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Commission

Behaviour of Whales in Relation to Management

INCORPORATING THE PROCEEDINGS OF
A WORKSHOP OF THE SAME NAME HELD IN
SEATTLE, WASHINGTON, 19–23 APRIL 1982

Edited by

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Preface

It is almost four years since the International Whaling Commission held a Workshop on the behaviour of whales in relation to management. Prior to that meeting cetologists studying behaviour and cetologists studying population dynamics had kept themselves to themselves, apart from the occasional complaint from the behaviour people that modellers took no account of their work and the riposte from the modellers that until the behavioural observations were quantified it was impossible to incorporate them into models.

The Workshop did not attempt to answer outstanding management questions. What it did was to bring cetologists from both disciplines together to review current behavioural knowledge of cetaceans and identify those areas of management where behaviour was important. This served two important purposes:

(1) it showed management scientists how current behavioural knowledge could assist them in their work;

(2) it suggested new areas of behavioural research which would materially assist future management of whale stocks.

Four years is a long time between the holding of the meeting and the publication of this small volume, but in fact the delay in publication, for financial and logistical reasons, has inadvertantly had some beneficial effect. It has allowed the inclusion in the volume of nine recent papers which are to some extent the fruit of the contacts made during the Workshop. The report itself has been left largely unaltered apart from the inclusion of references to work carried out after the Workshop on topics which had been addressed there.

The published papers have been grouped into broad subject categories rather than chronologically. The first four papers review aspects of cetacean behaviour in the light of current behavioural thought on other mammalian species. This approach, along with comparative studies within the order Cetacea, is particularly important if any insight is to be obtained into the behaviour of the more oceanic and hence difficult to study species such as the rorquals.

The following four papers address some of the more recent methodological approaches to studying cetacean behaviour and examine how these can assist in management problems. Since the paper on the use of acoustic techniques was written, acoustic studies have considerably enhanced the census work on the bowhead whale, *Balaena mysticetus*, in Alaska (e.g. see Clark, 1986; Ko, Zeh, Clark, Ellison, Krogman and Sonntag, 1986—both published in *Rep. int. Whal. Commn* 36).

In the next section, five papers concentrate on two species of whale, the gray, *Eschrichtius robustus*, and the bowhead. Aerial observations have improved our knowledge of fundamental aspects of these species' behaviour, from migration and distribution patterns to possible reproductive strategies, and this work is reflected here. The gray whale has been extensively studied in its winter breeding grounds using several behavioural techniques and one of the papers presents a synthesis of this information and suggests how it might be relevant to other baleen whales. Behavioural work on this species in its summer feeding grounds in the Arctic holds many practical difficulties but such studies are now beginning as reported in the paper by Bogoslovskaya.

The final paper in the volume shows the value of behavioural studies, and in particular the technique of individual identification, for management. Large numbers of individual whales have now been identified in various studies and this paper reviews these data in the light of standard mark-recapture theory and makes practical suggestions to field workers as to how they should use such data to obtain population estimates.

I should explain the apparently incomprehensible code numbers at the top right hand corner of some of the papers. The IWC publishes a 'List of Scientific Committee Documents from 1960 to the Present' in which papers are listed by meeting, and place of publication, where appropriate, indicated. All meeting papers are assigned a code unique to that meeting. Thus for example in

SC/36/PS27

SC refers to Scientific Committee, 36 refers to the 36th Annual Meeting (held in 1985!) and PS27 refers to the 27th paper submitted to the Protected Species sub-committee; while for meetings other than annual meetings, e.g.

SC/A82/BW1

SC is as before, A82 refers to April 1982 and BW1 refers to the 1st paper presented in the Behaviour Workshop. The codes are thus included to allow easy cross-reference for subscribers to the 'List'. Those papers without code numbers (Brownell and Ralls, Swartz) were written specifically for the volume.

On a similar vein, I should explain the apparent inconsistency in the spelling of behaviour. Our policy is to allow American authors to use American spellings and the rest of the world to use 'English' spellings!

Finally, I would like to thank all those who have assisted in the production of this volume: Michael Tillman who not only most ably chaired the workshop but also put a considerable degree of effort into the report; the many reviewers, anonymous and otherwise who refereed the submitted papers; and Stella Bradley, Vivien Catchpole and Anne-Florence Dujardin who typed, re-typed and proof read many of the manuscripts.

GREG DONOVAN
Cambridge
17 March 1986

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REPORT OF THE WORKSHOP

Edited by M. F. Tillman and G. P. Donovan

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1. INTRODUCTION

At its 32nd Annual Meeting in 1980, the International Whaling Commission received a report on the meeting it had co-sponsored, held in Washington, D.C. in April/May 1980, concerning cetacean behaviour and intelligence and the ethics of killing cetaceans (Ovington, 1980 ms). It accepted a recommendation of that meeting that a workshop be established by the Scientific Committee for further detailed examination of those matters identified as being of greatest significance to the assessment and management of cetaceans (the Committee had previously considered this subject in 1978—IWC, 1979). Further it was agreed that this workshop should be held during 1981/82 (IWC, 1981a). The workshop subsequently met during 19–23 April 1982 at the National Marine Fisheries Service's Northwest and Alaska Fisheries Center, Seattle, Washington. Participants were welcomed by Dr William Aron, Center Director. A list of participants is given in Annex A.

2. IDENTIFICATION OF BEHAVIOURAL 'PROBLEM AREAS' RELEVANT TO MANAGEMENT

To help focus workshop discussions, the Chairman reviewed the Commission's current major management problems: stocks of minke whales subject to pelagic whaling, stocks of sperm whales subject to coastal whaling, and the Western Arctic stock of bowhead whales which is subject to an aboriginal/subsistence hunt. The Chairman pointed out that the most useful result of the workshop would be the provision of advice on how current assessment methods or management measures for these stocks might be revised to account for cetacean behavioural phenomena. He further noted that, although most behavioural research had been carried out on species which occur near coastal areas (e.g. gray, right, humpback and bowhead whales), reviewing these results would certainly aid the workshop in identifying relevant problem areas or even provide useful analogies for species which occur pelagically (e.g. minke and sperm whales).

2.1 ASPECTS OF SOCIAL BEHAVIOUR

2.1.1 Shifts in the age/sex structure of groups during and outside the breeding season

(i) *Breeding/calving areas*

Gray whales (*Eschrichtius robustus*). Swartz reported that gray whales use the lagoons of Baja California as breeding/calving areas from January to April. During migrations to and from the lagoons, temporal segregation of the population occurs according to sex, age and reproductive status (Rice and Wolman, 1971). In general, females migrate earlier than males and adults migrate earlier than immature animals. Late pregnant females lead the southward migration and arrive at the lagoons first, followed by recently ovulated females, then by immature females and adult males, and lastly by the immature males. On the northward migration, newly pregnant females lead, followed by adult males, then by anoestrous females, then by immature whales of both sexes and finally by cow/calf pairs.

Sexual behaviour is especially prevalent among the aggregations of animals which occur near (both inside and outside) the mouths of the lagoons. Mating appears to be promiscuous with no lasting pair bonds; often two or more males consort simultaneously with a female.

Animals in the lagoons appear to behave as two distinct groups (Swartz and Jones, 1981). Cow/calf pairs are different from other whales in their distributions, swimming patterns, group sizes and durations of stay. In Laguna San Ignacio, although the number of whales (excluding calves) reaches a maximum in mid-February (40% cow/calf pairs and 60% others), counts of whales other than cows with calves (breeding females, males, juveniles) peak in early February, while counts of cow/calf pairs peak in late March. Cow/calf pairs occupy the lagoon through mid-April (Swartz and Jones, 1981) whereas other whales utilize the lagoon for 1.5 to 2.0 months (January–February). In Laguna Ojo de Liebre (Scammon's Lagoon), counts of other whales peak in late January while cows with calves peak in mid-February. The number of other whales declines rapidly after mid-February, but cow/calf pairs stay until early March (Rice, Wolman and Withrow, 1981).

Although cow/calf pairs routinely travel the entire length of the lagoon, they tend to concentrate their activities away from sites frequented by other whales (Swartz and Jones, 1981). Other whales are concentrated near the entrance while cow/calf pairs are concentrated in the upper areas far from the entrance. Cow/calf pairs shift to the entrance area as it is vacated by other whales. Surveys indicate that 50% of the other whales, but only10% of cow/calf pairs, were in groups of two or more (excluding calves); and 57% of the other whales compared with 29% of the cow/calf pairs were transiting the lagoon, while the remainder were resting or milling within a specific area.

Based upon data obtained from both aerial and vessel surveys, Withrow reported that the vast majority of other whales spend the winter outside the lagoons in Bahia de Sebastian Vizcaino and Bahia de Ballenas.

Right whales (southern—*Eubalaena australis*, northern—*E. glacialis*). Clark reported that for the right whales of Golfo San Jose, Peninsula Valdes, Argentina, the succession of arrival at the breeding/calving areas is very similar to that described above for gray whales but that the utilisation of the Gulf is of longer duration, lasting 6–7 months. Females, including lactating and pregnant animals, are the first to arrive, in late autumn and early winter. Mothers with yearling calves typically remain with their calves for several weeks before leaving them at the Peninsula. For the first three to four months (mid-May to mid-August), females constitute the majority of whales seen within the Gulf. A few subadult males are occasionally seen during this period but adult males are not. In mid-August there is a sudden rapid influx of whales (adult females, adult males and subadults) into the Gulf with as many as 50 to 60 animals entering in a matter of seven to ten days. Since the maximum daily census of whales in the Gulf was never more than 100, this influx represents a high percentage of the total population seen there. The peak of the population occurs between mid-September and mid-October after which the numbers decline steadily until by mid-December, only mothers with newborn calves and a few subadults remain.

Data from individual sighting and sexing studies based on photo-identification indicate that the female population peaks during the last weeks of September, while the male population peaks three to four weeks later. This lack of synchrony between the female and male population peaks, and behavioural data which indicate that females observed copulating in the Gulf are not seen with calves the following year, suggest that it may not be a primary breeding area for these whales.

Mother/calf pairs reside in quite shallow water (5–10 m) and segregate from other groups found further offshore. The majority of whales that were individually identified but not sexed are small animals estimated to be between 8 to 12 m in length. These small whales very rarely participate in the large social or sexually active groups.

Female residence in the Gulf ranges from several weeks to four months with a great deal of individual variability, while male residence is typically between 30–40 days with much less variability than the females.

Cawthorn reported a similar pattern for the right whales off Campbell Island (51°S) except that the peak in August/September is followed by a quick decline in abundance. Best (1981) also described a pattern similar to that off Argentina for the right whales off South Africa. Anderson reported that the few observations obtained off the east coast of Australia indicate that cow/calf pairs occur inshore while mating groups are offshore.

Payne, Brazier, Dorsey, Perkins, Rowntree and Titus (1981) reported that none of the 30 individually photographed right whales from South Africa matched any photographs from Argentina. The higher incidence of white patches and blazes in the South African animals suggested that these are two separate stocks. Payne noted that one photograph of an individual from South Georgia was similar to that of a Peninsula Valdes whale, although it is unclear if an exact match was made or not. No other information exists concerning the specific migratory paths of right whales in the Southern Hemisphere.

Kraus and Prescott (1982 ms) reported for North Atlantic right whales that courtship and mating activity have been observed during August–September in the Bay of Fundy. The summer occurrence of this behaviour is unusual. Animals involved in sexual activity are offshore while cow/calf pairs remain inshore.

Humpback whales (*Megaptera novaeangliae*). Dawbin (1966) summarised the known migratory routes of Southern Hemisphere humpback whales and indicated that females at the end of lactation accompanied by their weaning yearling calves lead the migration to calving grounds, followed in succession by immature animals, mature males with resting females and finally females in late pregnancy. In the return migration, females in early pregnancy leave first, followed by immature whales, then resting females with mature males and lastly females in early lactation.

Some North Pacific humpback whales utilize the Hawaiian Islands as breeding/calving areas from January to April (Herman and Antinoja, 1977). Baker and Herman (1981) reported that the whales first appear off the island of Hawaii and then apparently move northwestward through the coastal waters of other islands in the chain as the winter season progresses. Baker reported that, although there is some tendency for cow/calf pairs to be segregated from adults in more shallow areas, they do mix with adult breeding groups, unlike gray whale cow/calf pairs. According to Darling, Gibson and Sibler (1983) groups of courting males tend to form around available females and exhibit competitive behaviour. Baker, Herman and Stifel (1981 ms) reported a seasonal peak in agonistic behaviour among humpback whales concurrent with the peak in seasonal abundance. They related this to the sudden increase in the abundance of males and females and possible changes in their reproductive states.

Distinct groups of sub-adults also occur on the breeding grounds. The distribution of groups upon the grounds is random and the duration of bonds between individuals within adult and sub-adult groups is very fluid, ranging from a matter of hours only to as long as a day. In contrast to gray whales, the peak number of calves occurs during the middle of the season rather than at the end. However, the peak percentage of calves occurs at the end of the season since females tend to stay latest (Herman and Antinoja, 1977; Herman, Forestell and Antinoja, 1980 ms). There is a tendency for average group size to increase from fewer than two to about three towards the middle and end of the season, with groups of five or more becoming increasingly more common as the season progresses (Herman and Antinoja, 1977; Herman *et al.*, 1980 ms).

A unique behavioural characteristic of humpback whales on breeding grounds is the singing of songs by adult males (Payne and McVay, 1971).

Cawthorn reported that limited winter observations at Tonga support the general finding that cow/calf pairs normally occur in shallow water.

Bowhead whales (*Balaena mysticetus*). Whether the bowhead whale utilises specific breeding/calving grounds is unknown. Nerini *et al.* (1984) stated that most evidence points toward calving occurring during the spring season. Foetuses obtained from females taken in the spring hunt are small, while those from the fall hunt are relatively large. There is an upward trend in calf counts as the season progresses with peak counts occurring in June–August. In terms of the extended calving period, April–August, there may be less synchrony in the bowhead than in other species. Since one might expect strong synchrony in high latitudes due to the strong seasonality of resources, the lack of it in bowheads may be symptomatic of their greatly reduced state.

Based upon icebreaker surveys, Braham, Krogman, Johnson, Marquette, Rugh, Nerini, Sonntag, Bray, Bruggeman, Dahlheim, Savage and Goebel (1980b) and Bruggeman (1982), reported that, during winter, bowheads are closely associated with ice, preferring loose ice rather than an open water habitat. Copulation is observed in late winter–early spring but no calves are seen. Mating behaviour is also seen during the spring (April–June) migration (Everitt and Krogman, 1979), but only rarely on summer feeding grounds in the eastern Beaufort Sea (Würsig, Dorsey, Fraker, Payne and Richardson, this volume). While describing the spring migratory route, Braham, Fraker and Krogman (1980a) commented that anecdotal evidence supports the hypothesis that age and/or sexual segregation occurs during the migration, as reflected by a series of 2–3 'waves' or 'pulses'.

Rorquals, Balaenoptera spp. Although specific surveys have not yet been undertaken to determine whether blue (*Balaenoptera musculus*), fin (*B. physalus*), sei (*B. borealis*), Bryde's (*B. edeni*) and minke (*B. acutorostrata*) whales have specific, localised areas for breeding or calving, the lack of positive evidence for their existence suggests rather that they return to broad, generalized wintering grounds located in temperate to tropical waters for these purposes.

According to Gambell (1968), sei whale migrations into winter breeding grounds show a predominance of sexually immature and female whales in the early months; mature animals and males predominate later. The proportion of newly pregnant animals amongst the mature females increases during the winter, but declines in the spring corresponding with the departure of pregnant females which leave first for the polar feeding grounds. Similarly with blue and fin whales, the males and pregnant females arrive first in the Antarctic, followed by the resting females and finally the lactating females and their calves. The return migration follows the same order, with the post-lactation females now joining the resting class (Mackintosh, 1942; Laws, 1961). The older blue and fin whales appear to precede the immature animals in both northerly and southerly migrations, in contrast to the sei whales, where the immatures do not penetrate beyond the Antarctic Convergence.

From information obtained from whaling operations from Durban in South Africa (30°S), Best (1982) noted that minke whales seem to be present in temperate waters of the southwestern Indian Ocean throughout the year, although during the austral summer and autumn the density is low and a large proportion of the whales present in the area are smaller, immature animals. In April–May the numbers begin to increase and remain at high levels from June–September. During the peak of abundance, mature males in the catches outnumbered females by more than 2 to 1. There thus appears to be segregation by sex during the winter migration, as well as segregation by size (and presumably age) in mature females, as the larger animals arrive later than the smaller ones. Unlike the other baleen whales in this area, separate northward or southward 'waves' of abundance are not seen. The winter migration appears to be more protracted and less well-defined than for fin or sei whales in these waters.

Observations of group size and composition indicate that minke whales form larger groupings in winter than they do in summer (Best, 1982). Since cow/calf pairs in August–September are usually accompanied by a mature male and groups of adults usually contain both sexes, pairing apparently takes place during this period. By December–February, cow/calf pairs are unaccompanied by other adults.

This pattern is similar to that described by Williamson (1975) for minke whales off Brazil (at 70°S) although the timing is somewhat different with the first animals arriving in late June–July and reaching a peak from September to November. The last animals leave in December.[1]

Sperm whales (*Physeter macrocephalus*). According to Best (1979), the basic social unit of the sperm whale appears to be the "mixed" school of adult females plus their calves and some juveniles of both sexes, normally totalling 20–40 animals. There is evidence that bonds between females in mixed schools may persist for years. The adult female component of mixed schools consists of animals of all ages and in all stages of the reproductive cycle, while the male component is mostly immature. Segregation of males (and some females) probably begins after weaning when schools of juveniles may be formed. Recruitment to schools of small bachelor males may take place from juvenile schools or from the mixed school directly. The female component of the juvenile schools presumably returns to a mixed school before puberty. Schools of small bachelors number 12–15, although

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[1] Editors' note: Brown (1983) reported the recovery of a minke whale marked in Antarctic Area III on 1 February 1980 recovered off Brazil on 11 July 1982 (3,900 miles away). This was the first direct confirmation of seasonal migration of minke whales from Antarctic to tropical waters. A second mark was recovered off Brazil in September 1985 at 07°04'S, 34°28'W (Rabay, pers. comm.) which had been marked at 62°44'S, 35°49'W on 7 January 1982 (Brown, pers. comm.).

these may aggregate to form much larger units. These schools appear to fragment as the members grow older, reach maturity, and form schools of medium-sized bachelors. A selection process may operate in the forming of medium-sized bachelor schools in which only males above a certain size migrate to the Antarctic for the first time. Schoolmaster bulls only join mixed schools during the breeding season when between 10–25% of mature males are involved in breeding activities.

For the Southern Hemisphere, Best (1979) concluded that mixed schools and schools of small bachelors have similar distributions and migratory cycles, even though socially segregated from each other. They appear to move to the equator in autumn and towards the subtropical convergence in spring. Schools of medium-sized bachelors move to the equator later in the year and return earlier than mixed schools and bachelors, while large males move to low latitudes last of all and depart soonest for high latitudes. This pattern correlates well with the differing distances that the various schools have to travel between tropical waters and their feeding grounds in higher latitudes. A rendezvous between the medium-sized and large bachelors and mixed schools probably occurs around mid-winter, in latitudes closer to the equator than to the subtropical convergence. A selection process apparently occurs in early spring and most of those males unsuccessful at gaining access to a mixed school migrate back to higher latitudes. It is unknown whether successful schoolmasters leave the mixed schools once breeding is completed and migrate to high latitudes or whether they remain behind for most of the summer. In general, males move greater distances than females, and mixed schools have considerably smaller 'home ranges' than do bachelor schools. From mark-recoveries, the migratory routes of females appear to be consistent from year to year.

On the breeding grounds, the majority of males of breeding age appear to be distributed allopatrically to the mixed schools but at large geographical distances between them (Best, 1979). This unusual pattern does not seem to allow for extensive replacement of schoolmasters once the selection process has been completed. While it may be concluded that the sperm whale has a polygynous social organization, its exact form is still unknown, and the workshop agreed that further extensive field observations are needed (and see Whitehead and Gordon, this volume).

(ii) *Feeding areas*

Gray whales. Most gray whales occupy the shallow waters of the northern and western Bering Sea and the Chukchi Sea from late May through October (Rice and Wolman, 1971). According to Bogoslovskaya *et al.* (1981; 1982) and Bogoslovskaya (this volume) gray whales feed here primarily in small groups of 2–3 animals or individually, with pregnant females being the most common individual feeders. Occasionally large aggregations of up to 200 animals lasting 1–2 days are observed on these grounds, but these may form as a consequence of sexual behaviour. While feeding, all members of a small group often maintain a steady breathing rhythm. Nerini reported that smaller animals tend to stay inshore.

Rice and Wolman (1971) noted the fact that not all gray whales migrate to the Arctic in the summer but many stay and feed in several areas along the west coast of the US and Canada. Darling (1984) reported that feeding aggregations occur annually off Vancouver Island, Canada, including groups of 6–15 animals comprising different sizes and ages. Small discrete groups (1–2 up to 3–4) of small yet apparently weaned animals also occur, associated with inshore kelp beds. Dahlheim reported that, off the Washington coast, gray whales appear to concentrate off river mouths.

Right whales. Recent studies of right whales on their Southern Hemisphere feeding grounds are not available. However, Ohsumi and Kasamatsu (1986) reported that Japanese sightings data indicate an area of concentration to the southwest of Australia which is similar to Townsend's (1935) historical plots of right whale catches around 40°S during late spring–early summer. No detailed information is available on the sex, size composition or behaviour of the animals sighted. Clark reported that in the spring right whales feed opportunistically upon copepods occurring on the surface of the Golfo San Jose, Argentina.

In their recent North Atlantic study, Kraus and Prestcott (1982 ms) reported that at least 61 right whales, including 7 cow/calf pairs, occur in the Bay of Fundy during the summer and fall. Morphometric analysis suggests that all animals classed as 'calves' are young of the year. Diving behaviour, defaecation, and analysis of faecal material indicate that these animals are feeding. Cow/calf pairs tend to remain inshore. Groups of adults segregated offshore are also involved in sexual activity during this period.

Humpback whales. Unlike the fluid relationships between individuals on the breeding grounds, Baker reported that prolonged associations between individuals seem to exist on Alaskan feeding grounds. Examples of 9–11 whales feeding together in synchrony are known, and in one case the same four individuals were observed in two groups 46 days and 90 miles apart. Aggregations of as many as 40 feeding whales within an area of a few square miles have also been observed, but individuals in these show no strong behavioural synchrony or prolonged social associations. Some site specificity is observed with the same group of individuals returning to Glacier Bay for over 12 years (Jurasz and Palmer, 1981 ms), although some exchange of animals between Glacier Bay and Frederick Sound further south is also known to occur. Segregation by size, age, sex, or reproductive condition is not seen; adult males do not appear to engage in competitive behaviour, nor does extensive singing occur (Baker *et al.* (1985), Jurasz and Jurasz (1979)) described the extensive repertoire of feeding modes exhibited by Alaskan humpback whales, including cooperation between members of groups. Hain, Carter, Kraus, Mayo and Winn (1981) also described the feeding behaviour of North Atlantic humpbacks.

Bowhead whales. Würsig *et al.* (this volume) reported that in the Canadian Beaufort Sea, bowheads occur in clusters or aggregations rather than being distributed randomly on feeding grounds. There is a tendency for cow/calf pairs to be segregated from other animals. Gross differences occur each year in group size and in the distribution of groups, which may be related to the influx of silt-laden water from the Mackenzie River and its subsequent influence upon productivity. Synchronization of behaviour is observed over extensive areas with animals orienting in the same direction. Feeding occurs on and below the surface and in some instances mud could be seen streaming from the mouth, although these animals probably were taking near-bottom swarms of mysids rather than infauna. Skim feeding at the surface in echelon formation was observed a number of times, with up to 14 bowheads in a single echelon.

Balaenoptera spp. Based upon catch data, Kasamatsu and Ohsumi (1981) concluded that Southern Hemisphere minke whales exhibit considerable temporal and spatial segregation of the sexes on their high latitude feeding grounds. Males tend to be most abundant in lower latitudes away from the edge of the pack ice while females tend to be most abundant in higher latitudes nearest the ice edge. However, males arrive earlier and stay longer on the feeding grounds than do females. Only adults are found on the feeding grounds; calves are observed only in temperate waters at lower latitudes in this season. Unlike other baleen whales, female minke whales apparently do not wean their calves on the Antarctic feeding grounds (Best, 1982). Temporal and spatial segregation of sexes in minke whales has also been reported off Brazil (Williamson, 1975) and in Norwegian waters (Jonsgård, 1980).

Joyce reported observing a loose aggregation of up to 100 minke whales exhibiting synchronous diving during Southern Hemisphere IDCR sighting cruises. Such aggregations are comprised of sub-groups having diverse compositions which vary with season and area. Average group size on the feeding grounds is four, which contrasts with normal groups of 1–2 animals when in transit.

Mitchell reported that North Atlantic minke whales usually move inshore in summer and disperse over their feeding grounds. Some cases are known, however, of offshore feeding concentrations of 100–200 animals.

Tarasevich (1967) found from North Pacific catches that fin whales form a variety of groupings upon their feeding grounds. During spring and autumn, solitary whales of both sexes are predominant. During the summer the following are observed: groupings of males (up to 8 members); groupings of females (up to 6); mixed groupings, with either males or females dominant (10–16 members, male dominant group; 5–11, female dominant); mixed pairs; solitary whales. Males tend to form the larger groupings. Generally, the larger and older mature fin whales occur alone or in groups of their own sex; the smaller and younger mature animals occur in mixed groups.

Donovan reported that fin and sei whales are most often seen alone or in small groups off Iceland and Spain.

Sperm whales. Best (1979) described the extreme spatial segregation of medium-sized and larger male sperm whales to high latitude feeding grounds. Evidence indicates that the degree of male segregation to higher latitudes, and hence the strength of the annual migration, increases with age. Mixed schools and schools of small bachelors remain at low latitudes in temperate waters during the summer feeding season. On their high latitude feeding grounds, adult males tend to be evenly distributed and do not form large, dense accumulations. Despite this tendency to be solitary, some short-term, localized feeding aggregations of adult males do occasionally occur.

2.1.2 Social tendencies of males as a function of age

(i) *Mysticetes*

Given their 1 : 1 sex ratio and the typical female breeding cycle of two or more years, the workshop concluded that there must necessarily be a surplus of adult males within mysticete populations during the breeding season. This circumstance might lead to competition between males for available females.

For coastal species (gray, humpback and right whales), competitive behaviour between males has been observed on their putative breeding/calving areas. However, for gray and right whales, it is unknown if this is where and when effective breeding takes place: for gray whales, it may occur during the southerly migration (Rice and Wolman, 1971). The workshop noted that the competition observed may not necessarily result in the largest adult males having exclusive access to an available female: in gray whales, a female may consort with several males and in right whales, the female may select a particular partner to the exclusion of other males. Only in humpback whales do males aggressively attempt to exclude other males from associating with females. However, the association between any individual escort is typically brief, lasting from a few hours to a day (Baker *et al.*, 1981 ms; Tyack and Whitehead, 1983).

For pelagic species (e.g., *Balaenoptera* spp.) insufficient information exists about mating behaviour or courtship to determine whether or not competition between males occurs (see Brownell and Ralls, this volume).

The workshop noted that nothing is known concerning the social tendencies of male bowhead whales and emphasized that efforts to increase behavioural knowledge of this species should be made.

Pryor noted that in small cetaceans, dominant males fulfil social roles other than a reproductive one, including scouting (investigating new phenomena), guarding (protecting or defending the herd) and food seeking. No behavioural studies have been undertaken of coastal or pelagic species which would confirm or deny the existence of these other behavioural roles for male mysticetes.

In some species of mysticetes, 'standing by' behaviour of adult males towards injured or dead adult females has been reported, notably for humpback whales. Most of these reports are anecdotal (see review by Caldwell and Caldwell, 1966), with the exception perhaps of some of the harvesting incidents noted by Tomilin (1935), Zimushko and Ivashin (1980), Bogoslovskaya, Votrogov and Semenova (1982) and Bogoslovskaya (this volume) for North Pacific humpback, fin and gray whales. Best also commented (see section 2.1.2(i)) that, for minke cow/calf pairs accompanied by adult males in putative breeding areas off South Africa, the male stood by if the female was killed. In many of the above cases, such standing by behaviour may result from a reproductive function rather than a protective one.

