary to that of the baleen whales, the sperm whale corpus luteum has no stem. It rises above the ovarian surface and is shaped like a ball (Fig. 17(2)). The diameter ranged from 58 to 160 mm. The size varied from 58 to

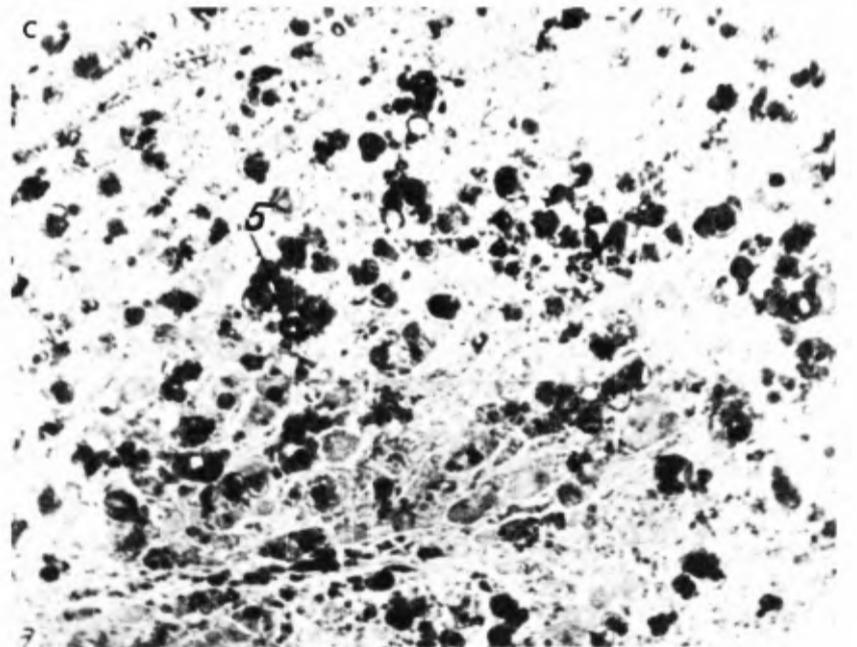
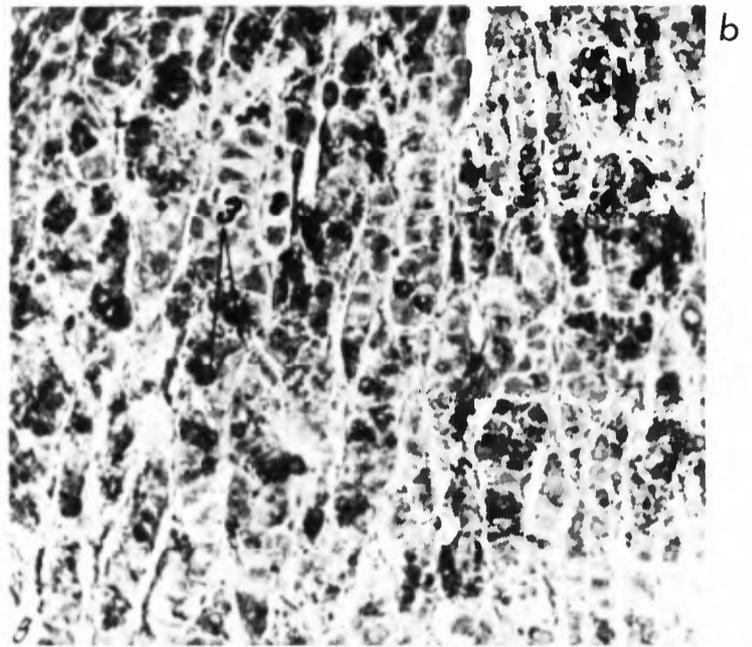
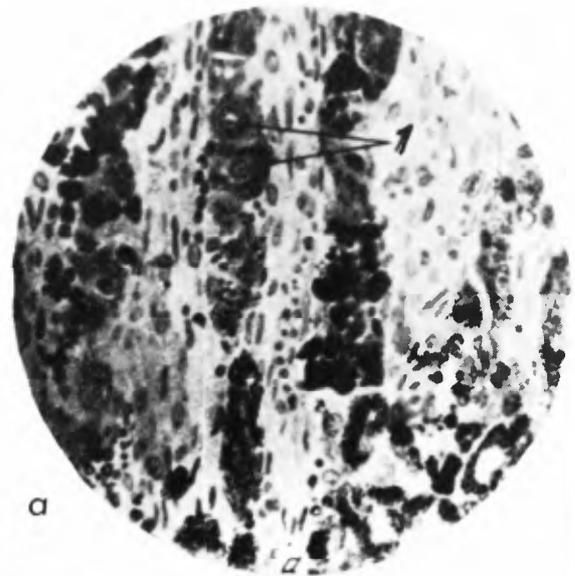


Fig. 18. Microphotography of the corpus luteum of pregnancy (from Chuzhakina, 1961). a - early stage, embryo - 1.8 cm; b - of calf-42 cm; c - of calf-374 cm.

113 mm in primiparous females. No crater was observed on the surface. A central cavity was present in 36.2%; sometimes it was not located in the centre (Fig. 17(2)).

The corpus luteum and the connective-tissue cells were arranged in a radial fashion during the first months of pregnancy (embryo length less than 18 mm). Luteal cells also extended radially and had a polygonal form, the lipid in small granules (Fig. 18a).

When the embryos reached 42 to 136 cm, luteal cells



Fig. 19. Regressing corpus luteum of pregnancy (from Chuzhakina, 1961). 1 - ovary; 2 - regressing corpus luteum; 3 - inner cavity of the corpus luteum.

appeared in the corpora lutea, bearing large drops of lipid (Fig. 18b). Later, the radial organization of luteal cells was disrupted, when the embryos measured from 199 to 276 cm; the first signs of regression were noted in many luteal cells; the lipid granules increased in size; and pycnosis and early karyolysis were observed.

Luteal cells were encountered encircled by connective-tissue layers to the end of pregnancy (embryos' length from 300 to 420 cm); most of the cells had large lipid granules, bright-orange or straw-yellow in color. Pycnosis and karyolysis were observed in 90% of luteal cells' nuclei (Fig. 18c).

#### Scar of the corpus luteum of pregnancy

In the first half of lactation, the scars were distinct (Fig. 19), though they were not sharply expressed on the surface. They had no constriction near the base. At the end of lactation such scars were not elevated. Areas of pale-brown color were most often clearly noticed on the surface.

At this stage of regression, the 50-87 mm scars consisted of dense connective tissue and xanthomatous

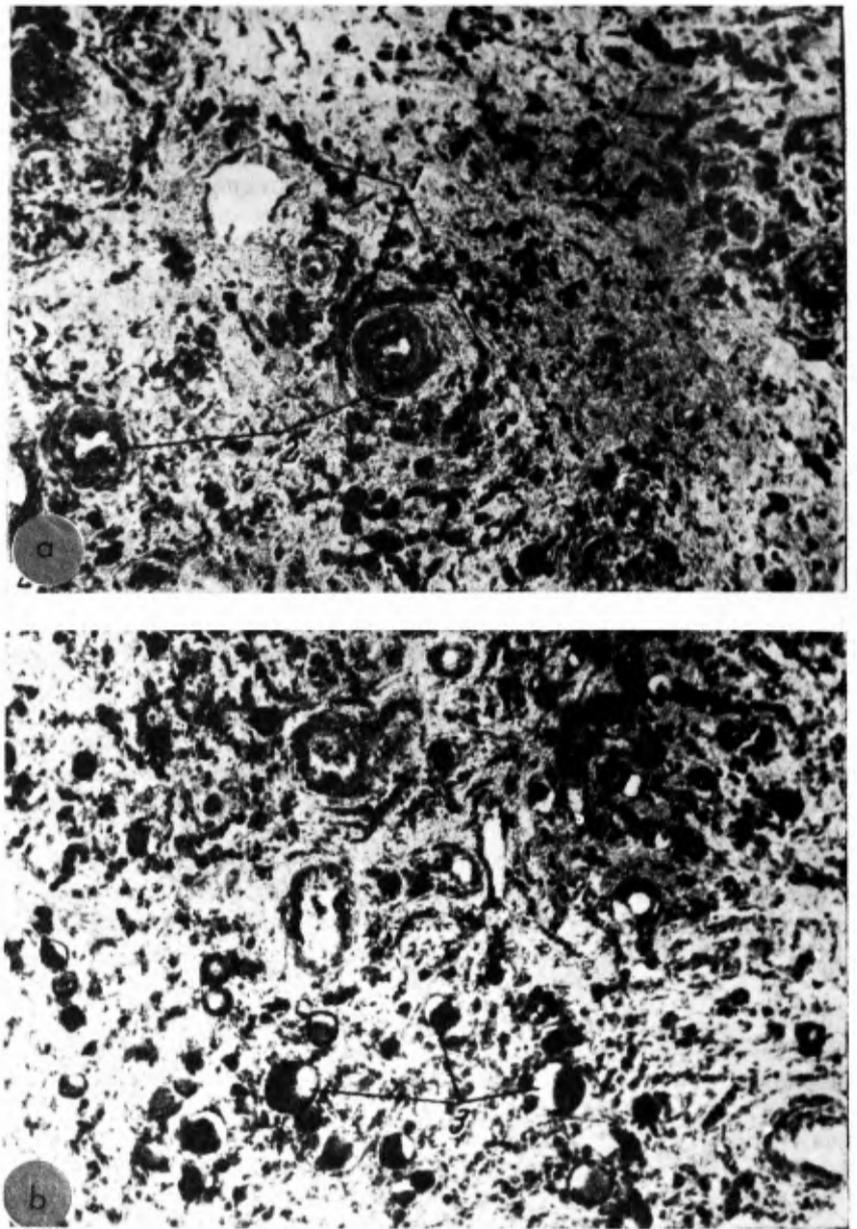


Fig. 20. Microphotography of the regression of the corpus luteum of pregnancy (from Chuzhakina, 1961). 1 - pseudoxanthomatous cells; 2 - blood vessels; 3 - filling of the lymphatic slits with fat.

cells having spherical shape, which could be noticed most often near the thick-walled blood vessels of different size (Fig. 20).

At the end of lactation the scars diminished to 21-33 mm and were not protruding on the surface. Many sclerotic blood vessels were seen on the surface of the cut; the few pseudo-xanthomatous cells were filled with fat. Hyalinosis was not noticed in the fibrous connective tissues.

Regression continues after the lactation period. The scars varied from 35 to 13 mm, became almost insignificant, and were located in the ovarian stroma (Fig. 21). The sectioned surface was most often ellipsoid and dark-brown to whitish (the latter scars are the oldest and are merged completely with the ovarian stroma). They consisted of connective tissue pierced with sclerotic vessels with hyalinosis (Fig. 22). Depending on the number of pseudo-xanthomatous cells, the scar acquired a yellowish or brownish tint. According to Chuzhakina, these scars persist during the whole life of the animal.

#### Atresia of follicles

According to Chuzhakina (1965), large atretic follicles from 40 to 76 mm were found in the ovaries of pregnant females (body length from 9.9 m to 10.7 m). Their diameters were 87 and 57 mm in a lactating female.



Fig. 21. Longitudinal cut through a sperm whale ovary and scars of corpora lutea of pregnancy. 1 – ovary; 2 – scar with connective-tissue nucleus; 3 – scar without a connective-tissue nucleus.

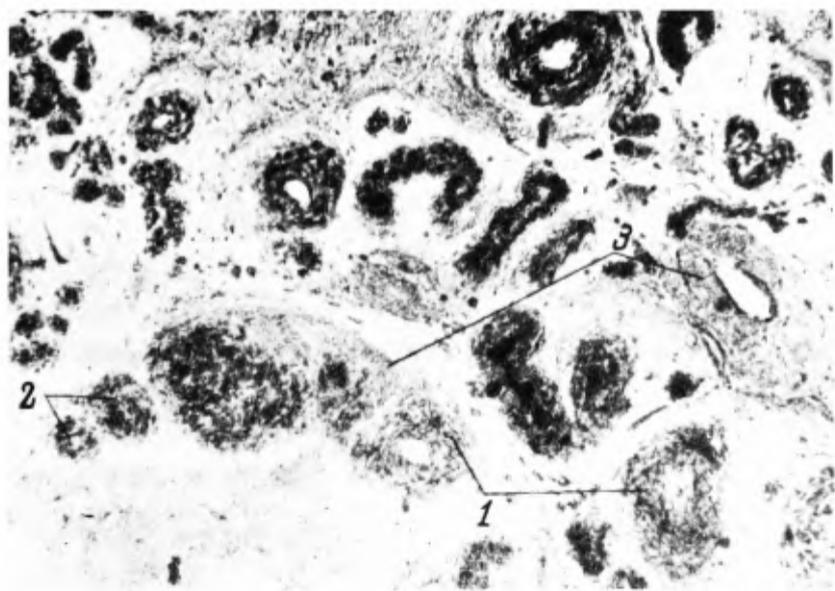


Fig. 22. Microphotography of an old scar of a corpus luteum of pregnancy (from Chuzhakina, 1961). Blood vessels: 1 – sclerosis, 2 – obliteration, 3 – hyalinization.

## DISCUSSION

### Multiple corpora lutea

Throughout the period from 1932/33 to 1967/68, cases of whales with 2 to 5 embryos (in fin whales up to 6) made up 0.85% of blue whale pregnancies, 0.94% in fin whales and 0.56% in humpback whales, whereas the rate was 2–3 times higher in sei whales (1.71%) (Ivashin, 1971). Two or more functioning corpora lutea of pregnancy were encountered most often in such cases. Thus, a female of a humpback whale off New Zealand (13.7 m in length) caught during the 1960/61 season had one functioning corpus luteum in the right ovary and three in the left ovary; embryos of 45 cm, 50 cm and 51.5 cm in length and embryonic membranes of a fourth were found in the uterine horns (Ivashin, 1971). During the 1973/74 season, twins were noted in 7 cases (0.48%) of minke whales. Three functioning corpora lutea of pregnancy were observed in their ovaries once, and two were found five times. When only one embryo was in the uterus, 15 females had two corpora lutea in their ovaries, 4 females had three and one animal had four corpora lutea (Ivashin, 1976).

These cases show the possibility of simultaneous ripening of two or more Graafian follicles. Thus, several scars can be engendered. They may differ in size but they will be similar in appearance and structure. The presence of such scars can cause difficulties in determination of the number of pregnancies and the interval of births. The frequency of such occurrence, however, cannot greatly affect the statistics on the whole. This also is the case when a female has an ectopic pregnancy, or the embryo dies in development (Ivashin, 1960; 1963).

### Distinguishing scars of pregnancy from those of ovulation only

The methods used by Soviet scientists to distinguish between scars of corpora lutea of pregnancy and ovulation can be used for practical purposes in spite of the fact that the studies were small in scope.

## ACKNOWLEDGEMENTS

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# Reproduction and the Reproductive System in the Beiji, *Lipotes vexillifer*

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## ABSTRACT

Information about reproduction and the genital organs of five females and three males of *Lipotes* is reported. Gross appearances and tissue structures are described. The left and right ovaries of an immature female 192 cm in length had the same dimensions and weight and were similar in outer appearances. From the length of their foetuses, two pregnant females of 250 cm and 253 cm gave birth in February or in March. A newborn calf of *Lipotes* is about 70 cm long. The corpus luteum of pregnancy is fungiform. The structure of the corpus luteum of *Lipotes* is somewhat different from that for *Platanista gangetica*, *Platanista indi* or *Neophocaena phocaenoides*. The corpus luteum of *Lipotes* has no fibrous core, and its granulosa lutein cell is larger than that of other species, reaching 46  $\mu\text{m}$ . The vagina of *Lipotes* has more longitudinal and transverse folds than those of other species of freshwater dolphins. Besides the dense longitudinal folds, it has six rings of transverse folds which constitute a more perfect structure for preventing water from entering the uterine cavity.

As early as the end of the 18th century, biologists had conducted some research on reproduction in the freshwater dolphins *Inia*, *Pontoporia* and *Platanista* (Harrison, Boice and Brownell, 1969; Harrison and Brownell, 1971; Harrison, 1962; and Kasuya and Brownell, 1979). Detailed study on the subject did not begin until the 1970s when Harrison, Brownell and Boice (1972) summarized previous work, examined reproduction and the external features of the genital organs from new specimens of these genera, and made comparisons between them. No systematic work has yet been done on the reproduction of *Lipotes*, except for Chen and Chen's (1975) brief description of the external appearances of the genital organs.

Table 1

	Animal no.	Locality	Date	Length (cm)	Weight (kg)
Male	73-1409	Echeng	73/10	206.0	95.0
	79-1	Fankou	79/1/5	191.0	80.0
	80-1	Longkou	80/1/4	194.0	87.5
Female	74-1	Yanwo	74/1/21	250.0	224.0
	74-2	Yanwo	74/1/21	253.0	237.0
	79-2	Xintankou	79/1/25	245.0	142.5
	80-3	Chenglinji	79/1/11	192.0	63.6
	80-7	Jiayu	80/2/15	238.0	166.5

## MATERIAL AND METHODS

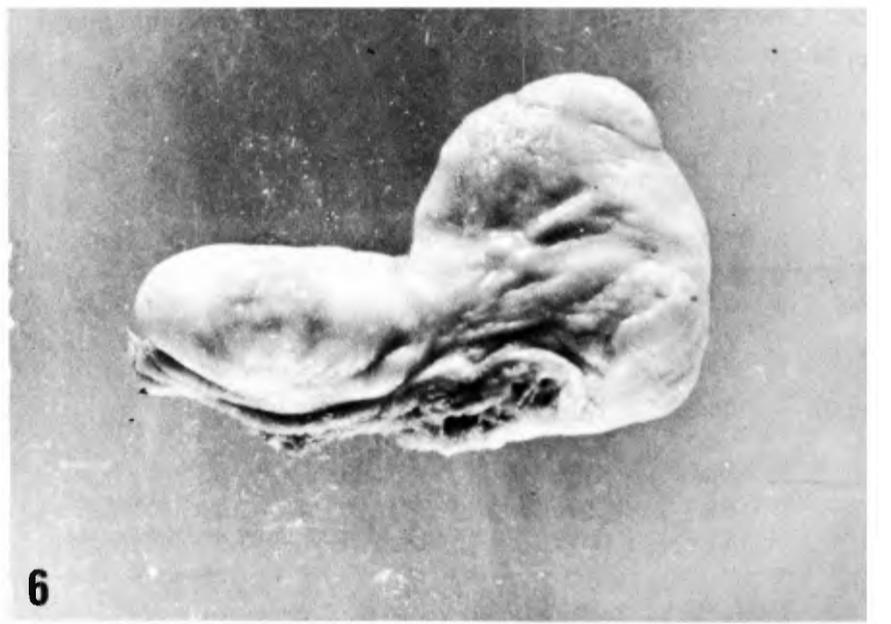
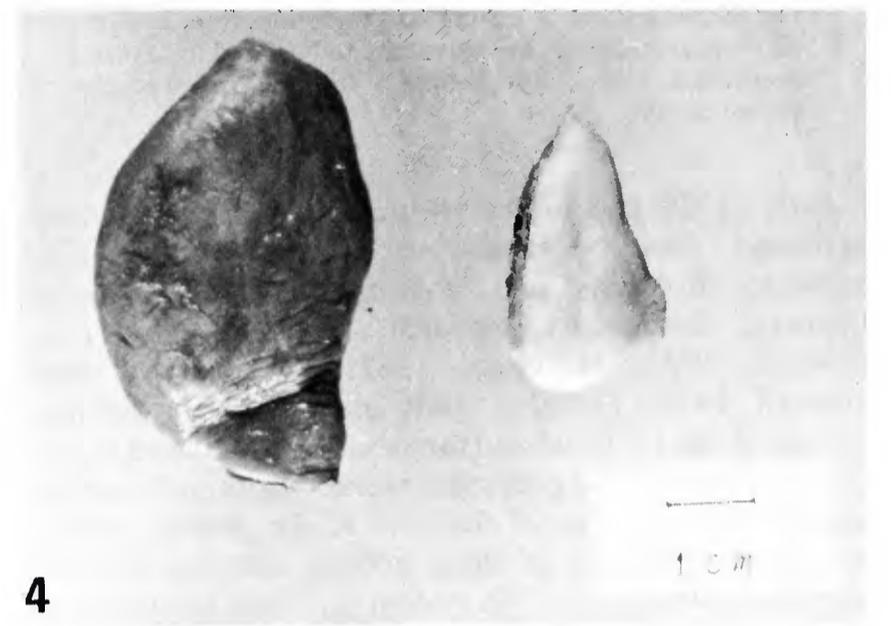
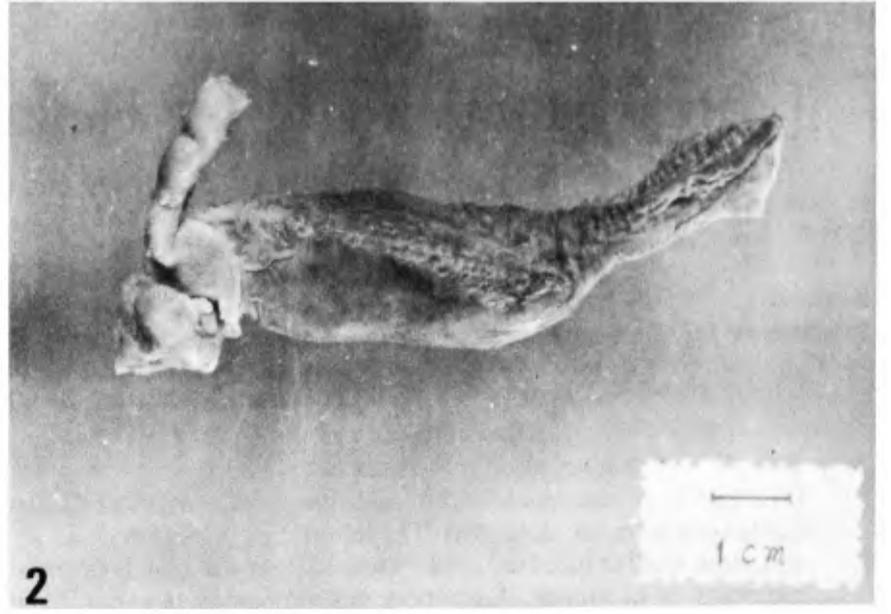
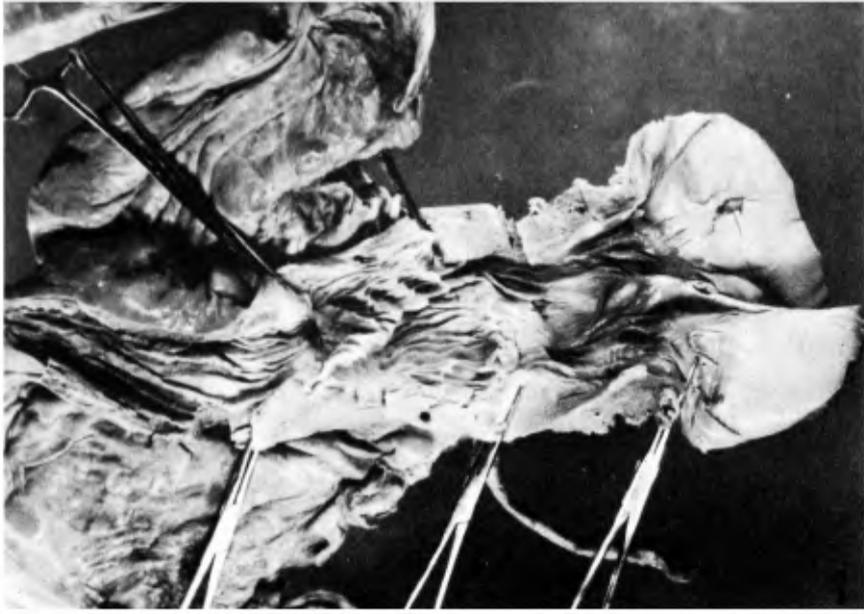
The material used here was taken from specimens obtained in the middle reaches of the Yangtze River in 1974–80 (Table 1). The genital organs of three males and five females were dissected, measured, weighed and photographed. Histological observations were made on each organ in the reproductive system.