Eisenberg (SC/A82/BW2) reviewed the social tendencies of male terrestrial mammals, noting that these not only vary as a function of age but also with respect to the form of the mating and rearing system. In general, males that have a polygynous mating strategy exhibit reduced parental care toward their offspring. Males having a monogamous mating strategy that has tended toward an obligate system with permanent pair bonds exhibit high parental care. Even in those forms exhibiting minimum parental care, the adult male may play a vital role with respect to sub-adult and dispersing males, which may associate with adult males and thereby learn aspects of foraging and habitat use that they otherwise would not. This is especially critical in those species where males and females segregate geographically and seasonally for foraging.

Kleiman (1981) reported that in obligately monogamous species of large mammals, it is common for older male siblings to remain within the family group in a non-reproductive state for an extended period, during which they typically serve as 'social helpers' by caring for or defending their younger siblings.

Based upon North Pacific catch data, Tarasevich (1967) concluded that the nucleus of the fin whale herd consists of mature males, around which non-breeding and young whales were grouped, with breeding females being widely dispersed in small groupings. Eisenberg noted that these observations, taken at face value, suggest a unique form of social organization involving an extended social role by adult male fin whales. Behavioural observations from the field are needed to verify this possibility.

After reviewing the available information, the workshop concluded that not enough similarities existed to make a general statement on the role of male mysticetes which could then be extended by analogy to pelagic species, particularly the *Balaenoptera* spp. The workshop believed that although sexual behaviours have been extensively documented only for coastal species, the role of male baleen whales may be more complicated than can be discerned from shore-based (or nearshore) observations. The workshop agreed that further research on mysticete behaviour with special attention to pelagic species, and particularly minke whales, is necessary.

(ii) *Sperm whales*

Since schools of large- and medium-sized bachelor sperm whales do segregate geographically and seasonally from mixed schools, the adult males may play a critical role with respect to sub-adult males. As pointed out in Eisenberg's review (SC/A82/BW2), the sub-adult males may learn aspects of foraging and habitat use by associating with adults. However, data are lacking to show that this occurs.

Reviewing anecdotal material, Caldwell and Caldwell (1966) found that adult females frequently stand by in the vicinity of injured adult females while adult males may also approach an injured female. However, juvenile males always flee when one of their pod is injured. Also based on anecdotes, Caldwell *et al.* (1966) found that large males are usually implicated in unprovoked attacks on vessels. Other than the anecdotal accounts in these reviews, no information exists which would indicate that male sperm whales fulfil an important or essential role other than a reproductive one.

Best (1979) reviewed evidence that the primary breeders are large males age 25 and above (45 ft and greater). However, in their analysis of reproductive tissues, Best, Canham and MacLeod (1984) indicated that medium-sized males, between 20–25 years of age (40–45 ft), are physiologically capable of contributing effectively to breeding. From this one might deduce that medium-sized males could replace large males in breeding schools following depletion of the numbers of large males. However, as yet no behavioural observations have been obtained which demonstrate that medium-sized males are socially capable of accomplishing this apparent physiological possibility.

2.1.3 Mother/young dependencies, their duration and the success of rearing young as a function of mother's age

(i) *Mother/young dependencies*

The workshop noted that the dependency of calves upon lactating females must last at least until weaning occurs. Table 1 reviews the available estimates of lactation periods for large cetaceans. A major difference is the relatively short lactation period of mysticetes compared to sperm whales. In fact, Best *et al.* (1984) provided new data indicating that some sperm whale calves may suckle for an extended period beyond two years.

Table 1

Lactation periods observed in large Cetacea

Species	Lactation period (mo.)[1]	Source
Gray whale	7	Rice and Wolman (1971)
Right whale	10–14	Thomas (this volume)
	[6–7]	Klumov (1962)
Humpback whale	10.5–11	Chittleborough (1958)
Bowhead whale	[12]	Nerini *et al.* (1984)
Blue whale	7	Mackintosh and Wheeler (1929)
Fin whale	7	Laws (1961)
Sei whale	6	Gambell (1968)
Bryde's whale	unknown	—
Minke whale	[6]	Best (1982)
Sperm whale	24	Best (1974)

[1] Parentheses indicate value based on poor evidence.

In general, mysticetes seem to have a lactation period of one year or less. According to Laws (1961), female fin whales wean their calves before reaching high latitude feeding areas. However, based upon a case of prolonged lactation, Best (1966) concluded that the evidence for 6–7 months as the duration of lactation in fin whales is far from conclusive. Jonsgård (1951) suggested that most minke whales are weaned before they enter Norwegian waters from lower latitudes. Female gray, blue and sei whales apparently wean their calves on the feeding grounds. Only female humpback whales (Chittleborough, 1958) and apparently female right whales are known to provide any care beyond the summer period, weaning their calves on the calving/breeding grounds the following winter. Baker reported observing an incidence of weaning on the Hawaiian grounds, confirming Chittleborough's (1958) conclusion that humpback calves are almost invariably weaned at the end of the autumn migration in low latitude waters relatively poor in plankton. Thomas (this volume), and Clark and Dorsey reported observations of female right whales 'abandoning' yearlings at Peninsula Valdez. Although nothing is known about the length of lactation in Bryde's whales, the workshop noted that if they behaved like other Balaenopterids, it would probably be in the range of 6–12 months.

While the dependence of mysticete calves on mothers and, hence, the caregiving of mysticete mothers, apparently is about a year or less, Best *et al.* (1984) reported the surprising result for sperm whales that suckling may extend up to age 7 or 8 in females and up to age 13 in males. These results came from tests which detected the presence of lactose in stomach contents of captured calves. Since the segregation of males from mixed schools seems to finish by an age of 15 years and the mean age of their departure may be as low as 4–5 years (Best, 1979), it is likely that most animals (at least the males) leave their parent school once they have been weaned. The weaning of juveniles apparently corresponds with the calving season (February–March[1]) rather than the breeding season (October–December[1]), so that as one set of juveniles is being weaned a new set of calves is being born (Best, 1979).

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[1] In the Southern Hemisphere.

Marsh and Kasuya (this volume) concluded that the long association between adult females and offspring during extended suckling, which seems to occur in the short-finned pilot whale and sperm whale, may be a period of 'required learning', as first suggested by Brodie (1969).

Best *et al.* (1984) postulated several possible explanations for the extended suckling of sperm whale calves. Firstly, there may be opportunistic suckling by older juveniles of lactating females with young calves in the same school, although this seems unlikely since it might jeopardize the survival of the younger animal and may be contra-indicated by the strong mother–calf bond observed. Secondly some of the large juveniles 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 stress of the female and renew familial ties between it and its offspring in the school. Finally, as found in elephants and some other terrestrial mammals, female sperm whales may suckle several calves, thereby sharing in the rearing process as well as forming social bonds within the school.

By analogy with other mammals, Marsh and Kasuya (this volume) suggested that the milk supply in cetaceans can be expected to dry up towards the end of the next pregnancy at the latest but that barren females can continue to lactate for an extended period provided they are appropriately stimulated. Thus large juveniles with milk traces in their stomach could be the offspring of females who have ceased to bear young.

In response to the observations of Marsh and Kasuya (this volume), Oldfield suggested that reproductive females may prolong lactation for their most recent calf if they have missed a subsequent opportunity or opportunities to reproduce. She noted further that the 'required learning' hypothesis proposed by Brodie (1969) is a possible evolutionary explanation for three of the other mechanisms proposed as proximate explanations for the presence of lactose in stomachs of older juveniles within family groups: kin-sharing of lactation responsibilities among females in the family group; prolonged lactation by post-reproductive females; and prolonged lactation by fecund females that for some reason have missed an opportunity for subsequent reproduction. The two other explanations, opportunistic suckling versus resumption of suckling by older calves, and the idea of extended suckling of calves throughout most of the juvenile period may be viewed as proximate explanations as to how older calves may continue to obtain lactose via one or more of the three proximate mechanisms.

Although unable to decide between these explanations, the workshop concluded that extended suckling would certainly increase the survival of juvenile sperm whales. The sperm whale has apparently adopted investing its energy in calf rearing as a reproductive strategy, while mysticetes apparently favour investing their energy in calf bearing.

(ii) *Success of rearing young as a function of mother's age*

Pryor reported that in captive odontocetes, successful rearing of young might be dependent on age since firstborn calves are often lost. In a review of this problem, Ridgway and Benirschke (1977) reported that, while calf survival was negatively correlated with primiparous females in *Tursiops truncatus*, stillbirths and deaths of newborn animals in captive dolphins and porpoises also tended to be associated with the length of parturition, possibly the lack of a stable social group, and wild-captured pregnant females. The workshop also noted that lack of rearing success might be associated with keepers' inexperience in handling births and newborn animals. In his review, Wilson (1975) indicated that, for many terrestrial mammals, females may not be successful mothers if denied the opportunity of caring for young as prepubertal juveniles. Noting that this latter observation might indicate experience rather than age as a primary factor, the workshop concluded that both age and experience may be involved in determining rearing success.

Marsh and Kasuya (this volume), after reviewing mammalian patterns of age-specific fecundity, concluded that for several odontocete species (e.g. the sperm whale, short-finned pilot whale and spotted and spinner dolphins) the duration of lactation (calculated from the ratio of lactating to pregnant females) seems to increase with maternal age concomitant with a drop in pregnancy rate. This increase could be at least partially the result of a reduction in prenatal mortality with increasing maternal age and experience. They further concluded that these species appear to invest less in calf bearing, but more in calf rearing, with increasing maternal age and experience.

The working group hypothesised that the older female sperm whales may be serving as 'nurses', suckling calves besides their own, as has been observed in the African elephant (Douglas-Hamilton and Douglas-Hamilton, 1975). Although observations of this behavioural role are lacking, such shared suckling is consistent with the apparent sperm whale strategy of optimising calf rearing. Given the apparent mysticete strategy of maximising calf bearing, one might not expect to observe in these species a behavioural change with age in regard to rearing calves.

2.1.4 Changes in 2.1.1 and 2.1.3 as a function of stock size

(i) *Mysticetes*

The workshop found no evidence that structure, social tendencies of males or mother/young dependencies vary as a function of stock size in mysticete populations. However, some evidence exists that age at sexual maturity (or first parturition) may vary with stock size in the *Balaenoptera* spp. and this in turn may affect rearing success, since rearing success may vary as a function of age (section 2.1.3(ii)).

Mizroch noted that observed trends in age at maturity may have resulted from biases in sampling. She noted that early maturing animals might be under-represented in catches since they might die early due to the stress of experiencing more reproductive events. Oldfield also observed that the magnitude of the effect of a decrease in age at sexual maturity would depend on the lifespan of the species. The workshop concluded that the magnitude of observed declines may thus have been over-emphasized and that the extent of the effect would depend on the lifespan of the species, being larger in short-lived minke whales than in relatively longer-lived fin whales.[1]

The workshop noted that one of the usual theoretical expectations of a declining age at sexual maturity is that it will contribute to increased rates of net recruitment. However in his analysis of age distributions of Southern Hemisphere fin whales, W. G. Clark (1984) found that despite the apparent increase in pregnancy rates

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[1] Editors' note: Since this meeting there has been considerable discussion concerning possible changes in age at maturity of minke whales. See, for example, Cooke (1985), Kato *et al.* (1985) and IWC (1984, pp. 78–9; 1985, pp. 76–7).

and the apparent decrease in the age at sexual maturity, recruitment rates fell rather than rose after the 1930s. The workshop noted that behavioural phenomena might well be responsible for this outcome.

The workshop observed that a possible consequence of a declining age at first parturition might be reduced rearing success (leading to reduced calf survival) resulting from a shortened period of prepubertal caring. Although it is presently unknown whether prepubertal caring experience is necessary in mysticetes, most evidence indicates that it is not. That is, for most of the mysticete species previously reviewed by the workshop (gray, right, humpback, fin, sei and minke whales), females with calves tend to be isolated or segregated temporally and/or spatially from juvenile females, which may restrict their opportunities for caring for young. This would make it unlikely that W. G. Clark's (1984) findings are the result of shortened prepubertal caring experience.

Oldfield suggested, and the workshop agreed, that an alternative biological explanation for falling recruitment rates might be that adult female survival declined due to the stress of experiencing more reproductive events and/or to potentially longer exposure to the fishery. That is, by growing more quickly to the size of sexual maturity, such females would be exposed relatively longer to these sources of stress or mortality. In addition if such a female is unsuccessful in her first reproduction efforts, she is further vulnerable to harvesting because she does not attain protected status through presence of a calf [IWC regulations do not permit the taking of animals accompanied by calves].

(ii) *Sperm whales*

The workshop found evidence in Best (1980) which suggested that the possible calf rearing role of older female sperm whales may change as a consequence of reduced stock size. Utilizing the accumulation of corpora albicantia as an index of relative age, he compared age-specific pregnancy rates from Durban during a period of relatively higher stock size (1962–65) with those from a period of lower stock size (1973–75), and found a general increase in pregnancy rate (and see Holt, 1980). Furthermore, the extent of the observed increase was greatest in the oldest females (those with the highest corpora count), suggesting that the high proportion of unsuccessful ovulations seen in such animals in the earlier period must have declined. The workshop noted that a compensatory mechanism might therefore exist in which the older females increase their investment in calf bearing.

The workshop had previously discussed the finding of Best *et al.* (1984) that medium-sized male sperm whales seemed physiologically capable of breeding effectively. It noted that at the special meeting on western North Pacific sperm whales, the Scientific Committee had agreed that at least to some extent, medium-sized males could replace large males in breeding schools following depletion of the numbers of large males (IWC, 1983). However, the Scientific Committee had further concluded that there were insufficient data available to quantify the effect that such replacement might have on pregnancy rates, as would be necessary if the 'La Jolla' pregnancy rate model (e.g. see IWC, 1981b, pp. 100–1) were to be revised. The workshop reiterated its observation that behavioural data are lacking which demonstrate that medium-sized males are socially capable of assuming an effective reproductive role if large males are removed.

Noting that the harvest of sperm whales is directed at 'surplus' males, the workshop was concerned about the behavioural effects on a population of reducing the numbers of large males and discussed the role that surplus males might play. Best reported that tooth scars begin appearing on the heads of 39–40 ft males, coinciding with the onset of effective physiological ability to breed, that below that size range few such scars occurred, and that in females there was no relation between age and scarring. Based on the presence of wounds and scars attributable to intraspecific fighting on males above a certain size, Best (1979) and Kato (1984) concluded that considerable competition may occur for 'possession' of a mixed school and that this competition is restricted to large males. However, as Best (1979) pointed out, the form and degree of this competition is unknown and, indeed, the scars on large males may represent the results of disputes within bachelor schools in establishing a dominance hierarchy, rather than in competition for access to females. Best (1979) further speculated that some sort of mating priority to rendezvous with females, thus avoiding or at least reducing the number of more serious disputes that might arise over access to females. The workshop agreed that field observations are needed to determine the nature and degree of the competition between surplus males. The workshop found no evidence that the age at sexual maturity (or at first parturition) of female sperm whales varies as a function of stock size. However, Ohsumi pointed out that, due to the policy of harvesting primarily males, female stock sizes may not have been reduced enough to evoke a response. Although declines in female age at maturity had been observed in such highly social, long-lived species as northern fur seals, southern elephant seals and African elephants (Fowler, 1981), the workshop noted that harvests from these included substantial numbers of females and not just males.

2.1.5 Evidence of minimum school size required for breeding

(i) *Mysticetes*

The workshop could not determine if there is a minimum number required for effective breeding within mysticete populations since their social organization remains unknown.[1] However, it did note that the apparently slow recovery of some stocks (such as right whales) may be the result of social disruption caused by low numbers. The appearance of asynchronous breeding cycles, as postulated earlier for bowhead whales, may be symptomatic of low numbers. The workshop also noted that inbreeding depression, as observed in some terrestrial mammal populations having reduced numbers, may be responsible for slow recovery, although as pointed out by Soulé (1980) effective population sizes for most asocial species are on the order of only 50–100 animals. Eisenberg observed that, for coastal species, habitat rather than numbers might be the limiting factor in recovery.

(ii) *Sperm whales*

The workshop observed that the Scientific Committee currently assumes that (if females remain relatively unexploited) sperm whale pregnancy rates remain constant as the density of socially mature males declines, until reaching a crucial threshold level. When the ratio of socially mature males to adult females falls below 2 : 15, it is then assumed that pregnancy rates decline linearly to zero as a function of male density. The threshold ratio incorporates an arbitrary 'reserve' of

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[1] Editors' note: for a fuller discussion see IWC (1984, pp. 136–7; and 1986a).

one extra breeding male (IWC, 1983). As previously noted, this so-called 'La Jolla' model does not account for the possibility of medium-sized males contributing to effective breeding (Best *et al.*, 1984). In accounting for this possibility, the workshop noted that modellers might assume either that pregnancy rates do not decline as quickly as implied by a linear relationship or else that the true threshold occurs at some much lower adult male density than previously defined. On discussing the possibility of such thresholds in other polygnous species, the workshop concluded that it is reasonable to expect such thresholds and further that one would expect a definite, abrupt decrease in pregnancy rates to occur at very low relative densities of adult males.

The workshop also recalled that, among some primates, several females must be available to rear young successfully. While noting that female sperm whales might share in calf rearing, the workshop had no data available on the minimum number required in a school to ensure calf survival.

2.1.6 The role of reproductively senescent animals on social organization

(i) *Mysticetes*

Marsh and Kasuya (this volume) found no evidence for reproductive senescence of females in any of the baleen whales studied. Moreover, despite indications of an age-related decline in the ovulation rate of several species, little evidence was found for a parallel decline in the pregnancy rate (e.g. Mizroch, 1981a). Based on the available histological evidence, the workshop also concluded that reproductive senescence does not occur in male baleen whales.

The workshop could find no evidence that the role of female mysticetes changed with age. This would be consistent with the apparent mysticete strategy of emphasizing calf bearing at the expense of calf rearing.

(ii) *Sperm whales*

Marsh and Kasuya (this volume) found no evidence for an age-specific climacteric in any of the sperm whale populations studied. Post-reproductive animals probably occur, but in fairly low numbers and there is no evidence that they are of particular significance to their populations.

Rather than focusing on the occurrence of senescence in sperm whales, the workshop believed it more useful to examine the role of older, mature females. The workshop recalled its earlier conclusion that older females appear to invest relatively more energy in calf rearing and less in calf bearing than younger females and that they might be serving as nurse, suckling calves besides their own.

Pryor commented that, in some domestic mammals, older females have leadership positions. This also appears to be the case for the matriarchal African elephant (Douglas-Hamilton and Douglas-Hamilton, 1975; Wilson, 1975). Best (1979) in commenting on the selective culling of large individuals from elephant herds, suggested that the older, larger females exerted a strong coordinating and protective influence over the remainder of the herd, such that their removal caused the leaderless survivors to amalgamate with other herds. However, Best (1979) found no evidence that school sizes of sperm whales observed during the 19th century, when substantial numbers of females were taken, differed markedly from those observed, when relatively few are taken.

The workshop also noted the possibility that, as for the African elephant (Douglas-Hamilton and Douglas-Hamilton, 1975) older females are the repository of 'cultural' information for the herd or school, i.e. retaining knowledge of migratory routes, locations of feeding grounds, etc.

2.1.7 Effects on schools of removals of some members

(i) *Mysticetes*

The workshop noted a lack of conclusive evidence for mysticetes concerning the effects of removing one age or sex as opposed to another. However, Best reported, for minke cow/calf pairs accompanied by males in putative breeding areas off South Africa that, if the male were killed, the cow and calf would depart but that, if the female were killed, the male would stand by. Upon reviewing standing by behaviour reported for some other mysticetes (Caldwell and Caldwell, 1966; Tomilin, 1935; and for gray whales see Bogoslovskaya, this volume), the workshop observed that such behaviour may result from a reproductive rather than a protective function (section 2.1.2 (ii)). Thus, it was speculated that, if disparate removals of one class or another did occur, the effects might be greater on the breeding grounds than on the feeding grounds.

(ii) *Sperm whales*

The workshop concluded that the removal of adult male sperm whales would have obvious consequences to reproductive success if their number fell below a critical threshold density. Given the possibility that medium-sized males might breed effectively, this threshold might occur at lower male densities than previously thought. However, no data are available to quantify where this threshold occurs nor to establish how pregnancy rates behave at densities below it. Moreover, behavioural observations are still lacking which indicate that medium-sized males are socially capable of assuming an effective reproductive role.

The workshop noted that, although the selective culling of older female sperm whales would remove those having the lowest reproductive rates, this might ultimately be deleterious to the population's survival. The older females may contribute to the sperm whale's strategy of maximizing the success of calf rearing by sharing the burden of suckling calves and, indeed, by possibly serving as nurses. Removing them might reduce rearing success and hence reduce net recruitment to the population. Moreover, at times of reduced stock size, older females of low fertility apparently can resume a calf-bearing role (Best, 1980). Consequently, if they are removed, the population could lack an important measure of resiliency against stress.

Finally, the workshop noted that the evidence from terrestial behavioural ecology indicates that for large mammals, old females may serve as leaders within a population and help transmit important selective behaviours to younger animals. While the consequences of their removal are not specifically known, the workshop believed that the elimination of their accumulated experience would likely be disadvantageous and at least have a disturbing effect on the population.

2.2 SITE FIDELITY

2.2.1 Core areas used for mating, calving, and feeding

(i) *Coastal mysticetes*

Calving areas. The workshop observed that only gray and right whales seemed to have definite core areas to which females repeatedly return for calving and rearing of calves on their winter grounds. Buhr and Leatherwood (SC/A82/BW9) reviewed the evidence for the gray whales' fidelity to particular lagoons and concluded that the species demonstrates 'weak' fidelity. Citing results from his studies, Swartz reported that several females repeatedly return to Laguna San Ignacio both with and without calves, 5 years consecutively in some cases. Although no information is available on whether the animals enter more than one lagoon, he believed that his observations suggest strong site fidelity. Based on the results of photo-identification studies of right whales, Payne (1984) reported that known females repeatedly returned to the same site for calving at Peninsula Valdez. He further reported that some calves repeatedly returned in winter as juveniles and that subadults and males generally occurred each year in the same locations near these areas.

The workshop also observed that, although humpback whales seemed to have definite core areas for calving and rearing calves on their winter grounds, some intermingling between these core areas apparently occurred. Based upon limited North Pacific photo-identification data, Darling (SC/A82/BW7) and Darling and Jurasz (1983) reported that, although the same adult humpback whales repeatedly returned to the Hawaiian grounds, some interchange occurred between Hawaii and the Mexican wintering ground (and see Baker *et al.*, 1985). Moreover, it was noted that the songs recorded on these two grounds in the same year were identical, thus providing further evidence of mixing.[1] The workshop also noted that, in the North Atlantic, a small number of photographs suggested the occurrence of mixing between Caribbean calving areas, particularly between Silver and Navidad Banks (Katona *et al.*, 1980). The workshop speculated that the humpback whale might be a species which demonstrates fidelity to several calving/breeding locations rather than a single one.

Mating areas. While some coastal mysticetes have definite core areas for calving purposes, the workshop noted that these same areas may not be important for mating purposes, even though mating behaviour has been observed there. Withrow reported that the vast majority of gray whale mating activities occurred in bays and shallows outside of the lagoons. Rice and Wolman (1971) provided evidence that significant mating occurred during the gray whale's migration prior to arrival at the lagoons. Clark reported behavioural observations indicating that female right whales observed copulating at Peninsula Valdez do not give birth there the following year; these observations suggest that this winter ground may not be an area where conception occurs. In the Bay of Fundy, Kraus, Prescott, Turnbull and Reeves (1982) reported that North Atlantic right whales were observed mating on a summer feeding ground. Braham reported that the mating of bowhead whales might be correlated with the occurrence of temporary ice blockages along the route during the population's spring migration which would facilitate social interactions. The workshop could only find circumstantial evidence that effective breeding of humpbacks occurs on their winter core areas, and Ohsumi noted ship sightings which indicated that North Pacific humpback whales are also distributed offshore during the winter.

The workshop concluded that, except perhaps for humpback whales, fidelity to core areas for breeding purposes may not be important for coastal mysticetes if conception occurs elsewhere. Since there are some terrestial analogues for

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[1] Editors' note: see also IWC, 1985, p. 122.

conception occurring during migrations (barren ground caribou, saiga and blue wildebeest), the workshop could identify no good reasons why it could not occur for mysticetes. Mitchell noted that, consequently, a core time rather than a core area might be the important factor in assuring fertilization.

The workshop agreed with Ohsumi that space available on so-called winter breeding areas may not be a limiting factor for coastal mysticetes since effective mating apparently occurred elsewhere. However, the workshop pointed out that available space on the winter grounds may be limiting if specific habitat needs are required for rearing calves. Ohsumi observed, though, that rearing success must also be a function of the availability of food to females on feeding grounds.

Feeding areas. The workshop noted that specific core feeding areas have been observed for gray, humpback, bowhead and North Atlantic right whales. Darling (1984) reported for gray whales that strong fidelity occurred to a feeding area off of Vancouver Island, with several individuals returning repeatedly over a span of 8 years. As reported by Jurasz and Palmer (1981 ms), some site fidelity is found among North Pacific humpback whales with a number of individuals returning to Glacier Bay repeatedly during 1967–1978. Baker also noted that movement occurred between specific areas within the southeastern Alaska feeding ground. Based upon photographic reidentifications of North Atlantic humpback whales, Prescott *et al.* (1981 ms) found that no interchange has occurred between the Gulf of Maine/Nova Scotia feeding ground and the Newfoundland/Labrador ground, although mixing of whales from these two areas has been observed on the Caribbean calving grounds.[1] Based on photographs, Kraus and Prescott (1982 ms) reported that two individual right whales identified in the Bay of Fundy summer ground during 1980 were reidentified there in 1981.

Fraker remarked that the distribution and behaviour of bowhead whales on summer feeding grounds varied yearly so that patterns, if any, could not yet be discerned (Ljungblad *et al.*, this volume).

(ii) *Balaenoptera* spp.

Calving/mating areas. The workshop noted its earlier summary that Balaenopterids do not have specific core areas for breeding or calving but rather return to broad, generalized wintering grounds for these purposes. Mackintosh (1966) concluded that the available evidence for blue and fin whales is insufficient to establish a clear and concise pattern of winter distribution in relation to land masses, water masses and times of year. He further cited evidence that these species do not assemble in concentrated breeding areas, as do humpbacks, although he believed that a certain degree of grouping on the grounds was more likely to occur than wide dispersal.

Noting the dearth of systematic observations on the presumptive Balaenopterid breeding or calving grounds, the workshop agreed that it could not yet conclude that breeding aggregations do not occur. Noting evidence for extended Balaenopterid breeding seasons (4 or more months long: Mackintosh and

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[1] Editor's note: for further discussion of this see IWC, 1984, pp. 135, 141–3; IWC, 1985, p. 122; and IWC, 1986b. This last reference notes that four sub-adults had moved from one feeding aggregation to another. It was postulated that this may be similar to the phenomenon seen for other species where juveniles disperse further than adults. To date, no adults have been found to move between feeding aggregations.

Wheeler, 1929; Laws, 1961; Gambell, 1968; Best, 1982), the workshop speculated that breeding aggregations might occur, but be of short duration and spread over the breeding period. Payne and Webb (1971) observed that the ability of some Balaenopterids to emit loud, low frequency (<20 hz) sounds which travel great distances might be a mechanism obviating the need to aggregate on specific areas to find mates. The workshop agreed that systematic observations of Balaenopterid behaviour on breeding/calving grounds located in temperate and tropical waters are required.

Feeding areas. Pelagic stocks of blue, fin, sei, Bryde's and minke whales do not appear to have specific core areas for feeding purposes, but rather return to large, generalized summering grounds located in temperate, sub-polar or polar waters for this purpose (Mackintosh, 1965; 1966; Best, 1982). As shown by tagging data, animals disperse on these grounds, with much travelling and overlapping of stocks occurring during the feeding season, although the dispersal of fin and sei whales perhaps may not be so wide as that of minke whales. This dispersal and movement apparently is in response to the 'patchy' and dynamic nature of the planktonic species upon which the Balaenopterids feed, although various plankton do tend to appear consistently in a given general area year after year.

Mitchell (concerning blue, fin and sei whales off the coast of Nova Scotia and Newfoundland), Dorsey (concerning the minke whales of Puget Sound, Washington), Würsig (concerning the fin whales of the Sea of Cortez), Wolman (concerning the fin whales of Prince William Sound, Alaska), and Oldfield (for fin whales off Long Island, New York) noted that some feeding aggregations of Balaenopterids do consistently occur in nearshore areas during summer. Mitchell particularly emphasized that off the east coast of Canada, three species returned consistently to the same feeding areas, although following different migration schedules and routes and exhibiting different behavioural patterns. Dorsey (1983) also observed that the feeding area available to Puget Sound minke whales apparently had been partitioned by three distinctive groups, with recognized individuals photographed repeatedly in the same area in summer and early fall over a span of five years.