<sup>1</sup> This paper is a revised version of a paper originally published in Chinese (Chen, Liu and Lin, 1982).

## ANATOMY OF THE FEMALE REPRODUCTIVE SYSTEM

### The vagina

Anterior to the ostium vaginae is quite a large oval protuberance, to the left of which is the urethra with the orificium urethrae in the vestibule of the vagina. The length of the vagina in one specimen (79-2) was 14.4 cm. Based on structure and color, the vagina could be divided into lower and upper sections. The lower section was near the ostium vaginae, 6.8 cm in length, and dark gray in color. Its wall was basically smooth, with a few shallow longitudinal folds. There was an obvious fold at the juncture of the ostium vaginae and the vestibule of the vagina, but no hymen was visible. The tissue of the lower vagina was divided into three layers. The membrane externa was of loose connective tissue. The lamina muscularis was smooth muscle with crisscross fasciculi. The submucous layer was very thick. The epithelium was of stratified squamous tissue. The membrana propria consisted of thick and fine connective tissue. The upper section of the vagina extended from the lower section to the ostium uteri. It was 7.6 cm long, a little longer than the lower section. Its color was light yellow. Its wall was covered with dense folds which were deep, leaf-like and crisscrossed. Although the number, color and distribution of the folds in *Lipotes* vary slightly, the basic features are the same, i.e. the upper section of the vagina is covered with thin leaf-like longitudinal folds. In addition to these there are several rings of transverse folds facing the lower section of the vagina. Since this section is filled with these dense longitudinal and transverse folds, no cavity is visible. Thus, this structure plays an important part in preventing water from entering the uterine cavity. The histology of this section is similar to that of the lower section, except that many tooth-like processes protrude from the surface. The epithelium is columnar (Plate 1, Fig. 1).



## PLATE 1

Fig. 1. Photograph of the uterine chamber, cervical canal, upper and lower vagina of 79-2.

Fig. 2. Photograph of the testis of 80-1.

Fig. 3. Photographs of the ovaries of 80-3.

Fig. 4. Photographs of the ovaries of 74-1. The right ovary contains corpora albicantia, the left ovary has a corpus luteum.

Fig. 5. Photograph of a section through the corpus luteum of 74-2.

Fig. 6. Photograph of the left ovary of 80-7 with corpora albicantia.

Table 2  
Dimensions of vagina and uterus (cm)

No.	Length of uterus	Length of vagina	Length of cervix	Width of septa	Left horn	Right horn
*74-1	250.0	18.0	12.7	—	70.0 × 20.0	19.0 × 15.0
*74-2	253.0	22.0	12.8	14.8	52.0 × 18.0	49.0 × 16.0
79-2	245.0	14.4	5.0	7.6	14.0 × 3.5	12.6 × 4.0
80-3	192.0	8.0	3.0	4.1	7.4 × 3.0	5.5 × 2.9

\* Pregnant.

### The uterus

The cervix uteri was 5 cm in length (specimen 79-2). The transverse folds of its external opening were especially thick. It resembled a triangle in longitudinal section. In a nonpregnant specimen, the cervix uteri was narrower than the vagina. Its external shape resembled a tube. Its inner wall consisted of several coarse and short longitudinal folds. During pregnancy, these folds disappear and are replaced by a soft, smooth lining, and the vagina becomes distinctly thicker.

The uterus is bicornuate and asymmetrical. The left horn was larger (14 × 3.5 cm) than the right (12.6 × 4.0 cm) in specimen 79-2. The uterus is held in position in the pelvic cavity by a broad ligament. A septum divides the uterine cavity in two, one leading to the right horn, the other to the left. In a nonpregnant female, the uterus resembles an anchor. Its inner wall is covered with longitudinal folds like those in the cervix. The thickness of the uterine wall in one specimen was 0.5 cm. During pregnancy the entire uterus expands greatly, with its base stretching upward so that the uterus resembles a bag. Its inner wall, like that of the cervix, is covered by a soft and smooth lining. The wall becomes thinner, only 0.2 cm thick (Table 2).

The wall of the uterus is thick, consisting of endometrium, lamina muscularis and serosa. The serosa is the membrane covering the uterus, while the lamina muscularis is made up of thick smooth muscle with muscular fibrous fasciculi of each layer arranged in different directions. The endometrium contains uterine glands covered with single-layered columnar epithelium. Many small processes protrude inward towards the uterine chamber from the lining epithelium of the pregnant uterus. The epithelial cells are loosely arranged. The epithelium of the external folds of the cervix is columnar. The smooth muscle layer is especially thick.

### The ovaries

The ovaries are flat and oval-shaped, but their form changes greatly with physiological conditions (Plate 1, Fig. 3). The oviduct is quite short, only 2 cm or so, but its fimbriated area is quite large, about 5 cm in diameter.

Specimens 74-1 and 74-2 were from pregnant females. The left ovary of each female contained a large corpus luteum, measuring 4.55 × 3.2 × 1.8 and 3.9 × 3.1 × 1.1 mm. Only the right ovary in both cases contained corpora albicantia. The left ovary was about 3 times as large as the right one (Plate 1, Fig. 4).

The corpus luteum is covered by a thick connective-

tissue membrane. Its thickness reaches 68–120  $\mu$ m. A longitudinal section of a left ovary (Plate 1, Fig. 5) shows that the fungiform corpus luteum is divided into many tiny sections of different dimensions by various large and small blood vessels and connective-tissue septa. However, no main septa are seen radiating inwards towards a small fibrous core. The corpus luteum is filled with large, growing polyhedral granulosa lutein cells. The cells are vacuolated and developing normally. Their dimension may reach 20–30  $\mu$ . Some cells are binucleate. The theca lutein cells are much smaller in dimension and number. From the point of view of histological structure and stage of pregnancy, the corpora lutea in specimens 74-1 and 74-2 were obviously functional (Plate 2, Fig. 6).

In specimens 74-1, 74-2 and 80-7, corpora albicantia were present, protruding from the surface of the right and left ovaries. The surfaces of the corpora albicantia were covered with numerous pleated cicatrices (Plate 1, Fig. 6). In the histological sections of the ovary, corpora albicantia are also visible with well developed blood vessels surrounding them (Plate 2, Fig. 3). The corpora albicantia in specimens 74-1 and 74-2 were greatly regressed (Table 3).

The ovary is covered by a tunica albuginea, 34  $\mu$ m thick. Primary follicles could be seen on its cortex (45  $\mu$ ), but the number of vesicular follicles is small (Plate 2, Fig. 4). The medulla also contained atretic follicles and numerous arterial and venous blood vessels (Plate 2, Fig. 5). The corpora illustrated in specimens 74-1 and 74-2 were old.

### The mammary gland

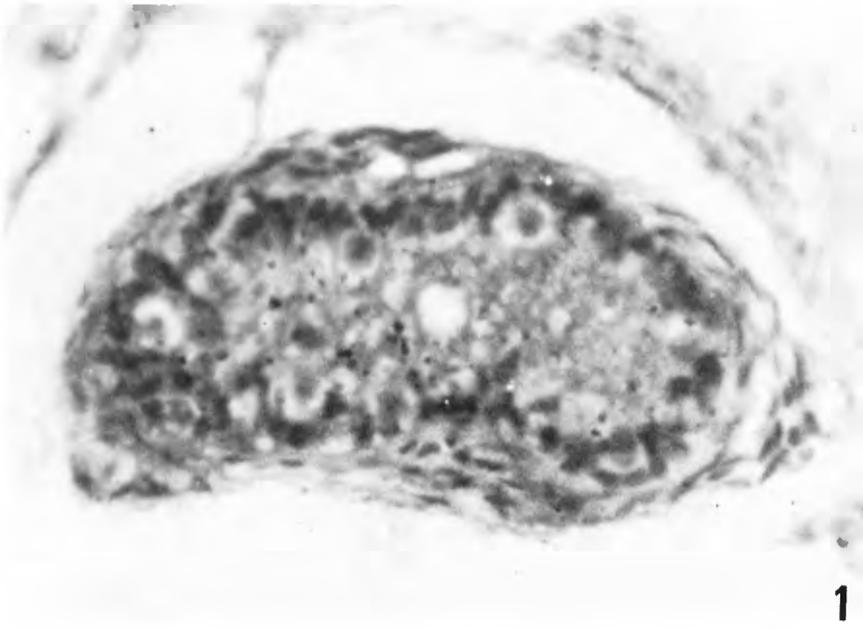
The nipple is about 2–3 cm long. The bases of the projections are connected with the two U-shaped mammary glands, which laterally join and anteriorly extend towards the umbilicus. In this respect *Lipotes* is different from the delphinids, whose mammary glands remain separate.

In specimen 80-7, the left mammary gland was 30 × 10.5 × 1.5 and the right 27.5 × 9 × 0.8 cm.

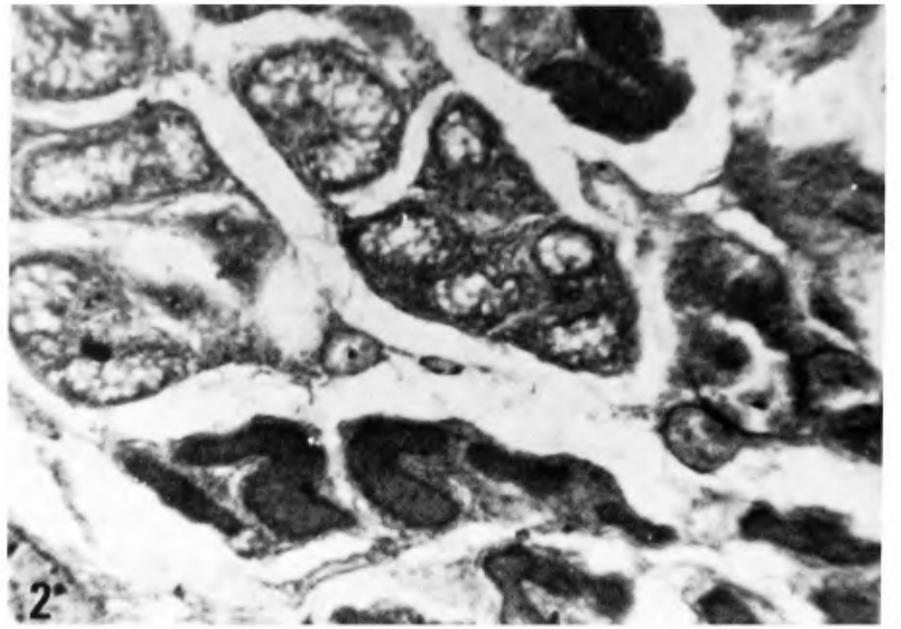
## ANATOMY OF THE MALE REPRODUCTIVE SYSTEM

### The testes

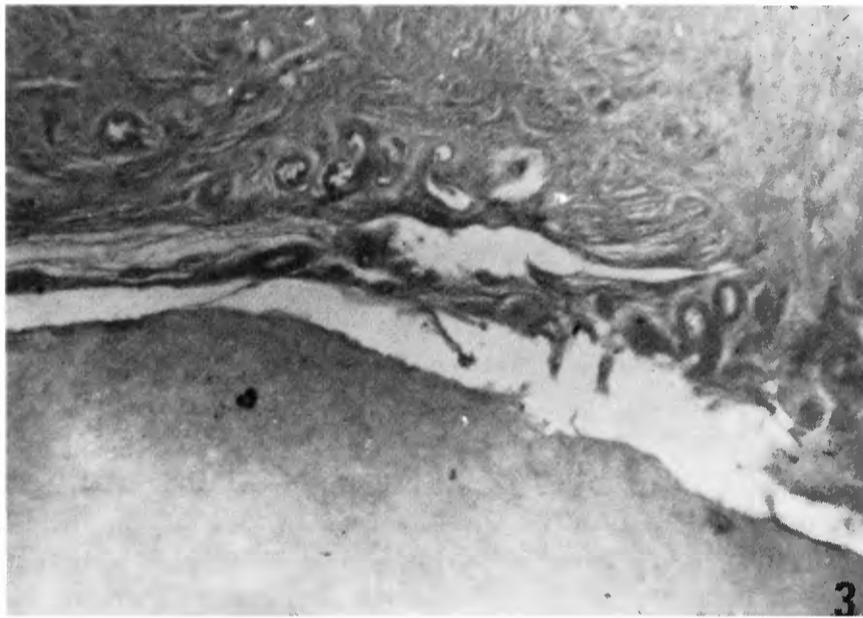
Specimen 73-1409 had ovoid testes 6.5 × 3 cm (Plate 1, Fig. 2). The testes in specimen 79-1 were similar in appearance to those in specimen 73-1409 and measured 4.3 × 1.9 cm.



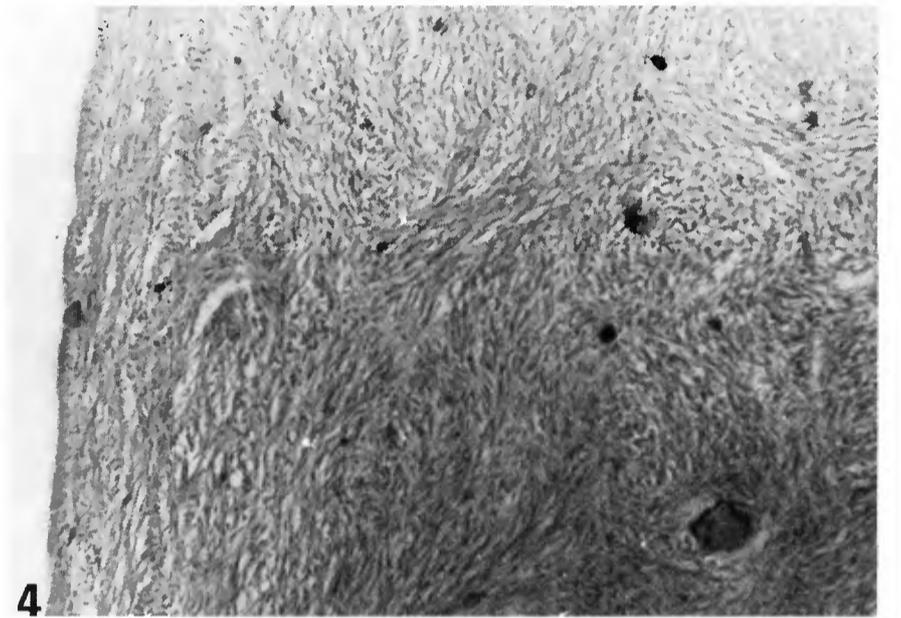
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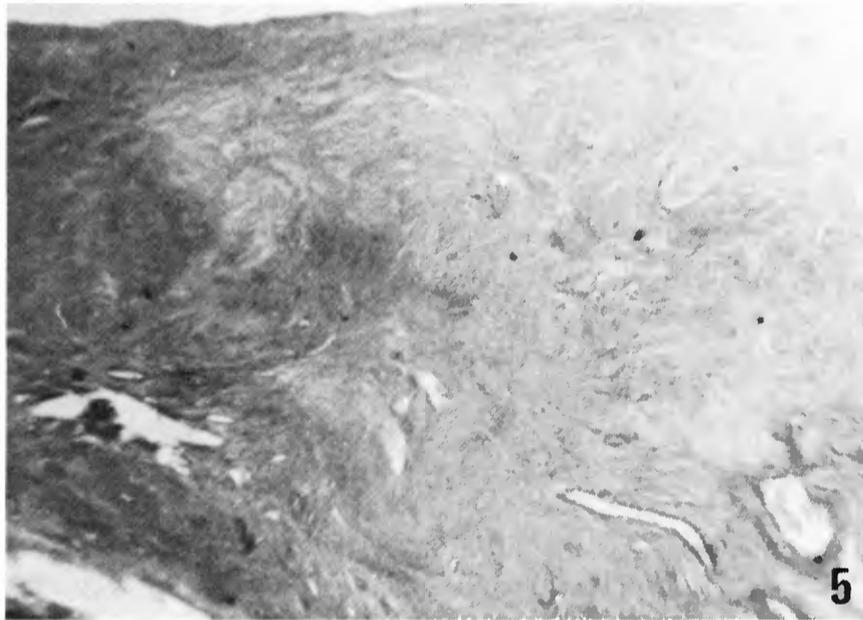
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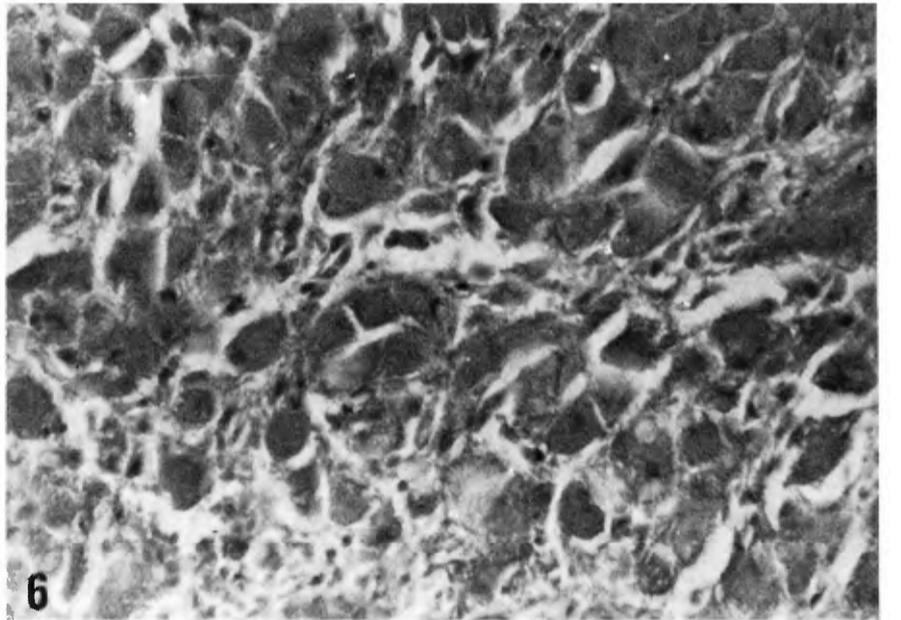
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4



5



6

## PLATE 2

Fig. 1. Photomicrograph of a section of the testis of 79-1. 15 20.

Fig. 2. Photomicrograph of a section of the seminiferous tubules in 79-1. 15 32.

Fig. 3. Photomicrograph of the corpus albicans of 74-2. 15 20.

Fig. 4. Photomicrograph of the cortex of the left ovary of 74-2. 15 20.

Fig. 5. Photomicrograph of the atretic structure in the left ovary of 74-2. 15 20.

Fig. 6. Photomicrograph of the corpus luteum in the left ovary of 74-2. 15 20.

Table 3  
Details of reproductive organs of *Lipotes*

Animal no.	Date of death	Locality	Length (cm)	Weight (kg)	Ovaries (g)				Comments
					Size (cm)		Weight (g)		
					L.	R.	L.	R.	
80-3	80/1/11	Chenglinji	192.0	63.5	1.6 × 0.6 × 0.3	1.6 × 0.4 × 0.4	0.3	0.3	Immature
80-7	80/2/15	Jiayu	238.0	166.5	3.65 × 1.9 × 0.85	3.4 × 1.85 × 1.2	3.6	4.3	L. One corp. alb. 0.8 × 0.4 R. One corp. alb. 0.8 × 0.4
79-2	79/1/25	Xintankou	245.0	142.5	2.6 × 1.75 × 0.9	2.7 × 1.8 × 0.9	1.3	2.0	L. Five corp. alb. 0.7 × 0.7 R. One corp. alb. 0.7 × 0.8
74-1	74/1/21	Honhu	250.0	224.0	5.2 × 3.2 × 1.8	3.1 × 1.8 × 1.0	16.0	2.7	Pregnant left horn: foetus 73 cm L. Corpus luteum 4.5 × 3.2 × 1.8 L. One corp. alb. 0.6 × 0.5 R. One corp. alb. 1.0 × 0.6
74-2	74/1/21	Honhu	253.0	237.0	5.7 × 3.2 × 1.2	3.6 × 2.1 × 1.3	13.5	5.8	Pregnant left horn: foetus 54.5 cm L. corpus luteum 3.9 × 3.1 × 1.1 L. Two corp. alb. 0.75 × 0.6 R. Five corp. alb. 1.0 × 0.8

Animal no.	Date of death	Locality	Length (cm)	Weight (kg)	Testis and epididymis (g)				Comments
					Size (cm)		Weight (g)		
					L.	R.	L.	R.	
79-1	79/1/5	Fankou	191.0	80.0	4.7 × 1.9 × 1.0	—	7.0	—	Active
80-1	80/1/4	Longkuo	194.0	87.5	5.4 × 3.1 × 1.0	4.8 × 1.4 × 0.9	20.0	15.0	
73-1409	73/10	Echeng	206.0	95.0	—	6.5 × 3.0 × 2.5	—	30.0	Active

The surface of the testis is smooth and covered with a serous membrane. The tunica albuginea of the testes is 140–225 μ thick. The septa divide the testes into numerous lobules. The diameter of the tubules was 32–46 μ in cross section (79-1). Many seminiferous tubules appeared to have central cavities. Obvious differentiation of spermatocytes could be seen. One or more layers of spermatogonia mixed with some primary spermatocytes were present. Secondary spermatocytes were present. On the inner surfaces of a few seminiferous tubules pear-shaped heads of spermatids could be seen. No mature free sperm were seen. We conclude that the testes in specimen 79-1 were active (Plate 2, Figs 1 and 2).

#### The ductus deferens

Downward from the base of the epididymis to the neck of the bladder there is a short ductus deferens connected with the urethra. The ductus deferens in *Lipotes* is not coiled like that in other cetaceans, but is thick, short and straight. The ductus deferens of specimen 73-1409 was only 13.2 cm long, yet its outer diameter was 0.7 m.

#### The penis

Like other cetaceans, *Lipotes* has a curved coiled penis. In a flaccid state, it is concealed completely within the body. The smaller specimen 79-1 had a penis 11.3 cm long and 1 cm in diameter. The penis of the larger specimen 73-1409 was longer and thicker, 30 cm × 4.8 cm at the base.

## DISCUSSION

### Breeding seasonality

No definite record has been made so far of the mating season for *Lipotes* in the Yangtze River. However, the parturition period can be inferred to be in February and March based on reproductive condition of the specimens examined.

Two pregnant females were obtained on 21 January 1974 in the Yaohu section along the middle reaches of the Yangtze River. The lengths and weights of their foetuses were 54.5 cm, 2.5 kg (male) and 73 cm, 4.5 kg (female). The foetuses were nearly fully developed, indicating that parturition would occur soon.

On 29 May 1979, in the Wuhan section of the River, a young female was caught, 95 cm in length and 9.5 kg in weight. Presumably it had been born about two months earlier.

When we did an ecological study of the Yangtze River, we could often see calves swimming by the side of their mothers in the months of April and May. Most of them were about 100 cm in length and 10–15 kg in weight. Calves of such a size are rare in the Yangtze River in November and December; only those of medium size can be seen then. Based on the lengths of foetuses and calves, we suggest that the period of mating is probably in April or May.

### Age and length at sexual maturity

It is difficult for us to determine age and size at maturation because we have not yet obtained sufficient material. The three males, measuring 191–206 cm long,

had reached sexual maturity. Compared with the testes of other freshwater dolphins and *Neophocaena phocaenoides*, the testes in *Lipotes* are small. In the largest male (Specimen 73-1409) the testes weighed only 30 g.

Among five females, two were pregnant (specimens 74-1 and 74-2). They measured 250 and 253 cm in length, respectively. The foetuses were both in the left uterine horns. Each of the pregnant females had a large corpus luteum in the left ovary surrounded by numerous blood vessels containing granulosa lutein cells and theca lutein cells. These corpora were obviously functional. Specimens 79-2 and 80-7 of length 245 and 238 cm were not pregnant. No corpora lutea were present in their ovaries, but corpora albicantia were present. What type these corpora albicantia belong to has not yet been determined. Judging from the sizes and appearances of their ovaries, we assume that these females were sexually mature. Specimen 80-3 measured 192 cm. Its left and right ovaries were very small, and no corpus luteum or corpora albicantia could be seen. This specimen was considered an immature. From the above examples we may assume that females probably do not reach sexual maturity until their length is over 200 cm.

#### Comparisons of reproductive anatomy in platanistids

While basic form of the structure of the reproductive system in *Lipotes vexillifer* is similar to that of other cetaceans, it has some peculiarities. The inner walls of the cetacean vagina have longitudinal and transverse folds, but in different species the folds differ in depth and number. They even may disappear in some species (Yablokov, 1972). Unlike in *Neophocaena phocaenoides* where the vagina has only longitudinal folds (Harrison and McBrearty, 1973-74), the vagina of *Lipotes* has six rings of transverse folds. These longitudinal and transverse folds all concentrate in the upper part of the vagina. The ring bordering the vagina and the cervix almost seal off the uterus. The folds may play the role of a pump. Moreover, they may also effectively prevent water from entering the uterus. This structure apparently plays an important role in *Lipotes*' adaptation to copulation and parturition in water.

The structure of the ovaries and corpus luteum and

corpora albicantia are also slightly different from those in other freshwater dolphins. In the corpus luteum of *Platanista minor* and *P. gangetica*, the connective tissue septa radiate inwards towards a small fibrous core (Harrison, 1972), but the septa in the corpus luteum of *Lipotes* do not lie in a radial arrangement, and no fibrous core is seen. The structure of the corpus luteum of *Lipotes* observed under the microscope is obviously different from that of *Pontoporia*. The connective-tissue septa in *Pontoporia* are arranged in parallel, separating the granulosa lutein cells into parallel columns each containing a few cells. Similar to the situation in *Platanista minor* and *Neophocaena phocaenoides* (Harrison, 1972; Harrison and McBrearty, 1973-74), the connective tissue in *Lipotes* divides the corpus luteum into different-sized roughly spherical small segments, each containing a large quantity of lutein cells. The granulosa lutein cells of *Lipotes* (usually about 18-23  $\mu$ ) are bigger than those of *Platanista gangetica* (15  $\mu$ ), *Pontoporia* (18-23  $\mu$ ), and *Neophocaena phocaenoides* (20  $\mu$ ). The largest may reach 46  $\mu$ .

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# Anatomic and Pathologic Observations of Female Reproductive Organs in the Short-finned Pilot Whale, *Globicephala macrorhynchus*

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## ABSTRACT

Abnormal findings made during a study of female reproductive tracts in *Globicephala macrorhynchus* include a granulosa cell tumor in an older female, papillary calcific scars on the ovarian surface of two animals, and a degenerating unimplanted embryo that was destined to be aborted. In addition, a nonpregnant female was found to have a large, functional corpus luteum. The latter two cases suggest that not all corpora albicantia identified necessarily represent completed pregnancies.

There have been only few reports on pathologic findings of reproductive tracts made in cetacean autopsies. Most studies concentrate on the ovarian morphology concerning corpora lutea and scars; also mentioned at times are the presence of parasites or scars of former parasitic lesions. Some tumors were discussed by Rewell and Willis (1950) and Cowan (1966) reviewed the pathology of 55 pilot whales, giving a few additional references to tumors, cardiac and infectious diseases. Parasitic disease was his principal finding as well. An 'intersexual' fin whale was described by Bannister (1963), and Kawamura (1969) described a thoracopagous ('Siamese') sei whale fetus. Gray and Conklin (1974) reported a transposition of vessels in a bottle-nosed dolphin twin fetus, and vaginal calculi in spotted dolphins were discussed by Sawyer and Walker (1977). In other surveys of reproductive organs of Cetacea virtually no pathologic findings were made (Harrison, 1949; Simpson and Gardner, 1972). Papillary lesions and other virus infections have been reported by Smith and Skilling (1979) without affecting the reproductive tract, however. Other pathologic reports are scarce. It is for this reason that we have documented these unusual findings made during the examination of the reproductive organs of 298 female *Globicephala macrorhynchus* (Marsh and Kasuya, 1984). The age estimates were based on dentinal and/or cemental layer counts (Kasuya and Marsh, 1984).

### *Case 1, Accession No. 13-6:*

This female was 353 cm long and had an estimated age of 34.5 years. Her reproductive organs were classified as resting; one medium and 14 old corpora albicantia were counted in the ovaries after routine slicing and macroscopic examination as outlined by Marsh and Kasuya (1984). The right ovary contained a buff-colored spherical tumor, 9.7 mm in mean diameter. Histologically it was composed of uniform polyhedral cells that possessed only scant cytoplasm. The nuclei were uniform and lacked mitoses. The tumor compressed slightly the



Fig. 1. Whale 13-6. Granulosa cell tumor in the right ovary of *G. macrorhynchus*. Normal ovarian stroma (above) is slightly compressed. Tumor is composed of uniform cells. (Frozen section, H and E  $\times 60$ ).

adjacent ovarian stroma (Fig. 1). Fat stains (as detailed in Marsh and Kasuya, 1984) showed slight, finely distributed sudanophilia.

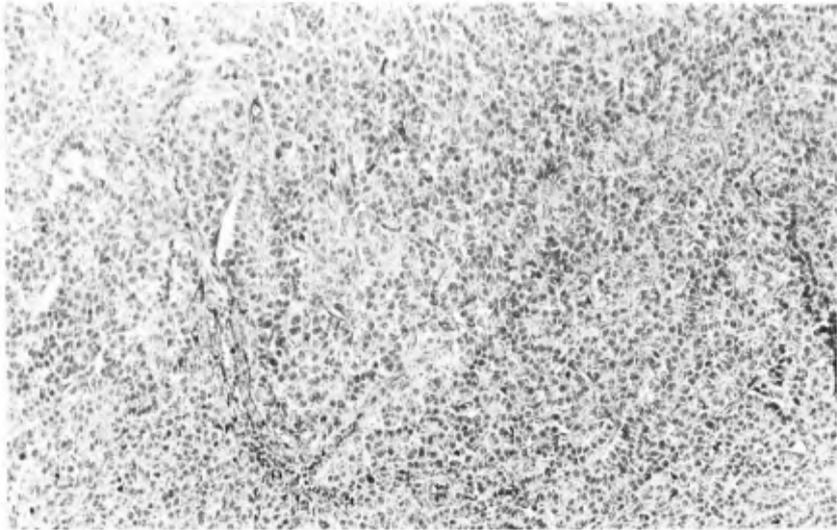


Fig. 2. Details of granulosa cell tumor showing occasional Call-Exner bodies (top left) and rows of cells. (Frozen section, H and E  $\times$  160).

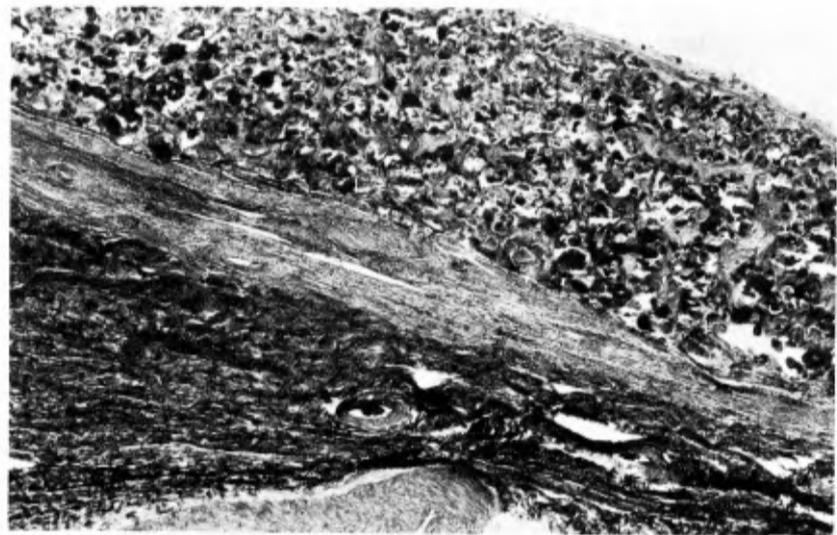


Fig. 3. Irregular foci of purplish calcification in plaques that lie peripheral to ovarian cortex (below). (Frozen section, H and E  $\times$  60).

The tumor had no cavity and the orientation of cells and vasculature differed substantially from that of a corpus luteum, the only normal structure with which the lesion could be confused. The tumor cells were usually arranged in rows and, occasionally, into pseudofollicles (Fig. 2). The latter were very similar to Call-Exner bodies and for these reasons the tumor is best interpreted as a granulosa cell tumor.

#### Case 2, Accession No. 11-19:

The reproductive activity of this 351 cm long female with an estimated age of 44 years was classified as 'resting'. Greyish irregular encrustations less than one mm in thickness were present on the surface of both ovaries. Microscopically these plaques consisted of irregular foci of calcification, not unlike psammoma bodies known from other types of pathologic specimens. The calcifications were encased in a thin sheath of connective tissue and appeared to be external to the ovarian capsule (Fig. 3).

There were no inflammatory cells, scars from parasites or epithelial elements admixed with the calcific lamellae (Fig. 2). The lamellae were superficial and did not appear to be related to corpora albicantia. Rather, they would appear to be related to peritoneal adhesions. Similar lamellae were also observed on the surfaces of the ovaries

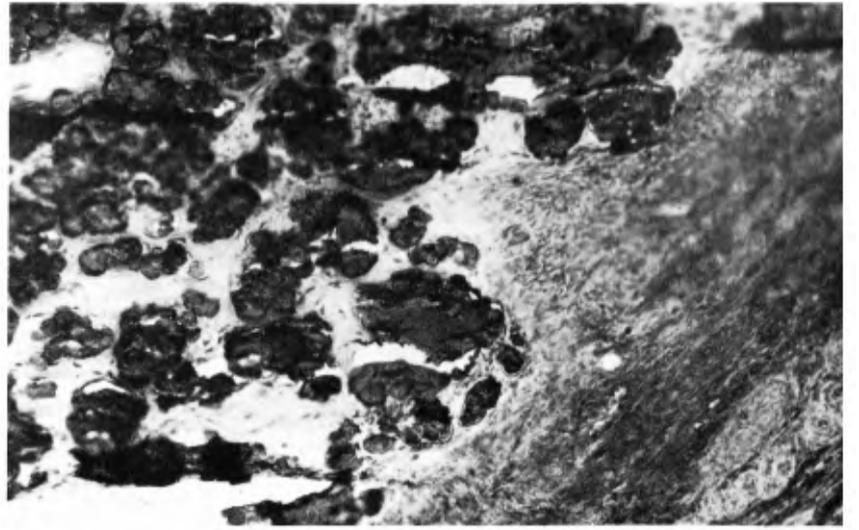


Fig. 4. Irregular calcific lamellae on the surface of ovary (Gomori's Trichrome  $\times$  250).



Fig. 5. Corpus luteum in left ovary (hemisected) of non-pregnant *G. macrorhynchus*. The cells are deep yellow and, histologically, they are well preserved, appearing to be fully functional.

of Accession No. 24-7 (body length 375 cm). This 'resting' female, the oldest *G. macrorhynchus* examined, was estimated to be 62 years old.

#### Case 3, Accession No. 24-9:

This female measured 371 cm in length and was thought to be 37 years old; it is one of the oldest whales studied showing evidence of recent ovulation (Marsh and Kasuya, 1984). It is remarkable in that an active, well-stimulated corpus luteum was present that measured 4.5 cm in greatest diameter (Fig. 5), representing one of the largest corpora seen in this species (Marsh and Kasuya, 1984). There was no evidence of pregnancy. On dissection of the uterus, no implantation site or fetus could be found. The endometrium (Fig. 6) had a nonpregnant appearance. It was edematous and had tubular secretory glands but lacked the superficial vascular network that is so typical of early pregnancy in *Stenella* species (Benirschke, Johnson and Benirschke, 1980). Thus, *G. macrorhynchus* is another cetacean in which it is probable that sterile ovulation may occur.

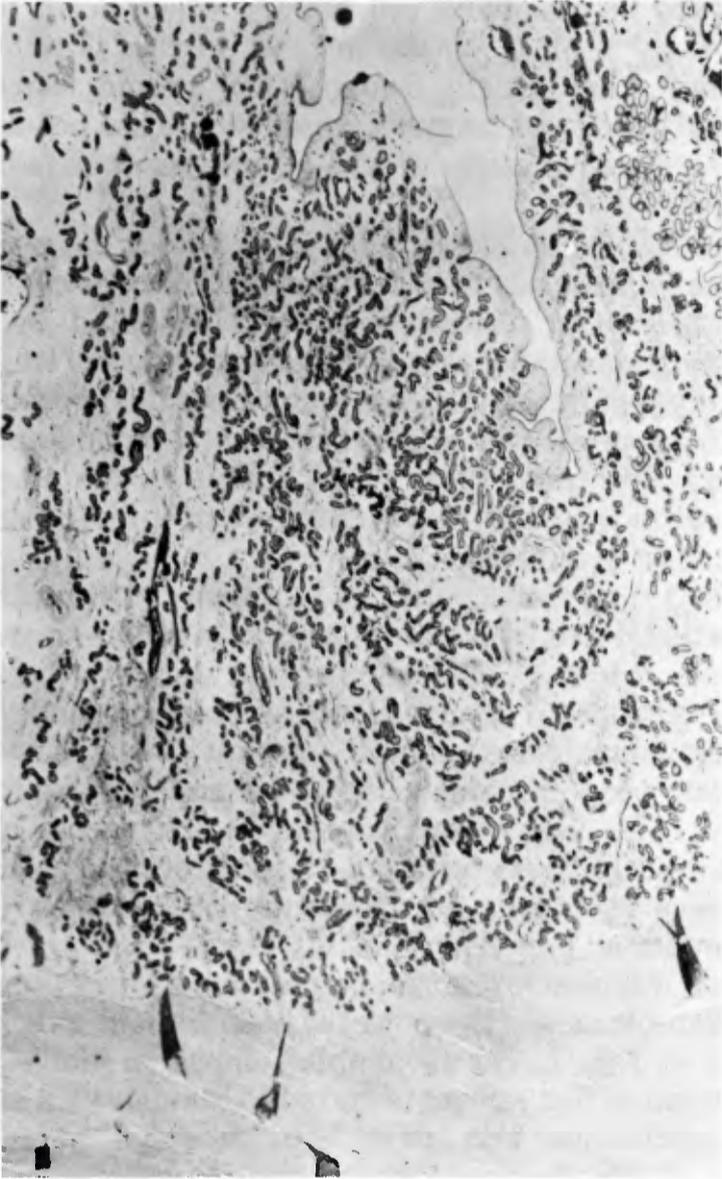


Fig. 6. Section of endometrium of non-pregnant *G. macrorhynchus* with corpus luteum. (H and E  $\times$  16).



Fig. 8. Cross section of membranous sac shown in Fig. 7. Above is outside, vacuolated epithelium, presumably trophoblast. The structure is avascular. (H and E  $\times$  250).

*Case 4, Accession No. 25-1:*

Fig. 7 illustrates the structure found in the right uterine horn of this whale which was 364 cm long and estimated to be 28 years old. As an apparently functional corpus luteum 35 cm in diameter was found in the right ovary, the whale was first classified as pregnant. However, on closer examination, an implanted pregnancy was not found. The sac shown in Fig. 7 was composed of a delicate membrane made up of connective tissue and vacuolated epithelium on one surface (Fig. 8). It is interpreted to represent the chorioallantoic connective tissue covered by trophoblast of an unimplanted placental sac. The structure identified by a black arrow (Fig. 7) was composed of amorphous eosinophilic debris associated with numerous refractive ovoid bodies of unknown origin. The structure identified by a long, thin arrow at the left was the remnant of a degenerating

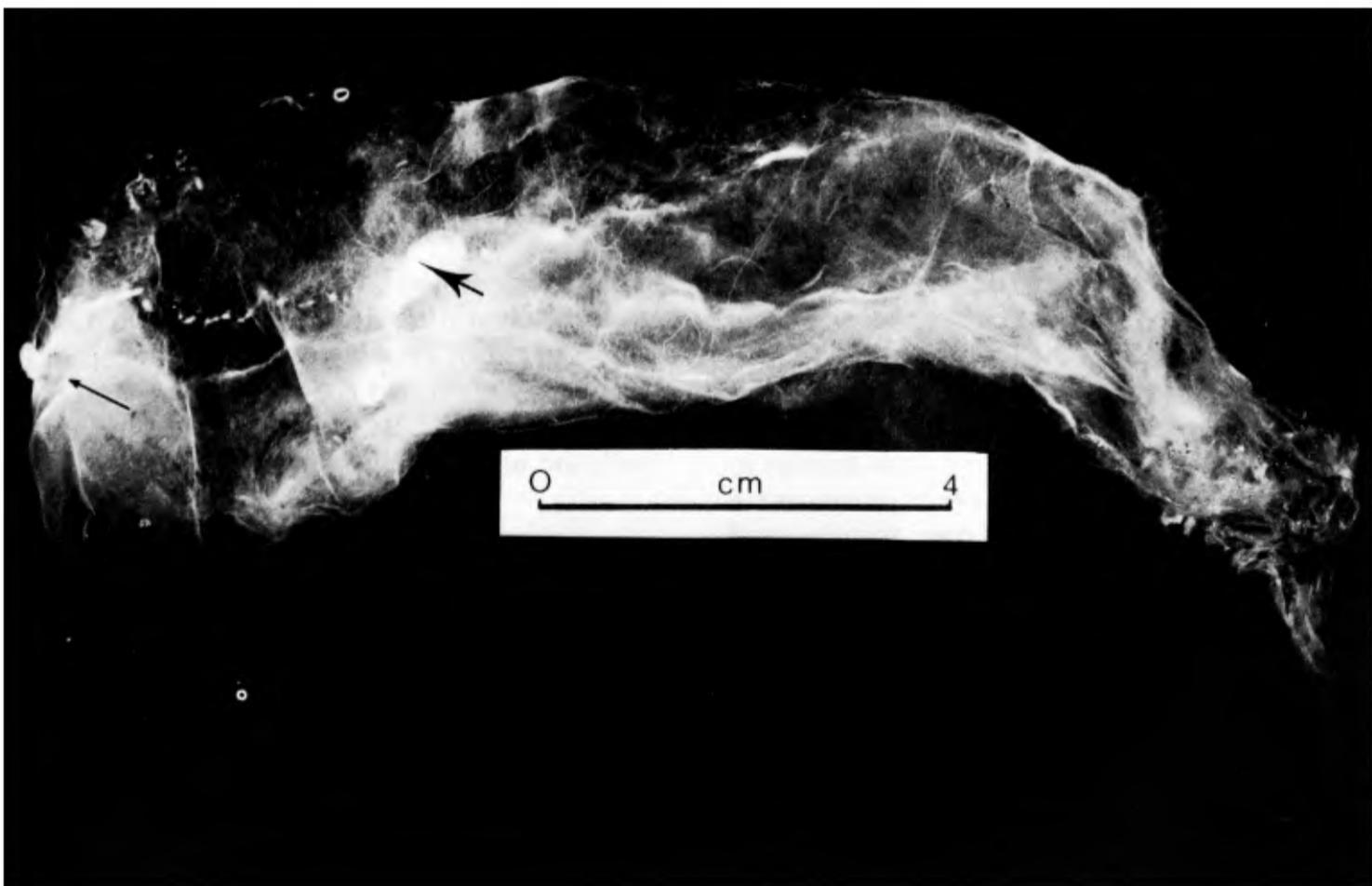


Fig. 7. Preimplantation placental sac with degenerating embryo. At left (thin arrow) is the remnant of embryo shown in Figs 9 and 10. The large arrow indicates an irregular calcified mass, perhaps representing yolk sac.