Noting this evidence for the partitioning of available inshore resources by Balaenopterids, the workshop speculated that the offshore forms may not be as panmictic as previously thought and that the potential for behavioural 'order' may still exist offshore. The workshop believed that the evidence at least indicated the presence of behavioural flexibility in Balaenopterids such that they would be able to take advantage of a wide variety of ecological situations.

(iii) *Sperm whales*

Based upon mark-recapture data, Best (1979) concluded that in general, home ranges for mixed schools of sperm whales are probably considerably smaller than those of bachelor schools. Berzin (1971) proposed that each school has its strictly defined winter ground, but as the area of summer habitat is vast, the schools cross extensively from one foraging ground to another, returning in autumn to their respective wintering grounds. However, Best (1979) pointed out that there is insufficient evidence to support this theory. Best remarked that the limited mark-recapture evidence that is available suggests that females are consistent in returning with regard to time and with regard to a limited wintering area.

The workshop noted that while the wide dispersal of females (mixed schools) on the feeding grounds may be a function of oceanographic features, some evidence pointed to male sperm whales aggregating near definite topographical features, such as shallow banks or canyons, on their feeding grounds. However, the fidelity of males to these features is unknown.

The workshop agreed that it could make no conclusive statement about the sperm whale's need for, or use of, core areas for breeding, calving, or feeding. It further observed that a definite need exists for further research incorporating systematic sightings, particularly on the wintering grounds.

2.2.2 Known migratory routes among these areas

(i) *Mysticetes*

The workshop noted that studies have confirmed the general north–south pattern of migration between feeding and calving/breeding areas for all species of mysticetes: blue and fin whales (Mackintosh, 1966), sei whales (Gambell, 1968), Bryde's whales (Ohsumi, 1980), minke whales (Best, 1982), gray whales (Rice and Wolman, 1971), right whales (Best, 1981), humpback whales (e.g. Darling and Jurasz, 1983; Whitehead, 1982; Dawbin, 1966) and bowhead whales (Braham *et al.*, 1980a). It acknowledged, however, that except for gray and bowhead whales, very little else is known about the specific routes, if any, followed by most mysticetes. Noting that Pike (1962) and Rice and Wolman (1971) had earlier described the narrow, nearshore route followed by gray whales, the workshop observed that recent surveys throughout the species range and a gray whale recently radio-tagged by Bruce Mate confirmed their conclusions regarding the timing and route, (see Jones, Swartz and Leatherwood, 1984).

Darling reiterated that photo-identification studies suggested the occurrence of an east–west component in North Pacific humpback whale migrations, in that an exchange of individuals had occurred between the Hawaiian and Mexican breeding/calving areas. Photo-identification data suggest that interchange or mixing of humpback whales does not occur between the major Western North Atlantic feeding grounds, although they do mix on the breeding grounds (e.g. see IWC, 1984; 1985).

(ii) *Sperm whales*

Best (1979), describing the general north–south migrations of mixed schools of sperm whales and bachelor males, concluded that males generally move greater distances than females. He further concluded that the limited mark-recapture data available suggest that the migrating patterns and routes of females (mixed schools) may be consistent from year to year. The workshop noted that except for these general observations, little else is known about the timing and specific routes, if any, followed by sperm whales.

Mitchell summarised marking data for male North Atlantic sperm whales and suggested that it may indicate a considerable degree of mixing: a male marked in Nova Scotia was recovered in the Spanish coastal fishery. The workshop noted that the Scientific Committee was unable to reach agreement about the degree of mixing of male North Pacific sperm whales as evidenced by available marking data (IWC, 1983). Although the available data suggest males have a much wider geographic dispersion than females, the workshop agreed that further observations are needed to ascertain the nature and degree of male dispersion. Martin (1982) reported on a link between male sperm whales of the Azores and

Iceland—the head of an Azorean harpoon was discovered in an animal flensed at Iceland.

2.2.3 Changes in these areas or routes as a function of stock size

Klinowska (SC/A82/BW1) analysed secondary sources of historical catch data for the West Greenland bowhead whale and concluded that continued catching caused the most southerly extremes of the range of this whale to be abandoned, or at least less regularly visited. After analysing primary historical catch records for the Western Arctic bowhead whale, Dahlheim, Bray and Braham (1980), Bockstoce and Botkin (1983) and Braham (1984) concluded that the pre-exploitation feeding areas were vastly larger than contemporary ones, and that this population seems to have been eliminated, for reasons not completely understood, from the use of large parts of its once greater range. After examining a variety of historical records, Best (1981) concluded that South African right whales may not now range as far north in winter as they did formerly. Payne reported that Argentine right whales do not now range as far south as they apparently did according to Townsend's (1935) charts of historical catches. However, Ohsumi and Kasamatsu (1986) reported that, based on modern sightings data, right whales south of Western Australia occurred in the same range defined by Townsend's (1935) charts. Gambell and Kasuya observed that modern catch records and the recent Japanese sightings data suggest that, as the numbers of southern blue and fin whales were reduced, the range and abundance of sei whales increased.

The workshop agreed that the weight of this evidence suggests a tendency for mysticete populations to condense their ranges to focal areas as numbers are reduced. Several participants urged caution in making this interpretation, however, noting that only careful analyses based upon primary historical data sources are to be trusted.

Other than the above possibility, the workshop believed that most changes observed in core areas or migratory routes of both mysticetes and sperm whales are probably related to oceanographic perturbations or to disturbances resulting from human activities rather than to changes in stock size. For example, Nishiwaki and Sasao (1977) concluded that ships and boats disturbed the migration routes of Baird's beaked whales on the Boso whaling ground and of minke whales on the Yobiho whaling ground, both off Japan. Reeves (1977) described the abandoment of Laguna Guerrero Negro by gray whales following the onset of barge traffic and associated dredging required for transport of salt. Finally, Ohsumi (1981) concluded that the season of availability of sperm whales to Japanese coastal whaling stations over recent years changed as a function of trends in oceanographic conditions.

The workshop also noted anecdotal evidence from Mitchell, for fin whales off Nova Scotia, and from Best, for sei whales off South Africa, that these populations persisted on the same general migratory route despite severe depletion by whaling.

2.3 PERIODICITY IN BREEDING CYCLE

2.3.1 Evidence for annual as opposed to 2 or 3 year cycles

(i) *Mysticetes*

Table 2 reviews the available estimates of breeding cycles for large cetaceans. An obvious difference is the relatively short breeding cycle of mysticetes compared to sperm whales. Although the sperm whale has a relatively longer gestation period than mysticetes, 15–16 months (Best *et al.*, 1984) versus 10–13.5 months. (Mackintosh, 1965; Rice *et al.*, 1981), this difference in breeding cycle may be due in part to the sperm whale's longer lactation period (Table 1).

On reviewing the physiological evidence for plasticity in breeding cycles, the workshop noted that only small proportions (10–20%) of mature female humpback whales (Chittleborough, 1958), southern fin and blue whales (Mackintosh and Wheeler, 1929; Laws, 1961) and sei whales (Gambell, 1968) experienced post-partum or post-lactation ovulations, while a large proportion (≥80%) of minke whales did (Best, 1982). Moreover, some examples of Southern Hemisphere female fin and blue whales which were simultaneously lactating and pregnant have been found (Mackintosh and Wheeler, 1929; Laws, 1961). The workshop consequently believed that the physiological possibility of reducing the average breeding cycle to below 2 years existed within all these species. However, given the very great differences between observed proportions of post-lactation ovulations, the workshop noted that only in minke whales might the average cycle approach one year while in the other species it might only be reduced slightly below 2 years. Moreover, Oldfield cautioned that, for the larger mysticetes, nothing is known about the rearing success of females which have experienced a one-year interbirth interval, or about the survival of their calves to the end of the first year of life. With regard to behavioural observations, Swartz (this volume) reported that, based upon individually identified animals returning to Laguna San Ignacio, female gray whales have intervals of 2 or more years between calves. Payne (1984) reported similar observations for individually identified Argentine female right whales, although the intervals most often observed were 3 or more years, rather than 2. Darling (SC/A82/BW5) and Glockner-Ferrari and Ferrari (1984) reported for Hawaiian humpback whales that intervals of one year between

Table 2

Breeding cycles observed in large Cetacea

Species	Breeding cycle (yr)[1]	Type of data	Source
Gray whale	2 or more	Harvest	Rice and Wolman (1971)
		Behavioural	Swartz (this meeting)
Right whale	3	Behavioural	Payne (1984)
	[2]	Harvest	Klumov (1962)
Humpback whale	1–2	Harvest	Chittleborough (1958)
	1–3	Behavioural	Darling (SC/A82/BW5) Glockner-Ferrari and Ferrari (1984)
Bowhead whale	[3]	Harvest	Nerini *et al.* (1984)
Blue whale	2	Harvest	Mackintosh and Wheeler (1929)
Fin whale	2	Harvest	Mackintosh and Wheeler (1929)
Sei whale	2	Harvest	Gambell (1968)
Bryde's whale	[2]	Harvest	Best (1977)
Minke whale	1–2 (14 mo ave)	Harvest	Best (1982)
Sperm whale	4–5	Harvest	Best *et al.* (1984)
	3	Harvest	Clarke *et al.* (1980)

[1] Parentheses indicate values based on limited data.

calves had been photo-documented for 3 females and that other cases have been reported.

Although the possibility of flexibility in breeding cycles seemed to exist in some mysticetes, the workshop was unable to decide whether such populations could vary their breeding cycles as a function of stock size. Citing evidence of pregnancy rates increasing temporally as stocks of Southern Hemisphere blue, fin, and sei whales declined, as well as their variation as a function of baleen whale biomass (Gambell, 1975), Gambell concluded that breeding cycles must necessarily vary as well. However, Mizroch argued that observed trends in vital rates may have resulted from inappropriate statistical treatment of data (Mizroch, 1980; 1981b; Mizroch and York, 1984). Noting that the basic conflict arose over whether appropriate analyses had been done, the workshop agreed that reexamination of the underlying basic data would be appropriate.

(ii) *Sperm whales*

Best *et al.* (1984) reviewed the evidence for breeding cycle length in sperm whales and found that 4–5 years, including 2 or more years of lactation, is the normal interval between calves. No evidence for an annual cycle was found. However, Clarke *et al.* (1980) proposed a 3-year cycle for the severely exploited Southeastern Pacific sperm whale, which included only one year's lactation. However, Best *et al.* (1984) found it difficult to reconcile this anomalous result with conclusions reached elsewhere and recommended that a fuller analysis of the reproductive material collected in Chile and Peru might help clarify the situation.

On considering the possibility of the breeding cycle changing as a function of female stock size, the workshop noted that the Scientific Committee had assumed that a density-dependent reduction from 5 to 4 years occurs, corresponding to a change in pregnancy rates from 20% to 25% (IWC, 1980). The workshop also noted that that the evidence of Clarke *et al.* (1980) supported the view that such a reduction in cycle is possible when stock sizes are reduced. Moreover, it recalled that Best *et al.* (1984) provided data indicating an increased pregnancy rate followed exploitation at Durban, with the extent of the observed increase being greatest in the oldest females (those with highest corpora counts).

Despite this evidence for density-dependent changes in breeding cycles, the workshop observed that changes in pregnancy rates might result from a confounding interplay of several factors in severely reduced populations. Although the breeding cycle might be reduced as a consequence of exploitation of female sperm whales, it was also possible that improved pregnancy rates resulted from an improved sex ratio, i.e. females were reduced to such numbers that available adult males could then more effectively mate with them. Mizroch again urged that appropriate statistical techniques be used to ensure that trends were not the result of inappropriate pooling of data. The workshop agreed that the interpretation of relevant data is confounded by a number of factors deserving of further analysis. It also observed that behavioural observations are lacking regarding the ability of female sperm whales to reduce their breeding cycle in response to reduced female abundance.

2.3.2 Movement into and out of social groupings, and movement to known core areas as a function of phase of reproductive cycle

The workshop agreed it had discussed this topic under agenda items 2.1.1 and 2.2.1.

2.4 REACTIONS TO VESSELS

2.4.1 Which species avoid and which species are attracted to vessels and

2.4.2 Changes in respiration, vocalization, or movement in response to vessels

The workshop discussed these two agenda items jointly.

(i) *Species review*

Gray whales. Swartz reported for gray whales in Laguna San Ignacio that, although it is difficult to obtain close-up photographs early in the season, this task becomes progressively easier as the exposure to boat traffic increases. Under conditions of light traffic in the lagoon, he noted that most whales are not disturbed and about 5% will actually follow boats. Dahlheim reported that the attraction is mainly for small boats with idling engines and that outboard engine noise occurred in the same frequency ranges as gray whale signals (i.e. vocalisations). She also noted that gray whales vocalised more frequently in the presence of outboard engine noise. Swartz further reported that, during the southerly migration, where much small boat traffic is encountered off southern California, gray whales only rarely follow boats and more often avoid them.

Humpback whales. Baker *et al.* (1982 ms) studied the effect of vessel traffic on the behaviour of humpback whales in Southeastern Alaska during the summer of 1981. Vessel experiments were designed to simulate obtrusive (active harassment), unobtrusive (benign observations) and passby (no diversion to observe) conditions whose results were compared to control (no vessel present) conditions. As compared with control conditions, the obtrusive condition produced a striking decrease in the average interval between blows, an increase in total dive time, and an increase in maximum dive intervals. This effect moderated considerably as the vessel distance increased and the obtrusiveness of its behaviour decreased. Aerial behaviours (breaches, tail slaps, pectoral slaps), surface feeding behaviour, and changes in pod composition occurred so infrequently and with such variability that they were judged an unreliable measure of the effect of vessel traffic on whales. In a few instances, though, intense aerial displays were observed in apparent response to vessel activity. Baker further reported that no approaches to vessels were observed.

Cawthorn reported for Tongan humpback whales that the animals instantly fled upon being approached closer than 25 yds. He attributed this to their having been hunted by Tongan natives who used dynamite.

Bowhead whales. Fraker *et al.* (1982 ms) and Fraker (1984) reported that for feeding aggregations of bowhead whales in the Beaufort Sea, no whales were attracted and all tended to avoid vessels if approached. The whales began moving away at a range of 0.8–1.0 km and first tried to outrun the vessel but then moved perpendicular to the vessel's track as they were overtaken. While running, the whales spent less time at the surface (had increased dive times) and had fewer blows per surfacing, although the interval between blows was about the same. Although the whales scattered for some time afterward, they remained in the same area. Hence, he believed this to be a short term response. He also noted that sound is probably the stimulus.

Balaenoptera spp. Mitchell reported that during a 3-year study conducted from land near Les Escoumins, north shore of the Gulf of St Lawrence, 232 visual observations were unsystematically collected of surface activity of one or two minke, fin or blue whales near a vessel. Of these, 172 cases occurred where whale responses could be evaluated and the vessel passed within 500 m (visual estimate) of the whales. Of the 172 cases, whales departed the immediate vicinity on close approach of a vessel in 25 instances (15%). Of the 147 cases (85%) where the whales remained, 40% showed changes in diving duration, blowing sequences, and surfacing period (Mitchell and Ghanimé, 1982 ms). It is not known how representative these observations are of whale–vessel interactions within the study area.

With regard to ship-seeking or ship-avoiding behaviour of Southern Hemisphere minke whales, the workshop noted three recent studies (IWC, 1982a). A parallel ship investigation conducted during the 1980/81 IDCR/IWC minke whale cruise provided insufficient data to draw statistically significant conclusions whether either behaviour existed, but nonetheless gave no positive indication of ship-seeking (Butterworth *et al.*, 1982). A second experiment investigating response of minke whales to an icebreaker using a helicopter showed that whales encountered while the vessel was moving did not exhibit either behaviour; however, while the vessel was stationary, it was frequently approached by whales (Leatherwood *et al.*, 1982a). An analysis of observed headings of whales relative to the survey vessel, using data collected during the 1979/80 and 1980/81 IDCR/IWC minke whale cruises, suggested ship avoidance rather than seeking (Horwood, 1981; Butterworth and Best, 1982). The Scientific Committee (IWC, 1982a) concluded that clearly there is no evidence of ship-seeking behaviour while moving at survey speeds, but that there may be some evidence of ship avoidance by southern minke whales. Donovan (1982 ms) noted that although there was no evidence of ship seeking behaviour by Bryde's whales while moving at survey speeds, apparent ship seeking occurred when the survey vessel was almost stationary, during an IWC/IDCR sightings cruise in Peruvian waters in 1982.

Sperm whales. Lockyer (1977) reported that schools of sperm whales readily disperse and form smaller groups when a vessel approaches. This was observed regularly during marking cruises, implying that the mean numbers of whales diving together in a group during a chase probably constitute the minimum group sizes usually found. On giving chase the whales would simultaneously dive when the ship approached within 300 m, scattering in different directions underwater before resurfacing in smaller groups. It was frequently clear the diving to shallow depths (50–100 m) was an escape response to the vessel. Whales were often alarmed by sudden surface engine noise as when the ship went from idle to full ahead to give chase to a resurfacing group.

The workshop noted that other odontocetes also react to sound as a stimulus. Fraker (1977 ms) reported that white whales of the MacKenzie Delta in reacting to oil development vessels apparently could detect their sounds at 3,000 m, based on audiograms, and responded at 2,400 m by moving away. Pryor reported that *Stenella* spp. would react to tuna vessels at distances of 5–7 km: when a vessel drifted, porpoises oriented at random, but when engines were turned on, they moved away and this movement became even stronger as the vessel got underway.

(ii) *Generalisations*

From the above review, the workshop observed a general tendency for most species to avoid moving vessels. Moreover, it observed a general tendency for whales to respond by increasing the length of dive times as they moved away. In the case of sperm whales it was noted that they tended to split and reform in smaller groups. The workshop noted that such avoidance behaviour and responses would result in whales being missed along survey tracklines and that density estimates based upon sightings data would therefore likely be biased downward.

Although the above general tendencies were noted, the workshop also observed that great individual variation in behaviour and responses occurred between and within species. It believed that the results of whale–vessel interactions would also depend upon where or when the encounter occurred, with whales responding differently while breeding, feeding or migrating (see Gunther, 1949). The workshop also noted that the behaviour of the vessel involved could be a factor, with whales responding only if changes in pitch or intensity of engine noise occurred. It also noted that habituation might occur or alternatively that there may be no response until stimuli reach a cumulative threshold level. The workshop consequently believed that all these factors must be considered on a case-by-case basis when quantifying any sightings correction factors.

2.4.3 Changes in reaction to vessels in response to being tagged previously

(i) *Mark-recapture experiments*

The workshop discussed the possibility that, due to their previous ‘experience’, tagged whales would more likely avoid catcher vessels than would untagged animals. As a consequence of this possibility, the number of recovered tags might be biased downward, leading to overestimates of abundance.

Watkins (1981) concluded for radio tagging experiments involving fin and humpback whales in Prince William Sound, Alaska, and Bryde’s whales near Puerto La Cruz, Venezuela, that there was little visible response to the implantation of the whale tag, but there was reaction to the manoeuvring of the boat and to sudden underwater sounds. There was no evidence that the whales recognized the tagging boat, with successful approaches occurring for retagging the whales or for re-examining the tags. Johnson reported similar results for radio-tagged humpback whales in southeastern Alaskan waters.

Reviewing Mate’s radio tagging experiments on gray whales in Laguna San Ignacio, Swartz reported that, for whales which could be approached for tagging, little obvious response occurred upon being tagged. Moreover, tagged animals could be easily approached for close-up re-examination of the implanted tag. Withrow reported for experiments using streamer tags on gray whales in Laguna Ojo de Liebre that chasing was the problem, not being tagged.

Darling reported for killer whales in British Columbia waters that previously culled pods could be easily approached on subsequent occasions. However, Cawthorn reported for Discovery marking experiments on sperm whales off New Zealand that the position of the ‘hit’ on the whale’s body was important: whales envincing a strong reaction to being tagged could not be approached the following day.

Gunther (1949), commenting on the response of fin whales to marking, reported that they are disturbed by the sound of the ship, by the report of whale-marking guns and by the impact of the marks. At the sound of the ship they moved off gently, but at the report of the gun, or when hit by a mark, they sometimes bolted to a safe distance and then slowed down. The most timid took flight on approach of the ship; the less timid took flight on approach but allowed themselves to be overtaken after pursuit. After previous encounters, some schools allowed a ship to approach but went out of reach immediately after one of their number had been hit; other schools allowed repeated approaches, although, after every round of hitting, the whales took temporary flight. Thus some whales grew less approachable, others more so under this treatment. On some occasions whales did not flee or even seemed attracted to the ship. On these few occasions the whales were, or had been, preoccupied with feeding. Another characteristic was the tendency of large schools to split into smaller groups upon being chased. Donovan noted that in his experience, (with blue, fin, sei, Bryde's, minke and sperm whales) whales were more disturbed by near misses than hits (to which there was usually no apparent reaction).

From this sparse evidence, the workshop generally agreed that whales were more likely to react to being chased by a vessel than to the act of tagging. Although long term effects did not seem to occur, the workshop was unable to conclude definitely whether a tagging encounter (including the chase) would cause a whale to avoid catcher vessels on subsequent occasions. The workshop believed that research was needed involving double tagging using visual marks. In this manner Discovery-marked animals could be reidentified and their behaviour observed to see if they tended to avoid catcher vessels more than their companions.

(ii) *Capture 'stress'*

The workshop noted that Stuntz and Shay (1979 ms) had reported the likelihood that there is some unobserved mortality occurring after *Stenella* spp. are released from tuna purse seines. This mortality, which probably occurs at quite low levels, may be related to the capture stress syndrome observed in terrestrial mammals. That is, the chasing and encircling of dolphins by small speedboats operated by tuna fishermen may result in such a stress syndrome.

Noting that chasing whales occurs in both whaling and tagging experiments, some workshop participants were concerned that capture stress may be occurring, leading to mortalities if not to reduced biological fitness of the affected stocks. It was noted that cumultive effects of chasing, as in whaling, may be more problematical than an occasional chase, as in tagging. Although large cetaceans are adapted (as diving mammals) to major shifts in blood chemistry, no data were available which would enable the workshop to determine if capture stress is a significant problem.

2.5 PATTERNS OF RESPIRATION

2.5.1 The effects on sightability of various swimming speeds and respiratory cycle lengths

and

2.5.2 Aerial displays other than respiration that affect sightability

The Scientific Committee, on reviewing factors affecting sightability of whales (IWC, 1982b), concluded that sighting cues vary by species (and its individual size, group size, and behaviour) and by weather. For example, flocks of birds sometimes congregate near porpoise schools, and can indicate the presence of a porpoise school well beyond the range it could normally be sighted. Large cetaceans cue their presence by their blow, their body, the splash when they blow, jump or spy-hop, their body colour below the water surface and the slick or ring that persists on the water's surface after diving. Different cues predominate under differing weather conditions, e.g., blows are sometimes obvious in calm, relatively clear weather, while body form plus blows become the principal cues in more disturbed weather conditions.

The Scientific Committee also believed that systematic collection of data on the submergence and respiratory patterns of different whale species might assist in modelling, at least, the maximum proportion of animals that might be seen on the trackline (IWC, 1982b). Leatherwood *et al.* (1982b) summarised available data on the respiration patterns and diving behaviour of large cetaceans, killer whales and bottlenose whales. Although incomplete, the workshop believed it to be thorough enough that its general conclusions were still valid. That is, the authors believed that, despite the considerable research on whales over the years, their respiratory patterns continue to be poorly documented and the information which is available is variable in method, quality, extent and format. Much of it is anecdotal and hardly adequate to support development of numerical correction terms accounting for whales missed along survey tracklines. The authors further commented that one is struck by the variability in diving behaviour of all species studied: overall, the patterns appear to vary significantly by time of day, season, geographical area, environmental conditions, number present, dominant behaviour of the group, its age composition, presence of the survey platform and perhaps other factors.

The workshop noted a lack of information in Leatherwood *et al.* (1982b) regarding diel patterns of respiratory or diving behaviour. Such patterns might bias sightings or results from other assessment techniques. Swartz and Jones (1981) concluded that time of day and direction of tidal current appear to shape the overall movements of gray whales in lower San Ignacio Lagoon. Hourly whale movements suggest a diurnal pattern of two active periods: early morning activity with a net flow of whales into the upper lagoon followed by a late afternoon period of activity with a new flow of whales into the lower lagoon. Superimposed on this pattern is a tendency for whales to move with rather than against the tide. Swartz reported that increased sightability occurred during the two activity periods.

Würsig *et al.* (this volume) reported for bowhead whales in the Canadian Beaufort Sea, that no apparent diel patterns are observed although differences occur during the season depending on whether the whales are feeding in or migrating through the area. However, Watkins *et al.* (1981) reported for radio-tracking experiments upon fin and humpback whales that both species had shorter dive times during the dark.

Klinowska (this volume) reviewed available information on diurnal rhythms in Cetacea and concluded that, although the evidence is of varying quality, taken as a whole it shows that regular diurnal behaviour occurs in all families. The review also pointed out that in assessment models, a linear relationship is presumed to exist between stock density and catch-per-unit-effort as measured by catch per catcher day's work adjusted by various multipliers. Moreover, in sightings theory, it is assumed that density of whales is proportional to sightings per unit of searching time. These assumptions may not hold true if whales have diurnal rhythms in appearance or in 'catchability'. Not only would whales be more likely to appear at certain times of day, but bad weather at these times, mechanical breakdown or other reasons for not operating might lead to underestimates of abundance.

Moreover, operations would more likely be timed to take advantage of maximum probability of appearance of whales, thus possibly overstating abundance.

With regard to sighting surveys, the workshop observed that diel patterns would only become important if they affected the proportion sighted along the trackline or the estimates of group size. The workshop also noted that the mobility of whales complicates line transect analyses since the theory was developed for stationary objects.

The workshop concluded that adequate data were not yet available to quantify the possible effects of diel behaviour patterns. Moreover, it noted that currently available data on swimming speeds of whales were inadequate for the task of analyzing the likely effect of mobility on estimates of abundance. The workshop agreed that long term radio tracking experiments might provide an appropriate data base for addressing these areas of concern.

2.6 PATTERNS OF VOCALIZATION

2.6.1 Use of sounds in conjunction with sightings to assess age/sex of groups

(i) *Mysticetes*

Gray whales. Dahlheim reported on a newly initiated investigation of gray whale acoustic behaviour in Laguna San Ignacio which indicated that those animals are extremely vocal in the breeding/calving season. The work has not progressed far enough to indicate whether vocalizations indicate age or sex differences of individuals.

Right whales. C. W. Clark (1982; 1983) concluded that the activity, size and sexual composition of groups of right whales were correlated with the types of sounds produced. The most discrete types of sounds were associated with long distance contact situations, while the highly variable, acoustically complex sound types were associated with groups of socially active whales. Clark elaborated that 'up' calls function as contact signals, used to communicate over long distances and when whales are attempting to come into physical contact. Once the animals meet, this type of call is no longer produced. High frequency tonal calls are produced when whales form groups and become excited. Pulsive calls are produced in agonistic contexts, as when several males compete for a female in a very large group (6–10 animals). He would expect a population of right whales that is dispersed over a large area, but maintaining itself as an acoustic herd, to produce mainly 'up' calls, while one that is engaged in a lot of social interactions and sexual activities to produce mainly 'high' or 'pulsive' calls. The workshop noted that these results pertained to a closed gulf in the calving season, which may or may not be a specialised situation.

Clark observed that cows and calves are surprisingly quiet and become vocal only when separated. He speculated that the silence may be an adaptive response to killer whales or other predators.

Humpback whales. Baker and Darling reported that apparently only male humpback whales produce songs on the calving/breeding grounds. They also noted that only short or fragmentary songs are heard irregularly on feeding grounds. Payne and McVay (1971) reported that songs change from year to year and recent studies show that, within a population, the song changes most during the breeding season (Payne, K. *et al.*, 1983; Winn *et al.*, 1981). Tyack (1981) suggested that one of the functions of singing may be to convey to conspecifics the age and sex of the singer.

Winn *et al.* (1975) utilized both passive acoustic and visual techniques to estimate abundance of humpback whales in the West Indies. A comparison of estimates indicated that consistently fewer animals were estimated by the acoustic method. A major difficulty was that, since only single animals produced calls and pairs, trios and juveniles did not, the number of non-callers had to be added to callers to obtain an estimate. The ratio of non-callers to callers was obtained by observation and probably represented the greatest weakness of the acoustic method. Based upon five years of observations that all single adults produced calls, some continuously for extensive periods, the authors were not concerned about the possibility of missing some single animals due to non-calling.

Bowhead whales. Johnson *et al.* (1981) examined the feasibility of using passive acoustic monitoring to census bowhead whales during the spring migration past Pt Barrow. In 1979 experiments, the system demonstrated its usefulness as a tool in support of visual counting, indicating to counters the presence and location of whales that otherwise would have passed by unobserved. However, in the much wider lead encountered in 1980, the system proved less effective because some whales passed so far away that they were heard only faintly, if at all, and increased wave action produced more background noise, which further obscured the fainter vocalizations. Braham *et al.* (1980b) expressed the view that, with the systems tested, it probably was not feasible to census bowheads acoustically. Major uncertainties remained regarding the proportion of passing whales that vocalize and its constancy through the migration season, from year to year, and from location to location. However, Awbrey and Clark stated that acoustic censusing techniques could definitely augment visual censusing efforts.[1]

Clark and Johnson (1984) note that bowhead and right whales have very similar repertoires, especially for sounds lower than 400 Hz.

Balaenopterids. The workshop was unaware of any evidence indicating that the age or sex composition or activities of groups of Balaenopterids could be distinguished from vocalizations.

(ii) *Odontocetes*

Killer whales. Thomas *et al.* (SC/A82/BW10) reported that geographic variation in vocalizations has been documented in killer whales and is suspected in short-finned pilot whales. Based upon an analysis of the recordings of wild animals, Ford and Fisher (1982) concluded that the killer whale dialect system represented a potentially useful technique for identifying populations and determining their social organization. Dahlheim and Awbrey (1982) found that by using multi-discriminant analysis, individual captive killer whales could be distinguished by variations in vocalizations. Such variation might reflect discrete breeding populations.

Dahlheim (1980 ms) also noted that individual, group and sexual information had been found in her examination of the calls of captive killer whales. Observing

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[1] Editor's note. Acoustic monitoring was successfully used in this context during the 1985 spring bowhead census, e.g. see Clark, Ellison and Beeman (1986), IWC, 1986b.

that much of her work is based on captive animals, the workshop foresaw a problem of identifying in the wild which animal is vocalizing.

Sperm whales. Møhl *et al.* (1981) outlined an acoustic approach for determining the length of sperm whales. By this technique the interpulse interval within a click is correlated to the length of the spermaceti organ, which in turn is correlated to the length of the whale. However, the workshop queried the statistical basis of the two required correlations, noting that only two observations (of 9 m and 21 m animals) were available for the former and that the latter actually used length of head, rather than length of spermaceti organ. Moreover, Clark reported that, from recent observations of the click trains of a captive sperm whale, he could not detect any secondary pulses in extremely good samples of click trains. He noted Watkins' suggestion that the secondary pulses were merly a reflection of the click pulse off the surface and not related to the length of the animal at all. The workshop agreed that the basis of the approach required further careful examination.

2.7 OTHER PROBLEM AREAS

2.7.1 Behaviour near ice

Ohsumi reported that Southern Hemisphere minke whales invade the loose pack ice. The numbers which do so are unknown but certainly IWC/IDCR sightings vessels have not been able to enter these areas and determine the scope of the problem. The workshop noted some positive evidence indicating extensive use by minke whales of the leads and pools occurring inside the pack ice: (1) The density of minke whales is highest at the pack ice edge and they have a definite tendency to flee into it, as when chased by killer whales; (2) sightings of minke whales inside the pack ice had been obtained by South African vessels (Condy, 1977); (3) noting the tendency for females to segregate closest to the pack ice edge, Best recalled the situation in Area IV in 1979/80 where the proportion of females in Japanese catches was relatively low and it was claimed that the animals had invaded the ice (Furukawa, 1981). The workshop agreed that although it had no means of judging the magnitude of the problem, occurrence of such behaviour would imply that sightings surveys underestimated abundance.

2.7.2 Photographic techniques

Fraker reported that he had successfully identified 32 individual bowhead whales from aerial photographs based upon their distinctive colour patterns and markings. Moreover he had been able to estimate their lengths using an accurate radar altimeter and standard photogrammetric techniques. Overflights were made at 500 ft. The workshop agreed that this promising approach should be used to determine the length frequency distribution of the bowhead population and, perhaps, to develop a basis for mark-recapture estimates of abundance. It noted that the summer range might be the best location for this work since long days, good weather, and little segregation occurred there.[1]

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[1] Since the Workshop there has been a substantial amount of work on this topic, for example see Fraker (1984), Würsig *et al.* (this volume), Ljungblad *et al.* (this volume), IWC (1986b).

3. REVIEW OF BEHAVIOURAL PROBLEM AREAS, THEIR POSSIBLE EFFECTS, POSSIBLE MANAGEMENT ACTIONS NEEDED AND PROPOSED RESEARCH

The workshop agreed that it would consider these items together for the three major species/stocks identified earlier: South Hemisphere minke whales, sperm whales and bowhead whales; and that the results of the discussions would be presented in the form of the table (Table 3) which is included on pp. 37–46.

4. RECOMMENDATIONS

The workshop identified one major problem area for each of the species identified as key species for management and recommends that work on these areas should be undertaken as a matter of urgency.

4.1 MINKE WHALES

The major problem concerning the minke whale is the determination of what changes, if any, have occurred in its reproductive cycle as a result of the changes in density of the balaenopterid species in the Antarctic due to whaling. The workshop recommends that a working group which includes Gambell, W. G. Clark and Mizroch, re-evaluates the proposed density-dependent responses of balaenopterid whales in the Antarctic (re. pregnancy rates, age at sexual maturity, recruitment rates) and reports to the IWC Scientific Committee by the 1983 Annual Meeting.

4.2 SPERM WHALES

Throughout the discussions it was clear that there is a general lack of field observations of the social behaviour of sperm whales. The workshop recommends that priority be given to the design and support of field studies of sperm whale social behaviour, particularly emphasizing mixed schools and associated schools of adult males during the breeding season.

The workshop also recommends that the proposed density-dependent responses of sperm whales (re. pregnancy rates as a function of male/female ratio, breeding cycles as a function of female density) be examined with the aim of developing more realistic models.

4.3 BOWHEAD WHALES

There is a serious lack of data on the general biology and biological parameters for this species. The workshop believes that aerial photogrammetric surveys on the feeding grounds represent the best method of obtaining the information required to assess the status of this stock and to enable a rational management programme to be established. It recommends that such surveys be carried out as soon as possible. If the surveys take place during the period the whales are on the feeding grounds they will give information on:

(a) gross production (calf counts)
(b) population structure (size of animals and groupings)
(c) segregation by age/sex on the migration streams (by reference from times of first arrival of e.g. cows with calves)
(d) core feeding areas, if these occur

(e) size at sexual maturity and calving interval (if known animals are followed through a series of years).

If for logistic or other reasons the survey period is restricted then the usefulness of the information on these items will be lessened.

4.4 OTHER RESEARCH RECOMMENDATIONS

In addition to the above proposals the workshop agreed that the research projects identified in its report and in particular Table 3 should be classified into three types:

Type 1—Proposals for which the highest priority should be given and which should be implemented immediately.

Type 2—Proposals which would provide useful information in the longer term and which should be initiated within the next 2 years.

Type 3—Proposals which contained scientific merit but which would not provide information relevant to management, or proposals which could not be implemented until suitable technology became available.

Table 3 (see text)

Effect on stock assessment	Effect on management measures	Possible management actions	Research needed
2.1.1 Shifts in the age/sex structure of groups during and outside the breeding season			
(a) Minke			
May not be important since the IDCR cruises cover most of the population within 200 miles of the ice edge, i.e. the available population since this is the area of whaling operations.	Since the proportion of females in the catch is greater due to segregation by sex, then the sex ratio in the available population will change with time in favour of males (also see 2.3.1).	Several theoretical possibilities are available which have associated practical problems. (i) Set catch limits by sex: operationally impossible since males and females cannot be distinguished at sea; (ii) since females are predominant close to the ice, then take catches away from the ice edge: problematical due to the fall in density of whales and the poorer sea/weather conditions with distance from the ice edge; (iii) the current IWC method which is to set a total catch limit which ensures that replacement yield of females is not exceeded (although this may in fact exacerbate the imbalanced sex ratio).	The possibility of extending IDCR cruises to cover warmer waters to investigate possible segregation in these areas should be examined. Information may be obtained particularly in conjunction with Brazilian whaling operations. **Priority 1**
(b) Bowhead			
No direct information. The low calf counts obtained in several studies (e.g. see Cubbage and Rugh, 1982) may be either real, an artifact of sampling technique, or imply segregation of mothers and calves in the survey/census area.	Information on recruitment rates is essential if rational management measures are to be developed.		The aerial photogrammetric methods used by Fraker in the summer feeding areas (Canadian Beaufort Sea) should be expanded in extent and time (see 4.3). **Priority 1**
(c) Sperm			
The segregation by age, sex and time presents problems in several areas of stock assessment, e.g. sightings surveys, pregnancy rates (see below).	These are discussed under the more specific items later in this Table.	The segregation of sperm whales could potentially be used to protect different segments of the population, e.g. confining catches to between 40°-50° latitudes would confine catches to mainly medium sized males (although some large males migrating through these latitudes may be taken).	Further consideration of the value of geographical limits should be undertaken, in the light of current sperm whaling operations. **Priority 2**

Effect on stock assessment	Effect on management measures	Possible management actions	Research needed
2.1.2 Social tendencies of males as a function of age			
(a) Minke			
-	-	-	Further examination of the possibility of seasonality in sperm production in males (Best, 1982) is necessary. Seminal fluid counts with respect to weight and age should be made. **Priority 1, 2**
(b) Bowhead			
-	-	-	Although the data base will be small, the landed catch should be carefully examined for information on maturity of males. **Priority 1, 2**
(c) Sperm			
Important in modelling pregnancy rates (see 2.1.4).	See 2.1.4	See 2.1.1 for possible ways of achieving protection for certain categories of males.	Behavioural observations are required to obtain information on the cause of scarring, how and which males rendezvous with female schools, how long they stay, etc. As the technology develops, radio and satellite tracking may become very useful (see 4.2). **Priority 1,3**
2.1.3 Mother/young dependencies, their duration and the success of rearing young as a function of mother's age			
(a) Minke			
Important in estimating recruitment rates if success in rearing young is affected by the fall in age at maturity.	Important to have accurate estimates of recruitment since catch limits are currently based on estimates of replacement yield.	-	Females taken in warmer waters, e.g. Brazil, should be examined to determine length of lactation and IDCR cruises should be extended to warmer waters to observe mothers and calves (see 2.1.1). **Priority 2**

Effect on stock assessment	Effect on management measures	Possible management actions	Research needed
2.1.4 Changes in 2.1.1-2.1.3 as a function of stock size			
(a) Minke			
At present, changes in the age at first parturition are the driving force of the BALEEN model, and thus any bias in the estimation of this will affect stock assessment.	This may affect estimation of replacement yield, upon which current catch limits are based.	-	A thorough re-examination of the available data should be carried out and the question of bias in the estimates of tm at either end of the time series be investigated (see 4.1). **Priority 1**
(b) Sperm			
The current 'La Jolla' pregnancy rate model assumes that only 25+ year males can fertilise females, although evidence from Best et al. (1984) that this is not true is generally accepted. Due to the catch histories of most populations this does not significantly affect current stock assessments.	The pregnancy rate model is critical to the calculation of catch limits and MSY levels under the present IWC Management procedure, and to any population predictions.	It may be considered necessary to introduce management actions which protect certain segments of the population (see 7.1 above) in addition to or instead of those currently in force.	A quantitative application of the role of medium sized males as discussed by Best et al. (1984) should be developed as soon as possible. **Priority 1** A general survey of the role of 'surplus' males in mammalian populations should be undertaken. **Priority 2** The available data for Division 9, where females are greatly depleted should be examined with respect to possible changes in age at first parturition (although noting the problem that the age at recruitment is generally greater than the age at sexual maturity). **Priority 2**

Effect on stock assessment	Effect on management measures	Possible management actions	Research needed
(b) Bowhead			
-	-	-	Information may be obtained from the Canadian Beaufort Sea using aerial photogrammetric methods and known individuals (see 2.1.1 and 4.3). **Priority 1** The examination of logbooks to find times when calves first taken may be a useful approach: examination of the published Scoresby logbooks should be carried out as a pilot project. **Priority 2, 3**
(c) Sperm			
At present juvenile mortality is estimated from the balance equation.	Current management regulations include the protection of cows with calves as a means of protecting lactating females, under the assumption that calves will be with their mothers.	If shared suckling is confirmed then the regulations concerning cows accompanied by calves may need to be re-evaluated, with the aim of protecting all females.	A literature survey of terrestrial mammals to examine the nature and extent of shared suckling should be undertaken. **Priority 2** Examination of blood proteins of all females in schools should be carried out to examine in-school relationships. **Priority 2** Long term observations utilizing and extending present photo-identification and passive tracking techniques are needed which may well require the development of new techniques. **Priority 3**

Effect on stock assessment	Effect on management measures	Possible management actions	Research needed
2.1.5 Evidence for minimum school size required for breeding or changes in school size with density which may affect assessments			
(a) Minke			
The sightings estimates obtained from the IDCR cruises utilise school size and numbers of schools seen (with sightability obviously affected by size of school). Any changes in school size with density would critically affect these estimates and may affect catch-per-effort values.	-	-	Examine the available data for trends between school size and density for (a) minke whales within the Antarctic; (b) fin whales in the Antarctic with time (data for Areas II and III from Discovery Reports and IV and V from Japanese expeditions) in conjunction with krill distribution. **Priority 1, 2**
(b) Sperm			
See 2.1.4 in connection with La Jolla pregnancy model.	See 2.1.4	See 2.1.4.	See 2.1.4. The possibility of examining logbooks to obtain some information on school size and even changes in school size over the period of the fisheries should be investigated. **Priority 2**
2.1.6 The role of reproductively senescent animals in social organisation			
(a) Sperm			
Selective harvesting of females due to size limits (see next column) has probably occurred too late in the catch history of fisheries in most areas to affect estimates of current numbers.	The role of the female within the school appears to change with age, e.g. lower pregnancy rates but higher lactation rates for older females. The minimum size limits currently (30ft) and historically (35ft; 38ft) in force are higher than the length at sexual maturity, and thus selection of females over this length may affect calculations of MSY levels, replacement yields and population via either pregnancy or juvenile mortality rate changes.		The implications of selective harvesting (e.g. due to size limits) within the context of current whaling operations should be examined. The available age-specific fecundity rate data from South Africa should be analysed. **Priority 1, 2**

Effect on stock assessment	Effect on management measures	Possible management actions	Research needed
(b) Bowhead			
-	The IWC Scientific Committee has recommended in recent years that if any bowhead whales are taken they should be "sexually immature animals (less than 12m long) in order to maximise reproduction in the short term." The long term implications of such a policy are uncertain and have never been assessed quantitatively.	This depends on the outcome of the research identified in the next column.	The long term implications of the current policy concerning the taking of immature animals should be examined as thoroughly as is possible given the lack of direct information of biological parameters for this species. The workshop agreed that it was not appropriate to apply data from mysticete species other than right whales to this species and that the question of using right whale data must be investigated. **Priority 1**
			See earlier items
2.1.7 Effects on schools of removal of some members			
(a) Sperm			
See items 2.1.2, 2.1.3, 2.1.4, 2.1.6.	See earlier items	See earlier items	See earlier items

Effect on stock assessment	Effect on management measures	Management action	Research needed
2.2 SITE FIDELITY			
2.2.1 Core areas used for mating, calving and feeding and 2.2.2 **Known migratory routes among these area.**			
(a) Minke If such areas exist within the feeding grounds then this will affect mark-recapture estimates from the IDCR cruises (also see 2.2.2 and 3).	Current catch limits are set for each of the six traditional IWC Management Areas. If smaller 'core' areas exist then there is a possibility of localised groups being removed. Knowledge of the distribution and relationship between animals in both their breeding and feeding grounds is important in the determination of management areas.	Depends on outcome of the next column.	The mark-recapture data being accumulated from the IDCR cruises should be examined to obtain some information on the issue of 'core' areas. **Priority 1,2.** The feasibility of photo-identification of minke whales in the Antarctic should be examined in a small area, for example McMurdo Sound. **Priority 2.** The development of long term visual tags (scarring?) should be encouraged. **Priority 2.** There is definite need for systematic sightings to be carried out in areas where breeding grounds might be. In particular the possibility of extending the IDCR cruises should be investigated. This would also be a useful Ocean Sanctuary. **Priority 1.** Further marking of animals in the Brazilian whaling grounds should be undertaken which may give information on breeding/feeding ground relationships. **Priority 1.** Again, satellite tracking, when the appropriate methods become available, could be extremely useful. **Priority 3.**
(b) Sperm The length-and-age-specific assessment techniques used for sperm whales require that the correct catches allocated to sub-areas within the North Pacific. Problems exist in finding the correct allocation of catches for the northern North Pacific.	-	-	It is of prime importance that a thorough reanalysis of the available marking data is undertaken. **Priority 1.** A research programme incorporating sightings, and radio and visual tracking should be designed for the North Pacific. **Priority 1,2.** As they develop, satellite tracking techniques will be very useful for this purpose. **Priority 3.**
(c) Bowhead	-	-	The aerial photogrammetry techniques discussed under 2.1 may give some information on 'core' areas on the feeding grounds of the Canadian Beaufort Sea. **Priority 1**

Effect on stock assessment	Effect on management measures	Management action	Research needed
2.2.3 Changes in these areas or routes as a function of stock size			
(a) Minke and Sperm			
If such areas exist they could affect stock assessments. (i) Sightings: extrapolation to areas outside the survey area would be affected, although bias should be avoidable using appropriate techniques. (ii) Catch-per-unit effort (CPUE) estimates: if animals have a preferred central area then as animals are removed from it, animals outside will enter, thus maintaining CPUE values whilst stock size declines. If animals return to the same area each year then pelagic operations in particular could remove local stocks whilst maintaining CPUE values, by changing operational areas within the large management Area.	See 2.2.1	-	See 2.2.1
2.3 PERIODICITY IN BREEDING CYCLE			
2.3.1 Evidence for annual as opposed to 2 to 3 year cycles			
(a) Minke			
At present the 'true' pregnancy rate for minke whales used in the BALEEN model is 0.78 consistent with a calving interval of about 15 months (IWC, 1982a). This means that females cannot maintain a regular cycle for long, i.e. will eventually give birth too late in a season to either ovulate or be fertilised and will enter the resting phase.	-	-	Thorough examination of animals in warmer waters is needed, particularly those taken off Brazil, to determine the proportion of females in different reproductive states. **Priority 1**

Effect on stock assessment	Effect on management measures	Management action	Research needed
2.3.2 Movement into and out of social groupings, and movement to known core areas as a function of phase of reproductive cycle			
(a) Sperm			
See items under 2.1 and 2.2	See items under 2.1 and 2.2		See items under 2.1 and 2.2
2.4 REACTIONS TO VESSELS			
2.4.1 Which species avoid and which species are attracted to vessels and **2.4.2 Changes in respiration, vocalisation or movement in response to vessels**			
(a) Minke and Sperm			
This is of importance to estimates obtained by sightings, mark-recapture and, if it varies with experience (age) of the animal, those based on CPUE data.	-	-	Experiments carried out in the IDCR cruises in the Southern Hemisphere should be continued and extended to the Northern Hemisphere. **Priority 1, 2** Experiments carried out using an ice-breaker and helicopter (Leatherwood et al., 1982a) should be duplicated using a catcher boat to see if type of vessel is important. **Priority 1, 2** The theoretical implications of response to vessels should be examined thoroughly. **Priority 1**
(b) Minke			
This will clearly effect sightings assessments (e.g. numbers seen along the track line, see 2.5)	-	-	A research programme to investigate this should be developed as a matter of some urgency in view of the implications for sightings assessments. **Priority 1**
2.4.3 Changes in reaction to vessels in response to being tagged previously			
(a) All			
This will, if it occurs, clearly affect mark-recapture estimates.	-	-	Experiments with visual tags may give some indication of whether the response to vessels changes. The incidence of double-marked whales marked on separate occasions should be examined. **Priority 2**

Effect on stock assessment	Effect on management measures	Management action	Research needed
2.5.1 The effects on sightability of various swimming speeds and respiratory cycle lengths **2.5.2 Aerial displays other than respiration that affect sightability**			
(a) Minke and Sperm			
These are of particular importance for the probabilities of sighting an animal on the trackline (IWC, 1982b).	-	-	In view of the importance of stock estimates from sightings data: (i) field data on the swimming speeds of undisturbed whales (especially minke, sperm and bowhead) should be obtained; (ii) a theoretical appraisal of various respiratory cycles on sightings models should be carried out. **Priority 1** Radio tags can give detailed information on respiratory cycles in the 'undisturbed state' and also on within-day changes in behaviour which may affect sightings estimates. **Priority 1, 2, 3**
2.6 PATTERNS OF VOCALISATION			
2.6.1 Use of sounds in conjunction with sightings to assess age/sex of groups, stock identity and size distribution			
If sounds can be used in conjunction with sightings then this will improve the quality of sightings estimates.	Stock identity is important in assessing stock size and catch limit allocation.	-	Research on the use of vocalisations in the areas outlined under this item should be continued and its potential for minke, sperm and bowhead whales assessed. **Priority 2**
2.7 OTHER PROBLEM AREAS			
2.7.1 Behaviour near ice			
(a) Minke			
If large numbers are in open water areas behind the pack ice this will bias the sightings estimates downwards	-	-	Studies within pack ice zones should be undertaken in cooperation with research teams already there to establish the importance of the problem. **Priority 1** In addition a systematic programme including correlation with the degree of ice cover should be designed and initiated. **Priority 2**
2.7.2 Photographic techniques (see 2.1.1)			

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Appendix B

RESUMES OF PAPERS PRESENTED TO THE MEETING AND REFERRED TO IN THE REPORT BUT NOT PUBLISHED IN FULL IN THIS VOLUME—PROVIDED FOR INFORMATION ONLY AND NOT TO BE CITED WITHOUT AUTHOR'S PERMISSION

SC/A82/BW1. WINTER HABITS OF THE BOWHEAD WHALE [(*Balaena mysticetus*) IN WEST GREENLAND FROM 1799 to 1836 IN RELATION TO DRIFT AND ICE CONDITIONS. *M. Klinowska, Dept Anatomy, University of Cambridge, Cambridge CB2 3DY, England.*

Published information on the habits of the bowhead whale in winter in West Greenland was compared with published information on catches in the area and a measure of drift ice in Davis Strait. Five decades, starting in 1804, were selected for detailed analysis, although not all information about habits, catch and ice was available for the whole period. For the first three decades, information on habits was available and a number of changes were noted, most marked at the most southerly station, Holsteinborg, towards the extreme of the winter range. Here, as catching proceeded, instabilities appeared and habits became more dependent on climate, whereas at Godhavn, further north, the changes are less marked. Climate (as measured by ice) was an important factor in the variability of habits in the third decade when catching was at a peak, but in the second decade catches played a greater role. The findings are discussed in relation to the traditions of local people, who rely on memory and observations of habits to reach their conclusions about the health of hunted populations. It appears that although differences were detected in these data as catching proceeded, it is most unlikely that these would have been apparent to local observers. [10 pp. + 6 tables]

SC/A82/BW3. WORKSHOP ON THE BEHAVIOR OF WHALES—A COMMENTARY. *J. F. Eisenburg, National Zoological Park, Smithsonian Institution, Washington D.C., 20008, USA.*

Two topics on the agenda of the workshop are addressed to give some perspective on the manner in which terrestrial species respond to various challenges in the habitats they occupy. (1) Social tendencies of males as a function of age: such tendencies vary with age and further with respect to mating and rearing system—in general males with a polygynous mating strategy exhibit reduced parental care although they may play a vital role with respect to sub-adult and dispersing males who learn from them aspects of foraging and habitat use, particularly in species where males and females segregate geographically and seasonally for foraging; males with a monogamous mating strategy that has tended towards an obligate system with permanent pair bonds exhibit a high parental care index. (2) Role of reproductively senescent animals in social organisations: there appears little evidence to indicate that reproductively senescent individuals have an important role in natural populations of terrestrial mammals—for females post-reproductive animals have a high probability of dying and it must also be remembered that low fecundity is density dependent and that at high densities there may be low fecundity in younger females but these should not be considered equivalent to senescent animals; although in some species males have been shown to live a relatively long time after ceasing to participate in reproduction they are often solitary or live in small groups and play little or no role in the social grouping which carries out normal reproductive and rearing activities. [11 pp. + 5 figs + 2 tables]

SC/A82/BW5. A NOTE ON THE BREEDING CYCLE OF NORTH PACIFIC HUMPBACK WHALES. *J. D. Darling, West Coast Research Foundation, Box 49296, Four Bentall Centre, Vancouver BC, Canada V7X 1L3.*
Repeat cow sightings of humpback whales (based on fluke patterns) for the period 1976/77–1980/81 are presented. There were three cases of cows seen with new calves in consecutive years, in four cases cows were seen which gave birth at least every second year (it is not possible to be sure they did not give birth in intervening years). In five out of six cases where a cow was seen the year after having a calf, without a calf, it was seen with another adult. Although escort whales are usually males, on one occasion an 'escort' whale was seen two years later with her own calf. The percentage of cows following an annual breeding cycle is unknown. [2 pp. + 1 table]

SC/A83/BW7. MIGRATORY DESTINATIONS OF NORTH PACIFIC HUMPBACK WHALES. *J. D. Darling, West Coast Research Foundation, Box 49296, Four Bentall Centre, Vancouver BC, Canada V7X 1L3.*
A comparison of fluke photographs from Hawaii, Mexico, Alaska and British Columbia, Discovery mark recaptures, and songs suggests that whales which summer in Alaska and winter in Hawaii or Mexico could also visit the western North Pacific, Ryukyu, Bonin, Mariana Islands area in some years. This raises the possibility that humpbacks in the North Pacific comprise a single 'stock', with animals more nomadic than generally thought. [2 pp. + 1 fig.]

SC/A82/BW9. SITE FIDELITY IN GRAY WHALES. *R. D. Buhr and S. Leatherwood, Hubbs Marine Research Institute, 1700 South Shores Road, San Diego, CA 92109, USA.*
The California gray whale (*Eschrichtius robustus*) undertakes an annual migration from Arctic summer feeding grounds to winter calving grounds in Baja California and the Gulf of California. Analysis of observations of reaction to disturbance in lagoons and stock depletion data suggests that gray whales demonstrate weak site fidelity, adhering to a set of environmental constraints (mainly temperature) in the choice of calving lagoons. These observations are consistent with population recovery of gray whales following marked depletion in the 19th century, and further suggest that separate breeding populations in the California stock do not exist. [12 pp.]

PAPERS

EVIDENCE FOR REPRODUCTIVE SENESCENCE IN FEMALE CETACEANS

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ABSTRACT

Information on changes in the age–specific ovulation rate, corpora-specific pregnancy rate and age–specific pregnancy rate are reviewed for various populations of twelve odontocete and six mysticete species. Despite indications of an age-related decline in the ovulation rate of several mysticetes, there is little evidence for a parallel reduction in the pregnancy rate. It seems likely that post-reproductive females occur rarely, if at all, in the populations of baleen whales that have been studied. In contrast, there is convincing evidence for a substantial age-related decline in fecundity usually accompanied by an increase in the duration of lactation in several, but not all, of the odontocetes studied, and for the existence of post-reproductive females in some populations. The most striking example is the short-finned pilot whale off the Pacific coast of Japan. In some other odontocete species, the specimens on which the data is based need to be re-evaluated. Theoretical explanations for the presence of post-reproductive females and for changes in the reproductive role of a female with age are considered.

INTRODUCTION

The fecundity rate of most wild large mammals climbs from puberty and then levels off. Although the 'plateau' is invariably convex (Caughley, 1977), the decline in fecundity is usually limited to old animals whose mortality rate is so high that large samples are needed to detect the curvature. In most species, a significant post-reproductive phase appears to occur only when the mortality rate is artificially lowered by conditions of domestication or captivity.

In marked contrast to this general trend, our recent carcass study of the short-finned pilot whale off the Pacific Coast of Japan (Kasuya and Marsh, 1984; Marsh and Kasuya, 1984) suggested that females in this population cease to breed when they still have a mean life expectancy of 14 years. Our result has prompted this review of the incidence of reproductive senescence in female cetaceans.