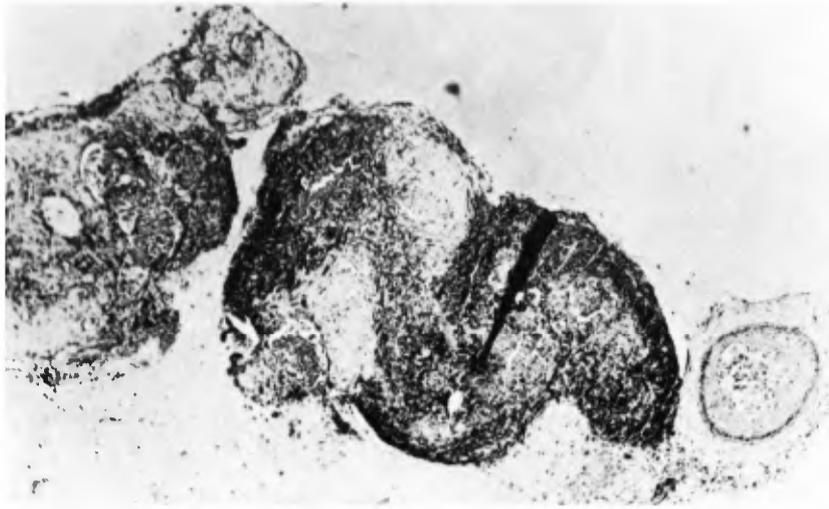


Fig. 9. Structure indicated by thin arrow on Fig. 7, representing degenerating embryo. (H and E  $\times$  64).

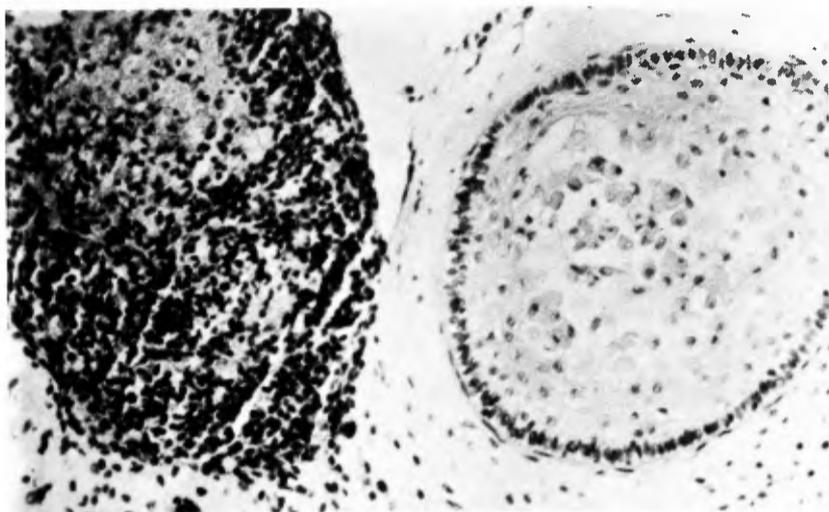


Fig. 10. Portion of previous figure at higher magnification. The squamous epithelium (? amnion) at right is readily identified and appears viable. Structure at left is degenerating embryo with collapsed vessels and coagulated blood without recognizable red blood cells. (H and E  $\times$  250).

embryo (Figs 9, 10). This whole structure is interpreted to represent a degenerating preimplantation stage of pregnancy and may be similar to what in other species is described as 'cystic placental mole' (Jubb and Kennedy, 1970).

## DISCUSSION

Cowan (1966) performed a systematic pathologic study of 55 animals of the related species *Globicephala melaena* and reviewed the major pathologic lesions that had been described in cetaceans to that date. He found no granulosa cell tumors of the ovary. Previously, however, Rewell and Willis (1950) described three such lesions in their review of whale neoplasms. The other lesions were a uterine leiomyoma, papilloma of the tongue and mucinous cystadenoma of the ovary. The granulosa cell tumors reported by these authors were a cystic 3-cm mass in a blue whale, *B. musculus*, and two tumors in fin whales that were also described as being cystic. Histologically, they were classical and similar to our first description in *Globicephala* from Accession No. 13-6 (Case 1). We assume, from the size of this tumor (Figs 1 and 2), that it was of recent origin. Whale 13-6 had presumably been reproductively active, as it has 15 corpora albicantia. However, at 34 years it would have been nearing the age at which *G. macrorhynchus* become post-reproductive in the population studied (Marsh and Kasuya, 1984). This

is typical for granulosa cell tumors, which occur most commonly in older females in other species. Granulosa cell tumors are usually benign. Their steroid secretory activity varies and cannot be predicted from histologic appearance. The uterus of whale 13-6 was not available for study.

Calcific plaques as seen on the surface of the ovaries in Case 2 apparently have not been described. They differ from the rather characteristic scars produced by the frequent parasitic deposits in the genital organs of whales. The origin of the plaques is unknown but it is speculated that they represent the healing process of an inflammatory process. Both the whales which exhibited such plaques were old and probably would have been post-reproductive for at least several years.

Case 3 is presented solely to document the presence of a functional and large corpus luteum in a non-pregnant *G. macrorhynchus*. The endometrium shows no inflammatory changes or other evidence of recent implantation, and an unimplanted embryo was not found. Thus, a pregnancy can probably be ruled out and, judging from the size of the corpus luteum, we expect that it would have become a sizeable corpus albicans had the animal lived.

Case 4 represents an apparently degenerating pre-implantation pregnancy in *G. macrorhynchus*. The embryo was clearly degenerating but must have supplied the allantoic mesenchyme for the membranous structure shown in Fig. 7. The trophoblast appeared viable but implantation had not yet occurred. Although such large pre-implantation sacs have been recorded in other cetaceans (Benirschke, Johnson and Benirschke, 1980), the present specimen would be expected to have aborted had the animal lived because of the degeneration found in the minute embryo. Whether 'resorption' of such a pre-implantation specimen could take place must remain speculative; however, the possibility of such structures becoming future vaginal calculi must be considered (Sawyer and Walker, 1977). This is particularly so since crystalline mineral deposits were already seen in the embryonic structure.

## ACKNOWLEDGEMENTS

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# A Vaginal Mass, Containing Fetal Bones, in a Common Dolphin, *Delphinus delphis*

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## ABSTRACT

Vaginal calculi in cetaceans are composed of calcium phosphate compounds identical to those found in mammalian bone. We report the occurrence of fetal bones in the vagina of *Delphinus delphis*. Both the left ovary and the left endometrium showed evidence of a recent pregnancy. The possibility of other calculi having formed from aborted embryos is suggested.

## INTRODUCTION

Vaginal calculi have been reported from *Delphinus delphis* by Harrison (1969), who described them as hard, flattened formations containing both organic and inorganic material, and suggested that they were remnants of vaginal plugs of coagulated seminal fluid. Sawyer and Walker (1977) described the presence of vaginal calculi in *Stenella attenuata* and summarized eight similar occurrences of calculi in *D. delphis* and *Lagenorhynchus obliquidens*. X-ray diffraction showed the calculi to be composed of calcium phosphate compounds identical to those found in mammalian bone. We report here the occurrence of a vaginal fetus in *D. delphis*.

## MATERIALS AND METHODS

The present specimen of *D. delphis* was stranded on 11 May 1979 in Encinitas, California, USA (lat. 33° 02' 48" N, long. 117° 17' 54" W). The specimen (WFP 595) was 176 cm long, weighed 54 kg, and displayed two scars from healed shark bites. Primary cause of death was diagnosed as hemorrhagic pneumonia, with contributory causes being duodenal ulceration and liver abscesses. Trematodes, *Nasitrema* sp., were present in the air sinuses, but no associated brain lesions were evident.

## RESULTS

The vagina contained an ovoid mass of firm material held together by mucoid secretions. On gentle dissection, 35 individual bones clearly derived from an embryo were identified, among which were 15 identifiable ribs (2.0 × 0.1 cm), fragments of skull, and pelvic bones (Fig. 1). No vertebrae were present and the largest bone measured 2.5 × 2.0 cm.



Fig. 1. Fetal bones found in the vagina of a common dolphin, *Delphinus delphis*.

The mucosa-serosa thickness of the left uterine horn was 0.5 cm, that of the right horn 0.15 cm. Histologically, the left endometrium was edematous and congested, showing evidence of recent pregnancy (Fig. 2). Some glands contained dense precipitations representing remnants of degenerate placenta. The right endometrium was inactive.

The left ovary measured 3.2 cm in greatest diameter and contained one large (1.2 cm) corpus albicans, two smaller and older corpora albicantia, and Graafian follicles. The large corpus albicans showed evidence of recent involution of a corpus luteum (Fig. 3), and presumably corresponds to the abortion event. The right ovary contained primordial eggs and Graafian follicles, but no corpora albicantia.

The vaginal wall was normal and inactive.

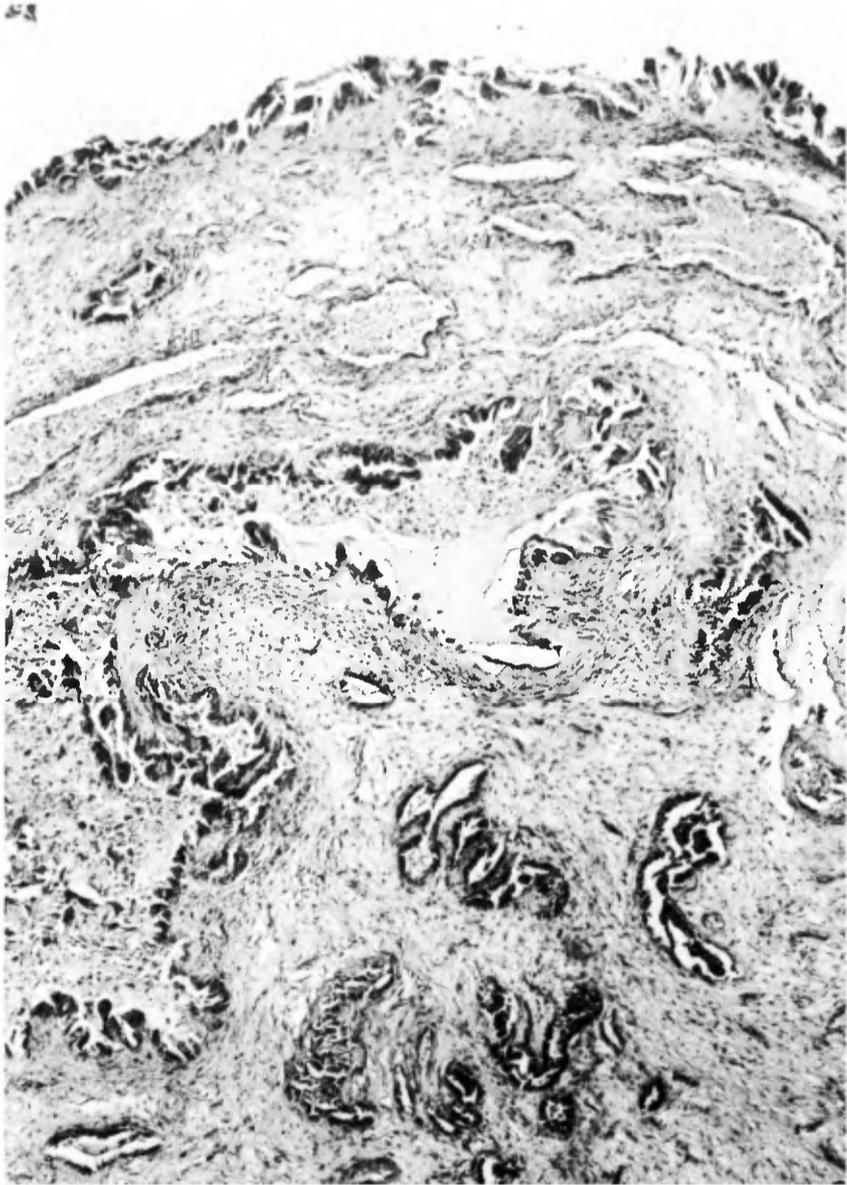


Fig. 2. Left endometrium, showing edema and hyperplasia of recent pregnancy. Lumen above. Several glands are distended and contain debris. (H & E  $\times 16$ ).

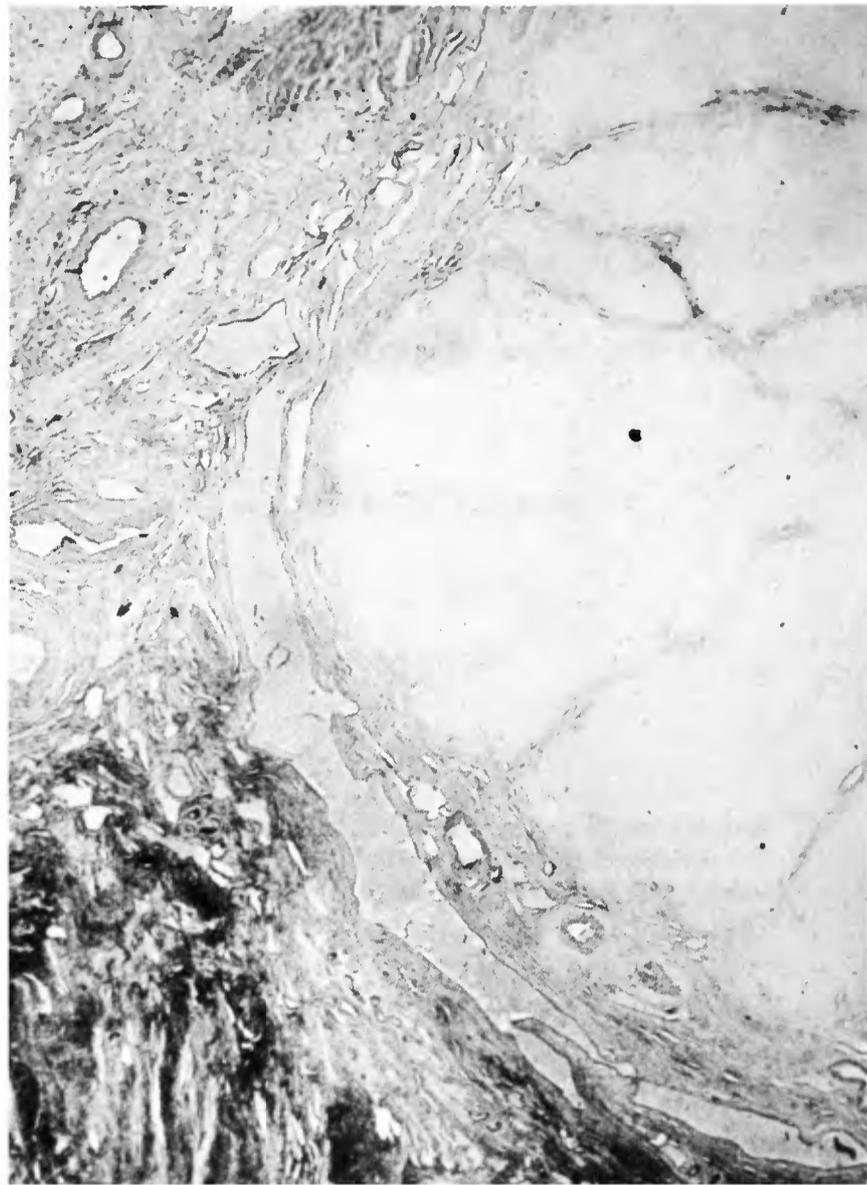


Fig. 3. Corpus albicans of left ovary (homogeneous white mass on the right) showing evidence of recent involution of corpus luteum. (H & E  $\times 16$ ).

### DISCUSSION

Harrison (1969) suggested that vaginal calculi were salt-impregnated remains of vaginal plugs, while Sawyer and Walker (1977), based on their X-ray analyses, proposed that something other than cervical or seminal fluid was being trapped in the vagina. The cross sectional structure of the calculi they analyzed indicated formation by concentric layer crystallization for an unknown time period.

This is the first report of a vaginal encrustation containing an aborted embryo in Cetacea. If embryonic bones were to become crystallized over time after being trapped in the vagina, other vaginal calculi could conceivably have arisen from aborted embryos. All reported occurrences of cetacean vaginal calculi have been in sexually mature animals. Harrison (1969) stated that the occurrence of vaginal calculi was 4% in *D.*

*delphis*, though he made no mention of the source or size of the sample. The percent occurrence of calculi in other cetacean species is not known.

Other calculi which are found should be examined for evidence of fetal bones which may be progressively crystallizing or coalescing.

### ACKNOWLEDGMENTS

We thank Pat Robards, California Department of Parks and Recreation, who collected the specimen.

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# Hormonal Evidence of Spontaneous Ovulation in Captive Dolphins, *Tursiops truncatus* and *Delphinus delphis*

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## ABSTRACT

Baseline plasma levels of progesterone and total immunoreactive estrogens were determined for four captive female bottlenose dolphins, *Tursiops truncatus*, and two captive female common dolphins, *Delphinus delphis*. Female bottlenose dolphins were kept as pairs with or without males and bled biweekly for one year periods. Female common dolphins were kept as a pair without a male and bled biweekly for a two year period.

Baseline progesterone levels less than 1 ng/ml were indicative of 'resting' or anestrus females. One common dolphin and three bottlenose dolphins did not exhibit ovulations. Episodic fluctuations of progesterone from baseline to 22.1 ng/ml were observed in two bottlenose dolphins kept with and without a male and from baseline to 15.5 ng/ml in one common dolphin. These cycles of progesterone were considered to be indicative of ovulation. No episodic fluctuations of estrogens were observed in the bottlenose dolphins and two were observed in the one common dolphin which ovulated. Estrogen levels on a biweekly sampling schedule did not appear to be useful.

It was concluded for captive females of *T. truncatus* and *D. delphis* that (1) they can be anestrus for at least a one-year period, (2) they can be polyestrous with an observed maximum of three cycles/year for *T. truncatus* and seven cycles/year for *D. delphis*, (3) the females of *T. truncatus* had spring cycles whereas no conclusion about *D. delphis* seasonality could be made, and (4) these two species can exhibit spontaneous ovulations.

Since reproductive events are hormonally mediated, monitoring hormonal levels in animals has proven to be effective in elucidating ovulatory cycles. Gonadal function can be inferred from the gonadal steroid levels in females, since folliculogenesis can be monitored by changes in levels of estrogens (and estrus if it occurs) and episodic fluctuations in progesterone reflect luteal function, i.e. corpus luteum formation as a result of ovulation (Loskutoff, Ott and Lasley, 1983). Immunological techniques have been used to monitor gonadal steroid hormones in a wide variety of domestic animals, such as the goat, cow, sheep, pig, horse (Cole and Cupps, 1977; Hafez, 1974; Hogarth, 1981; McDonald, 1975), in some exotic animals such as the alpaca, elephant, rhino, okapi, primate (Fernandez-Baca, Hansel and Novoa, 1979; Hodges, Czekala and Lasley, 1979; Kassam and Lasley, 1980; Loskutoff, Ott and Lasley, 1982; Ramsey, Lasley and Stabenfeldt, 1980), and in humans (Ross, Cargille, Lipsett, Rayford, Marshall, Scrott and Rodbard, 1970; Tepperman, 1974; VandeWiele, Bogumil, Dyrenfurth, Ferin, Jewelewicz, Warren, Rizkailah and Mikail, 1970).

In the past, gonadal steroid studies on whales have consisted of gross measures of bioactivity which consisted of injecting whale ovarian extracts into mice or rabbits and measuring progestational effects on the uterus (Callow, Laurie and Parkes, 1935; Bomskov and Unger, 1938; Jacobsen, 1941). Prelog and Meister (1949) identified progesterone in the corpora lutea of whales, and Kristofferson, Lunaas and Velle (1961) identified 20 beta and 20 alpha-hydroxypregnene-4-ene-3-one in *Balaenoptera physalus* ovaries. With the advent of specific and sensitive radioimmunoassays (RIA), studies have been conducted on long-term captive dolphins. Sawyer-

Steffan, Kirby and Gilmartin (1983) and Sawyer-Steffan and Kirby (1980) reported that hormonal studies in *Tursiops truncatus* were feasible for monitoring ovulations and diagnosing pregnancies. Kirby, Cornell, Schroeder and Andrews (In prep.) reported on the comparisons of progesterone levels in six species of captive odontocetes and concluded that plasma progesterone levels could be used to study pregnancies and ovulations in odontocetes.

Several studies of delphinid steroid hormones have indicated the occurrence of infertile cycles or spontaneous ovulations. Sawyer-Steffan *et al.* (1983) and Sawyer-Steffan and Kirby (1980) speculated that *T. truncatus* is capable of infertile cycles, but no conclusions about spontaneous vs induced ovulation could be made since males were present with the females. Kirby *et al.* (In prep.) found infertile cycles and spontaneous ovulations in females of *T. truncatus*, *Orcinus orca*, *Stenella longirostris*, *Globicephala macrorhynchus*, *Delphinapterus leucus*, and *Delphinus delphis* kept with or without males.

The purpose of this study was to synthesize information from longitudinal hormonal studies on captive females of *T. truncatus* and *Delphinus delphis*, and progesterone baseline data for females of these species kept with and without access to male dolphins.

## METHODS

### *Subjects and sample collection*

Two pairs of adult *T. truncatus* females and one pair of adult *D. delphis* females were each maintained in separate circular fibreglassed-redwood tanks (10 × 2 m). One pair of bottlenose dolphins (A and B) were bled biweekly for two years (1978 and 1980), but only had access to a

Table 1

Animal	Age (years)	Length (cm)	Year Aged
<i>Tursiops truncatus</i>			
A	13	231	1980
B	19	242	1980
C	20	227	1980
D	16	261	1980
<i>Delphinus delphis</i>			
E	8½-9	178	1981
F	16	180	1981

mature adult *T. truncatus* male during 1978. The other pair of bottlenose dolphins (C and D) were bled bi-weekly for one year (1978) and were with a mature adult male of *T. truncatus* for the entire year. The females of *D. delphis* (E and F) were bled biweekly for two years (1979 and 1980) without access to any males. Blood samples were obtained by draining the tanks to strand the animals. The dolphins were placed on foam rubber pads and kept moist during the bleeding procedure. Blood was taken from the dorsal or the ventral aspect of the tail fluke (Ridgway, 1965). Plasma was stored in glass vials at  $-4^{\circ}\text{C}$  until analyzed.