DEFINITION

We define a female as reproductively senescent or post-reproductive if she can no longer either conceive or sustain a successful pregnancy because of age-related changes to her reproductive system.

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IDENTIFICATION OF POST-REPRODUCTIVE FEMALES

Lactation status

Once lactation has been established it can be maintained by the stimulus of regular suckling. If the mother subsequently becomes pregnant, milk production will usually cease towards the end of the gestation period at the latest, but barren females can continue to lactate for extended periods (Lascelles and Lee, 1978). Thus, animals which suckle for a prolonged period can be post-reproductive (according to our definiton) and still lactating. Lactation status is not therefore a reliable indicator as to whether or not a female is post-reproductive.

Ovarian examination

Although the ovaries have been reported to become atrophic in post-reproductive women, rats, mice and hamsters (for references see Labhsetwar, 1970), actual data are scanty. The ovaries of a post-reproductive female are not necessarily 'shrivelled and prune-like'. As Labhsetwar (1970) pointed out, the accurate determination of weight changes is complicated by the tendency of old gonads to undergo pathological change, and by the positive correlation between body weight and ovarian weight. Thus reliance on macroscopic examination of ovaries alone is not a good method for identifying post-reproductive females.

The available evidence (e.g. Zuckerman, 1956), although based on very few species (none of which is cetacean), suggests that in mammals there is no renewed proliferation of oocytes beyond foetal or early post-natal life. 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 cell population is exhausted or the animal dies (Talbert, 1977). Antral follicle production is always in excess of the number which ovulate. The antral follicles that 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. Females with a severely depleted or exhausted oocyte stock are thus post-reproductive. However, using this standard to classify an individual cetacean as post-reproductive not only demands a more extensive histological study than is usually feasible (particularly in the case of a large whale), but will also tend to underestimate the number of post-reproductive females in a population as discussed below.

An age-related decline in pregnancy rate is not dependent solely on ovarian status but on the sum of the total age changes to the reproductive tract. For example, most strains of laboratory rodents become post-reproductive long before their ovaries become depleted of oocytes (Jones, 1970). The decline in fertility, moreover, cannot be explained on the basis of a decline in oocyte number for several reasons including (a) removal of half the oocyte population by unilaterial ovariectomy does not appreciably affect litter size; and (b) prevention of ovulation by prolonged steroid dosage of mice does not counteract the decline in fertility (for references see Jones, 1970).

The possible factors involved in the age-related decline in the fertility of laboratory rodents have been discussed (Talbert, 1968; Biggers, 1969 and Finn, 1970). The overall opinion is that a major factor limiting the number of offspring produced is ageing of the uterus. Experimental evidence suggests that the ageing uterus fails to respond adequately to the stimulus given by the implanting blastocyst. The onset of uterine ageing appears to be unaffected by parity and investigations into the morphology of the ageing uterus has not revealed the cellular basis of its failure to maintain embryos (Finn and Porter, 1975). Verifying the presence of large numbers of ovarian follicles does not confirm that a female is still reproductive.

Studies of age changes in rodent reproductive cycles have been reviewed by Talbert (1977). Following the cessation of reproductive cycles, laboratory rodents tend to have periods of constant oestrus (in which the ovaries contain large numbers of follicles of various sizes), and/or repetitive pseudo-pregnancy (when the ovaries contain many large functional corpora lutea). Ascheim (1964–65) provided experimental evidence that these changes are probably the result of alterations in the pituitary-hypothalamic axis which interfered with cyclic gonadotrophin stimulation. Ovaries transplanted from old rats into castrated young rats performed in a regular cyclic manner for 3–4 months. Conversely, ovaries transplanted from immature into old rats assumed either a constant-oestrus or pseudo-pregnant condition according to the state of the recipient at the time it was ovariectomized. Thus an animal may be functionally post-reproductive and still have large follicles and/or corpora lutea in its ovaries.

Age changes in reproductive parameters

Age–specific fecundity

The only reliable indicator of the existence of post-reproductive females is the pattern of age–specific fecundity. Such data are often difficult to obtain for long-lived species such as most cetaceans, as samples need to be unbiased and sample sizes need to be large to obtain data from a meaningful number of old animals. A reliable means of estimating absolute age (often difficult for old animals) is essential if the carcass analysis approach is used. Behavioural studies of known individuals need to be carried out over many years if the presence of post-reproductive individuals is to be verified.

Unless all the females in a population cease breeding at approximately the same age, identification of post-reproductive females will be extremely difficult even with age–specific fecundity data.

As adequate age–specific fecundity data are available for few cetaceans, we have also examined other evidence for an age-related decline in fertility.

Age–specific ovulation rate

Usually calculated from the relationship between corpora count (number of corpora lutea plus corpora albicantia) and age (assuming that the corpora persist), the age–specific ovulation rate is not a completely reliable guide to the presence of post-reproductive females. Although a female who is no longer able to ovulate is post-reproductive, the converse is not necessarily true as discussed above.

Corpora-specific pregnancy rate

The corpora count has been used as an estimate of relative age for many cetaceans. It is not necessarily a good estimate, especially when the reproductive cycle is being considered. For most species, there is considerable individual variation in both the ovulation rate and the reproductive cycle, and they are, of course, interdependent. For example, Fig. 12 in Ohsumi (1965) demonstrates that the relationship between age and corpora count shows great individual variation in the sperm whale. Whales with 13 or more corpora range in age from 32 to 64 years, while whales 50 years and older have corpora counts ranging from 6 to 26.

In this discussion, we have concentrated on *changes* in corpora–specific or age–specific pregnancy rates. We have not, in general, considered the various sampling biases inherent in most data sets.

EVIDENCE FOR POST-REPRODUCTIVE FEMALES IN THE CETACEA

The data that we reviewed are summarized in Table 1 (Odontoceti) and Table 2 (Mysticeti).

Apart from the general problems discussed above, we also identified other problems which made some interspecific and intraspecific comparisons difficult.

Absolute age determination

For odontocetes, Sergeant (1962), Kasuya, Miyazaki and Dawbin (1974), Perrin, Coe and Zweifel (1976), and Perrin, Holts and Miller (1977) used dentinal layer counts only, and recognized that they had difficulties in estimating the age of old individuals. However, Kasuya (1976), Kasuya and Marsh (1984), Kasuya (1985) and Kasuya (unpublished) used cemental layer counts as well, enabling the age of old individuals to be estimated more reliably.

Ovulation rate

Perrin *et al.* (1976; 1977), included atretic leutinized follicles (corpora atretica) in corpora counts. We expect that the resultant over-estimation of the corpora count and ovulation rate would be greater in the case of older females.

Pregnancy rate

Ohsumi (1965) assumed that all animals with a corpus luteum were pregnant. However, it is possible for a female to be post-reproductive and still ovulating as explained above.

Proportion of females classified as senile or post-reproductive

The criteria used by different authors are compared in Table 3. All are likely to *underestimate* the proportion of post-reproductive females in a sample. For example, Marsh and Kasuya (1984) classified females less than 40 years of age as post-reproductive, only if their ovaries did not contain any corpora lutea, young or medium corpora albicantia, or macroscopic follicles that were not obviously atretic. However, they also showed that the proportion of corpora lutea for which no conceptus could be found was significantly higher in females more than twenty years of age than in younger females, suggesting that fertility was reduced *before* these whales ceased to ovulate.

The criteria used by Sergeant (1962) and Perrin *et al.* (1976; 1977), were even more exclusive. Marsh and Kasuya (1984) recognized that a female could be post-reproductive and still lactating, however, Sergeant (1962) and Perrin *et al.* (1976; 1977) did not. In addition, Perrin *et al.* (1976; 1977) classified resting females as senile on the basis of ovarian characteristics (Table 3) which applied to relatively few of the females classified as post-reproductive by Marsh and Kasuya (1984).

[*Text continues on p. 66*]

Table 1

Summary of evidence relating to the presence of post-reproductive females in various odontocete populations. All percentages rounded to nearest 1%. Resting females are mature but neither pregnant nor lactating. Corpora refer to corpora lutea (CL) plus corpora albicantia (CA) in both ovaries. All ages in years unless otherwise stated. GLGs are Growth Layer Groups. Annual pregnancy rate is proportion of mature females which are pregnant divided by length of gestation; apparent pregnancy rate is proportion pregnant not corrected for length of gestation. Where possible, the number of mature females studied has been counted directly from published figures or tables.

Reference	Location/source of information or samples	Sampling period	No. mature ♀'s studied	Age-related changes in ovulation rate (no. of ovulations per year)	Changes in corpora-specific pregnancy rate	Changes in age-specific pregnancy rate/calving interval	Other information	Conclusions regarding presence of post-reproductive ♀'s
Sperm Whale (*Physeter macrocephalus*)								
Chuzhakina (1961)	Kuril Is./ fishery	1951–55	Uncertain; total of 105 pairs of ovaries examined				No follicles detected in histological sections from ovaries of 5 ♀'s with 13–16 scars. CL and young CA also absent from these ovaries	*Inconclusive*; no evidence for an age-specific climacteric. Fertility is greatly reduced in ♀'s with high corpora count. However, the relationship between age and corpora count is very variable and whales with a high corpora count are not necessarily old, neither do old whales necessarily have a high corpora count. Best (1980) and Holt (1980) reported that the pregnancy rate of females with a high corpora count was higher after a period of intense exploitation
Ohsumi (1965)	North-west Pacific/ fishery	1960–62	Variable; total of 1069 ♀'s aged	*Declined* from 0.308 per year (♀'s aged 6–20) to 0.255 (♀'s aged 21–48)	*Declined* from 49% (♀'s with 4 corpora) to 14% (♀'s with > 18 corpora)	*Declined* from 40% (♀'s aged 9–20) to 22% (♀'s aged > 50)	All animals with a corpus luteum were classified as pregnant	
Best (1967)	West coast of South Africa	1962–64	103		Fertility *decreased* in ♀'s with 13–15 corpora; 0/22 ♀'s with ≥ 16 corpora pregnant		Follicular atresia increased in ovaries of ♀'s with ≥ 13–15 corpora	
Bannister (1969)	Western Australia	? 1962–1966	Uncertain; total of 256 ♀'s examined	*Declined* in ♀'s aged > 30				
Gambell (1972)	East coast of South Africa	1962–69	1029		*Declined* from 20–30% (♀'s with < 9 corpora) to 6% (♀s > 15 corpora)			
Clark *et al.* (1980)	South-east Pacific	1959–61	176	*Declined* in ♀'s aged > 20				
Bottlenose whale (*Hyperoodon ampullatus*)								
Christensen (1973)	Northern Labrador/ fishery	1971	20	Reportedly *constant* until age 24; but no correlation between corpora count and age after age 18 suggesting possible age-related *decline*			8% ♀'s resting	Inconclusive

Reference	Location/source of information or samples	Sampling period	No. mature ♀'s studied	Age-related changes in ovulation rate (no. of ovulations per year)	Changes in corpora-specific pregnancy rate	Changes in age-specific pregnancy rate/calving interval	Other information	Conclusions regarding presence of post-reproductive ♀'s
White whale (*Delphinapterus leucas*)								
Sergeant (1973)	Canadian Arctic/net fishery	1962–64	33	Apparently *constant* from age 8 GLGs (4 years) to age 50 GLGs (25 years)			3% ♀'s resting	Inconclusive
Khuzin (1963)	Kara Sea	unknown	21	Apparently constant until age 20				
Long-finned pilot whale (*Globicephala melaena*)								
Sergeant (1962)	Eastern Newfoundland/ driving fishery	1952–54 1957	529					5% mature ♀'s classified as senile (see text)
Short-finned pilot whale (*Globicephala macrorhychus*)								
Kasuya and Marsh (1984); Marsh and Kasuya (1984)	Pacific coast of Japan/driving fishery	1965–81	245 (from which ovaries examined)	*Declined* from 0.7 (age 7) to 0.14 (age 39). No recent ovulations in 49 ♀'s > age 40. Follicle concentration severely depleted in ovaries of old females	*Declined* from 60% (1 corpora) to 10% (> 13 corpora)	Apparent pregnancy rate *declined* from 65% (age 6–12) to 24% (age 30–36). 0/76 ♀'s age > 36 pregnant		24% mature ♀'s classified as post-reproductive (see text). Ovaries similar to post-menopausal human ovaries
Killer whale (*Orcinus orca*)								
Bigg (1982)	Vancouver Is. area/behaviour study	1973–81	26				65% of mature ♀'s did not calve during study period	Some barren ♀'s possibly post-reproductive
False killer whale (*Pseudorca crassidens*)								
Purves and Pilleri (1978)	Britain/mass strandings	1927	At least 30				10% mature ♀'s pregnant; 7% lactating	Absence of pregnant ♀'s age >41 in Kasuya's sample indicates presence of post reproductive ♀'s
		1936	At least 29				17% mature ♀'s pregnant	
Kasuya (unpublished)	Japan/driving fishery	1979–80	67			0/12 ♀'s age >41 were pregnant	15% mature ♀'s pregnant; 25% lactating; 60% resting	
P. B. Best (pers.comm.)	South Africa/ mass stranding	1981	Uncertain; total of 41 ♀'s				3% pregnant; 15% lactating	
Bottlenose dolphin (*Tursiops truncatus*)								
Kasuya (unpublished)	Japan/driving fishery	1979–80	151			Annual pregnancy rate *declined* from 50% (age 10) to 34% (age 30–35)	Resting ♀'s *declined* from 21% adult ♀'s (age <10) to 11% (age 30–35). Pregnant/lactating ♀'s present in all age groups from 15–40 years	Inconclusive; no evidence of age-specific climacteric

Striped dolphin (*Stenella coeruleoalba*)									
Kasuya (1976)	Pacific coast of Japan/driving fishery	1971–75	121		Apparently *constant* for ages 5–25; *declined* significantly for ages 26–43				Inconclusive; apparent *decline* in fecundity after about age 30
Kasuya (1985)	Pacific coast of Japan/driving fishery	1967–80	387				Mean calving interval *increased* with increasing maternal age in age range 5–55 yrs	Resting period increased from < 0.2 y (young ♀'s) to 1 y (♀'s > age 30)	
Spotted dolphin (*Stenella attenuata*)									
Kasuya *et al.* (1974)	Pacific coast of Japan/driving fishery	1970–73	164			Proporation of pregnant ♀'s *decreased* from 23% (1–6 corpora) to 19% (7–12 corpora) to 11% (13–18 corpora)			Perrin *et al.* (1976) identified 1.3% ♀'s as senile (see text). Animals with similar ovaries also seen by Kasuya (unpublished). Apparent *decline* in fecundity with age in both populations. Perrin *et al.*'s data need re-evaluation because of (1) technical difficulties with age determination; (2) inclusion of corpora atretica in corpora count
Kasuya (1976)	Pacific coast of Japan/driving fishery	1970–73	106		Assumed *constant* for individuals > age 7; limited evidence for *decline* ♀'s age > 33				
Kasuya (1985)	Pacific coast of Japan/driving fishery	1970–78	257				Mean calving interval shows *no significant change* with age	Resting period *increased* from 0.6 years (♀'s < age 25) after which it increased with age. Pregnant/lactating ♀'s all < age 20.5	
Perrin *et al.* (1976)	Eastern tropical Pacific/tuna seine fishery	1972	195		Highest in newly mature ♀'s; nearly *constant* in ♀'s > 12 GLGs		Apparent pregnancy rate *decreased* nearly linearly from 60% (8–10 GLGs) to 30% (> 15 GLGs		
Spinner dolphin (*Stenella longirostris*)									
Perrin *et al.* (1977)	Eastern tropical Pacific/tuna seine fishery	1971–75		Variable; data on post-reproductive females based on 536 ovary pairs	Apparently *constant* for first 10 years after first ovulation; then *declined*		Apparent pregnancy rate *decreased* after about 12 GLGs		1% of females classified as senile (see text). Apparent *decline* in fecundity with age. Data need re-evaluation because of technical difficulties as for *S. attenuata*
Harbour porpoise (*Phocoena phocoena*)									
Gaskin and Blair (1977)	Western north Atlantic/various	1968–73		Uncertain; total of 41 ♀'s examined	No significant correlation between corpora count and age				Inconclusive

Table 2

Summary of evidence relating to the presence of post-reproductive females in various mysticete populations All percentages rounded to nearest 1%. Corpora refer to corpora lutea (CL) plus corpora albicata (CA). All age estimates in years unless otherwise stated. Apparent pregnancy rate is porportion of mature females sampled which are pregnant not corrected for length of gestation. The number of whales sampled has been taken directly from published figures or tables whenever possible

Reference	Location/source of information or samples	Sampling period	No. mature ♀'s studied	Age-related changes in ovulation rate (no. of ovulations per year)	Changes in corpora-specific pregnancy rate	Changes in age-specific pregnancy rate/calving interval	Other information	Conclusions regarding presence of post-reproductive ♀'s
Blue whale (*Balaenoptera musculus*)								
Laurie (1937)	Antarctic/fishery	1934–36	1011		Data show *no* evidence of substantial *decline* up to maximum of 34 corpora			Inconclusive
Fin whale (*Balaenoptera physalus*)								
Laws (1961)	Antarctic/fishery	1925–54	Variable 900		% frequency of pregnancy or post-oestrus stages *does not vary significantly* between ♀'s with 0–40 to 50 corpora; may be some decline in animals with > 50 corpora		% of corpora which represented pregnancies *declined slightly* in females with > 30–50 corpora	No evidence for presence
Gambell (1976)	Antarctic/fishery	1955/61–1963/64	348	Ovulation rate *declined* from about 1 (♀'s which had been mature for 5 years); to 0.6 (♀'s which had been mature for > 30 years)			Gambell interpreted change in ovulation rate as a density-dependent response to whaling	
Lockyer and Brown (1979)	Iceland/fishery	1975–77	Uncertain; ovaries examined from 111 ♀'s	Apparently *constant* at 0.62				
Mizroch (1981)	Antarctic/fishery	1965/66–1977/78	Uncertain; 1556 ♀'s sampled	Some evidence of *decline* with age from 0.881 at age 11–20 to 0.49 at age 21–40. Low value of 0.131 for age 41–60 attributed to technical problems		Proportion-pregnant did not change significantly in the age range 11–>51		
Sei whale (*Balaenoptera borealis*)								
Gambell (1968)	Antarctic/fishery	1960/61–1965/66	476		Apparent pregnancy rate *constant* for ♀'s with 1–25 corpora			No evidence for age-specific climacteric

Table 2 *continued*

Masaki (1976)	North Pacific/ fishery	1952–73	904	*Declined* from 0.604 (♀'s age <23) to 0.438 (♀'s age >24). Ovulation rate *apparently close to 0* for small sample of ♀'s > 35 y. Mean annual ovulation rate apparently *declined* over age range 9–43	Apparent pregnancy rate *constant* (70%) for ♀'s <20 corpora; *rapidly declined* to 0 (♀'s >30 corpora)	Apparent pregnancy rate *constant* (70%) ♀'s age 40; may *decline slightly* (in older ♀'s (eg 55% at age 50)	
Rice (1977)	Eastern north Pacific/fishery	1959–70	100	Calculated as 0.70 over all age groups. Possibly slightly higher in ♀'s < age 25; *considerably less in old ♀'s*			
Lockyer (1978)	Iceland/fishery	1967–75	41	Assumed *constant* at 0.66			
Antarctic minke whale (*Balaenoptera acutorostrata*)							
Ohsumi and Masaki (1975)	Antarctic/fishery	1971/72–1972/73	Uncertain; total of 1359 ♀'s studied	Assumed *constant* at 0.866 from age 6 to age 28; may be *some decline* after age 28		Apparent pregnancy rate *almost constant* to age 50	No evidence for presence
Masaki (1979)	Antarctic/fishery	1967/68–1976/77	Uncertain; total of 11,423 ♀'s examined	Assumed *constant* up to 20; data suggest *some decline* after age 20			
Kato (1982)	Antarctic fishery	1971/72–1979/80	Uncertain; but very large	Assumed *constant* at 0.883 (all Areas combined) for age range 6–20; some evidence of change after age 20			
Humpback whale (*Megaptera novaeangliae*)							
Chittleborough (1959)	Australia/fishery	1950's	Uncertain; 287 ♀'s aged	Assumed *constant* at 1.1 (may be higher at commencement of a two-year cycle—Chittleborough 1965)			Inconclusive
Robins (1960)	Eastern Australia/fishery	1952–54	25	Assumed *constant* at 1.48			
Gray whale (*Eschrichtius robustus*)							
Rice and Wolman (1971)	California/ fishery	1959–69	Uncertain; total of 150 ♀'s examined	Assumed *constant* at 0.52			Inconclusive

DISCUSSION

Occurrence of post-reproductive females in the Cetacea

In view of the large sample sizes collected from fisheries of several species, there is surprisingly little absolute age–specific fecundity data available for cetaceans. However, the information to hand (Table 2) indicates that despite indications of an age-related decline in the ovulation rate of several mysticetes (e.g. fin whale—Mizroch, 1981; sei whale—Masaki, 1976; minke whale—Masaki, 1979), there is little evidence for a parallel reduction in the pregnancy rate.

We conclude that post-reproductive females probably occur rarely, if at all, in the populations of baleen whales that have been studied. However, it should be pointed out that the true situation could be masked by bias due to the protection of lactating females. The magnitude of this bias could be age–specific if lactation is prolonged in older animals.

In contrast, there is convincing evidence for a substantial age-related decline in fecundity in several (but not all) of the odontocetes studied, and for the presence of post-reproductive females in some species. The short-finned pilot whale had a significant post-reproductive stage in its life history in the population studied (Kasuya and Marsh, 1984; Marsh and Kasuya, 1984), and, as detailed in Table 1, there are indications that at least some populations of killer whales and false killer whales may be similar.

In other odontocetes (e.g. sperm whales—Chuzakina, 1961; Oshumi, 1965; Best, 1967; 1980; Gambell, 1972; spotted dolphins—Kasuya *et al.*, 1974; Perrin *et al.*, 1976; spinner dolphins—Perrin *et al.*, 1977; and long-finned pilot whales—Sergeant, 1962), the specimens on which the evidence for post-reproductive females is based need to be re-evaluated. However, it does seem that the fertility of at least some individuals declines to a low level after mid-life, even though the climacteric (if it occurs) may not be age–specific. For example in the sperm whale, reduction in fecundity is most marked in females with a high corpora count (Table 1); these whales are not necessarily extremely old (see Fig. 12, Ohsumi, 1965). It should also be noted that the corpora-specific pregnancy rate was a poor indicator of the presence of post-reproductive females, compared with both the age–specific ovulation rate and the age–specific pregnancy rate, in the population of *G. macrorhynchus* studied by Kasuya and Marsh (1984) and Marsh and Kasuya (1984).

Theoretical Considerations

Usually there will be no selection to maintain, and often selection will indirectly eliminate, post-reproductive stages (Hutchinson, 1978). However, as pointed out by Williams (1957) and Hamilton (1966), an obvious explanation for their existence is the factor of parental care. The vigour of the post-reproductive adult can be attributed to the beneficial effects of its continued survival on the survival and reproduction of its descendents. We would thus expect post-reproductive females to be more likely to occur in species in which the major burden of parental care falls on the females and in which the period of offspring dependence is long relative to both the lifespan and the modal birth interval. We would also expect post-reproductive females to be particularly important to species (like cetaceans) which bear one young at a time and have a low life-time productivity.

Table 3
Criteria used by different authors to classify female odontocetes as post-reproductive (senile). CL are corpora lutea; CA are corpora albicantia

Category	Sergeant (1962)	Perrin *et al.* (1976, 1977)	Marsh and Kasuya (1984)
Age	Not considered	Not considered	All ♀'s > 40 years irrespective of the status of ovaries or mammary glands
Ovarian status	CA numerous but regressed; follicles (if numerous) small and filled with yellow fluid	Small regressed ovaries, with 10 to 15 old CA; no CL or young CA; typically with very small Graafian follicles	♀'s < 40 years whose ovaries contained no CL, young or medium CA, or macroscopic (non-atretic) follicles
Mammary status	Regressed	Inactive	Either active or inactive
Uterus	Frequently cornified and with fluid-filled cysts	Not considered	Not considered

At least some of the odontocetes we have identified as exhibiting a marked decline in fecundity after middle age and which, therefore, have a greater or lesser proportion of post-reproductive females, do indeed have the characteristics outlined above. Sperm whales (Best, 1979), killer whales (Bigg, 1982), pilot whales (Sergeant, 1962; Kasuya and Marsh, 1984) and false killer whales (Purves and Pilleri, 1978) are all sexually dimorphic and presumably polygynous (Ralls, 1977). Male parental investment is therefore expected to be relatively low. Although the Stenellids are less dimorphic, there are no data to suggest that males are involved in direct parental care.

There is mounting evidence that the association between the mother (and/or other adult females in the school) and young can be long in some of these species. For example, Kasuya and Marsh (1984) studied the age composition of whole schools taken in the driving fishery for pilot whales and suggested that suckling might sometimes last up to eight years in females and 13–15 years in males. Best (1979) presented direct evidence of the suckling status of male sperm whale calves up to age 13. The mean length of lactation and mean calving interval in sperm whales (Best, 1968; Gambell, 1972) and short-finned pilot whales (Kasuya and Marsh, 1984) are certainly less than these extreme values. As both species probably begin to eat solid food when less than a year old (P. B. Best, pers. comm.; Kasuya and Marsh, 1984), the nutritional value of a long lactation may be limited. However, this prolonged lactation clearly indicates a long association between mother (and/or other adult females in the school) and offspring. The long-term behaviour work of Bigg (1982) provided compelling evidence that young killer whales remain associated with their mothers into adulthood even though the minimum birth interval observed (three years) was much shorter than the pre-reproductive period (more than seven years).

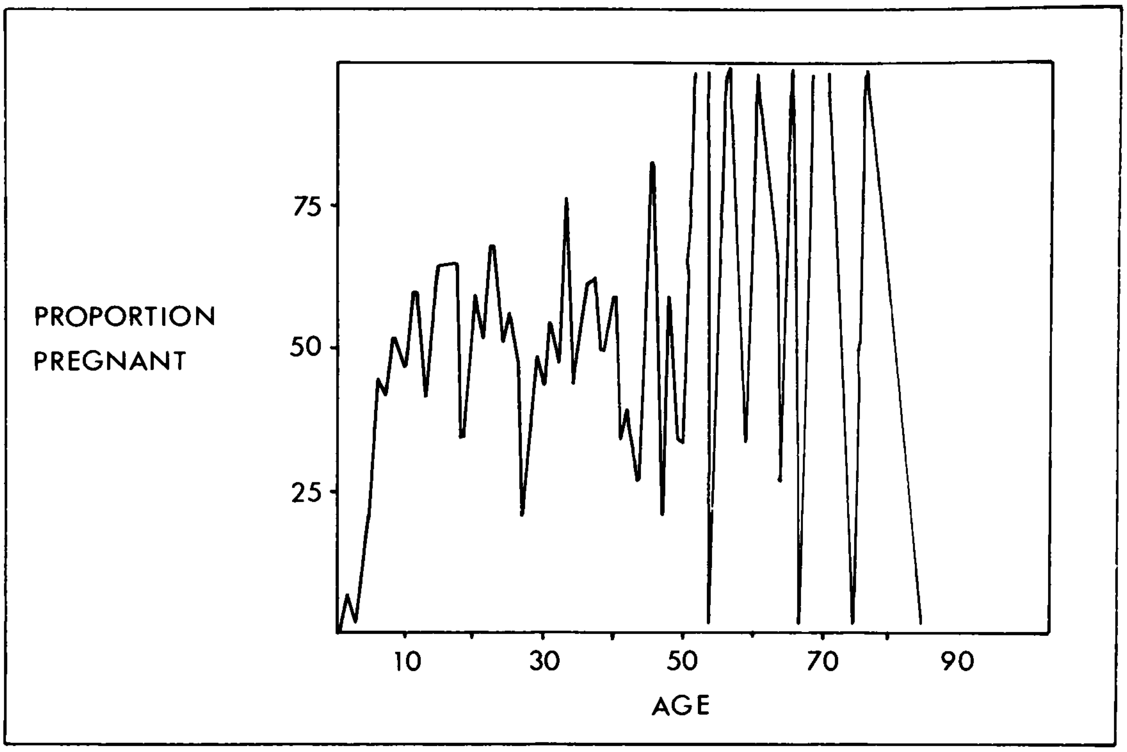

Fig. 1. Fin whale pregnancy rate (proportion pregnant) by age in IWC Area IV. Note that there is no evidence of an age-related decline. Reprinted from: Mizrooh, S. A. 1981. Analysis of some biological parameters of the Antarctic fin whale (*Balaenoptera physalus*). *Rep. int. Whal. Commn* 31: 425–34.