At least one year prior to the beginning of these studies teeth were extracted from the bottlenose dolphins (Ridgway, Green and Sweeney, 1975), and the teeth were used to age the animals by the method of Hui (1980). Teeth were extracted from the common dolphins after the study and aged by the method of Hohn (1980). Lengths were standard, from the tip of the lower jaw to notch in the tail fluke (Norris, 1961; see Table 1).

#### Radioimmunoassays (RIA)

Plasma was assayed for progesterone and total immunoreactive estrogens as described by Sawyer-Steffan and Kirby (1980) using their hexane-modified techniques of Anderson, Hopper, Lasley and Yen, (1976) for progesterone. Co-chromatography validation of celite chromatography for progesterone in *T. truncatus* was reported by Sawyer-Steffan and Kirby (1980). Co-chromatography verification of celite separation of *D. delphis* progesterone was performed by running hexane extracted plasma (10:1 v/v) on a 2:1 (v/v) celite:propylene glycol column, collecting seven 0.5 ml iso-octane fractions. Each fraction was counted for radioactivity and RIA for progesterone immunoactivity. The interassay coefficient of variation (CV) for progesterone was 11.3% ( $n = 13$ ) and for total immunoreactive estrogens was 6.2% ( $n = 6$ ). Sensitivity of the progesterone assay was as low as 30 pg/ml and for estrogen was as low as 3 pg/ml.

Plasma samples with progesterone levels less than

1 ng/ml were evaluated as baseline levels. Samples with progesterone greater than 3 ng/ml were evaluated as indicative of ovulation. Pregnancy was diagnosed in those cases in which progesterone levels were elevated above 3 ng/ml over an extended period of time (Sawyer-Steffan *et al.*, 1983; Sawyer-Steffan and Kirby, 1980). Values between 1 and 3 ng/ml were considered indeterminate, unless subsequent samples indicated that the progesterone levels were continuing to rise.

## RESULTS

The mean baseline level of plasma progesterone ( $P$ ) for the four females of *T. truncatus* was  $0.18 \pm 0.04$  ng/ml ( $n = 133$  samples). Progesterone levels ranged from less than 1 ng/ml to 22.1 ng/ml in animals where elevated  $P$

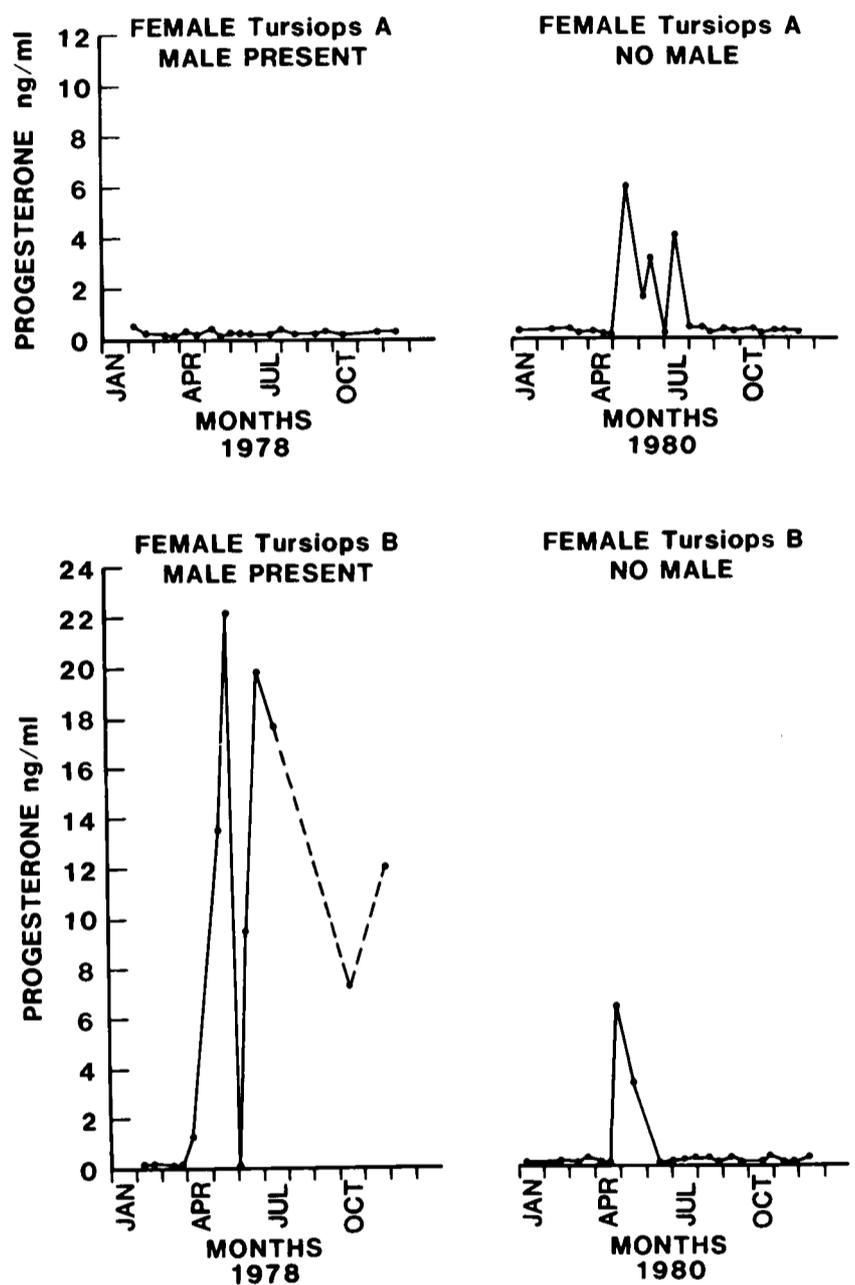


Fig. 1. Plasma progesterone levels in two captive females of *Tursiops truncatus* ('A' and 'B') maintained together with a mature *T. truncatus* male (1978) and without access to a mature male (1980).

Table 2

Baseline plasma progesterone ( $P$ ) and total immunoreactive estrogens ( $E_t$ ) in captive female *Tursiops truncatus* and *Delphinus delphis*

Species	No male present				Mature male present			
	$n$	$\bar{x}P \pm \text{CI}$ ng/ml	$n$	$\bar{x}E_t \pm \text{CI}$ pg/ml	$n$	$\bar{x}P \pm \text{CI}$ ng/ml	$n$	$\bar{x}E_t \pm \text{CI}$ pg/ml
<i>Tursiops truncatus</i>	36	$0.15 \pm 0.03$	43	$31 \pm 3$	97	$0.21 \pm 0.05$	101	$23 \pm 2$
<i>Delphinus delphis</i>	73	$0.48 \pm 0.08$	45	$33 \pm 5$	—	—	—	—

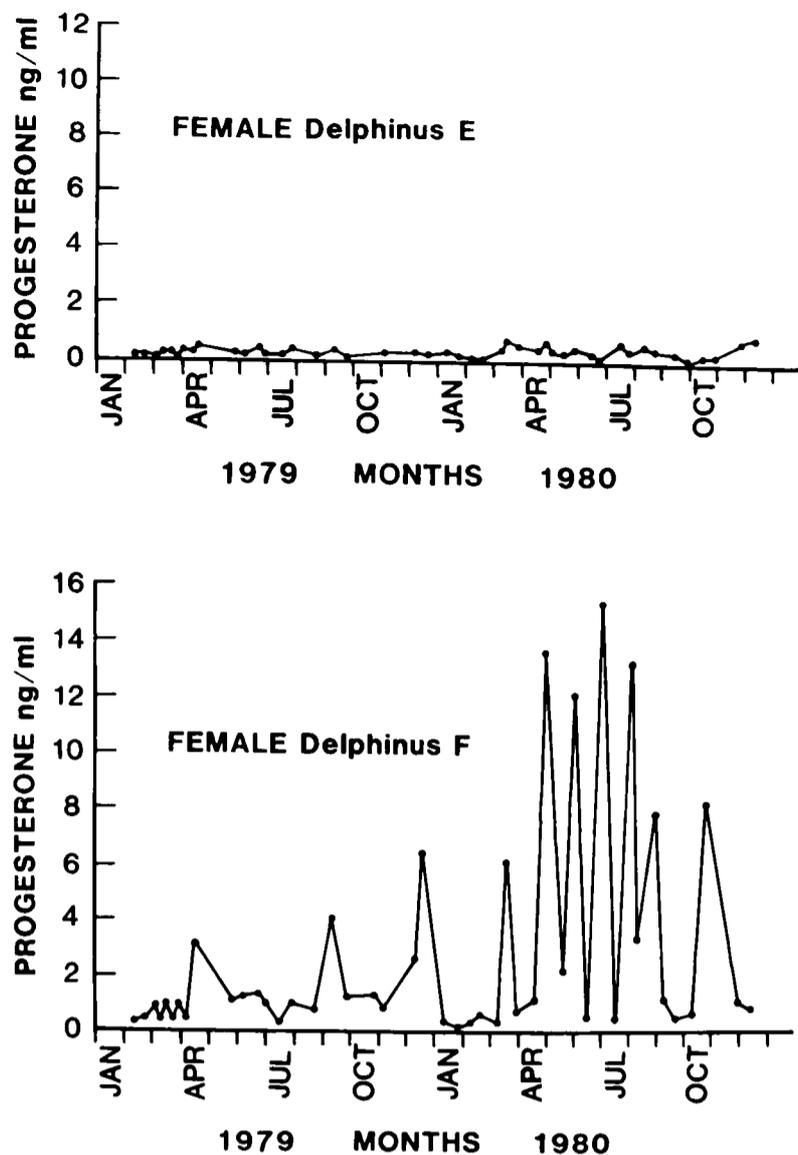


Fig. 2. Plasma progesterone levels in two captive females of *Delphinus delphis* ('E' and 'F') maintained together for two years without access to a male.

was not maintained (i.e. animals were not pregnant). The maximum number of cycles observed during the study was three (Table 2). The mean total immunoreactive estrogen (Et) levels were  $23 \pm 2$  pg/ml when a male was present and  $31 \pm 3$  pg/ml when no male was present. No episodic fluctuations of Et were observed. Of the 94 *D. delphis* samples evaluated, the mean *P* baseline level was  $0.48 \pm 0.08$  ng/ml with episodic fluctuations ranging from less than 1 ng/ml to 15.5 ng/ml. The maximum number of cycles during the study was ten (Female F, Table 1). The mean Et level for 94 samples was  $33 \pm 5$  pg/ml with two periodic fluctuations observed of 79 pg/ml (April, 1980) and 80 pg/ml (July, 1980) for Female F, although plasma was not available for Female F from May and June for estrogen analysis.

Comparison of plasma from *T. truncatus* females A and B in the presence of males to plasma levels for A and B without males is shown in Fig. 1. From the figure it can be seen that (1) female A was anestrus for 1978, when a male was present, while female B ovulated two times and was impregnated on the second cycle, (2) each female ovulated when no male was present, (3) each female cycled at approximately the same time of the year (spring/summer), and (4) the profiles of the cycles with and without males were similar. Female A had episodic *P* fluctuations May through July 1980 with no male present, with a maximum of three sequential cycles. Female B ovulated twice and became pregnant in 1978 and ovulated again in 1980 when no male was present. The second pair of bottlenose dolphins (C and D) kept

with a mature male (1978) were anestrus for the one year period and are not shown, but had a profile similar to that of *T. truncatus* A, 1978, in Fig. 1.

Episodic fluctuations were observed for *P* in one of the common dolphins (F) while the other female (E) was anestrus for the two year period. Female F exhibited three periods of *P* elevation in 1979 and seven in 1980 (Fig. 2).

## DISCUSSION

The primary objective of this study was to determine whether episodic fluctuations of progesterone and estrogens occur in captive females of *T. truncatus* and *D. delphis* that do not have access to males. This would be consistent with the hypothesis that these two species are spontaneous ovulators. It was disappointing that observable estrogen cycles were not always associated with progesterone cycles, but this may have been an artifact of the sampling time schedule in that the follicular phase may be of short duration relative to a two-week sampling schedule. Obviously, macroscopic analysis of the ovaries is necessary to confirm the relationship between episodic fluctuations of progesterone and ovulation. Still, it is generally agreed that in mammals, where captive studies have been performed, episodic progesterone levels are associated with functional corpora lutea from ovulations. Considering that (1) progesterone is produced by only three endocrine glands (corpus luteum, placenta, adrenals), (2) while adrenal progesterone may be reproductively significant in the rat (Feder, 1981) and in the armadillo (Nakakura, Czekala, Lasley and Benirschke, 1982), it is not significant to the luteal phase in higher mammals such as humans (Tiez, 1976), and (3) adrenal progesterone has never been reported to be released in episodic surges similar to luteal or placental excretion patterns, the relationship between episodic progesterone surges and ovulations is reasonable.

Sawyer-Steffan and Kirby (1980) and Sawyer-Steffan *et al.* (1983) reported baseline *P* levels in captive females of *T. truncatus* as less than 1 ng/ml with a mean of 0.3 ng/ml. In this study, the mean baseline level for *T. truncatus* was 0.2 ng/ml and 0.5 ng/ml for *D. delphis*. Progesterone levels less than 1 ng/ml are generally considered indicative of lack of luteal activity in other mammals (Hendricks and Meyer, 1977). Kirby *et al.* (In prep.) and Wells (1984) observed similar levels in four other species of odontocetes, with mean *P* levels of 0.2 to 0.4 ng/ml for *Stenella longirostris*, *Orcinus orca*, *Lagenorhynchus obliquidens*, and *Globicephalamacrorhynchus*. Episodic *P* fluctuations from baseline to 22 ng/ml were reported for ovulations in *T. truncatus* (Sawyer-Steffan *et al.*, 1983) which are similar to observed levels in this study in which *P* levels fluctuated from less than 1 ng/ml to 22.1 ng/ml. The *D. delphis* females exhibited similar progesterone profiles of ovulation from baseline levels to 15.5 ng/ml. Each species exhibited multiple cycles, with *T. truncatus* ranging from none to possibly three cycles in a year, and *D. delphis* ranging from none to seven cycles within one year. In both species, females were observed to be anestrus for a one-year period, and the *D. delphis* female E was anestrus for two years. The *T. truncatus* female A was anestrus for one year, as was

the second pair of bottlenose dolphins (C and D) for the same year. *T. truncatus* females A and B (Fig. 1) exhibited cycles during April through July. *D. delphis* female F exhibited no specific seasonality, with cycles occurring during spring, summer, and winter of one year, and during spring through late fall of the next year. Occasionally three to five weeks passed between samples, so that one apparent cycle may have actually been two cycles.

Sergeant, Caldwell and Caldwell (1973) suggested that *T. truncatus* females reach sexual maturity at an average length of about 235 cm. Animal C was captured in 1971 at a length of 227 cm, produced a calf in 1973, and has remained at 227 cm (through 1982), considerably under the length at which females generally became sexually mature. The smallest sexually mature females mentioned by Sergeant *et al.* (1973) were also 227 cm long. It is possible that Animal A was not yet sexually mature in 1978 even though she was 11 years of age. In 1974 she was 226 cm in length, in 1980 231 cm and in 1982 245 cm. Another possibility is that length at attainment of sexual maturity varies among populations (Perrin and Reilly, 1984).

Ovulations may be spontaneous in other cetacean species. Some mysticete females have been found to cycle more than once in a season and to cycle when males were not in season (Slijper, 1966). In the same paper it was mentioned that *Globicephala macrorhynchus* and possibly *Pseudorca crassidens* may experience one to three ovulations either simultaneously or in close temporal association as determined histologically. In some odontocetes (*Lagenorhynchus*, *Globicephala*) ovulations may be spontaneous, as evidenced by large numbers of corpora relative to body length (Harrison, 1969; Harrison, Boice and Brownell, 1972; Sergeant, 1962). Yet, it has been proposed that other species of odontocetes are reflex ovulators as evidenced by low numbers of corpora relative to body length and by active corpora lutea usually associated only with pregnancy, under the assumptions that corpora persist throughout the lifespan of the female and that all corpora albicantia are of past pregnancies. Harrison and McBrearty (1977) and Harrison and Ridgway (1971) did not find an active corpus luteum without pregnancy in *T. truncatus*. Perrin, Coe and Zweifel (1976) reported only 5.4% of mature females of *Stenella attenuata* had a corpus luteum without pregnancy. For *S. longirostris*, only 2.8% of the mature females had a corpus luteum without an associated fetus (Perrin, Holts and Miller, 1977). Harrison *et al.* (1972) reported that in the *Stenella* species they examined, the corpora of pregnancy persisted and that these species are induced ovulators as evidenced by the lack of ovulation in captivity. However, it should be pointed out that the corpora observed in the ovaries of a long-term captive female were assumed to be the result of pregnancies before capture, rather than the result of spontaneous ovulations in captivity. They also observed that in *D. delphis* not every corpus could possibly be attributed to past pregnancies, hence some corpora may have been the result of lutealized follicles or accessory corpora lutea. It seems likely that they could also have been attributed to spontaneous ovulations. However, there have been questions about the basic assumptions which underly the theory of reflex ovulations in

cetaceans. Benirschke, Johnson and Benirschke (1980) reported that histologically the corpus luteum of a non-fertilized spontaneous ovulation could not be distinguished in *S. attenuata* from a corpus luteum of early pregnancy and that the possibility of spontaneous ovulation should be examined. Harrison and Ridgway (1971) reported that *T. truncatus* females are induced ovulators because of the relationship between length of the female and number of corpora. However, they also reported relatively short sexually mature females with three or more corpora. Without histological examination of the uterus, it would not be possible to determine if these sexually mature females had ever been pregnant. Harrison and McBrearty (1977) speculated that *T. truncatus* females are induced ovulators because a female kept with an immature male had corpora in her ovaries, although they mentioned that this female could have spontaneously ovulated. Harrison *et al.* (1972) speculated that *T. truncatus* females are induced ovulators, although they observed females with corpora counts that were greater than the probable number of pregnancies for animals of that size class. As can be seen above, the only evidence for induced ovulation has been the low number of corpora found in captive animals and the fact that most corpora lutea could be associated with pregnancy. The possibility that corpora of infertile cycles do not persist as long as do the corpora of pregnancy is critical to any interpretation of ovarian scars. Harrison and Ridgway (1971) concluded that the number of corpora albicantia does not increase relative to female body length. The argument that these two corpora cannot be distinguished does not preclude that they may persist for different lengths of time.

Considering that (1) in captivity female dolphins might have an ovulation rate that is lower than that in wild dolphins and (2) for where it is known in wild marine mammals, the proportion of ovulations that result in pregnancy is relatively high (*Leptonychotes weddelli* 78%, Stirling, 1971; *Callorhinus ursinus* 80%, Chapman, 1961; *Phoca groenlandica* 84%, Sergeant, 1966), it would be impossible to state unequivocally that *T. truncatus* or *D. delphis* are induced ovulators. It seems likely that a number of delphinid species may be spontaneous ovulators, in light of a number of recent hormone studies of captive cetaceans that report episodic fluctuations of progesterone and/or estrogens (Kirby *et al.*, in prep; Sawyer-Steffan and Kirby, 1980; Sawyer-Steffan *et al.*, 1983; and Wells, 1984), and a number of ovarian studies (Benirschke *et al.*, 1980; Collet and Harrison, 1981; Marsh and Kasuya, 1984). Although hormonal evidence of spontaneous ovulation does not eliminate the possibility that dolphins are actually reflex ovulators in the wild, it does suggest that this question should be reviewed in a new perspective with respect to the literature on terrestrial mammals and with respect to what ovarian scars actually represent.

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## Note added in proof

Gross and histological examinations were made on the formalin-fixed ovaries from *T. truncatus* B and *D. delphis* F. In *T. truncatus* B, gross examination yielded a corpora count of five yellow scars in the left ovary and nine yellow scars and one obvious corpora albicans (CA) in the right ovary. Histological examination revealed that there were 13 to 15 old CA in addition to the obvious CA. Exact corpora counts are difficult in serially step-sectioned tissue because a CA on one slide may overlap with the edge of a second CA on the next slide. Hence, this female had a total corpora count of approximately 14 small old CA and one larger CA. She was known to have a

reproductive history of at least five ovulations and only one calf in captivity.

In the *D. delphis* F, gross examination yielded a corpora count of one possible degenerated corpus luteum (CL) associated with a cystic follicle in the right ovary and 8–10 yellow scars in the left ovary. Histological examination of the ovaries yielded a total corpora count of 1–2 degenerated CL and 11–13 CA. Three of these CA

were so old as to be very small and devoid of pigment and would probably have not been seen in gross examination. The relatively recent luteal tissue associated with the cystic follicle in the right ovary was not included in the total corpora count. These ovarian data suggest that gross corpora counts are not indicative of past pregnancies and that yellow scars are old corpora albicantia in these two species.

# Reproductive Behavior and Hormonal Correlates in Hawaiian Spinner Dolphins, *Stenella longirostris*

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## ASBTRACT

The distinction between the reproductive and social contexts of sexual behavior for dolphins is often difficult to make. This problem was examined through comparison of behavior patterns and steroid hormone concentrations in a captive colony of Hawaiian spinner dolphins, *Stenella longirostris*. Once every two weeks, behavioral observations were made over a 24 hour period, and blood samples were drawn for radioimmunoassays of testosterone in the male, and estradiol and progesterone in the two females. An apparent seasonal peak in testosterone was recorded for the male; possible ovulations were noted for the females. The amount of time spent in heterosexual swimming associations did not vary predictably relative to hormone levels. Genital-to-genital contact and mutual ventral presentations occurred most frequently during periods of high testosterone levels. Beak-to-genital propulsion appeared to be related to ovulatory events. All other kinds of contact, one-way ventral presentations, and chases occurred with equal frequency regardless of reproductive hormone levels, suggesting a more social context for these behaviors.

Knowledge of reproductive cycles is crucial to understanding any society of animals. The purpose of this study was to attempt to relate measurements of steroid reproductive hormone concentrations to concurrent observations of behavior patterns in order to distinguish between reproductive and social contexts of sexual behavior in Hawaiian spinner dolphins, *Stenella longirostris*, and to examine the effects of reproductive condition on school structure.

Timed relationships between hormonal events and the behavioral and physical correlates of reproduction are well known for other mammals. For example, close monitoring of hormone concentrations in study groups of rhesus monkeys (*Macaca mulatta*) has allowed precise determination of the timing of endocrine events associated with ovulations and has resulted in observations of strong correlations between mating behavior and hormone concentrations (Wilson, Gordon and Collins, 1982). Until recently there has not been an effective, harmless means of assessing the reproductive condition of dolphins. Now, radioimmunoassay analysis of steroid hormones, using small blood samples, provides a practical means of assessing reproductive conditions of both male and female dolphins. The technique has been applied to bottlenose dolphins (*Tursiops truncatus*) and common dolphins (*Delphinus delphis*) (Sawyer-Steffan and Kirby, 1980; Kirby and Ridgway, 1984). I attempt here to use a combination of radioimmunoassays and behavioral observations to see how well the two kinds of assessments support one another. Does overt sexual behavior closely track changes in blood-carried steroid hormones? Can particular behavior patterns be identified as having reproductive vs social contexts?

Delphinid social and sexual behavior has been described qualitatively for a variety of species, including bottlenose dolphins (McBride and Hebb, 1948; McBride and Kritzler, 1951; Tavolga and Essapian, 1957; Tavolga, 1966; Caldwell and Caldwell, 1972; Tayler and Saayman, 1972; Saayman, Tayler and Bower, 1973; Saayman and Tayler, 1977), common dolphins (Essapian, 1962), and members of the genus *Stenella* (Bateson, 1974;

Norris and Dohl, 1980). Puente and Dewsbury (1976) identified and quantified the occurrence of 'courtship and copulatory' patterns for bottlenose dolphins; from the frequencies they observed they determined that some patterns were more likely to be associated with copulation than were others. Several authors have recognized the importance of sexual behavior in both reproductive and social contexts (Saayman and Tayler, 1977; Norris and Dohl, 1980). Norris and Dohl state (page 845) '... sexual behavior and social communication are interwoven to such an extent that it is often impossible to separate true courtship and mating behavior from communicative behavior of other sorts.'

## METHODS

A captive colony of spinner dolphins held at Sea Life Park, Oahu, Hawaii, was sampled and observed regularly. From September 1979 until February 1980 the captive colony consisted of two males and three females ranging in estimated age from eight to sixteen years

Table 1

Composition of the Sea Life Park spinner-dolphin colony from September 1979 through June 1981. From February 1980 through June 1981, the colony consisted of only the three largest dolphins; only the data from this period are considered in the analyses presented in this report

Dolphin	Sex	Length (cm)	Age* (years)	Comments
Lioele	Male	183	16	Captured 2 September 1976
Kehaulani	Female	190	12	Captured 9 September 1976
Kahe	Female	191	11	Captured 15 June 1972
Apiki	Male	172	9	Captured 27 August 1976 Died 9 February 1980
Mahealani	Female	175	8	Captured 23 May 1974 Died 13 January 1980

\* Age in 1980 determined from analysis of growth layer groups in sectioned teeth (Myrick, Shallenberger, Kang and Mackay, in press.

(Table 1). From February 1980 through June 1981, the colony consisted of the three oldest dolphins: Lioele, a male, and Kahe and Kehaulani, both females. Lioele had a deformity of the spine as a result of an injury incurred two years previously. While the deformity did not prevent his participation in any major class of behaviors, the intensity of his involvement was typically less than for the other dolphins. The colony was maintained strictly for research in the 25 m diameter, 3 m deep Bateson's Bay. Human contact was limited to three feedings per day and biweekly blood sampling.

Blood samples were obtained every other Wednesday from 5 September 1979 through 29 October 1980. Additional samples were collected on 22 June 1981. For blood sampling, the dolphins entered an adjoining, smaller tank which was then drained until the dolphins could be handled individually on the shallowest portion of the sloping tank floor. The dolphins were restrained by two handlers, and blood was drawn from a large, superficial vessel on the dorsal aspect of the fluke. The 24–36 cc samples were centrifuged, filtered, and frozen prior to analysis.

Steroid hormone concentrations were measured using radio-immunoassay techniques. Serum from males was analyzed for testosterone (Smith-Kline Laboratory, Honolulu, HI; sensitivity = 0.05 ng/ml); samples from females were analyzed for estradiol (Smith-Kline Laboratory, Honolulu, HI; sensitivity = 1.9 pg/ml) and progesterone (V. Kirby, San Diego Zoo; sensitivity = 33 pg/ml). Progesterone was measured from February 1980 through June 1981.

Behavioral observations were made in conjunction with each blood-sampling session. The behavior patterns of the colony were monitored for the first ten minutes of every half hour through the twenty-four hours preceding or following hormone sampling. An observer at the side of the observation tank narrated behavioral events and times of occurrence into a tape recorder. The durations of heterosexual pairings and the frequencies of occurrence of all other behavior patterns considered to have sexual or social connotations were measured from the transcriptions of the tapes. The durations of heterosexual pairings were measured as the periods during which the dolphins swam and surfaced synchronously within approximately 2 m of each other, engaged in similar activities, and swam approximately side by side. Other behavior patterns were scored as one occurrence as long as the participants were together and engaging in the activity. If the dolphins separated to terminate the activity or to surface to breathe, and then engaged in the activity again, two occurrences were scored. The behavior patterns were further partitioned on the basis of the role of the participant. A dolphin was classified as 'giving' the behavior if it initiated or was the most active participant in a behavioral sequence; the more passive participant or the individual receiving the attentions of the 'giver' was classified as the recipient. Distinctions were sometimes difficult and some of the behavior patterns involved mutual participation.

Only observations made from February 1980 through June 1981, when the colony composition was stable and when progesterone was measured, are considered here.

The distribution of durations of heterosexual pairings and frequencies of occurrence of the behavior patterns

were compared relative to the concentrations of the reproductive hormones measured during the same period with a Kolmogorov–Smirnov Goodness of Fit test (Zar, 1974; 0.05 level of significance). Testosterone concentrations were considered 'high' if greater than 30 ng/ml, 'intermediate' if between 8–30 ng/ml, and 'baseline' below 8 ng/ml. 'High' estradiol concentrations were those over 90 pg/ml, 'intermediate' were between 50–90 pg/ml, and 'baseline' were below 50 pg/ml (this categorization scheme follows that of Wilson, Gordon, and Collins, 1982). Progesterone concentrations over 3 ng/ml were considered indicative of ovulation, 1–3 ng/ml concentrations were 'indeterminate', and below 1 ng/ml were 'baseline' (Wilson *et al.*, 1982; Kirby and Ridgway, 1984).

## RESULTS

### Steroid hormone concentrations

Serum testosterone measurements (Fig. 1) ranged from less than 1 ng/ml to over 60 ng/ml for the adult male (Lioele) monitored throughout the study. The values for the smaller males, Apiki and a dolphin that was tagged and released off the coast of the Island of Hawaii, were within the baseline range for Lioele (0–8 ng/ml). Lioele's testosterone titer increased significantly beginning in March 1980, reached maximum levels in June–July 1980, and returned to baseline in October 1980. A single sample from June 1981 was nearly identical to the highly elevated value from the same period during the previous year.

Estradiol concentrations were usually low or intermediate for both females (Figs 2 and 3). Elevated estradiol values were noted for Kahe in June 1981, and for Kehaulani in October 1979 and 1980.

Progesterone concentrations were highly variable for both females (Figs 2 and 3). The elevated progesterone values for Kehaulani in September–October 1980 suggested ovulations. The October surge in progesterone was preceded by elevated estradiol and low progesterone, perhaps indicating both the follicular and luteal phases of the cycle. Progesterone level in Kahe increased markedly in July 1980 and remained elevated at least through the end of the continuous observation period

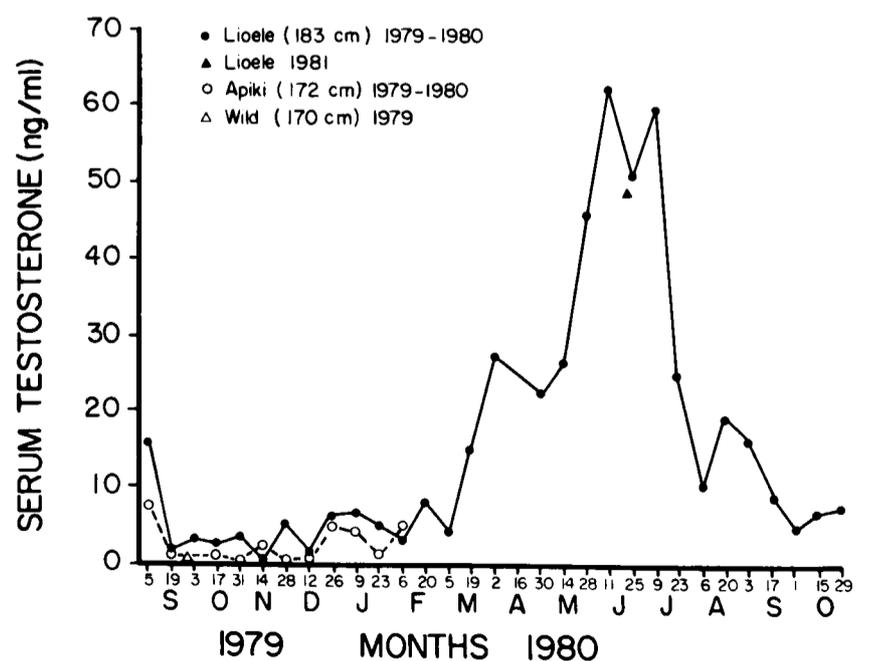


Fig. 1. Serum testosterone concentrations for three male Hawaiian spinner dolphins.

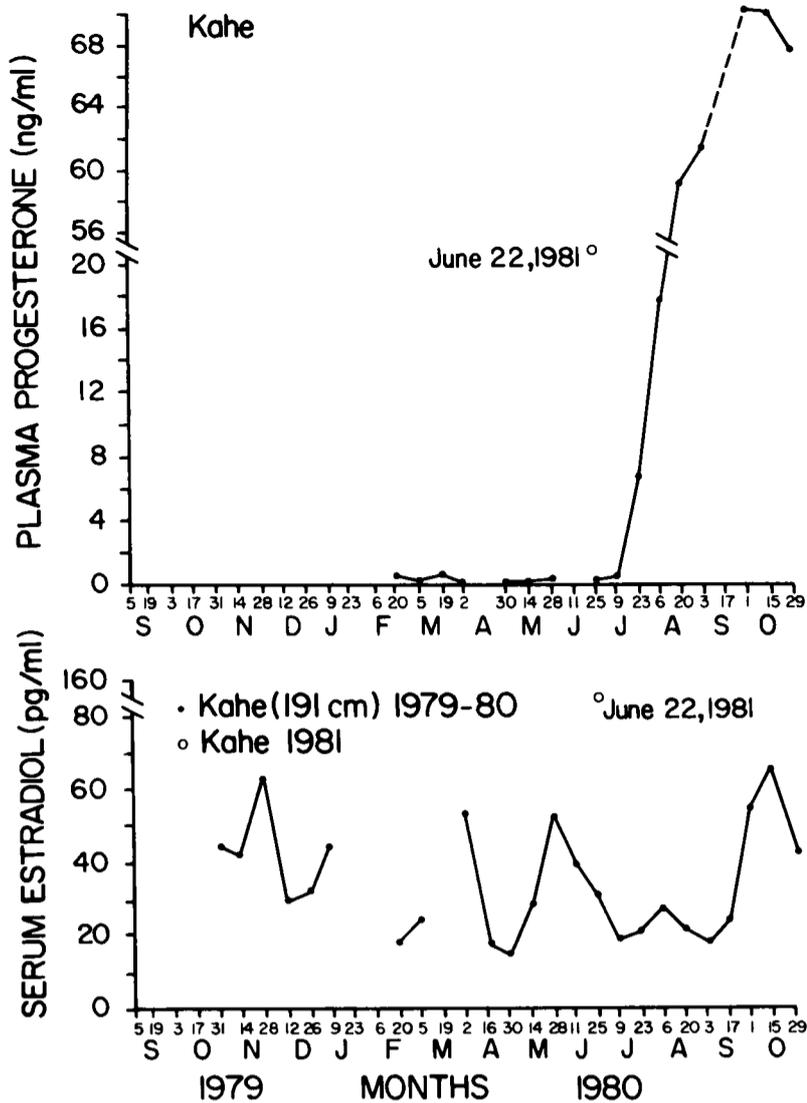


Fig. 2. Serum estradiol and progesterone concentrations for female Hawaiian spinner dolphin Kahe.

(October 1980). It was found to be elevated again in June 1981. Elevated progesterone values over prolonged periods are typically indicative of pregnancy, but no calf or aborted fetus was forthcoming.

**Durations of heterosexual pairings**

The amount of time spent by each dolphin swimming in association with a dolphin of the opposite sex did not appear to vary predictably with the hormone levels of any of the participants. Total time spent in each heterosexual pairing was calculated for each observation day. Comparisons of the distributions of these pair totals with the hormone concentration categories showed no significant differences from the random. In general, Lioele (♂) tended to spend more time with Kahe (♀) than with Kehaulani (♀). The mean proportion of the observation days each dolphin spent in each pairing, relative to the hormone categories, is presented in Table 2. Lioele spent the greatest proportion of time paired with females (49.8%), rather than swimming alone or in a trio, on the day when the females' progesterone concentrations were at their lowest value (1 April 1980). The next highest proportion of time in which Lioele was paired with females (36.1%) occurred on the day of Kahe's highest recorded estradiol concentration (22 June 1981). High estradiol concentrations and low progesterone concentrations are associated with the follicular phase of the female cycle, when estrus would be most likely to occur (Cupps, Anderson and Cole, 1969). However, as only one hormone concentration on these two dates could be considered indicative of imminent ovulation, these anecdotes are only suggestive of the possible role of female steroid hormone in influencing swimming associations.

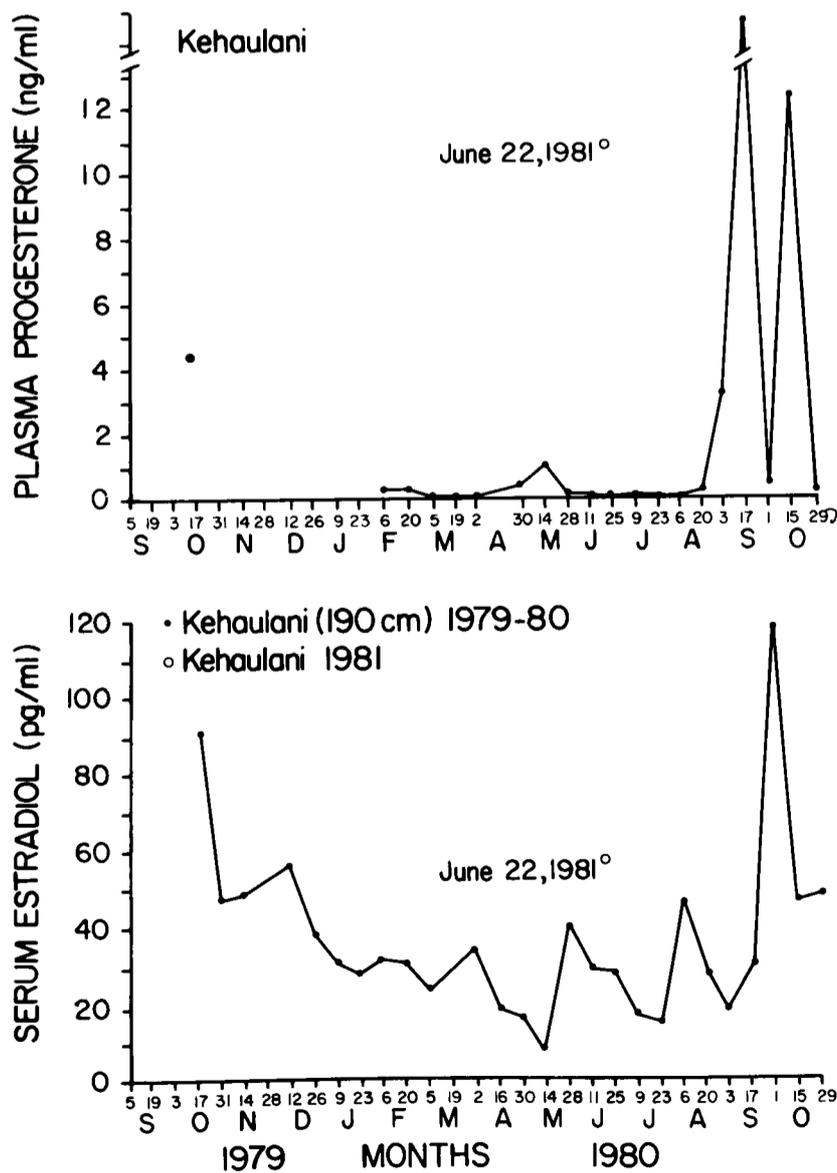


Fig. 3. Serum estradiol and progesterone concentrations for female Hawaiian spinner dolphin Kehaulani.

Table 2

Proportion of total observation time during which heterosexual pairings occurred, relative to steroid hormone concentrations. Means calculated from daily ratios of time paired: total observation time

	Lioele with Kahe		Lioele with Kehaulani	
	$\bar{X} \pm \text{s.d.}$	n (days)	$\bar{X} \pm \text{s.d.}$	n (days)
<b>Testosterone</b>				
Baseline (0-8 ng/ml)	0.24 ± 0.055	4	0.02 ± 0.018	4
Intermediate (8-30 ng/ml)	0.26 ± 0.097	9	0.04 ± 0.026	9
High (> 30 ng/ml)	0.18 ± 0.102	4	0.06 ± 0.028	4
<b>Estradiol</b>				
Baseline (0-50 pg/ml)	21.1 ± 7.44	11	3.9 ± 2.93	14
Intermediate (50-90 pg/ml)	24.8 ± 13.05	4	2.8 —	1
High (> 90 pg/ml)	33.0 —	1	4.3 —	1
<b>Progesterone</b>				
Baseline (0-1 ng/ml)	24.9 ± 11.25	7	4.7 ± 2.74	12
Intermediate (1-3 ng/ml)	— —	0	6.5 —	1
High (> 3 ng/ml)	23.4 ± 7.16	9	1.4 ± 1.44	3

Table 3

Heterosexual behavior patterns: male relations to females (no. occurrences/hr) relative to serum testosterone conc. of the male

Female behavior patterns relative to male (Lioele)	Lioele		
	Baseline (0–8 ng/ml) <i>n</i> = 4 days: 26.06 hours $\bar{X} \pm \text{s.d.}$	Intermediate (8–30 ng/ml) <i>n</i> = 9 days: 62.69 hours $\bar{X} \pm \text{s.d.}$	High (> 30 ng/ml) <i>n</i> = 4 days: 30.77 hours $\bar{X} \pm \text{s.d.}$
Genital–genital contact			
Mutual	0	0	0.13 ± 0.135
Beak-to-genital propulsion			
Give	0	0.02 ± 0.053	0
Receive	0.24 ± 0.480	0	0.03 ± 0.065
Other genital contact			
Give	0	0.02 ± 0.050	0.07 ± 0.130
Receive	0.11 ± 0.210	0.01 ± 0.043	0.03 ± 0.065
Non-genital contact			
Give	0	0.03 ± 0.062	0
Receive	0.08 ± 0.165	0.13 ± 0.290	0.17 ± 0.127
Mutual	0.25 ± 0.289	0.05 ± 0.076	0.17 ± 0.168
Ventral presentation			
Give	0.04 ± 0.080	0.03 ± 0.062	0.17 ± 0.168
Receive	0.29 ± 0.300	0.12 ± 0.149	0.03 ± 0.065
Mutual	0.08 ± 0.087	0.02 ± 0.050	0.23 ± 0.167
Chases			
Give	0	0.03 ± 0.066	0
Receive	0	0	0

### Behavior patterns

Six patterns of behavior with potential sexual connotations were identified and scored. Each of these patterns involved interactions between pairs, as noted by Bateson (1974). The six patterns are: genital-to-genital contact, beak-to-genital propulsion, other genital contact, non-genital contact, ventral presentations, and chases. *Genital-to-genital contact* was scored when the genital regions of both members of the heterosexual pair were in contact with each other. Intromission was difficult to observe, but was seen as part of this pattern. *Beak-to-genital propulsion*, as described by Bateson (1974) and Norris and Dohl (1980), involved the placement of the tip of the rostrum of a trailing dolphin in the genital slit of another, with the flukebeats of the trailing animal propelling the pair at slow speed. Occasionally the flukes of the propelled dolphin rested on the head of the other individual. This was usually a protracted behavior, and was scored once for each period of contact between surfacings. *Other genital contact* included all other occasions when the genital region of one dolphin was in contact with any part of the other dolphin. This category included such behavior patterns as inserting fins in the genital slit of another dolphin, or rubbing or stroking the genital region of the other dolphin. *Non-genital contact* included caressing of the dolphin by another, or both simultaneously, using the pectoral fins, flukes, rostrum, head, or flanks. Typical forms of non-genital contact involved one animal raising a pectoral fin while the other dolphin rubbed on the outstretched fin (we called it 'pec-whetting'). The pectoral fins of both dolphins sliced rapidly back and forth against each other. In a more passive pattern, swimming occurred with the pectoral fin of one animal in contact with the body of the other. Non-genital contact often involved an increase in swimming speed. *Ventral presentations* consisted of the tilting of the belly of one dolphin toward another, or

tilting by both toward each other simultaneously or in rapid alternation. This behavior pattern varied from a slight tilt of one partner to one rolling over beneath another with ventrum oriented upwards. *Chases* generally consisted of a pair of dolphins swimming rapidly, often with one dolphin behind the other. As used here, the term 'chase' does not necessarily imply that one animal was chasing the one ahead. Often the initiation of a chase was so sudden and synchronous that it was impossible to determine whether the activity was actually a 'chase' or a 'follow'.

These behavior patterns occurred with variable frequencies relative to the steroid hormone concentrations (Tables 3, 4 and 5). In general, most of the behavior patterns occurred less frequently between individuals of opposite sex than they did between the two females. All but genital-to-genital contact were observed in both heterosexual and female–female pairings.