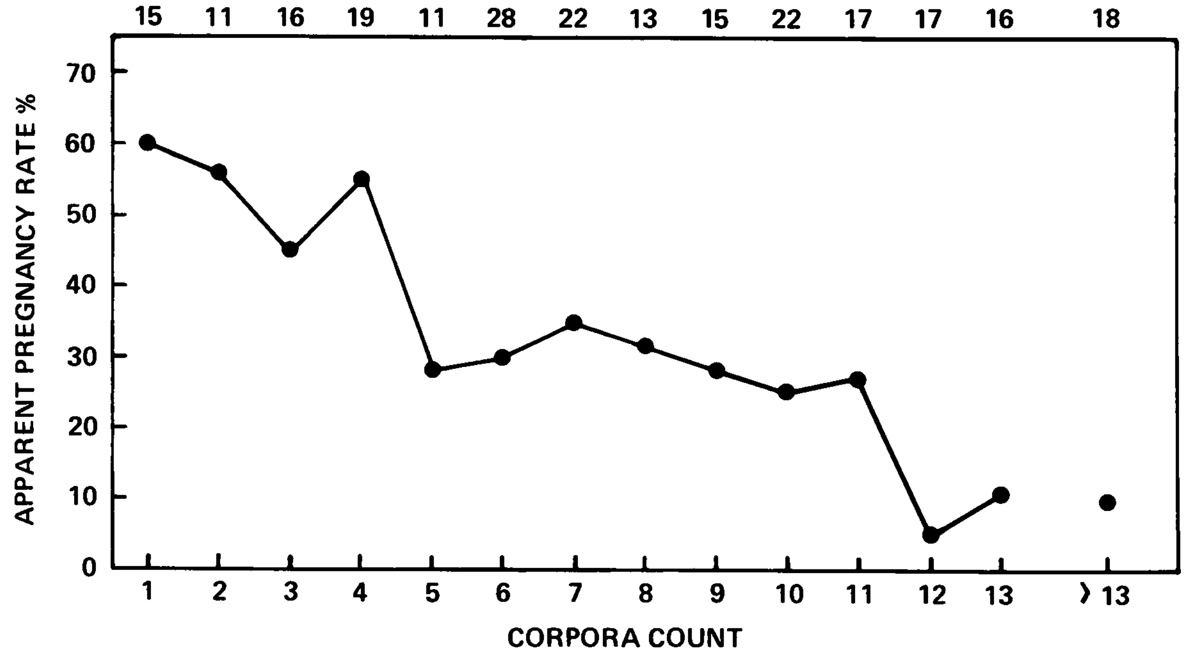

Fig. 2. Relationship between the apparent pregnancy rate and the corpora count in *Globicephala macrochynchus*. The numbers at the top indicate sample size. Note that pregnancies still occur in some females with a high corpora count.

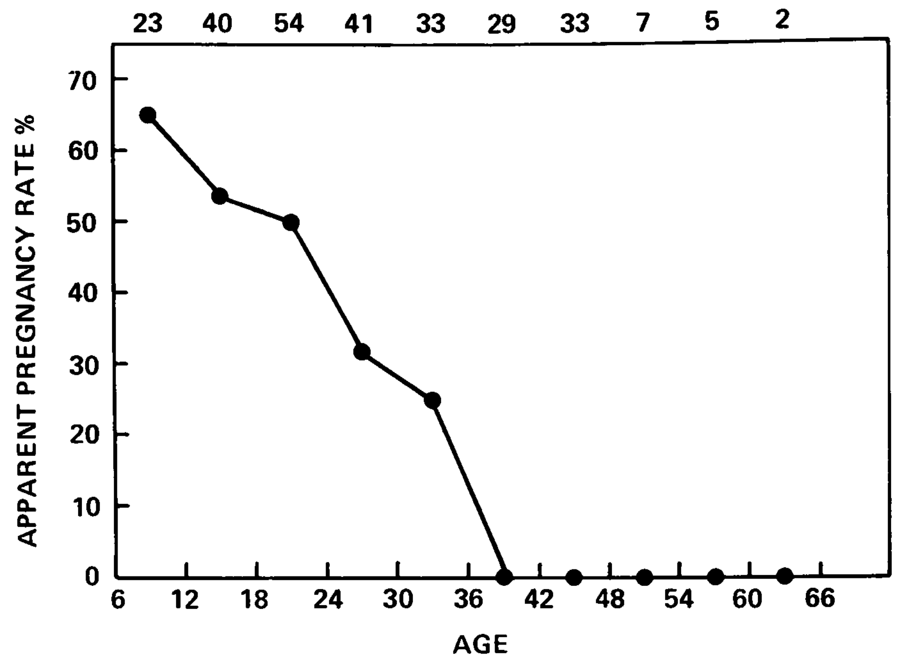

Fig. 3. Relationship between the apparent pregnancy rate of *Globicephala macrorhynchus* and age based on dentinal and/or cemental GLG counts. The numbers at the top indicate sample size. The data are from the same animals as those in Fig. 1. Note that none of the 76 females older than 36 years was pregnant. Data from: Kasuya, T. and Marsh, H. 1984. Life history and reproductive biology of the short-finned pilot whale, *Globicephala macrorhynchus*, off the Pacific coast of Japan. *Rep. int. Whal. Commn* (special issue 6): 259–310.

Post-reproductive females might also be expected to be more important to species in which the females live in stable, cohesive, kinship groups in which the survival of an old female might benefit not only her own offspring, but the offspring of other females (to whom she is also related) as well. Killer whales (Bigg, 1982), short-finned pilot whales (Kasuya and Marsh, 1984) and sperm whales (Ohsumi, 1971; Best, 1979) are thought to live in such groups. The school structure of spotted (Kasuya *et al.*, 1974), striped (Kasuya, 1972), and spinner dolphins (Norris and Dohl, 1980) seems to be more fluid, however nothing is known of the duration of sub-units within the schools, except that there is evidence that even female juveniles tend to segregate from the breeding schools at some stage after weaning (Kasuya, 1972; Kasuya *et al.*, 1974; Miyazaki and Nishiwaki, 1978; Kasuya, 1985).

Best (1979) pointed out that there are many similarities between the life history and the social structure of the sperm whale and the African elephant (*Loxodonta africana*). Elephants have a similar life span, produce one precocial calf at a time which is suckled for a prolonged period, are polygynous and live in stable, kinship groups. It is significant that post-reproductive female elephants have also been reported from wild populations (Laws, Parker and Johnstone, 1970; 1975).

A Strategy for maximum lifetime productivity

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 a post-juvenile phase characterised by an initially low but steadily increasing rate of mortality. The available evidence suggests that most female mortality patterns do conform to this shape (Ralls, Brownell and Ballou, 1980), but there are few data on the age–specific mortality rates of cetaceans. However, Kasuya and Marsh (1984) have shown that the mortality rate increases with age in adult female short-finned pilot whales

In species that produce few offspring during a lifetime and exhibit long lasting and overlapping maternal care for successive offspring, the death of the mother would substantially reduce the survival chances of several dependent offspring and, in species with co-operative care of young, the survival of other members of the group. In these circumstances, selection could be expected to favour females which terminate their reproductive life before the natural mortality rate rises steeply, particularly if reproduction in old age substantially increases the risk of mortality.

Changes in the role of an adult female with increasing age

With the inadequate data presently available and the different criteria used to identify females as post-reproductive (Table 3), we cannot make meaningful comparisons between different species or populations or within a population at different levels of exploitation. However, there are indications that the proportion of post-reproductive females can be very variable between populations of closely related species (e.g. long (Sergeant, 1962) and short-finned pilot whales (Kasuya and Marsh, 1984; Marsh and Kasuya, 1984); within a population before and after a period of intensified exploitation (e.g. sperm whales (Best, 1980; Holt, 1980)), and between different schools in the same population (e.g. short-finned pilot whales, Kasuya and Marsh, 1984).

Laws *et al.* (1975) pointed out that there were substantial differences between African elephant populations in the age of peak reproductive activity and in the proportion of inactive elephants. They claimed (without presenting supporting data on the age compositions of the populations involved) that the 'menopause' in elephants is density or habitat dependent. Eisenberg (1982) compared the age–specific mortality and fecundity curves (Croze, Hillman and Lang, 1981) and noted that the tenure of female African elephants in a post-reproductive state would be only a few years at best.

All these data suggest that post-reproductive females *per se* may not be of particular significance to their populations. Rather than focussing on the occurrence of reproductive senescence itself, we believe that it is more useful to examine changes in the role of an adult female as she gets older. In contrast to the situation in mysticetes where we have no evidence that this role does change with age, the duration of lactation seems to increase with maternal age concomitant with the drop in pregnancy rate in several odontocetes, e.g. sperm whales (see data of Gambell, 1972), short-finned pilot whales (Kasuya and Marsh, 1984), spinner dolphins (Perrin *et al.*, 1977) and striped dolphins (Kasuya, 1984). Thus these species appear to invest less in calf-bearing but more in calf-rearing with increasing maternal age and experience. This is in accordance with several evolutionary theories (see review in Clutton-Brock, Guinness and Albon, 1982) which predict that parents should invest more in their *current* offspring as their own potential for *future* reproduction fails. The scanty evidence that parental investment may increase with maternal age is summarized by Clutton-Brock (1984).

Calf-rearing in elephants is a cooperative effort. Although filial attachment seems to be present (infants tend to follow and remain close to their mothers even though they are in the company of other adult females (McKay, 1973)), calves are allowed to suckle from any lactating female in the group (Douglas-Hamilton and Douglas-Hamilton, 1975). We do not know whether communal nursing occurs in any odontocetes. If it does, it will provide definite evidence of an important role for older females who are spending an increasing proportion of their lives lactating. However, in the short-finned pilot whale population off the Pacific coast of Japan, most of the older adult females were classified as resting (Kasuya and Marsh, 1984). Behavioural studies are needed to determine the role of these animals in the school.

Pryor and Kang (1980) observed triads consisting of two adults with a small calf (estimated age 1–7 months) in schools of *Stenella attenuata* and *S. longirostris* encircled by purse–seine nets during tuna fishing. These triads were often composed of a young adult female, an older female and a calf. Pryor and Kang hypothesized that the presence of the two adults may have been necessary to assist in transporting young (but not neonate) calves during episodes of fast swimming (via the Bernouilli effect) and that providing such assistance may be an adaptive role for post-reproductive females.

The pattern of age–specific fecundity has evolved for each species to maximize lifetime productivity. In species that practise prolonged parental care and in which the care of successive offspring overlaps, the optimum strategy will be a continuous trade-off between investment in calf-bearing and calf-rearing. As discussed above, in several odontocetes (e.g. sperm whales, short-finned pilot whales, spotted and spinner dolphins), the young mothers seem to have the greatest investment in calf-bearing, the investment in calf-rearing increasing with age. Post-reproductive females have ceased to invest in calf-bearing, concentrating their energies on promoting the survival of their offspring and perhaps other members of the school as well.

Implications for the management of some odontocete fisheries

As discussed above, the females of polygynous, sexually dimorphic odontocete species in which fecundity seems to decline significantly after middle age, are either known to live in stable kinship groups or are expected to do so. Bigg (1982) has indicated that the effect of selective cropping on the reproductive rate of the killer whale (which definitely lives in such groups) seemed to have been limited to the pods which were cropped. In species such as sperm, pilot, killer and false killer whales, the removal of an entire pod or school such as occurs in a driving fishery, may not rapidly change the reproductive rate of the remaining pods or schools. The population reproductive rate may be expected to respond more rapidly to selective cropping from many schools rather than the entire removal of a few schools (Kasuya and Marsh, 1984).

The selective cropping of old females would be impracticable at present because of the impossibility of selecting them. If it were possible, it would remove females with a low reproductive rate and improve the population reproductive rate. However, it is also possible that the elimination of the accumulated 'cultural' information and experience of the old animals would reduce the survival of other members of the population. The net result of these two opposing effects is not known but we suggest that if cropping is to be practised it should not concentrate on the removal of old females.

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SC/A82/BW13[1]

DIURNAL RHYTHMS IN CETACEA—A REVIEW

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ABSTRACT

This review brings together information, of varying quality and from diverse sources, on rhythmic behaviour in cetaceans. Where data exist, regular diurnal activities are found in all Families. However, the question of whether such activities are regulated by internal biological clocks or are merely a reflection of prey habits has still to be resolved.

Whatever the underlying cause, diurnal organisation of behaviour might be a significant factor to be taken into account in population assessments based on catch-per-unit-effort or sightings surveys. If there are patterns of behaviour rendering animals more likely to be seen or caught at different times of day, temporal stratification of data may be required.

INTRODUCTION

Diurnal rhythms in many biological variables have been widely documented for many species of plants and animals and their circadian nature shown (Bunning, 1967). For the Cetacea, however, there have been rather few direct studies of diurnal rhythms and only one attempt to establish circadian periodicity (Hui, 1979). Some additional information can be gleaned from reports of whaling expeditions, from casual observations reported in little detail and from studies with other primary objectives. A further potential source of information in diurnal rhythms are whaling logbooks and field notes. The most apparent factor revealed by a literature survey is that the subject has been given little priority even in studies of captive animals. One reason for this apparent lack of interest is of course, the sheer practical difficulty in studying any aspects of the lives of these animals.

The general impression from the literature is that Cetacea, otherwise so perfectly adapted to their aquatic life, are entirely at the mercy of their environment in the organisation of their daily routine. Alternatively, their adaptation may have taken such a course that to have no fixed daily routine was the most advantageous way for a mammal to cope with life in the water. In either case a closer study of such unique plasticity would be of great interest to students of biological rhythms. Could there be a whole order of mammals with the circadian component of their biological clocks missing or inoperative?

The classical diurnal rhythm for study is the activity pattern—usually the gross resting/moving cycle. Can these aquatic mammals sleep or even rest, bearing in mind the need to rise to breathe at regular intervals and to maintain equilibrium in the water? Many prey species have marked diurnal rhythms in availability and perhaps apparent regular behaviour simply reflects the habits of the prey. It was with this in mind that I examined the available direct and indirect literature.

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[1] This paper was first presented to a meeting on cetacean behaviour and intelligence and the ethics of killing cetaceans in Washington DC, April/May 1980. In view of the lack of attention given to its subject it has been published here to stimulate discussion, although it only deals with literature up to 1982.

SLEEP

Until recently, the only information on sleep in cetaceans came from accounts of large whales apparently sleeping on the surface (with no details of time of day), for example in Christiansen (1962) or the review by Slijper (1979). Work on the electrophysiology of dolphins, mostly in the USSR, has now revealed some very interesting details.

Captive bottlenose dolphins (*Tursiops truncatus*) were implanted with electrodes and kept free-swimming in a tank for long periods—up to several months (Mukhametov, Supin and Polyakova, 1977; Supin, Mukhametov, Ladygina, Popov, Mass and Polyakova, 1978). Electroencephalograms (EEGs) and other electrophysiological activity were recorded. Supin *et al.* (1978) reported the waking state to be characterised by high frequency, low amplitude electrical activity and 'slow' sleep by low frequency, high amplitude rhythms. Stages of drowsiness (an alpha-like rhythm), light sleep (sleep spindles) and deep sleep (theta and delta activity) were distinguished. No 'rapid eye movement' sleep stage was identifiable because the usual physiological criteria are not applicable to dolphins. There was no prolonged and complete relaxation of skeletal muscles in any phase of sleep, since for respiration the animal must continuously maintain its position. Sleeping and waking states cannot be determined in dolphins on the basis of visual observation of the animals' mobility alone, since on occasions they were almost completely motionless while awake (on EEG criteria) and slight movements of the fluke and head were normal during sleep. The entire set of breathing movements could take place during 'slow' sleep hence revealing that the respiratory act does not require the dolphin to be awake. Sleep occurred under these experimental conditions at night.

Perhaps the most surprising finding was that the two brain hemispheres could generate synchronised (i.e. all electrodes registering similar patterns) and desynchronised EEG patterns *independently* as well as *simultaneously*. One hemisphere may show large-amplitude slow waves at three points while the other shows low-amplitude fast activity at corresponding points. The cycle became more marked after sleep deprivation. Similar findings, but based on only one night of recording, have been reported for another delphinid, the pilot whale, *Globicephala scammoni*[1] (Serafetinides, Shurley and Brooks, 1971–72; Shurley, Serafetinides, Brooks, Elsner and Kenney, 1969).

Koval'zon (1978), again using *Tursiops truncatus*, confirmed these epochs of asymmetry and found, using implanted electrodes, that temperature is also asymmetrical in the brain at these times. Large amplitude slow waves were associated with a more fluctuating thermogram and the hemisphere was slightly cooler. The other side, with low-amplitude fast activity, had a flat thermogram and was usually slightly warmer. Stage three sleep, with at least two-thirds of each scoring epoch occupied by delta waves of maximum amplitude, was only recorded unilaterally. Bilateral delta waves were only observed during barbiturate anaesthesia, when spontaneous breathing stopped. Thus bilateral 'slow' sleep is compatible with respiration, but unilateral deep 'slow' sleep appears to be incompatible.

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[1] There is some controversy over the taxonomy of pilot whales. Some believe there to be only one warm/temperate water species, *Globicephala macrorhynchus*, others treat the animals in the North Pacific as a separate species, *G. scammoni. G. melaena* is found in colder waters of all oceans except the North Pacific.

At least the bottlenose dolphin and the pilot whale seem to have solved the problem of sleep and to sleep at night (although see below), under experimental conditions. In spite of the caution by Supin *et al.* (1978), that sleep cannot be determined by observations alone, this is the only available method for most species for the forseeable future. Observational evidence is also needed to determine if this 'sleep' behaviour and its timing is real or an artefact of the experimental conditions.

RESTING BEHAVIOUR

McCormick (1979), comparing *Tursiops truncatus, Lagenorhynchus obliquidens* (Pacific white-sided dolphin) and *Phocoenoides dalli* (Dall's porpoise), in captivity, observed two kinds of resting behaviour in the first two species. In one, called by him a light sleep phase, the animal rested on the bottom for perhaps four minutes, then surfaced to breathe. In the other, a deeper phase, the animal maintained itself at the surface for prolonged periods, breathing in an automatic fashion. If this automatic behaviour is the equivalent to the sleep described by Supin *et al.* (1978), then another species can be added to the list of known sleepers. In contrast, the Dall's porpoise showed no such resting at any time. Unfortunately, neither the time of day nor the lighting regime were noted. Recently, McCormick recalled (pers. comm.) that the three species showed a graded resting behaviour, which he related to natural habitat and/or to adaptation to captivity. The most inshore species, the bottlenose dolphin, had adapted best to captivity and showed resting behaviour most clearly; the most oceanic species, the Dall's porpoise, had adapted very poorly and showed no resting behaviour; the white-sided dolphin, which occupies an intermediate habitat, had adapted fairly well but showed less resting behaviour than the bottlenose dolphin. He noted that most observations were made during the day.

In the field, however, Dall's porpoises have been observed to vary their daily activity. Morejohn (1979) gave considerable details of their behaviour and reported a 'period of quiet' with gentle respiration from mid-morning to mid-afternoon when the animals may have been sleeping. This contrasted with more active swimming, splashing and playing around the boat in the early mornings and late afternoons. Ridgeway (1966), described an early attempt to keep these porpoises in captivity and noted that they were hungrier and more active at night. They were also more responsive to training at night, fairly responsive in the early morning and least responsive at mid-day and in the early afternoon.

The above reports suggest that although variations in behaviour are seen when a species is studied alone, it is often in comparative studies that qualitative differences emerge. The importance of the conditions of captivity is also shown.

Pilot whales

Kritzler (1952) describes three newly captured *Globicephala macrorhynchus* as showing a nocturnal rhythm, feeding at night and sleeping during the day. This is in contrast to the *G. scammoni* report referred to earlier (Serafetinides *et al.*, 1971–72; Shurley *et al.*, 1969), which showed the EEG sleep pattern at night. Sergeant (1962), describing *G. melaena*, a different species inhabiting colder waters (Mitchell, 1975), found 'no evidence of diurnal feeding in the wild', but went on to describe daytime feeding close inshore on Sundays when no hunting took place and five herds thought to be feeding at the time of interception which varied between 07.00 and 11.30 hours. Slijper (1979) mentions pilot whales (species unspecified but probably *G. scammoni*) at Marineland aquarium, California, as being nocturnal when first captured. The one which remained for nine months gradually became more active during the day, adapting itself to the routine, but returned to nocturnal activity after the other dolphins (species unspecified) began to attack it. Another pilot whale 'slept' both by day and night. Whistles of *G. melaena*, sampled in the field, varied significantly with time of day, i.e. the midnight sample differed from the midday sample from the dusk sample (Taruski, 1979).

These reports suggest that pilot whales do have a diurnal activity rhythm. *G. macrorhynchus* appears to be active at night. Although the only example of a recorded sleep pattern is for a *G. scammoni*, and was displayed at night, the report of the captive animal at Marineland shows that this may have been due to acclimatisation in captivity. There is other evidence of behavioural plasticity in captivity and of individual differences in rhythmic behaviour. Brown and Norris (1956) reported *G. scammoni* in the wild to be dispersed in scattered feeding groups during the day but to travel together at night. *G. melaena*'s pattern is unclear.

The common dolphin

The common dolphin, *Delphinus delphis*, has been studied in the wild using radio-telemetric methods (Evans, 1971; 1982). The earlier study described long dives during the night, with groups stopping to 'mill' and possibly to feed around sunset and noon. The later study, however, revealed that the deep diving behaviour was in fact feeding behaviour. The prey species migrate to the surface after sunset and their level in the water column can be followed with acoustic instruments. On days when the ambient light level is reduced by fog or heavy overcast, the prey does not descend completely during the day and diving patterns similar to those normally observed after sunset continue intermittently during the day. But what does the 'milling' behaviour represent? Is it some form of resting? Are Brown and Norris (1956) correct in interpreting the grouping of *G. scammoni* at night as 'travelling', might they not also be resting?

A recent report by Hui (1979), of which only the abstract was available, described the only attempt so far located to test the circadian basis of activity in fairly constant conditions. He stated that in the wild, *Delphinus* are active at sunrise and sunset, showing minimal activity at midday. The behaviour of two captive, fasting animals, undisturbed during any of the 4-day experiment, except for sampling blood at 14.00 hours daily, was recorded on videotape. The average speed of each animal was computed for each half hour and showed random distribution. Tests for autocorrelation showed no periodicity of 12 hours or less. It was concluded that the diurnal pattern of swimming speed observed in the wild is not endogenous but reflects other rhythms for which the entrainment cues were absent in this experiment. However, on the basis of the abstract information, this seems a badly designed test for rhythmic activity. Not only were the animals fasting (many studies on other species have shown that this disrupts activity patterns, especially in the first few days e.g. Krieger, 1974; Bolles, 1963; Strong, 1957) but they were also subjected to blood sampling at a fixed time which must have had a disturbing effect. It would be interesting to know about the behaviour the day after this experiment ended, in view of the report by Supin *et al.* (1978) that sleep rhythms were more marked in *T. truncatus* after 60 hours of sleep deprivation. Would the animals have been 'catching up' on sleep? Or would they perhaps have been 'resting' during the fasting experiment as increased resting can be an effect of food deprivation (Bolles, 1963).

TIDAL RHYTHMS

These studies documenting either the presence or absence of tidal rhythms are inconsistent and it may be that the habits of the human observers or captors, based as they are on the solar day, are a confounding factor. Very many marine and other organisms exhibit tidal or lunar day rhythms, which persist in captivity even under seemingly unpromising conditions (Palmer, 1976; Klinowska, 1972). Tidal or lunar day activity is very rare in human groups so that if such rhythms are observed in animals there is usually good reason for accepting them as genuine and not entrained by observers.

Before comparing studies of tidal rhythms in cetaceans, a further excursion into taxonomy is necessary. There appear to be two main forms of the bottlenose dolphin, *Tursiops spp.* A large form, in general found in colder waters, is usually known as *T. truncatus*, while a smaller form from warmer waters often goes by the name of *T. aduncus*. The North Pacific populations, however, are sometimes described as *T. gilli.* Most field studies of *Tursiops* activity have been made close to shore.

Schevill and Backus (1960) refer to observations made during January 1954 of *T. truncatus* following a tidal routine off St Augustine, Florida. At low water they remained in the bay, as the tide rose they went up rivers and creeks with it so that at high water almost none were left in the bay, but by low tide they had returned. This is presumed to be a response to the tidal movement of prey. McBride and Hebb (1972), Irvine and Wells (1972) and Caldwell and Caldwell (1972) describe similar movements. Hoese (1971) gives a graphic description of *T. truncatus* fishing at low tide in a salt water marsh. The dolphins chased fish until their bow waves washed the fish onto a muddy bank. The dolphins then slid out of water and seized the prey. This particular behaviour had to be limited to about 30 minutes before or after low tide otherwise the mud bank was inadequately exposed.

In contrast, Saayman, Tayler and Bower (1973) noted no tidal component in the activity of *T. aduncus* in the wild or in captivity. In the wild these dolphins were most frequently seen in the early morning and late afternoon. Almost no sightings were made beween 13.00 and 14.00 hours, the times when captive mammals showed most activity. Feeding took place in the early morning and late afternoon in captivity. Tayler and Saayman (1972) describe the acclimatisation of newly caught '*T. truncatus*' (later papers make it clear that these are the same animals as those later described as *T. aduncus*). For the first few days they were constantly on the move. After about two weeks they began to remain stationary at night and after a further two weeks or so to swim more slowly by day. The authors suggested that no similar pattern of cessation of movement occurs in the wild. This is interesting in view of the reports of *T. truncatus* behaviour in captivity. It is surprising that no authors report either tidal, lunar day or month timing in captive *T. truncatus* in view of the number of reports of tidal behaviour in the wild, although Saayman and co-workers are the only group to have reported making a specific study.

The humpbacked dolphins, *Sousa spp.*, of Robbe Berg Point have also been studied in the field and in captivity by Saayman (1979). Most observations could only be made during daylight, but limited observations on the captive animals suggested that social interactions might occur quite frequently at night, particularly during the period of full moon. Activity in the wild seemed to depend more on the tidal cycle than on the time of solar day, but feeding periods did reveal a tendency to be longer in the early part of the day than at midday and in the afternoon. Their entire schedule, however, in the wild seemed based on the primary effect of the tides on feeding activity.

This emphasis on tidal based activity and even a suggestion of lunar timed behaviour in captivity, is impressive, particularly as the studies are based on several years of observations and subjected to statistical analysis. No less so are the observations on *T. aduncus* which frequented the same bay but showed no overt tidal timing. Since all other field studies examined emphasised the tidal feeding habits of *T. truncatus* in the field, this suggests either that *T. aduncus* has in general different rhythms or that these *Tursiops* have adopted different feeding habits in this area, because the inshore tidal feeding is exploited by *Sousa.*

Some species do appear to exhibit tidal behaviour in some situations in the wild but not in others. Würsig (1982) studied the dusky dolphin, *Lagenorhynchus obscurus*, by radio tracking and found that while travel direction of animals in the study bay was influenced by strong tidal currents—travel being with the currents at almost all times—animals more than 20 km from the mouth of the bay did not seem affected in this way by the tides. At night (00.15 to 00.45 hrs and 04.15 to 04.45 hrs samples) significantly shorter dives were recorded than during daylight hours. Peaks of long dives occurred during the 12.15–12.45 hrs and 16.15–16.45 hrs samples, and the number of long dives also increased around sunset or dusk. It appears that although the animals' direction of travel was influenced by the tides in some areas, the overall activity pattern was based on the solar day.

Kleinenberg, Yablokov, Bel'kovitch and Tarasevich (1964) referred to the apparent dependence of the white whale, *Delphinaterus leucas*, on the tides. In the White Sea it passed nearshore only at high tide and remained 2–3 km away at other times. It only entered rivers at high tides. The largest numbers of white whales were observed migrating along the shore during the period of high spring tides, more animals migrating at the beginning and end of this period than in the middle. The daily tidal habits are probably concerned with feeding since fish species taken are found inshore in large concentrations at high tide and deep water gives access to the shallows where benthic organisms, another food item, are found. Perhaps the most convincing evidence of tidal rhythms comes from the Gulf of St Lawrence where it is reported that traps were designed based on knowledge of the tidal movements of the animals.