Genital-to-genital contact occurred only in male–female pairs. Only three occurrences of genital-to-genital contact were observed. Intromission was observed once and was believed to have occurred during the other times but could not be confirmed. Erection was not seen at any time other than during this intromission. All the genital-to-genital contacts occurred when the male's testosterone titer was high (more than 48 ng/ml) (Kolmogorov–Smirnov  $D = 0.74, n = 3, p < 0.05$ ). Genital-to-genital contacts were not clearly related to female hormone concentrations, occurring at both baseline and high levels of estradiol or progesterone.

The occurrence of beak-to-genital propulsion was most closely related to the female hormonal cycle. The male rarely propelled the females; there was no clear relationship between the incidence of giving or receiving propulsion and testosterone concentration. However, the highest frequency of beak-to-genital propulsion occurred during the follicular phase of the only clearly-defined ovulatory cycle observed during this study. Kehaulani

Table 4

Heterosexual behavior patterns: female relations to male (no. occurrences/hr) relative to estradiol of the females

Behavior patterns relative to female	Kahe		
	Baseline (0-50 pg/ml) <i>n</i> = 11 days: 76.31 hours $\bar{X} \pm \text{s.d.}$	Intermediate (50-90 ng/ml) <i>n</i> = 4 days: 29.07 hours $\bar{X} \pm \text{s.d.}$	High (> 90 pg/ml) <i>n</i> = 1 day: 7.53 hours $\bar{X} \pm \text{s.d.}$
Genital-genital contact			
Mutual	0	0	0.26 -
Beak-to-genital propulsion			
Give	0	0	0
Receive	0.02 ± 0.048	0	0
Other genital contact			
Give	0	0.03 ± 0.065	0
Receive	0	0.11 ± 0.210	0
Non-genital contact			
Give	0.06 ± 0.111	0	0.13 -
Receive	0	0	0
Mutual	0.05 ± 0.074	0.17 ± 0.135	0.27 -
Ventral presentation			
Give	0.04 ± 0.067	0.14 ± 0.198	0
Receive	0.04 ± 0.069	0.13 ± 0.133	0.40 -
Mutual	0	0.07 ± 0.078	0.40 -
Chases			
Give	0	0	0
Receive	0.01 ± 0.045	0	0
		Kehaulani	
	<i>n</i> = 14 days: 98.12 hr	<i>n</i> = 1 day: 7.53 hr	<i>n</i> = 1 day: 7.26 hr
Genital-genital contact			
Mutual	0.01 ± 0.035	0	0
Beak-to-genital propulsion			
Give	0.01 ± 0.035	0	0.96 -
Receive	0	0	0
Other genital contact			
Give	0	0	0
Receive	0.02 ± 0.070	0	0
Non-genital contact			
Give	0.05 ± 0.089	0.03 ± 0.065	0
Receive	0.02 ± 0.051	0	0
Mutual	0.01 ± 0.037	0.03 ± 0.065	0.28 -
Ventral presentation			
Give	0.06 ± 0.098	0	0
Receive	0.13 ± 0.035	0	0
Mutual	0.04 ± 0.067	0	0
Chases			
Give	0	0	0
Receive	0	0	0

propelled Lioele seven times on 30 September when her estradiol titer was the highest of the study, and when her progesterone was at a low level. This resulted in a significant difference in the occurrence of beak-to-genital propulsion relative to Kehaulani's estradiol titer ( $D = 0.82, n = 8, p < 0.01$ ).

Mutual ventral presentations, in which both the male and female tilted their bellies toward each other, were significantly related to testosterone levels ( $D = 0.44, n = 10, p < 0.05$ ) and Kahe's estradiol concentrations ( $D = 0.67, n = 5, p < 0.05$ ). The frequency of occurrence of mutual ventral presentations was not consistent for all the females, suggesting that the significance of Kahe's relationship may be due to the coincidental result that her highest estradiol value and Lioele's high testosterone concentrations occurred together on 22 June 1981.

No significance was found in the comparisons of the hormone concentrations and frequencies of occurrence of

other genital contacts, non-genital contacts, chases, or one-way ventral presentations.

### DISCUSSION

Although sample sizes were small, the frequencies of occurrence of three behavior patterns appeared to be closely linked to changes in reproductive hormone levels. Genital-to-genital contact and mutual ventral presentations occurred most frequently when the male's testosterone concentrations were high. Beak-to-genital propulsion appeared to be related to ovulatory or associated events. All other contact, chases, and one-way ventral presentations were not significantly related to hormone concentrations, and presumably were typically used in more social than reproductive contexts. Dolphin copulations occur with the two participants oriented ventrum to ventrum; thus the actual mechanics of mutual

Table 5

Heterosexual behavior patterns: female relations to male (no. occurrences/hr) relative to progesterone of the females

Behavior patterns relative to female	Kahe*		Kehaulani		
	Baseline (0-1 ng/ml) n = 7 days: 49.98 hours $\bar{X} \pm \text{s.d.}$	High (> 3 ng/ml) n = 9 days: 61.58 hours $\bar{X} \pm \text{s.d.}$	Baseline (0-1 ng/ml) n = 12 days: 84.96 hours $\bar{X} \pm \text{s.d.}$	Intermediate (1-3 ng/ml) n = 1 day: 6.35 hours $\bar{X} \pm \text{s.d.}$	High (> 3 ng/ml) n = 4 days: 28.21 hours $\bar{X} \pm \text{s.d.}$
Genital-genital contact					
Mutual	0	0.03 ± 0.090	0.01 ± 0.038	0	0
Beak-to-genital propulsion					
Give	0	0	0.09 ± 0.276	0	0
Receive	0.02 ± 0.061	0	0	0	0
Other genital contact					
Give	0.02 ± 0.049	0	0	0	0
Receive	0	0.05 ± 0.140	0.03 ± 0.083	0	0
Non-genital contact					
Give	0.05 ± 0.125	0.05 ± 0.077	0.05 ± 0.089	0	0.07 ± 0.085
Receive	0	0	0.01 ± 0.038	0.15 -	0
Mutual	0.04 ± 0.063	0.14 ± 0.120	0.02 ± 0.081	0	0.07 ± 0.078
Ventral presentation					
Give	0.06 ± 0.073	0.06 ± 0.143	0.06 ± 0.097	0.31 -	0
Receive	0.06 ± 0.076	0.09 ± 0.152	0.02 ± 0.055	0	0
Mutual	0.02 ± 0.049	0.06 ± 0.136	0.05 ± 0.071	0	0
Chases					
Give	0	0	0	0	0
Receive	0.02 ± 0.050	0	0.01 ± 0.043	0	0

\* No serum progesterone concentrations between 1-3 ng/ml were measured for Kahe. Serum samples on 11 June 1980 were too small for progesterone analysis; thus, only 16 blood sampling days are considered for Kahe.

Table 6

Occurrence of behavior patterns within heterosexual and homosexual pairings, as observed in three delphinid genera: *Stenella* (S), *Tursiops* (T) and *Delphinus* (D)

Behavior pattern	Sexual composition of pairs			Association with copulation	
	M-F	M-M <sup>ab</sup>	F-F	With	Without
Genital-to-genital contact	STD	ST		STD	ST
Beak-to-genital contact	ST	S	S	ST	ST
Other genital contact	STD	ST	S	STD	STD
Non-genital contact	STD	ST	S	STD	STD
One-way ventral presentations	ST	c	S	ST	ST
Mutual ventral presentations	STD	c	S	STD	ST
Chases	ST	S	S	ST	ST

<sup>a</sup> No observations of M-M or F-F *Delphinus* combinations were available from the literature.

<sup>b</sup> The only available descriptions of M-M *Stenella* combinations are reported by Bateson, 1974.

<sup>c</sup> Ventral presentations not considered in the descriptions of Bateson, 1974.

Sources: McBride and Hebb, 1948; McBride and Kritzler, 1951; Tavalga and Essapian, 1957; Essapian, 1962; Tavalga, 1966; Caldwell and Caldwell, 1972; Tayler and Saayman, 1972; Saayman, Tayler and Bower, 1973; Bateson, 1974; Puente and Dewsbury, 1976; Saayman and Tayler, 1977; Norris and Dohl, 1980.

ventral presentations are similar to genital-to-genital contact, and mutual ventral presentation is known to serve as a precursor behavior to copulation, for example, in *Delphinus* (Essapian, 1962).

Some of the behavior patterns were not correlated with hormonal events. Many delphinid courtship and copulatory patterns may be used in contexts outside of reproduction. Non-reproductive contexts may be identified when the behavior patterns occur between inappropriately-matched individuals (but it is possible that sexually-aroused individuals may use patterns with inappropriate partners). Copulations between males (Bateson, 1974), attempted matings between male calves and their mothers within several days of birth (Caldwell and Caldwell, 1972), or beak-to-genital propulsion between two females (Bateson, 1974) could scarcely be considered reproductive, yet each of the patterns have been described as a courtship pattern when engaged in by adult dolphins of different sexes. Table 6 summarizes occurrences of behavior patterns in heterosexual or homosexual pairs of dolphins of three genera and shows that most of the behavior patterns are observed in both homosexual and heterosexual combinations. Though this table sometimes suffers from a lack of observations of homosexual behavior in some of the available literature, the similarities in patterns across genera and widespread occurrence of patterns in both kinds of pairings is noteworthy. Other behavior patterns have been included in lists of courtship and copulatory patterns for *Tursiops* and *Delphinus*, such as head-butting, mouthing, leaping, vocalizing, tailslaps and headslaps. Head-butting and mouthing have not been reported for *Stenella* spp.

It may be more difficult to identify the context of behavior patterns involving heterosexual pairs of adults than of homosexual pairs, but knowledge of the reproductive condition of members of heterosexual pairs can be useful in distinguishing between reproductive and other social contexts. Puente and Dewsbury (1976) found that *Tursiops* behavior patterns they termed 'courtship' occurred more frequently on days during which copulations occurred than on days without copulations. However, all of their observations were made during the presumed breeding season (McBride and Hebb, 1948; McBride and Kritzler, 1951; Tavalga, 1966), and no data are available for comparison with frequencies outside of the breeding season. It would be expected that behavior patterns most closely linked to reproduction would increase in frequency during the reproductive season. Similar behavior patterns observed at other times of the year or between inappropriate participants could be assumed to occur as part of the ordering of dolphin schools, or developing or maintaining relationships between individuals. Changes in the frequency of mating activity and durations of heterosexual pairings on a seasonal basis have been reported for *Tursiops* in several locations (McBride and Kritzler, 1948; McBride and Hebb, 1951; Tavalga, 1966; Saayman and Tayler, 1977). For example, males are reported to spend more time with females during the spring, and more copulations occur then. In one case it was reported that female-female social interactions were curtailed in the spring (Saayman and Tayler, 1977). These changes were presumed to coincide with the breeding season, but no precise measures of the reproductive condition of the involved dolphins were made.

The lack of significant relationships between duration of heterosexual pairings and hormonally determined reproductive condition differs from descriptions of *Tursiops* behavior, where such associations seem clear (Tavalga, 1966). This difference could be related in these observations to a possible inability of the deformed male to maintain swimming associations of long duration. It could also reflect interspecific differences in school structure. Spinner dolphins often swim in large schools of mixed sex, whereas coastal bottlenose dolphins often swim in single-sex schools that occasionally meet and mix for periods of variable length with schools of the other sex (Norris and Dohl, 1980; Wells, Irvine and Scott, 1980). The constant availability of members of the opposite sex within a school may preclude the need to change typical swimming association patterns.

Acoustic recordings have not been made consistently throughout any of the studies reported in the literature, making comparisons of occurrence of vocalizations difficult. Leaping, head-slaps and tail-slaps have been observed in the present study as 'punctuation' signalling the initiation or termination of bouts of social behavior involving pairs of dolphins.

The hormonal determination of reproductive condition in males may be simpler than in females, as the period of elevated testosterone concentrations may be prolonged, as shown in Fig. 1. Ridgway and Green (1967) identified a 'definite seasonal rut' in male *Lagenorhynchus obliquidens* and *D. delphis*, during which there was a

significant increase in the size of the testes, prostate, and muscles associated with the reproductive organs. Perrin and Henderson (1984) observed similar changes in male spinner dolphins in the eastern tropical Pacific. Kirby and Ridgway (1984) measured significant seasonal increases in testosterone levels in male *Tursiops*. Very few comparative data on hormones in *Stenella* spp. are available. Sawyer-Steffan and Kirby (1980) reported testosterone values of 0.5 ng/ml to 6.7 ng/ml for four immature specimens killed in the tuna-seine fishery; these values were less than or equal to the baseline values for Lioele.

Female reproductive condition may be more difficult to determine because of the short-lived nature of the hormonal events surrounding ovulation. If spinner dolphins follow the typical ovulatory cycle described by Cupps, Anderson and Cole (1969), then elevated estradiol values in conjunction with low progesterone concentrations, followed by reduced estradiol levels and a progesterone surge, should define an ovulation and presumably should define the time during which behavioral estrus should occur. Measurements of estradiol surges alone are not enough to indicate imminent ovulations. Biweekly measurements of progesterone and estradiol may be insufficient to document each ovulation, as suggested by the fact that only one presumed ovulation was clearly indicated in 8.5 months of continuous measurements of two females (Fig. 3). Rather than the long breeding season suggested for the males, the breeding season for the females during one year may consist of an unknown number of brief periods of receptivity associated with multiple ovulations. Multiple ovulations per season have been suggested from the data from the tuna-seine fishery. Perrin, Holts and Miller (1977), Perrin, Coe and Zweifel (1976), and Perrin and Henderson (1984) reported variations in ovulation rates for *Stenella* spp. with age with the younger adults showing evidence of more (up to 4) ovulations per year. Ridgway and Kirby (1984) reported multiple spontaneous ovulations in captive *D. delphis*. Benirschke, Johnson and Benirschke (1980) provided evidence from the examination of ovaries of *Stenella* spp. that spontaneous ovulations may occur. Few hormone data are available for comparison, but Sawyer-Steffan and Kirby (1980) found progesterone and estradiol levels from their *Stenella* specimens to be similar to levels obtained from pregnant and non-pregnant *Tursiops*, and these levels are comparable to those reported here. As noted by Tayler and Saayman (1972) and Puente and Dewsbury (1976), receptivity in the female is critical to the completion of courtship patterns, and such receptivity is likely to be closely related to the reproductive condition of the female. More data are needed to document this relationship adequately.

More frequent blood sampling in association with observations of the patterns of social behavior of dolphin groups may provide more clear-cut determinations of the contexts of the observed behavior patterns and thereby provide the basis for better understanding the mechanisms utilized by delphinids in ordering their schools and developing and maintaining interindividual relationships.

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**Abstracts of Symposium Papers not Published in this  
Volume**



## Abstracts of Symposium Papers not Published in this Volume

(see PARTICIPANTS for authors' addresses, p. v–viii)

### Molecular Hybridization in Cetaceans

Ú. Arnason

#### ABSTRACT

Earlier studies showed a conservation of two DNA satellites in the balaenopterids. The lighter satellite was demonstrated only in the balaenopterids, whereas repeated sequences related to the heavier satellite have been shown to occur both in the bowhead and in odontocete materials.

In the present study a Hind III restriction fragment was isolated from killer whale DNA. The fragment was nick-translated and hybridized according to the Southern blot technique to restricted DNA of the following species: *O. orca*, *L. albirostris*, *P. phocoena*, *D. leucas*, *B. acutorostrata* and *B. mysticetus*. The highest degree of hybridization was registered between *O. o.* and *L. a.* These two species showed identical lengths of restriction fragments whereas fragment sizes in the other species were somewhat larger. Substantial hybridization was recorded between *O. o.* and *P. p.* and *D. l.* respectively. The hybridization between *O. o.* and *B. a.* was somewhat lower and between *O. o.* and *B. m.* almost nonexistent. While the results show a remarkable conservation of highly repeated DNA among most of the materials studied it is not known whether the very low degree of hybridization between *O. o.* and *B. m.* is due to a limited occurrence of the sequence in *B. m.* or is caused by divergence of the same original sequence in the two species.

The present results coincide with the cetacean karyological conservatism which has been demonstrated earlier in considerable detail. The results of the molecular hybridization and the karyological studies are consistent with the previously advocated view that, as compared with terrestrial mammals, inbreeding in marine mammals is limited, and differentiation of new populations and speciation is very slow.

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### Sperm Whale Growth and Reproduction – A New Method of Assessment

J. R. Beddington and J. G. Cooke

#### ABSTRACT

Sperm whales, *Physeter macrocephalus*, have been exploited for some considerable time, both in the Southern Ocean and in the North Pacific and North Atlantic Oceans. During the history of this exploitation, data have been obtained in great detail on the length composition of the catch. By contrast, biological information on the sperm whale reproductive performance is scanty. Utilizing a population model and the full data on the length distribution of the sperm whale catch, a method is developed which enables the reproductive performance of sperm whales over time to be assessed. These results are then tested against available biological data.

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## Baleen Whales and their Food Supply in the Southern Ocean: the Effect on Reproduction

J. R. Beddington and B. Grenfell

### ABSTRACT

Baleen whales in the Southern Hemisphere have been substantially exploited and the history of exploitation has been accompanied by extensive data collections on the biological parameters of reproductive success. Although the data collection lacks the statistical design for elucidating comprehensively the patterns of reproductive performance, nevertheless the analysis-of-variance techniques applied to these data sets have enabled the main temporal patterns to be elucidated. These indicate an increase in reproductive performance with time, but the increase is occurring in a quasi-cyclic manner. An explanation for the quasi-cyclic phenomenon is provided by modelling the natural history of the main prey species of the baleen whale and assessing the interaction between the decreasing whale population and their prey.

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## Ovarian Characteristics, Corpora Lutea and Corpora Albicantia in *Delphinus delphis* Stranded on the Atlantic Coast of France<sup>1</sup>

A. Collet and R. J. Harrison

### ABSTRACT

Efforts have been made by several investigators to differentiate between corpora albicantia derived from corpora lutea of pregnancy and those from corpora lutea of a cycle, of pseudopregnancy, of abortion, and of a secondary or accessory type.

The ovaries of 19 females of *D. delphis* stranded on the Atlantic coast of France have been examined, of which 8 were immature (from 163 to 189 cm) and 11 were mature (from 195 to 208 cm). Young retrogressing corpora lutea (in neither pregnant nor lactating females), lutealized follicles, corpora atretica, and corpora albicantia have been described in mature females. The corpora albicantia could be divided into two types: the first with considerable acellular hyaline material arranged in lobules, the second with little more than coils of obliterated blood vessels and sparse hyaline material. One female of only 195 cm showed fourteen corpora albicantia, and another of 208 cm exhibited eighteen corpora albicantia; in both cases most of the corpora were from the second type. It would seem unlikely that these animals would have had, respectively, fourteen and eighteen young, as there is to date no evidence of rapidly increasing population of *Delphinus* in these waters, nor of an excessive postnatal mortality. It is therefore argued that sexual maturity might be marked by the onset of a variable number of successive oestrous cycles not resulting in pregnancy, until that particular individual attains the status of breeding cow within the social structure of its school.

<sup>1</sup> Published in 1980 in *Aquatic Mammals*, 8(1): 69-76.

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## Sea World's *Tursiops* Breeding Project

L. H. Cornell

### ABSTRACT

An overview of Sea World, Inc.'s *Tursiops* breeding project including information on the animals which compose the breeding group, methods of pregnancy determinations in both captive and wild animals, captive environmental considerations and additional information on pre- and post-natal care. The data includes information on 14 births from the spring of 1978 to the spring of 1981.

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## Census of Captive Marine Mammals in North America: Preliminary Observations on Reproductive Parameters in Captive Cetaceans

D. A. Duffield, L. H. Cornell and E. D. Asper

### ABSTRACT

Information has been compiled relating to captive breeding programs in the United States and Canada as part of a broader Census of Captive Marine Mammals in North America (1976) and a subsequent Census Up-Date (1979), sponsored by Sea World and Hubbs-Sea World Research Institute. Data are presented relating to the following reproductive parameters in captive cetaceans: the actual age of reproductive *competence* in males versus females; abortion and still-birth rates – relation to female age and experience, and implications for population reproductive strategies in the wild; timing of births in captivity; and comparative growth and development rates in captive-bred calves.

Although preliminary, these observations suggest areas for future evaluation of wild and captive reproductive parameters in cetaceans and pinnipeds.

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## Biochemical Variability in *Tursiops* and *Delphinapterus*, Application to Evaluation of Population Dynamics

D. A. Duffield, D. K. Odell, E. D. Asper, S. Searles, W. E. Evans, K. J. Finley and M. A. Fraker

### ABSTRACT

Electrophoretic comparisons of blood and tissue proteins have been undertaken in *Tursiops* and *Delphinapterus*, to initially identify the variability present in these populations, and to test the use of protein variants for evaluating the degree of population discreteness and the presence of possible population interactions. Comparisons include Atlantic versus Pacific populations and a variety of sample locations within each of these systems.

As time does not permit a detailed description of all findings, this paper is designed to illustrate conclusions pertinent to the use of this technique as a tool for evaluation of population structure and dynamics in cetaceans. These are that: (1) the levels of protein variability present in populations of both species are more than adequate for use in population comparisons; (2) composition of the sampling units to reflect immediate social units (as illustrated in *Tursiops*) allows a much greater evaluation of relationship and population structure based on genetic comparisons of individual protein profiles, than samples taken on an individual animal basis; (3) maternal-foetal or mother-calf comparisons provide an extremely valuable tool for detection of inter-population exchange; and (4) evaluation of representative population samples over 2-3 consecutive years from any one sampling location is essential for detecting transient, but reproductively effective exchanges between populations.

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## Influence of Stress and Disease on Reproductive Success in Cetaceans

J. R. Geraci

### ABSTRACT

There are interesting relationships between the outcome of pregnancy and the genetic, medical, and psychological history of the prospective mother. Most of our information comes from observations of women and from studies on laboratory animals. Few, if any, direct correlations have been made in cetaceans, partly because the animals are inaccessible, and partly because we have not been very determined in our effort.

In this paper, I adopt the premise that cetaceans, like other groups of mammals, are subjected to biological and environmental factors that influence reproductive success. The case can be made easily for environmental contaminants that threaten the reproductive welfare of dolphins which accumulate them from a vast oceanic reservoir. Genetic factors related to inbreeding, psychological stress provoked by noise, and disruption of parental and social bonds affect pregnant women, terrestrial mammals, and, undoubtedly, whales and dolphins.

With a slight twist in approach, we can draw upon some findings in cetaceans to better understand the influence of stress and disease on their reproductive activity. In this context we examine adrenal disorders that affect nearly all mature female Atlantic white-sided dolphins, *Lagenorhynchus acutus*, widespread infections in the mammary glands of odontocetes, and the peculiar affinity of some larval cestodes for the genital region of males and females.

Using these direct and extrapolated data, an attempt is made to identify certain features of life history and environment that may affect reproductive success in cetaceans.

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## Aspects of the Estimation of True Population Pregnancy Rates

J. W. Horwood

### ABSTRACT

Four characteristics of the fishery of exploited whale stocks are reviewed in relation to the estimation of true population pregnancy rates. These all tend to lead to biases in the sampled data. The four features are; (i) the geographical segregation of different components of the population, (ii) the differences in age-specific pregnancy rates, (iii) the time of sampling of the population, and (iv) the effects of protection from fishing of parts of the population. Examples of these are discussed, with a description of how some of them have been coped with.

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## Effect of Exploitation on the Reproductive Parameters of Two Species of *Stenella* off the Pacific Coast of Japan<sup>1</sup>

T. Kasuya

### ABSTRACT

The striped dolphin, *S. coeruleoalba*, in Japanese coastal waters has been exploited longer and heavier than the closely related spotted dolphin, *S. attenuata*, in the same region, and decrease of population is known to have occurred. The response of the populations to the exploitation based on data collected in the past 28 years is analyzed here.

Females of the lightly exploited spotted dolphin attain sexual maturity at an age between 8 and 12 years. In the striped dolphin, however, maturation starts 3 years earlier and is completed at 12 years. This results in a small difference in the mean age at maturity of 9.3 years versus 8.0 years. This is overridden by a difference in age composition caused possibly by higher mortality rate and increasing recruitment rate in the latter species. The proportion of adults in the female population is estimated as 52–56% in the former species and as low as 35–42% in the latter, more exploited species. The mean calving interval in the spotted dolphin of 4.7 years is contrasted with 2.0–2.5 years in the striped dolphin in the late 1970s. The difference is caused by the limitation of high reproductive activity to young ages and by longer lactating and resting periods in all age classes of the less exploited species. The recent shortening of calving interval in the more exploited species is related to decrease in the length of lactation. These facts suggest that the shortening of calving interval was brought on firstly by the decrease in length of resting period followed by that of lactating period, secondly by the extension of age of high reproductive activity toward older age classes, and thirdly by the increase of young females of high reproductive rate as the result of the change in age composition.

It is suggested that dolphin populations may respond to change of density more in the reproductive cycle than in growth. However, it is left to be studied if the change of length of lactation inevitable in the process might influence survival of calves. (All the estimates in this abstract are provisional and liable to change.)

<sup>1</sup> A revised version of this paper will be published in *Sci. Rep. Whales Res. Inst., Tokyo* 36.

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## Hormonal Evaluation of Ovulations and Pregnancy in Captive *Tursiops truncatus*

V. L. Kirby

### ABSTRACT

The most accessible model for studying cetacean reproductive endocrinology is the bottlenose dolphin, *Tursiops truncatus*. Animals bled over regular time periods can provide baseline data on oestrus, ovulation, pregnancy, lactation, and gestation length, as well as information about rates of these events. Reproductive events in wild cetaceans can be elucidated by monitoring the reproductive hormones progesterone ( $P$ ) and total immunoreactive estrogens ( $E_t$ ) in captive cetaceans.

Reproductive events in captive females of *T. truncatus* were monitored by a modified radioimmunoassay for the gonadal steroids. In addition to random sampling of females, longitudinal studies were conducted. Females were bled monthly for 1–2 year periods and biweekly for two 1-year periods. Baseline  $P$  levels below 1 ng/ml ( $\bar{X}$  0.3  $\pm$  0.1 ng/ml) were indicative of 'resting' females, neither pregnant nor ovulating, and of lactating females. Females exhibiting  $P$  levels above 3 ng/ml, ranging to approximately 20 ng/ml, were considered to have ovulated. Cycle length was estimated to be around 25–30 days, an estimate which is limited by the frequency of sampling per cycle.  $P$  levels which fell into the range of 1–3 ng/ml were not designated as ovulations without further sampling that indicated ovulation. Animals observed with elevated  $P$  levels (especially 30–50 ng/ml) longer than 6–8 weeks were diagnosed as pregnant. Correct diagnosis is dependent upon time elapsed between samples.  $P$  levels fluctuated throughout monitored pregnancies between 5 to 50 ng/ml. Very early pregnancy cannot be distinguished hormonally from ovulation. Although the sample size is small relative to probable individual variation, certain events have clearly been observed. Data are presented which show that (1) some females are anestrus thru a year's period, (2) some females cycle once for a year, (3) some females can ovulate 2–3 cycles in a year (within 1 season) or more. Females with males have exhibited infertile cycles. Females without males have exhibited spontaneous ovulations. Estrogen levels were so low ( $\bar{X}$  21  $\pm$  5 pg/ml) with no observed changes indicative of folliculogenesis that current methods of measurement have no diagnostic value.

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## A Review of the Stranding and Occurrence of Cetaceans along the Indian Coasts with Notes on their Reproductive Biology

M. D. K. Kuthalingam and K. Venkataramanujam

### ABSTRACT

Data on the mass and individual strandings of cetaceans throughout the vast stretch of the Indian coasts are presented. The numbers of beached carcasses, their distribution and composition by species and age are indicated and their period of occurrence are given. The location of catch, stranding-locality maps and numbers caught are provided. The accidental exploitation of the cetaceans is also described.

The morphometric characters of the sperm whale, *Physeter macrocephalus*, recorded from the east coast of India after a lapse of 90 years, are discussed in detail. Data on the false killer whale, *Pseudorca crassidens*, noted in different coastal areas of India, together with stages of maturity, length and weight are given. The occurrence, distribution and stranding of the rorquals (*Balaenoptera physalus*, *B. musculus* and *B. edeni*) are dealt with. Distribution and size range of the Indian finless porpoise, *Neophocaena phocaenoides*, are reported. The reproduction of cetaceans and the scope for their development are also discussed.

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## Biological Similitude and Cetacean Reproductive Parameters

D. M. Lavigne

### ABSTRACT

Cetaceans, because of their size and habits (and existing legislation) are not usually the ideal subjects for studying life-history parameters associated with reproduction. It would, therefore, be useful to have some underlying theory, or empirically-determined generalizations with which to compare existing data, to predict relationships between various parameters, and to generate reasonable approximations of parameter values as an interim solution when empirical data are lacking entirely.

A consideration of large-scale, interspecific comparisons of metabolic rate/body size relationships suggests that numerous reproductive parameters are scaled to predictable power functions of body size. These parameters include a variety of 'biological times', e.g. age at maturity, generation time, gestation time and life span; they also include a variety of biological rates, e.g. birth rates,  $r_{\max}$ , and individual growth rates. Comparisons of pairs of parameters reveal a number of relationships which are independent of body size among 'metabolically similar' animals, e.g. net reproductive rate,  $R_0$ , the relationship between  $r_{\max}$  and generation time, age at maturity and growth rate, and the relationship between production and respiration in population energy budgets.

These large-scale relationships cannot be used indiscriminately to predict relationships at smaller scales, e.g. over a smaller range of body sizes, as is usually found within a single mammalian order such as the Cetacea. Nonetheless, they do appear to permit a variety of predictions about life history parameters, and in some cases at least, the interpolation of a parameter estimate can be justified when data are lacking entirely.

The specific problem of estimating cetacean reproductive parameters for stock assessment and management seems to provide an ideal opportunity for testing the practical utility of large-scale interspecific relationships for predicting and interpreting small-scale interrelationships, both between and within individual species comprising a single order.

## Reproductive Seasonality in Multi-herd Groups of Northern Offshore Spotted Dolphins, *Stenella attenuata*, and Age-Related Reproductive Parameters for Females

A. C. Myrick, Jr

### ABSTRACT

Tooth dentine of spotted dolphins contains annual growth layer groups (GLGs) which consist of about 13 lunar monthly layers (LMLs) each. LMLs were counted in teeth from approximately 300 males and females less than five years old. Back calculations of LMLs from the data of death obtained the approximate month of birth ( $\pm 1$  month). Most animals killed in a given purse-seine set or in a series of sets made in a given area over a few days were born either in the same month or about six months later. Animals taken in other sets at a different position and date were born in a different month or six months later. The implications of these findings are (1) that spotted dolphins may maintain discrete multi-herd breeding groups comprised of ephemeral herds and confined to rather small geographic ranges, and (2) nonpregnant females may have a obligatory ovulation rate of twice per year.

## Collection, Storage and Preparation of Cetacean Reproductive Materials

† M. Nishiwaki

### ABSTRACT

Methods of storage of reproductive materials vary according to the aims of the study. When the aim is examination of sexual maturity in relation to body length of animals, it is desirable to collect fresh ovaries and testes from as many individuals as possible. It is best for scientists to do the actual collecting in the field; otherwise, problems of storage occur. If no specialists are in the area and no one can come quickly, materials must be preserved by the most effective method. Among useful methods, preservation with salt is helpful, especially in an isolated area. Salted samples of reproductive organs are presented for reference and comparison.

## Hybrids Between *Pseudorca crassidens* and *Tursiops truncatus gilli*<sup>1</sup>

† M. Nishiwaki and T. Tobayama

### ABSTRACT

A hybrid between *Pseudorca crassidens* and *Tursiops truncatus gilli* was born on 3 May 1981 at Kamogawa Seaworld, and the calf looks in good health and is swimming in the pool. This mother had given abortive birth to a calf in 1979. In the same pool, another female of *T. truncatus gilli* also gave abortive birth to a near-term calf on 6 July 1981. In the pool, the only mature male was an individual of *P. crassidens*; thought to be father of the hybrids. Detailed information on the three hybrids is given.

Another incident of hybridization in Japan is a calf born to a male of *Grampus griseus* and a female of *T. truncatus gilli*. It has lived more than 1,000 days in Enoshima Marineland and is still alive. The well known hybrid between *Steno bredanensis* and *T. truncatus gilli* at Sealife Park of Hawaii has been reported to have died.

<sup>1</sup> Published in 1982 in *Sci. Rep. Whales Res. Inst., Tokyo* 34: 109–21.

## Reproductive Biology of Pygmy Sperm Whales, *Kogia breviceps*, Stranded in Florida

D. K. Odell, E. D. Asper and J. E. Reynolds, III

### ABSTRACT

The pygmy sperm whale is, after *Tursiops*, the most common stranded cetacean along the southeastern coast of the United States. Systematic collection of stranded cetaceans along the entire east coast of Florida began in 1975. Examination of over 100 *Kogia* stranding records (published and unpublished, mostly Florida) suggests a seasonal pattern with stranding peaks in winter and fall. Adult males and adult females strand in approximately equal numbers. The males conform to the bimodal seasonal pattern better than the females do. Adult, non-pregnant females, pregnant females, and females with calves stranded at similar frequencies. Pregnant, lactating females have stranded. Most pregnant females were found in January and February. The smallest adult female examined was 260 cm total length. The mean length of adult females was 303 + 22 cm; adult males 307 + 29 cm. Juveniles stranded with a conspicuously low frequency. This may indicate different patterns of distribution for different age classes.

## Interspecific Relationships Among Biological Parameters Concerned with Reproduction in the Cetacea

S. Ohsumi

### ABSTRACT

Interspecific relationships are useful in checking the accuracy of estimates of a biological parameter, if there are good relationships concerned with the parameter and an accurate estimate of another biological parameter of the same species.

I examined interspecific relationships among several kinds of combinations of several biological parameters which are concerned with cetacean reproduction, such as body length at birth, body length at sexual maturity, pregnancy rate, gestation period, etc., by use of previously reported figures of these parameters for 40 cetacean species and stocks.

Clear interspecific relationships were observed in some combinations of some biological parameters, such as the relation between asymptotic body length and body length at sexual maturity. The relationships exhibit some patterns concerned with differences of taxonomic sub-class and sex. A single interspecific relationship is observed in the combination of asymptotic body length and body length at sexual maturity in female cetaceans, but Mysticeti and Odontoceti have different interspecific relationships between asymptotic body length of females and body length at birth. On the other hand, no clear interspecific relationship is observed in some combination of biological parameters, such as between age at sexual maturity and growth rate at the first year of age.

## Reproductive Rates and Breeding Area Occupancy in the Southern Right Whale, *Eubalaena australis*

R. Payne

### ABSTRACT

Since 1970 we have maintained a long-term study of a population of southern right whales at Peninsula Valdes, Argentina. Using aerial photographs of distinctive callosity patterns, we have been able to identify over 580 animals, 75% of which we have seen more than once (a few individuals have been seen up to 18 times). Of this group, 66 have had at least 2 calves and 9 of these have had at least 3. Adult males tend to visit Valdes every year, whereas females in their prime calf-bearing years are usually seen only every third year, when they are accompanied by a calf – not in the year before giving birth, when it might be expected that they would be impregnated. This means that Peninsula Valdes is used by 3 different groups of calf-bearing females. It also suggests that although mating behavior and intromission are commonly observed in the area, productive matings in this population occur either at a different time of year or elsewhere.

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## A Technique for Estimating Reproductive Parameters of Small Cetaceans from Vertical Aerial Photographs

W. L. Perryman, M. D. Scott and P. S. Hammond

### ABSTRACT

An aerial photographic survey was conducted off the west coast of Mexico to acquire length-frequency data on dolphin stocks affected by the tuna purse-seine fishery in the eastern tropical Pacific. This study was funded by the Inter-American Tropical Tuna Commission (IATTC), and the scientific party was comprised of personnel from the IATTC and the National Marine Fisheries Service (NMFS). The study was designed to develop and evaluate techniques for photographing dolphin schools, measuring lengths of dolphin images from aerial photographs, and using these data for calculating reproductive parameters. The camera systems onboard included a 230-mm-format cartographic camera, two 115-mm-format aerial reconnaissance cameras, and four Hasselblad 55-mm-format cameras. The camera systems were mounted vertically in the deck of an AT-11 aircraft. Although all of these camera systems have been used successfully to collect imagery for length determination of large cetaceans, only the 115-mm-format cameras produced photographs of adequate quality for dolphin length measurements. Of the 100 schools photographed, 29 were of suitable quality for length-measurement analysis. Due to their light grey color and unique swimming behavior, spinner dolphins (*Stenella longirostris*) were found to be more vulnerable to photographic sampling than the other species encountered. Preliminary analyses of some length data from schools of the Costa Rican race of spinner dolphins have revealed that groups of lengths of small animals can be identified which correspond to age groups approximately 6 months apart up to an age of 1½–2 years. Analyses are proposed to try to describe the data using a limited age-structured model from which estimates of reproductive rate can be obtained.

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## Behavioral Aspects of Cetacean Reproduction

K. W. Pryor

### ABSTRACT

Reproductive success of highly social animals depends not only upon the fitness of individuals but upon maintenance of the social structure of the group. For example the removal of heavily-tusked, often post-reproductive females from elephant herds has been found to lead to the massing together of younger females and offspring in large groups which are destructive to the environment.

In the highly social cetaceans, behavioral aspects of reproductive success may vary widely from species to species, or even within species. For example, sexual dimorphism, usually an indicator of polygyny (a few males mating with many females, many males not mating at all) is present in *Stenella longirostris* in the eastern tropical Pacific; yet in the same species in Hawaii, the sexes are virtually indistinguishable, suggesting pair formation or even polyandry. Cooperative care of young, especially during high-speed travel, has been observed in captive and wild cetaceans of several species, and may help to explain the presence in cetacean herds of viable post-reproductive females. Long-term parental care (4+ years in *Stenella attenuata* and in *Orcinus orca*) can be affected by high predation levels, but the ensuing increased reproductivity of individual females may not represent increased reproductive fitness of a population. Management of cetacean species should include awareness of the probable behavioral dynamics affecting reproduction, on a group as well as on an individual level. Current research in the evolution of behavior and in behavioral ecology offers new analytic tools to the study of cetacean reproduction.

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## Induced Reproductive-cycle Events in *Tursiops truncatus*

J. P. Schroeder

### ABSTRACT

The Naval Ocean Systems Center has made some unprecedented moves to develop a model program to provide data that will ultimately define the events of the reproductive cycle of *Tursiops truncatus*. As a result of these studies, an artificial insemination program, or a controlled breeding program, will be established leading to the propagation of dolphins from those already in captivity.

The length of the oestrous cycle in *Tursiops truncatus*, the duration of oestrus, its seasonality and the optimum time for fertilization are events that require the accumulation of much data before a complete picture of breeding *Tursiops* can be obtained. Spontaneous ovulation, reflex ovulation, or both, are key events that have received much attention in recent years.

Injections of pregnant-mare serum gonadotropin and human chorionic gonadotropin coupled with blood sample collection and radioimmunoassays has generated data that are presented. Indications are that exogenous hormone manipulation of the dolphin reproductive system can result in management of reproductive-cycle events and that, if other events interface correctly, could produce pregnant dolphins.

The number of animals involved, their husbandry, specific dose ranges of PMSG and HCG and sample collection are presented. Breeding data retrieval leading to a breeding data bank are also discussed.

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## Patterns of Life Histories in Delphinidae

D. E. Sergeant

### ABSTRACT

In Delphinidae, we can trace a series of grades of increasing complexity with the following features: (a) an increase in body size; (b) an increase in size of male relative to female; (c) an increase in the lengths of pregnancy and lactation and hence in the total reproductive cycle; (d) an increase in sociality. True sociality appears to be achieved by a long delay in attainment of male sexual maturity together with an absence of aggression by adult males and females towards adolescent animals of both sexes. These features are particularly marked in the subfamily Orcininae, which includes the genera *Globicephala* (pilot whales, blackfish) and *Pseudorca* (false killer) among others. Mass strandings are particularly marked in these social species.

Long reproductive cycles and sociality have therefore evolved together in Delphinidae. Long parental care and epimeletic (care-giving) behavior reduce juvenile mortality. Absence of aggression reduces adolescent mortality. Fecundity is density-dependent, lactation being sharply reduced in length in females of a thinned-out population. (Probably a fertile-lactation oestrus is the result of a higher nutritional plane). However, social behavior probably results in continued care of the early-weaned calf. Populations of the highly social odontocetes are therefore regulated largely by mass mortality, and explanation of mass strandings must be sought at the ecological level. There is good evidence in *Globicephala melaena* and *Lagenorhynchus acutus* that mass strandings occur at high population levels. Search for proximate causes of mass strandings could include examination of at-sea controls and stranded animals for stress phenomena.

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## Annual Calf Production of Gray Whales, *Eschrichtius robustus*, in Laguna San Ignacio, Baja California Sur, Mexico

S. L. Swartz

### ABSTRACT

The number of calves produced each year by gray whales wintering in Mexico was largely underestimated because previous studies of breeding whales terminated before cow/calf pairs reached peak numbers within the lagoons. Studies of northward migrating gray whales failed to identify substantial numbers of cow/calf pairs because they also terminated prematurely and presumed an offshore migratory route for these whales.

Breeding gray whales were studied during four consecutive winters in Laguna San Ignacio, one of four major breeding sites along the Baja California coast. Timetable of lagoon occupation and distribution of female whales and their calves were determined from weekly boat transects. Aerial surveys conducted during one winter were compared with simultaneous boat surveys. Pregnant and post-partum females arrived in the lagoon throughout January and occupied the portion of the lagoon farthest from the entrance. Counts of these whales increased throughout February and March, and appeared to stabilize in early April at approximately 150 pairs. In March and April cow/calf pairs shifted their distribution to the portion of the lagoon nearest the entrance and approximately 120 pairs remained in this area at the termination of the field studies in late April of each year. Cow/calf pair counts in Laguna San Ignacio are compared with similar counts in Scammon and Black Warrior Lagoons. Annual gray whale calf production, departure from the lagoon, difficulties with survey techniques, and rate of migration past central California and Oregon are discussed.

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## Mother-infant Interaction and Behavioral Development in Southern Right Whales, *Eubalaena australis*

P. O. Thomas and S. M. Taber

### ABSTRACT

A quantitative study of infant behavioral development and mother-infant interaction in 12 individually identifiable southern right whale pairs was conducted from August to December 1979 at Peninsula Valdes, Argentina. A period of continuous rapid travel soon after birth is hypothesized to develop calf swimming confidence, to enhance the ability of the thin, nonbuoyant calf to rise to the surface to breathe, and to hinder detection by predators. Subsequent slowing of travel at 2-4 weeks of age leads to an increase in resting behavior by the mother and an increase in play by the calf. Calf play is centered around the mother and may function to develop motor skills in behaviors useful in social, reproductive, and other contexts as an adult, though in play calves exaggerate behaviors and combine them in ways that are not identical to adult behavior. Days before departure from the nursery area, rapid travel again predominates, presumably functioning to prepare mother and calf for the subsequent migratory period. Nursing comprises about 5% of the pairs' diurnal behavior throughout the season but the length of individual bouts increases with calf age. The mother's need to conserve bodily reserves during her four-month fast at this time may conflict, in terms of individual reproductive strategies, with the calf's need to develop motor abilities through energy consumptive play. Commencement of migration appears independent of calf age or size and is probably spurred by the mother's requirement for food or other factors.

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## Use of Aerial Survey Sightings to Determine Seasonality of Calving in *Tursiops truncatus*

N. B. Thompson

### ABSTRACT

Aerial survey sightings of *Tursiops truncatus* were collected during flights over various study areas. All flights were completed under NMFS contract by Mar, Inc. and were conducted over:

1. Indian-Banana River, FL; May, Aug., Nov., 1980;
2. Charlotte Harbor, FL; July, Oct., 1980; Jan., Apr., 1981;
3. Apalachicola, FL; June, Sep., Dec., 1980; Mar., 1981;
4. Mississippi Sound, MS; June, Sep., Dec., 1980; Mar., 1981 and
5. Rockport, TX; May, Aug., Nov., 1980; Feb. 1981.

When possible, animals are identified as adult, juvenile and calves; based on relative size. All adults and juveniles are considered non-calves for the purpose of the paper. Measures used to test for significant differences between months, and between offshore and inshore flights include: total calves sighted; calves/herd, and proportion of calves sighted relative to the total number of animals sighted. While there were no significant differences found in the Indian-Banana River, differences were found between inshore and offshore flights and between months at the other four survey areas. These differences suggest that there may be a distinct calving season, in conjunction with significant inshore-offshore movements of *Tursiops*.

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