The narwhal, *Monodon monoceros*, inhabits almost the same waters as the white whale, but no reports of any tidal behaviour were found. Both species have been kept in captivity, but their activity does not seem to have been studied (Mitchell, 1975). This may be an example of two species sharing similar habitats through variations in behaviour patterns and warrants further study.

Not all cetaceans encountered feeding near shore show tidal patterns. For example, a large humpback whale, *Megaptera novaeangliae*, seen by Schevill and Backus (1960) over a period of ten days, was usually contacted near 13.00 to 14.00.

If it had kept a constant relation to the tides it would have appeared seven hours later by the end of the observations period. The whale appeared to be feeding.

One study points to the possibility of a lunar rhythm in a deep water species, the sperm whale (*Physeter macrocephalus*). Holm and Jonsgård (1959) investigated the belief of many whalers that sperm whale catches were related to moon phases, using information from Norwegian Antarctic whaling expeditions between 1950 and 1956. The catch per catcher for each season did not show any obvious relationship to the moon phases, but if only days with 'very large' (40+) catches were considered, most were found to occur at full and new moon. When days with a minimum of thirty whales per expedition were taken the pattern is much clearer, with the largest concentrations appearing around new moon. The authors also took the positions of the expeditions during the season into consideration by comparing whaling activity on the banks and in deep water. On average, activity was less at the banks than in deep in water, although bank whaling had given the largest yield at all phases of the moon. A small number of effective catcher days work (CDW) on the banks had resulted in a larger number of sperm whales caught per CDW, except under a waning moon. Large daily catches were more frequent near the banks.

Even setting aside any methodological criticisms, interpretation of this report is difficult. The whales may move to the banks and congregate there towards full moon, possibly because the tides made food more available there at that time. This implies that the whales have some means of monitoring the lunar month. An alternative explanation, particularly in view of the whalers' beliefs, is that the expeditions may have simply moved to the area at certain times of the lunar month, although the whales were equally available in all areas. This is not entirely satisfactory, as it seems unlikely that the whalers' belief has no foundation at all and the whalers would not move away from the banks if there were not times when the whales were not so plentiful. It would be interesting to see if the data warrant a statistical analysis and to examine and compare the data with the records of other expeditions.

If this lunar relationship of catches is substantiated, this has some relevance to studies involving effort data: (a) CDW would not be equivalent in terms of potential yield from one moon phase to another and from deep water to banks; (b) the number of full moon phases per season would need to be taken into account as would the moon phase and position of the expedition for days lost during a season.

DIURNAL ACTIVITY IN FRESHWATER SPECIES

Most Platanistidae, and some Delphinidae and Phocoenidae inhabit freshwater. The available literature suggests little difference in general in the occurrence of diurnal activity patterns between freshwater and marine species.

Layne (1958) and Layne and Caldwell (1964) described the activity of the Amazon river dolphin, the boutu (*Inia Geoffrensis*), in the wild and in captivity. While the dolphin was seen at nearly all hours, it was more in evidence in the early morning and late afternoon than at midday. There was a marked movement from the river to adjacent lakes from daybreak until 09.00 hrs but no observable peak in the opposite direction—the dolphins appeared to straggle back irregularly. There may have been movements at night, but these could not be observed. Respiration sounds indicated nocturnal activity. In captivity no marked diurnal cycle was noted, although observation by night was rare. Sleep-like behaviour was described during the day.

The activity of the Indus susu, *Platanista minor*, in captivity is described by Pilleri, Gihr and Kraus (1971). As the optical apparatus is much reduced in this species, the frequency and duration of sound emitted was taken as a measure of activity and recordings made over 24 hour periods. The two animals, a male and a female, were in separate tanks. An active and resting stage could be distinguished. The female was active from 18.00 to 03.00 hours and the male from 01.00 to 14.00. Fish food was given between 17.00 and 18.00 hours but consumed only during the night. Complete quiet (pump switched off, no outside noises) and darkness were needed for hunting to take place. The differences between periods designated 'active' and 'resting' were small, but clear. However a quantitative analysis should be undertaken and information on the exact lighting cycle provided. This study shows that careful recording of activities over 24 hours may reveal periodicities not easily apparent from short visits during the daytime. Herald, Brownell, Frye, Morris, Evans and Scott (1969) also describe the behaviour of a captive specimen. Their study revealed the eye to be a light gatherer rather than an image resolver; the animals showed no reaction to drastic changes in light intensity. Sound emission was monitored for 16 hours and no periods without sound were noted but this period was probably too short to reveal any small diurnal differences such as those noted by Pilleri *et al.* (1971).

Herald *et al.* (1969) noted that a boutu in an adjacent tank responded to reduced light intensity by more frequency sound emission. This is perhaps to be expected in a species with more developed eyes and is comparable with Powell's (1966) finding that the light–dark cycle influenced the incidence of vocal activity in *T. truncatus*. Although Herald *et al.* (1969) failed to demonstrate a change in sound emission in response to abrupt lighting changes in the Indus susu, Pilleri *et al.* (1971) noted that darkness was one of the required conditions for hunting activity. Their report also incorporates the only observation of a sex difference in activity pattern found in the literature, although further study is needed to see whether this is a true sex difference or merely two individual responses.

The freshwater delphinid, the tuxuci (*Sotalia fluviatilis*), also from the Amazon, is described as having a similar activity pattern to that of the boutu (Layne, 1958).

INFORMATION FROM WHALING OPERATIONS

This section is mainly concerned with the large baleen whales and the sperm whale. A large proportion of the literature on these species is concerned with topics relevant to whaling and to its management and very few studies have been made without the cooperation of whaling operations. In general, diurnal rhythms have received even less attention for harvested than for non-harvested species. Interpretation of any data is difficult without detailed information on the whaling operations and it is often not possible to separate genuine animal rhythms from artefacts caused by operating priorities or routines.

Diurnal activity of the Antarctic sperm whale was studied by Matsushita (1955), based on catch records and details of stomach contents for the 1953–54 season. Most helpfully, and unusually in cetacean literature, he provided a diagram showing daily duration of light, civil twilight, astronomic twilight and darkness at 60° South Latitude. At this latitude, astronomical twilight lasts all night during most of the catching season and it is only towards the end, in the latter half of March, that there are some hours of full darkness. This makes Matsushita's terms 'night' and 'day' somewhat imprecise. It is quite clear from a diagram of catch frequency for one ship in 1953–54 and from a table showing catches by the same ship in 1951–52 and 1952–53 and by another in 1952–53 and 1953–54, that fewer whales were caught at 'night' and that this is true for each ship each season. Whether this is an artefact of work routine is impossible to tell from the information given. Between 22.00 and 02.00 hrs, catches were low for all years and for all ships. Between 03.00 and 07.00 hrs the catch approximately doubled and increased further from 08.00 hrs to a peak about midday. Catches decreased slightly through the afternoon and evening and sharply after 21.00 hrs. Animals caught during the 'night' had full stomachs more often than those caught during the 'day'. Matsushita concluded that sperm whales feed during the 'night', diving deeply for their squid prey. A dive could take an hour or more, with pauses at the surface between long dives for respiration. During the day the animals are thought to remain near the surface and not move so actively.

Ohsumi and Satake (1977) studied sperm whales caught off the coast of Japan and found quite a different diurnal picture. These animals appeared to feed in the afternoon and to some extent in the early morning. A table indicated that more animals were caught in the early afternoon and mid-afternoon than at midday.

Lockyer (1977) found that the average depth and duration of dives in sperm whales off Durban, South Africa, showed an increasing trend in the evening compared with the rest of the day. The number of whales in a group diving together tended to increase during the day, groups in the evening being almost double the size of groups in the morning (although the 95% confidence limits indicate some overlap of mean ranges of group size). These observations related only to 9.5 to 10.9 m size whales, the only studied size category with sufficient data for examination. As this study is based on four seasons work, and almost 1,000 dives are reported in another section, the possibility that different size categories have different diurnal patterns of behaviour should be considered.

The above information, combined with the possible lunar related behaviour discussed earlier, reveals the sperm whale to show many of the expected characteristics of an animal with circadian timing. Although the detailed diurnal activity is different at different latitudes the patterns are similar, suggesting day length has some relation to behavioural organisation. An extension of these studies to night hours using sonar to detect activity would be useful.

Before considering reports of diurnal behaviour in the baleen whales, the diurnal habits of their principal food resource in the Southern Ocean, the krill (*Euphausia superba*) need attention. Marr's (1962) study revealed the life stages which form the principal food to have a fairly limited diurnal vertical movement. At night, they are mainly in the top 5 to 10 m of water while during the day they may migrate to depths of 40–50 m—not outside the range of baleen whales.

Ivashin (1961) reports on the periodicity of humpback whales (*Megaptera novaeangliae*) feeding in the Southern Atlantic. A diagram shows that whales caught in the early morning almost all had full or more than half full stomachs, while in the afternoon the proportion fell to below half and by 21.00 to 22.00 hrs almost all had empty stomachs. Within this overall pattern there was evidence that the whales may have taken food every three to four hours during daylight hours, at least in February. Ivashin speculated that meal frequency might have varied with available daylight hours, giving a maximum of six meals in January and a minimum of four in March. The observation that humpbacks do not feed at night is interesting in view of the habits of the krill and may reflect a preference by humpbacks to feed at deeper levels rather than on the surface.

Nishiwaki and Oye (1951) reported a tendency for baleen whales caught in the afternoon in the Antarctic to have empty stomachs and that fin and blue whales were early morning feeders. Marr (1962) also noted a tendency for early morning feeding in baleen whales in the North Pacific, with lower activity during the day and an increase in the evening. He noted that the gunners of the Arranmore Whaling Company, County Mayo, Ireland, used to maintain that the baleen whales they hunted were most plentiful on the surface at sunrise.

Nemoto (1959) ascribed all apparent diurnal patterns in whales to movements in prey species. For example when feeding on the euphausiid *Thysanoessa raschii* or on capelin (*Mallotus catervarious*), fin whales followed their migrations and showed the same marked rhythm. When feeding on the copepods *Calanus crustatus* and *C. plumchrus* the rhythm was less clear reflecting that these food species do not show marked diurnal migration in their summer forms which inhabit the upper water layer.

There is perhaps a way to resolve the question of whether baleen whales have marked diurnal rhythms or whether they are simply following those of food species, because these whales feed for part of the year and eat little during the winter sojourn in warmer waters. A comparison of behaviour during winter with that during summer feeding should serve to disentangle the feeding and the overall activity rhythms, if any.

Information on diurnal habits in baleen whales may be contained in whaling logbooks and journals, if they render whales more likely to be seen at certain times of day (e.g. by spending more time at the surface). To test this, a preliminary study of three voyages made by Captain Milne to the Davis Strait, using a microfilm copy of the logbooks in the Scott Polar Research Institute, Cambridge (MS 1159) in 1982, 1982 and 1983 was made. It is possible to collect sightings times and boat lowering times and construct daily activity patterns for each species. How far this gives an accurate picture requires further study, since recordings may not be complete, ship routines may preclude some sighting times and so on. Consideration might be given to adding another category to the recommended recording cards for analysis of old whaling records for time of event to facilitate such studies (IWC, 1983).

Modern whaling logbooks are required to contain details of the time of day each whale is caught, under IWC regulations although exact details of the timing of a single catcher do not seem to have been published. Some data are available, however. For example, Hylen and Holm (1965), using details from Norwegian whaling expeditions, worked out a theoretical catcher day, assumed to last from sunrise until the end of civil twilight or to midnight in high latitudes in summer and provided a nomogram to assist future studies where date and latitude are known. Their diagram, showing times when the first and last whale of the day were taken, is interesting in that the first whale was always taken at least an hour after sunrise in the high summer months of December and January and often three or four hours later. The last whales, in contrast were mostly taken between sunset and the end of civil or nautical twilight, whichever was the later. Is this a reflection of the habits of the whales or of those of the whalers? Do whalers prefer to work into the evening and begin work well after sunrise or are they following the habits of the whales?

Modern observations of whales may also yield information in diurnal activity.

For example the counting of bowheads in Alaska, which takes place every year and involves great effort to maintain continuous vigils (Braham, Krogman, Johnson, Marquette, Rugh, Sonntag, Bray, Brueggeman, Dalheim, Nerini and Savage, 1980). A figure from this report showing six hourly counts over a 19 day period looks as though some periodicity in appearance exists. A rough check of the counts showed the possibility of a small diurnal component, although tidal, weather and other factors may prove to be more important.

DIURNAL PATTERNS IN GROWTH LAYERS IN HARD TISSUE

One rhythm which cetaceans do show, in common with many other animals, is that of the growth of hard tissue. Growth lines in teeth, baleen and ear plug have been used for estimating the ages of many cetacean species (e.g. see IWC, 1980). These layers seem to be the result of some basic process since they are found in cetaceans kept in captivity as well as those living in the wild. They are not simply, for example, reflections of seasonal feeding. Using a petrographic microscope, which reveals changes in the crystallographic alignment, Myrick (1980) found very detailed fine layers in the teeth of the dolphin *Stenella attenuata*. In adults, the prenatal dentine contained 240 striae of Retzius, which are thought to represent daily records of prenatal growth, after the formation of the tooth. Postnatal dentine showed 13 regularly spaced accessory layers in each of the first five of six growth layer groups. These accessory layers were thought to reflect lunar cycles and each contained an average of 29 microlayers (lines of von Ebner) that may represent daily growth increments. The proposed lunar monthly layers corresponded well with the known ages of two specimens. If this method proves to be generally applicable, it gives a powerful, if somewhat tedious method of following life events.

CONCLUSION

In the introduction to this review a number of questions about rhythmic behaviour in cetaceans were posed. Evidence of varying quality has been assembled, which taken as a whole suggests that in all Families where data exist regular diurnal behaviour occurs. In two species details of the mechanism of sleep have been obtained. There is also some indication that differential diurnal behaviour may enable two species to exploit the same or very similar habitats without conflict. Solar day, tidal, and possibly lunar monthly patterns have been reported. Within species there are individual differences in behaviour, particularly in captivity, and the possibility of sexual differences cannot be ruled out.

The effects of the behaviour of prey species on diurnal organisation may be difficult to identify, particularly if prey with different behaviour patterns are taken in the same area. At least in baleen whales with an annual feeding/fasting cycle it should be possible to resolve this problem using studies during the fasting period for comparison. Studies of the smaller species might be made in captivity by varying feeding schedules.

Diurnal organisation of behaviour, whatever its underlying cause, ought to receive more attention in harvested species to determine if it is a significant factor to be taken into account in assessment techniques. Current assessment of whales depends very much on sightings surveys and assumptions of relationships between stock size and catch-per-unit-effort. If whales have diurnal rhythms in activity which render them more likely to be seen (or caught) at certain times of day, then temporal as well as spatial stratification of data may be required.

Perhaps, now that the subject has been reviewed in general, some of the detail needed—times, dates, places and lighting regimes—will be forthcoming so that even casual observations can be fitted into the overall picture. If the formidable practical problems can be overcome, it may be possible to explore the circadian parameters which must now be assumed to underlie the organisation of the diurnal patterns.

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NON-ACOUSTIC COMMUNICATIVE BEHAVIOR OF THE GREAT WHALES: ORIGINS, COMPARISONS, AND IMPLICATIONS FOR MANAGEMENT

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ABSTRACT

In small cetaceans, as in terrestrial mammals, some physical actions appear to serve a social, communicative function. These 'display' behaviors, including breaching, slapping the tail on the water, and emitting shaped bubble clusters, can communicate internal states such as fear, affiliation, aggressiveness, or annoyance. While many species of great whales exhibit similar behavior, the communicative functions of these actions in whales, if any, are not generally known. The author selected eleven behavioral displays that occur in small cetaceans for which specific communicative functions are known from captive studies. The author then surveyed a group of investigators studying great whales in the wild, to see if (a) the behaviors selected had been seen at all, and if so, in what species; and (b) if the investigator could ascribe a socially communicative function to such behavior. Every behavior had been seen in at least one species; some, such as breaching, in many. In eight of the eleven behaviors one or more observers reported communicative contexts and functions in whales as being similar to those seen in dolphins, in at least some circumstances, i.e. tailslaps in the presence of a disturbance.

Such signals may be useful management tools, for example as indicators of undue disturbance of whales by human intrusion. Survey results are presented in a table.

Every overt or perceivable behavior that a social mammal engages in may be said to be communicative, in the sense that the behavior can convey information to conspecifics. If I see you, a member of my species, engaged in eating, I know at once that food suitable to my needs is probably present in the environment. If I see or hear you belch, I know that you have eaten—and possibly I know a great deal more: that you may have over-eaten; that you may have eaten somewhat indigestible food; that you have eaten but may now be under stress, so that you are not digesting well and are consequently likely to be in a bad mood, and so on.

So it is with the great whales. Small, perhaps inadvertent actions of the individual, such as a change in respiration rate, a sudden move of flukes or fins, or even a change in the set of the eyelids, may convey information to other species mates and thus constitute communication. The absence of such changes is information too: this information might be described metaphorically as 'that other whale seems undisturbed; consequently I may assume that there is nothing disturbing to a whale like me in that sphere of the environment that its senses are measuring'.

We, with our fantastic ability to communicate verbally and to analyze learned information (the implications of a burp) sometimes think of communication as primarily or even exclusively, an active, intentional process on the part of the communicator. The mare whinnies to her foal and it runs to her side; the dolphin slaps its tail on the water, sounding an alarm which makes the whole school dive;

the human being says or writes words with the intention of making other human beings comprehend the communication. In fact, an enormous amount of the communication between animals is not given with the intention of influencing or informing others; but is nevertheless attended to, and often 'read', purposively, by species mates.

Since we communicate so avidly via the spoken word, we also sometimes make the anthropocentric assumption that communication is largely an acoustic phenomenon. However, even in the noisiest of species—flocking birds, monkey troupes, and so on—most of the information exchange is not carried on the acoustic channel, so to speak, but in gesture, movement, posture, expression and (in terrestrial mammals) sometimes scent production.

The exquisite complexity of acoustic signalling among small cetaceans began to fascinate researchers in the 1950s, and led to speculations that the acoustic production of dolphins was comparable to that of humans, in meaningfulness as well as complexity. In fact, recent studies show that most dolphin whistle and burst-pulse sound interchanges are highly stereotyped, like the acoustic interchanges of birds (Gish, 1979).[1]

In most cetaceans, as in birds, much of the information offered by sound production is exceedingly redundant. Redundancy, however, is not a conspicuous feature of information-giving behavior carried out in the physical mode: for example, an individual may 'startle' but once, and yet convey surprise or alarm to all around it, even individuals of other species.

The study of the informational content of the behavior of individuals has been for many years the province of classical ethology, the field of biology which concentrates on the evolution and function of behavior in the natural setting. Modern behavioral ecologists extend the uses of behavioral interpretation to the analysis of not just the relationships between individuals, but also relationships between groups, of groups to populations, and of populations to their environments. Of particular interest to these investigators are behavioral events which do not convey information merely as a 'byproduct', as does a startle, or an increase in respiration rate—but which appear to have evolved to serve a communicative function primarily. Such behaviors, which tend to be conspicuous, stereotyped and noticeably different from other events in the behavioral stream, are generally termed displays.[2] Displays communicate the internal state of affect of the individual doing the displaying (i.e. what it is 'feeling') and sometimes also its intentions. Typical displays in terrestrial birds, reptiles and mammals include stereotypic behaviors associated with courtship, aggression, submission, flight, greeting, affiliation and distress.[3]

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[1] While redundant and lacking complexity in informational content, dolphin acoustic exchanges may be exquisitely complex in engineering detail; for example, Atlantic bottlenosed dolphins are able to mimic each other's call-notes, or 'signature whistles', with such fidelity that computer analysis of original and mimic whistles, across 70 parameters, found them to be nearly identical (Gish, 1979).

[2] For an excellent general review of modern behavioral ecological theory see: J. F. Wittenberger, 1981, *Animal Social Behavior*, Duxbury Press, Boston.

[3] Two very typical examples of display behavior in human beings are laughing and crying. Like all such displays these are conspicuous behaviors, somewhat involuntary (consequently difficult to suppress), are sharply attended to by conspecifics, are capable of gradation in intensity (thus communicating the level of affect eliciting the display) and, as is the case in many social display behaviors, are rather contagious.

While behavioral biologists have learned an enormous amount about the nature, function, significance and development of social signalling in terrestrial mammals, little attention has been paid to this rich source of biological information in cetaceans. The behavioral literature on cetaceans is strikingly scanty (Defran and Pryor, 1980). Most of the literature refers only to observations on captive animals, and most of those are limited to the Atlantic bottlenosed dolphin (*Tursiops truncatus*), the species most commonly kept in captivity. This is in fact a rather anomalous species, the behavior of which cannot necessarily be extrapolated to other dolphin species, much less to the great whales. Of course the scantiness of the literature, and especially of field observation, is partly due to the extreme difficulty of observing the social behavior of cetaceans in the natural setting. Even when one has located animals, what they are actually doing takes place largely underwater and thus usually out of sight.

The paucity of information about cetacean social behavior however, is also partly due to the fact that so many of those who have observed and reported on cetacean behavior are not versed in or not even cognizant of this area of biological discipline, being engineers, physicists or the like. Because of the unfamiliarity of such investigators with mammalian social behavior in general, and because the extreme adaptations necessary for a totally aquatic life render this group so very different morphologically from terrestrial mammals, there seems to have arisen in both the public mind and the attitudes of the scientific community a tacit assumption that cetaceans cannot be compared behaviorally to better-known social animals. Even people who do not subscribe to any wishful thinking about intelligence seem to treat cetaceans as if the whole group somehow fell from Mars, behaviorally, rather than being normal products of evolution; as if they cannot be expected to show behavioral traits typical of other social mammals, such as dominance hierarchies, territoriality, collective defence, prolonged parental care and so on. In fact, it seems much more parsimonious to assume that cetaceans, while certainly varying from species to species in social structures, exhibit overall social adaptations directly analogous to adaptations of terrestrial social mammals (Ralls, Brownell and Ballou, 1980).

Fortunately, in the last decade, many field observational programs have been under way. Payne and others have studied the natural history and behavior of Southern right whales in Patagonia. Swartz heads an on-going study of the behavior of gray whales in St Ignacio lagoon, Baja California. A number of investigators are studying the humpback whale in several locations. In Hawaii, warm clear waters allow opportunities for extremely useful underwater observations which have done much to unravel the nature of social groupings in this species. Behavioral studies have also been undertaken on the bowhead whales in Pacific Arctic waters.

Comparative behavioral studies have been made of eleven species of small cetaceans in captivity (Defran and Pryor, 1980) and field behavioral studies have been made or are under way on numerous small cetaceans in the wild: the dusky dolphin, *Lagenorhynchus obliquidens*, (Würsig and Würsig, 1979); the Hawaiian spinner dolphin, *Stenella longirostris* (Norris and Dohl, 1980); the Atlantic bottlenosed dolphin, *Tursiops truncatus* (Wells, Irvine and Scott, 1980); the Black Sea bottlenosed dolphins *T. truncatus* (Bel'kovich, Agafanov, Efremenkova, Kosarovitsky and Kharitonov, 1978) and (Bel'kovich, Efremenkova, Ivanova, Kosarovitsky and Kharitonov, 1978); the Pacific spotted dolphin, *Stenella attenuata* (Pryor and Kang, 1979); and this list is by no means a complete review.

From these studies it is becoming evident that the social organization, feeding strategies, reproductive cycles, and other details of natural history may vary as widely between species in the cetaceans as they do, for example, in the primates; meanwhile however, there may be considerable correlation throughout the cetaceans in the form and function of their social signalling and communicative displays. For example, individuals of many species, from the largest whale to the most diminutive dolphin, have been observed to 'breach', or fall violently forward or sidewise on the water surface, when aroused or disturbed by external stimuli such as boat noise.

It seems reasonable to suppose that what is known of the communicative or informational function of such displays in small species might sometimes be applicable to large species exhibiting the same or similar behavior. The availability of some kind of comparative information might help to take whale behavioral events—breaching, the spyhop—out of the category of meaningless curiosities and into the category of useful biological information.

In preparation for this discussion, the author conducted a small survey among some scientists who are oriented toward behavioral ecology and who have recently been studying whale behavior in the field. Of a list of twelve display behaviors which have a known (or at least generally agreed-upon) communicative or social function in small cetaceans, how many had been seen in large whales, and in what species of whale? The results are presented in Table 1. Each of the ten respondents had seen six or more of the listed behavioral events in at least one species of great whale. Each event listed had been seen by at least one observer in at least one species. Many observers, especially those who work only from the water surface, were extremely reluctant, and understandably so, to assign any function, communicative or otherwise, to specific behavior. (Of course behaviors may indeed have different functions in different species or different circumstances; as breaching, for example, may be both a sign of affect and part of a feeding procedure in both small and large cetaceans). Other observers, however, reported with confidence the relationship of some behaviors to the circumstances which elicit them. By and large such interpretations agreed with similar interpretations for small cetaceans (see 'Comments', Table 1).

In overlooking the significance of behavioral events which may seem trivial in an individual instance, but which may carry real information for the whales, we overlook one of our own most available sources of biological information. A wider understanding of communicative behavior might have practical management advantages, providing, for example, evidence that a population is being disturbed, and to what extent; realistic interpretation of behavior before, during, and after pursuit and capture; analysis of social groupings and of the rise of abnormal social groupings; and better understanding of the effect of age- or sex-specific take on social structure. The social behavior of the great whales is a highly important part of their biology. Thanks to the techniques of modern behavioral ecology, it need not remain a closed book, but can begin to be a useful source of enlightenment about the biology of these mysterious and valuable beasts.

Table 1

Results of Behavioral Survey

Behavior[1]	Function in small cetaceans (when known)[2]	Whales species and number of observers reporting this behavior in this species[3]	
Slap tail on water: 'lobtail' or 'tailslap'	Annoyance; sometimes, warning signal.	Humpback (*Megaptera novaeangliae*)	6
		Southern right whale (*Eubalaena australis*)	5
		Bowhead (*Balaena mysticetus*)	2

Comments and interpretation
Behavior not seen: Norris ('not in baleen whales').
Seen, but no interpretation: Hudnall, Ellis, Thomas ('I cannot ascribe the function of annoyance to this behavior').
Annoyance: Tyack, Beamish, Curtsinger.
Herman: (Humpback) 'Frequently seen. May have . . . functions listed. Possibly as communication of location (doubtful in my opinion)'.
Würsig: (Bowhead) 'Directed towards conspecifics and airplanes'. (S. right) 'Directed towards conspecifics, airplanes, killer whales'.

Headslap; slap forward part of body on water	Annoyance; excitation	Humpback	3
		Bowhead	2
		S. right whale	3

Comments and interpretation
Not seen: Norris, Ellis, Beamish.
Excitation: Würsig (Bowhead, S. right); Curtsinger (S. right).
Hudnall: (Humpback) 'Head-lunge: excitation, above-surface visibility while swimming'.
Tyack: (Humpback) 'Excitation; occurs in large groups engaging in aggressive behavior'.
Herman: (Humpback) 'Common. More often in calves. Exuberence, excitement'.
Thomas (S. right whale) 'In presence of dusky dolphins; can't ascribe a "communicative" function though annoyance or excitation may have been there'.

Breach (throw much or all of body out of water and onto water surface)	Extreme annoyance; general arousal; (sometimes) play; also associated with feeding	Gray whale (*Eschrichtius robustus*)	4
		Fin whale (*Balaenoptera physalus*)	1
		Minke (*Balaenoptera acutorostrata*)	1
		Humpback	7
		S. right whale	6
		Bowhead	2

Comments and interpretation
Seen by all respondents.
Hudnall: (Humpback) 'High perspective and long-range vision; power, display; "surprise" tactic; play'.
Würsig: (Bowhead and S. right whale) 'General arousal, sometimes play'.
Tyack: (Humpback, S. right) 'appears to be contagious—one often sees more or less synchronized bouts'.
Beamish: (Humpback) 'Play, as well as communication (behavior produces loud underwater sounds)'.
Herman: (Humpback) 'Associated . . . with coming together, copulating, or disaffiliating . . .'.

continued

Table 1 (*continued*)

<table>
<tr><th>Behavior[1]</th><th>Function in small cetaceans (when known)[2]</th><th colspan="2">Whale species and number of observers reporting this behavior in this species[3]</th></tr>
<tr><td>Spyhop (rise partly out of water vertically)</td><td>Visual inspection of in-air environment</td><td>Gray whale
Humpback
Right whale
Bowhead
Minke
Sperm whale (<i>Physeter catodon</i>)</td><td>2
5
4
1
1
1</td></tr>
<tr><td colspan="4"><i>Comments and interpretation</i>
Seen by all respondents.
Visual inspection: Hudnall, Norris, Ellis, Würsig, Tyack, Beamish, Thomas ('in S. rights, but rare'), Curtsinger.
Herman: (Humpback) '<i>Sometimes</i> seen; not clear whether or not it is for visual inspection'.</td></tr>
<tr><td>Roll belly up, or sinks tail-first</td><td>Submissive displays</td><td>Gray whale
Humpback
Right whale
Bowhead</td><td>3
4
3
2</td></tr>
<tr><td colspan="4"><i>Comments and interpretation</i>
Not seen: Ellis.
Norris: (Gray whale) 'Female during mating attempts'.
Hudnall: (Humpback, gray) 'Play, courtship, feeding; tail-sinking only after spyhop'.
Würsig: (S. right, bowhead), 'Roll belly up, but question it's a submissive display'.
Tyack: (Humpback) 'Brief belly-up appears to be involved in manoeuvering'.
Thomas: (Gray, humpback, S. right, bowhead) 'Submission just doesn't jump out at me . . .'.
Herman: (Humpback) 'Not seen in functional context of submission'.</td></tr>
<tr><td>Ram or charge a conspecific</td><td>Aggression</td><td>Humpback
Gray whale
Bowhead
S. right whale</td><td>3
1
1
2</td></tr>
<tr><td colspan="4"><i>Comments and interpretation</i>
Not seen: Ellis, Beamish, Thomas.
Norris: 'Humpbacks thrash tails at each other'.
Hudnall: (Humpback, gray) 'Swim towards and brush against a conspecific; not aggression; courtship, play, mock aggression.
Tyack: (Humpback) 'Whales in large groups ram one another or beat each other with their flukes. Appear to be fighting over position as consort to female'.
Herman: (Humpback) 'Occasional. We assume male–male competition'.</td></tr>
<tr><td>Gape: open jaws widely underwater</td><td>Threat display</td><td>Humpback</td><td>3</td></tr>
<tr><td colspan="4"><i>Comments and interpretation</i>
Not seen: Ellis, Würsig, Beamish, Thomas, Curtsinger.
Norris: 'Humpbacks and balaenopterids in feeding'.
Hudnall: (Humpback) 'Mouth opens briefly to release massive bubbles of air . . . perhaps to deceive or frighten predator'.
Tyack: (Humpback) 'In large groups in which aggressive behavior is observed, will open their mouths slightly, sometimes several times in a row'.
Herman: (Humpback) 'Not seen. <i>Inflated</i> lower jaw, instead, in what appears to be dominance-threat'.</td></tr>
</table>

Table 1 (*continued*)

Behavior[1]	Function in small cetaceans (when known)[2]	Whale species and number of observers reporting this behavior in this species[3]	
Whistle-trail (long plume of bubbles from blowhole, accompanying sound production)	Visual and echolocatable accompaniment of 'calling' whistles, especially mother–young	Humpback	4
		Fin whale	1

Comments and interpretation
Not seen: Ellis, Thomas.
Norris: 'In humpbacks, but whether sound is part of it, I don't know'.
Hudnall: (Humpback) 'Practiced by young, never mother, and by courting males'.
Würsig: Not for certain.
Tyack: (Humpback) 'particularly in large groups, produce streams of bubbles more than 30 meters long but I doubt they are producing sounds . . .'.
Herman: (Humpback) 'Bubble trails common, but no associated sound identified. May be dominance display'.

Behavior[1]	Function in small cetaceans (when known)[2]	Whale species and number of observers reporting this behavior in this species[3]	
'Surprise' blow: large sphere of bubbles (10% body length of animal)	On first viewing some novel or unexpected but not frightening thing: i.e. 'Hunh?'	Gray whale	2
		Humpback	5
		S. right whale	2
		Bowhead	1

Comments and interpretation
Not seen: Ellis, Tyack, Beamish.
Norris: 'Grays blow underwater'.
Hudnall: (Humpback) 'To create a physical screen to manoeuver behind'.
Würsig: (S. right) 'When "awakened" by approaching boat'.
Thomas: (Humpback, S. right, bowhead) 'Can't correlate occurrence with function'.
Herman: (Humpback) 'Underwater blows seen sometimes in aggressive encounter'.

Behavior[1]	Function in small cetaceans (when known)[2]	Whale species and number of observers reporting this behavior in this species[3]	
Stroke or pat with flukes or pectoral fins	Affiliative behavior: sometimes sexual	Gray whale	2
		S. right whale	4
		Humpback	4
		Bowhead	2

Comments and interpretation
Not seen: Ellis, Beamish.
Norris: (Gray, right) 'Contact behavior is common in groups of mother/young'.
Affiliative, sometimes sexual: Hudnall, Würsig, Curtsinger, Tyack, Herman.
Thomas: (S. right, bowhead) 'Certainly occurs during affiliative behavior'.

Behavior[1]	Function in small cetaceans (when known)[2]	Whale species and number of observers reporting this behavior in this species[3]	
Bunching: (crowd together and travel at high speed)	Fear; flight	Humpback	3
		Right whale	1
		Sperm whale	1

Comments and interpretation
Not seen: Ellis, Beamish, Thomas.
Norris: 'Whales seldom group enough to show it'.
Hudnall, Tyack: (Humpback) 'In large groups in which males are competing for females; not flight'.
Herman: (Humpback) 'Sometimes, in response to a disturbance'.
Würsig: (S. right) 'You bet! When killer whales nearby'.

continued

Table 1 (*continued*)

Behavior[1]	Function in small cetaceans (when known)[2]	Whale species and number of observers reporting this behavior in this species[3]	
Show sclerae: (widen or roll eyes so whites show)	Fear or aggression	Gray whale	1
		Humpback	2
		S. right whale	1

Comments and interpretation
Not seen: Ellis, Würsig ('haven't been close enough to tell');
Beamish, Thomas, Herman.
Seen but no interpretation: Tyack, Curtsinger, Norris.
Hudnall: (Humpback) 'To focus attention on eye contact'.

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[1] Derived from Defran and Pryor, 1980; Pryor and Kang, 1979 and Martinez and Klinghammer, 1978. The behavioral displays or events selected here have been recorded in at least five species of small cetaceans, with apparently similar social functions in each species: Atlantic and Pacific bottlenosed dolphins (*Tursiops truncatus* and *T. gilli*), Pacific spotted dolphins (*Stenella attenuata*), rough-toothed dolphins (*Steno bredanensis*) and killer whales (*Orcinus orca*).
[2] 'Function' refers to the apparent primary circumstances or states of affect in which each behavior occurs; some may also have other, unknown functions, or may occur in other circumstances also.
[3] Respondents to this survey were: Peter Beamish, William Curtsinger, Richard Ellis, Louis Herman, James Hudnall, Kenneth Norris, Peter Thomas, Peter Tyack and Berndt Würsig.

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POTENTIAL FOR SPERM COMPETITION IN BALEEN WHALES

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ABSTRACT

We examine the size of the testes and penis, relative to body size, in relation to mating behavior for all ten species of baleen whales and interpret our findings in the light of recent theory on sperm competition.

Testes size increases with body size; however, individual species may have testes that are larger or smaller than would be predicted from their body size. Right whale testes can weigh almost one metric ton and are about six times larger than predicted. Bowhead and gray whales also have larger testes than predicted, while all the balaenopterids and pygmy right whales have testes near or below the predicted size.

The penises of right and bowhead whales are over 14% of body length, those of humpback and gray whales are over 11% and those of the other species range from 7.5 to 10.8%.

Theory predicts that males will compete to sire as many young as possible. This competition can take two forms. A male can either prevent other males from copulating with females he copulates with or copulate with females that have copulated with other males and displace their sperm. The latter is called sperm competition. In species where males compete primarily through sperm competition, females commonly copulate with more than one male, male–male interactions are not highly aggressive, and males have relatively large testes and long penises. The right, bowhead and gray whales fit this description and probably exhibit sperm competition. In species where males compete primarily by monopolizing females and preventing other males from copulating with them, females commonly copulate with only one male, male–male interactions are often highly aggressive, and males have relatively small testes and shorter penises. Although copulation has not been observed in humpback whales, they appear to be competing primarily in this manner. The mating systems of the pelagic balaenopterids and pygmy right whales are poorly known but these species do not appear to be selected for sperm competition.

INTRODUCTION

The intense competition among males of polygynous species for mating opportunities, indicated by threats and physical fighting, has been recognized for over a century (Darwin, 1859). More recently, it has been realized that sperm also compete in species where a female usually copulates with more than one male. Sperm competition was first described in insects (Parker, 1970) but evidence for its existence in mammals soon followed (Harcourt, Harvey, Larson and Short, 1981; Dewsbury, 1984; Hogg, 1984).

A common form of sperm competition is attempted displacement or dilution of the sperm of rival males. The males of species competing in this fashion have relatively large testes compared to those of related species in which females usually copulate with only one male (Harcourt *et al.*, 1981; Dewsbury, 1984; Hogg, 1984; Kenagy and Trombulak, 1986) and may also have relatively long penises (Parker, 1984; Smith, 1984). Both large numbers of sperm per ejaculate and multiple ejaculates within a short time period can be advantageous in species where sperm competition occurs. Larger testes are required to produce the large numbers of sperm needed under these conditions and the longer penises presumably help to deliver them closer to the ova.

Although nearly universal in odontocetes, competition for estrous females was once thought to be nearly absent in mysticetes (Norris, 1967). However, recent behavioral studies of humpback whales, *Megaptera novaeangliae*, have provided abundant evidence of aggressive interactions between males that appear to be competing for access to females (Tyack and Whitehead, 1983; Baker and Herman, 1984) and less violent interactions have been observed in right whales, *Eubalaena glacialis* (Payne and Dorsey, 1983), and gray whales, *Eschrichtius robustus* (Jones and Swartz, 1984). The extremely large size of right whale testes—the largest pair on record weighed nearly one metric ton (972 kg) (Omura, Ohsumi, Nemoto, Nasu and Kasuya, 1969)—suggests that sperm competition occurs in this species and perhaps in other baleen whales.

Here we evaluate relative testes and penis size and the potential for sperm competition among living mysticetes and relate these findings to current knowledge of their mating systems.

METHODS

Six genera of baleen whales are recognized. We place the right whale in the genus *Eubalaena*, following Schevill (1986); our specific names for the ten species follow Honacki, Kinman and Koeppl (1982).

We reviewed the literature for information on mating system and male–male interactions in mysticetes. For each species, we also compiled maximum body length and testes weight data for a particular sample from a specific geographic area. For all species except the Bryde's whale (*Balaenoptera edeni*) and the pygmy right whale (*Caperea marginata*), body lengths were converted to weights using the formulas in Lockyer (1976). These formulas have not been adjusted for blood and fluid lost during flensing and our calculated weights are thus about 94% of the live weight. As no length/weight formula is available for bowhead whales (*Balaena mysticetus*), we used Lockyer's formula for right whales. Our data for the Bryde's whale are from the Southern Hemisphere population. We therefore used the length/weight formula for that area given in Ohsumi (1980), as Lockyer's formula was based on the North Pacific animals. Our pygmy right whale value is the actual body weight of one individual (Ivashin, Schevchenko and Yukov, 1972).

Testes weights are for both testes and without the epididymides. Single testis weights were doubled for humpback and bowhead whales. Testes weights from animals on the breeding grounds were not available for all species. Testes weight increases with body weight in mammals regardless of breeding system (Kenagy and Trombulak, 1986). We therefore corrected for the effect of body weight by examining deviations from the line of best fit. We used the major axis line because some error was present in both measures of body weight and testes weight and the data were logarithmically transformed (Harvey and Mace, 1982).

Since we could not locate data on maximum penis length for all the species, we compiled data on the mean penis length of sexually mature males and analyzed these in relation to the mean body length of these same individuals. In three cases, we had to estimate mean penis length and mean body length from published figures and the accompanying text. These were: gray whale, Rice and Wolman, 1971: Fig. 36; sei whale (*Balaenoptera borealis*), Masaki, 1976: Fig. 11; and blue whale (*B. musculus*), Mackintosh and Wheeler, 1929: Fig. 139. The bowhead value was estimated by M. Nerini from a photograph.

RESULTS

Mating behavior and male–male interactions

Most available information is for the species that frequent coastal waters: the right, bowhead, gray and humpback whales.

Right whale

Apparent mating behavior has been seen in the populations off South Africa, Argentina and the eastern United States. The observations off South Africa and Argentina were made on the calving grounds. Observations on five groups of courting whales at Algoa Bay, South Africa, included one group of two males and a female (Donnelly, 1967). Saayman and Tayler (1973) observed several trios interacting in Plettenberg Bay, South Africa.

Mating is one of the commonest group behaviors observed off Argentina in winter and spring and numerous intromissions have been seen (Payne, 1972; 1976; 1986). Payne and Dorsey (1983) mention multimale mating groups and Cummings (1985) reports a copulation sequence between one female and three males with penises extruded. One particularly striking observation was made by B. Würsig (pers. comm.). A female was floating with her ventral surface upwards at the surface. Two males positioned themselves on opposite sides of her and each inserted his penis into her genital slit. One male then ejaculated, as judged by the waves of muscular contractions that moved from the base of his penis towards its tip for about 12 sec. The second, slightly smaller male, apparently did not ejaculate, as no contractions were evident while his penis was inside the female.

The observations off the eastern United States were made on the feeding grounds. Kraus (1986) reported that groups of courting right whales can include as many as 14 individuals engaging in what appear to be efforts by several males to copulate with one or more females. This activity lasts up to one hour with the whales continuously on the surface of the water.

Payne and Dorsey (1983) believe that male right whales interact aggressively, using their callosities (particularly the bonnet, which tends to be slightly larger in males) to bump and scrape each other. Much of their evidence derives from an analysis of scrape marks but there are a few supporting behavioral observations, e.g. on occasions one animal in a mating group will

> 'turn its head over and run the dorsal side of the head against another whale, making clear contact with the callosities. The animal on the receiving end immediately twists or writhes, so as to move its body away, while the whale doing the scraping adjusts so as to keep its callosities in contact with the recipient.'

Bowhead whale

Apparent sexual activity has been observed during the spring migration off northern Alaska in mid-March (Braham, Krogman, Johnson, Marquette, Rugh, Nerini, Sonntag, Bray, Brueggeman, Dahlheim, Savage and Goebel, 1980) and in May (Marquette, 1977; Everitt and Krogman, 1979; Carroll and Smithhisler, 1980). Würsig, Dorsey, Fraker, Payne and Richardson (1985) describe two apparent mating attempts in August. Groups of up to six whales may participate in sexual activities (Everitt and Krogman, 1979).

Although aggressive interactions between male bowhead whales have not been reported, this species has been observed to a much lesser extent than the right, gray and humpback whales.

Gray whale

All accounts of mating behavior in gray whales note that more than one male is commonly present (Gilmore, 1968; Walker, 1971; Samaras, 1974; Norris, Villa-Ramirez, Nichols, Würsig and Miller, 1983; Rice, 1983). Samaras (1974) thought that the most common group consisted of two males and a female but Norris *et al.* (1983) observed that as many as seven or eight such groups often coalesce within an area about 100 m in diameter and mating groups of up to 18 animals have been documented (Swartz, 1986). Mating groups may last for up to two hours but change composition as individual males leave or join (Jones and Swartz, 1984). Females 'repeatedly copulate with more than one male during the same mating bout' (Swartz, 1986).

Although males in mating groups may gently nudge each other, these interactions do not seem to be aggressive (Swartz, 1986). Males appear to take turns copulating with the female in the group until she terminates the bout by swimming away or turning her ventral body surface upwards at the surface of the water (Jones and Swartz, 1984).

Wolman (1985) noted that 'courtship behavior has been observed by numerous individuals on feeding grounds, along the migration route and on calving grounds (Fay, 1963; Gilmore, 1961; Houck, 1962; Sauer, 1963; Tomilin, 1957 and Darling, 1977)'. However, Darling (1977) pointed out that only males were involved in the 'courtship' behavior off Vancouver Island. It can be very difficult to identify the sexes of all the whales involved in apparently sexual interactions: in one case, it took several observers two and one-half hours to make certain that all three of the individuals in a group were males (J. Darling, pers. comm.).

Humpback whale

Several authors have described mating behavior on the breeding grounds (Tyack, 1981; Darling, 1983; Baker and Herman, 1984). Females are seen simultaneously and sequentially with more than one male and males are seen sequentially with more than one female. Frequently, one male is seen 'escorting' a female or a female and her new-born calf. Groups of up to 15 adults consisting of one female and many males have also been observed. Unstable groups of males form around presumably estrous females. Interactions among these males, which appear to be vying for proximity to the single female in the group, have been well-described by several authors (Baker, Herman and Stifel, 1981; Tyack, 1981; Darling, Gibson and Silber, 1983; Tyack and Whitehead, 1983; and Baker and Herman, 1984).

These interactions range from 'apparent displays and threat gestures to violent physical contact which can cause wounds' (Darling, 1983). 'Escort' males also react aggressively to the approaches of other males. 'Escorts' appear to be males competing for the right to accompany a female and eventually mate with her. However, copulation has never been reliably observed on the winter grounds, or elsewhere (Mobley and Herman, 1985). Behaviors associated with aggressive interactions include broadside displays, underwater exhalations, head lunges, physical displacement and 'charge-strikes' (Baker and Herman, 1984). Bleeding wounds have been observed on some of the competing males (Tyack and Whitehead, 1983).

Pygmy right whale

There are few observations of live individuals and nothing is known about their mating behavior. 'Behavior in the wild is unspectacular, probably making the species relatively inconspicuous at sea' (Ross, Best and Donnelly, 1975).

Rorquals

Little is known about courtship and mating in these pelagic species: minke whale (*Balaenoptera acutorostrata*); Bryde's whale; sei whale; fin whale (*B. physalus*); and blue whale. Even the precise breeding and calving grounds are uncertain in many instances (Mackintosh, 1966; Lockyer, 1984).

The best data are for minke whales in the Southwestern Indian Ocean (Best, 1982). From a whale catcher boat, Best was able to observe 14 groups containing a calf during August and September, when mating probably occurs. He was able to determine the sexes of the animals captured from these groups. Ten of the groups contained more than one adult and the commonest grouping was a female, an adult male and a calf. Animals were captured from six of these ten groups and all six groups are thus known to have contained at least one adult male. Five pairs of whales and one trio were also captured. Four of the pairs consisted of a female and an adult male, the other of two adult males. The trio consisted of a female and two adult males.

Testes size

We were able to determine the total number of males in all the samples from which we extracted data on testes weight but we could not determine the proportion that was sexually mature for the fin and sei whale samples (Table 1).

One of the two bowhead whales is clearly immature. The body length of the other individual was 15.2 m, which is near the maximum of 15.3 m reported in Nerini *et al.* (1984). However, Tarpley, Stott, Sis, Shively and Jarrell (1985) reported a 16.6 m male from the same population. The testes in the 16.6 m individual were not weighed but sperm were present and the mean seminiferous tubule diameter was 91.6 μm. The mean seminiferous tubule diameter of recently maturing males in seven species of baleen whales is 113 μm (Lockyer, 1984).

Maximum combined testes weights and estimated maximum body weights (from the same sample) for all living species of mysticetes are shown in Table 1. Analyses at the generic and specific levels gave similar general results. We present the analysis based on the specific level. As expected, testes weight increased with body size ($r = 0.75$). The major axis slope was 1.35 and a line with this slope is fitted through the points in Fig. 1. As there was no heterogeneity of slope among families ($\chi^2 = 1.05$), deviations from this line were calculated for all species (Table 1).

Relative testes size in the right whale far exceeded that in all other species. The bowhead whale and the gray whale also had larger testes than predicted from their body size. All other species, except for the pygmy right whale, had testes that were smaller than the predicted size.

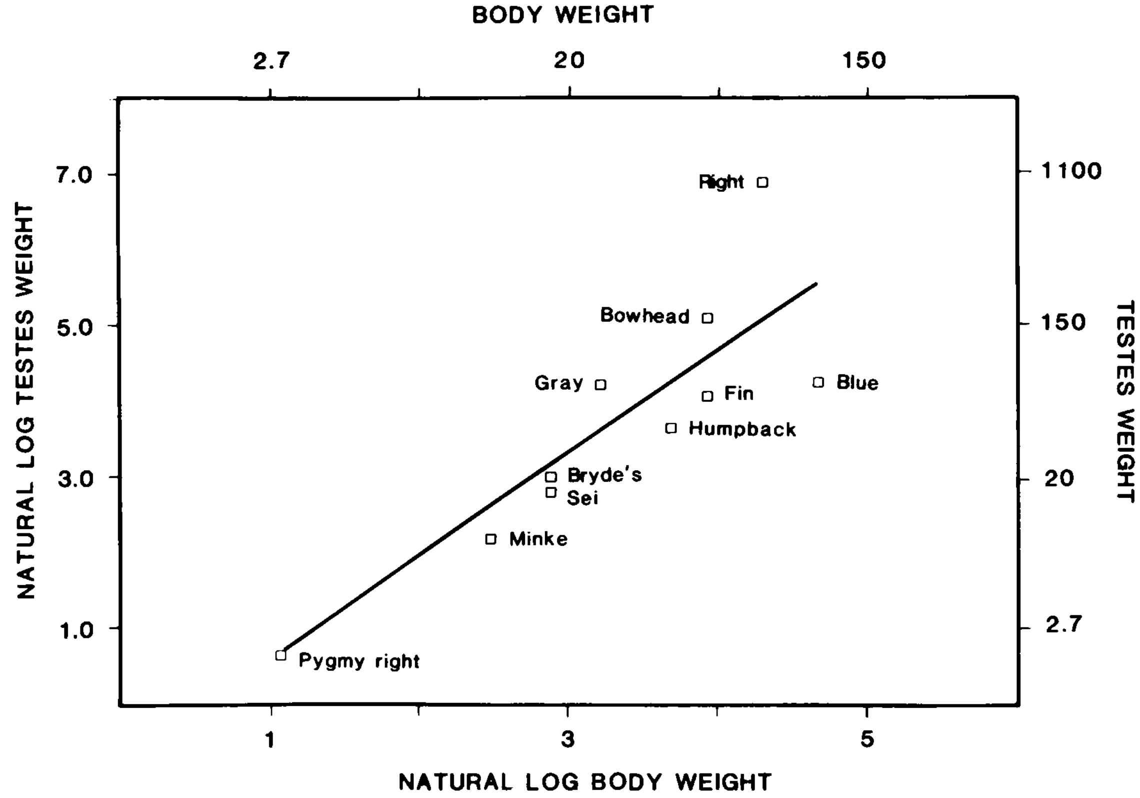

Fig. 1. Natural log of body weight (metric tons) plotted against natural log of combined testes weight excluding epididymes (kilograms) for all ten species of baleen whales. Most maximum body weights are calculated from body lengths using the formulas in Lockyer (1976). Maximum body lengths and testes weights are from within the same geographic area and study.

Penis type and length

Cetaceans have a fibroelastic type of penis like that of most artiodactyls (Slijper, 1938). This type of penis differs markedly from the vascular type found in primates and carnivores. The vascular type becomes considerably longer and thicker when it fills with blood during erection but this is not true of the fibroelastic type, which shows no increase in length and very little increase in width during sexual excitement. Penis lengths of dead cetaceans are thus similar to those of live males during sexual activities.

Data on mean penis and body length of sexually mature whales are shown in Table 2. Because penis length was not correlated with body length (r = 0.03), we could not perform an analysis similar to that on testes weight. Several authors reported that penis length increased at the time of sexual maturity (Mackintosh and Wheeler, 1929; Rice and Wolman, 1971; Masaki, 1976). Both right and bowhead whales have relatively long penises that are approximately 14% of their

Table 1. Maximum combined testes weight (excluding epididymides) and estimated maximum body weight of baleen whales. Body weights were calculated from maximum total lengths.

Taxon	Maximum Total Length (M)	Est. Body Wt. (MT)	Testes Wt. (Kg)	Predicted Testes Wt. (Kg)	Actual/ Predicted Testes Wt.	Sample Size		Source for total length and testes weight.
						Sexually Mature Males	Total Males	
Family Eschrichidae								
Gray Whale	13.3	25	67.5	36.49	1.85	123	166	Rice and Wolman, 1971
Family Balaenopteridae								
Minke Whale	9.8	12	8.8	13.44	0.65	67	205	Best, 1982; Best, pers. com.
Bryde's Whale	14.0	18	20.0	23.37	0.86	12	22	Best, 1977
Sei Whale	15.2	18	16.4	23.37	0.70	?	362	Mitchell & Kozicki, 1974
Fin Whale	20.4	51	58.3	95.15	0.61	?	436	Haug, 1981; Haug, 1978
Blue Whale	25.9	107	70.0	258.40	0.27	112	129	Ohno & Fujino, 1952
Humpback Whale	14.3	40	38.0	68.82	0.55	142	285	Nishiwaki, 1959
Family Balaenidae								
Pygmy Right Whale	5.5	2.9	1.9	1.98	0.96	2	2	Ivashin *et al.*, 1972
Bowhead Whale	15.2	51	163.0	95.15	1.71	1	2	Nerini *et al.*, 1984; Nerini, pers. comm.
Right Whale	17.1	74	972.0	156.80	6.20	7	11	Omura *et al.*, 1969

Table 2

Mean penis and body length of sexually mature baleen whales

Species	Mean Body length (m)	Mean Penis length (cm)	%	*n*	Reference
Family Eschrichtidae					
Gray whale	12.0*	138*	11.5*	85	Rice & Wolman, 1971
Family Balaenopteridae					
Minke whale	8.2	77	10.7	28	Best pers. comm.
Bryde's whale	13.8	128	10.8	27	Best pers. comm.
Sei whale	14.0*	130*	9.3*	119	Masaki, 1976
Fin whale	19.00	142	7.5	8	Ohsumi *et al.*, 1958
Blue whale	24.0*	225*	9.4*	?	Mackintosh & Wheeler, 1929
Humpback whale	12.1	134	11.1	48	Chittleborough, 1955
Family Balaenidae					
Pygmy right whale	6.00	56	10.6	1	Best pers. comm.
Bowhead whale	14.3*	200*	14.9*	1	Nerini, pers. comm.
Right whale	16.3	233	14.3	4	Omura *et al.*, 1969

* Estimated values see explanation in methods.

total body length. Although the bowhead data are for a single specimen, approximately the same percentage can be derived from other sources. Tomilin (1967) reports that the bowhead penis may reach a length of 2.4 m and cites Lepekhin (1805). Bowheads probably attain physical maturity at a body length of 15 to 18 m (Eschricht and Reinhardt, 1866) and the relative penis lengths of a 17 and 18 m male would be 14 and 13%, respectively. Gray whales (Fig. 2) and humpback whales have penises over 11% of their body length, and those of the other species range between 7.5 and 10.8% of body length.

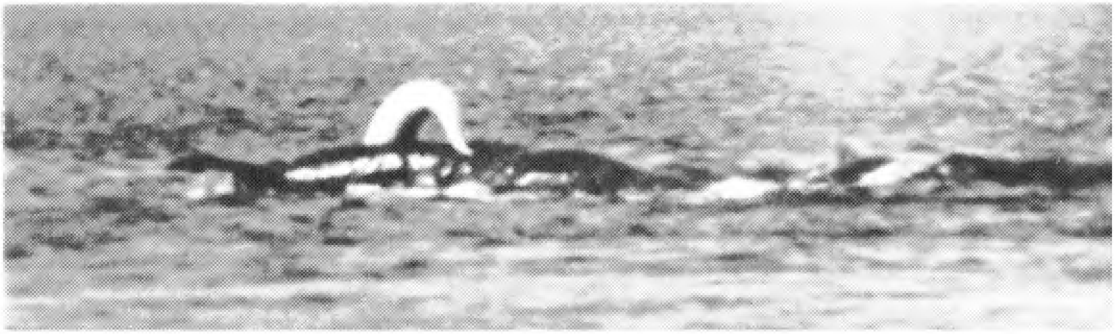

Fig. 2. The penis of a gray whale. Photograph courtesy of S. Leatherwood.

DISCUSSION

Difficulty of interpreting the behavioral data

Although the Eastern Pacific gray whale population is at or near historical population levels (Reilly, Rice and Wolman, 1983; Reilly, 1984), right, bowhead, humpback and blue whale populations have been reduced to small fractions of their original sizes. The effects of these reductions in population size on the size of mating groups and the intensity of male–male competition are unknown.

Another problem in interpreting the behavioral data is that much of the apparent sexual behavior observed in baleen whales probably does not result in pregnancy. Sexual behavior has been seen in the gray whale at all times of year and in all parts of the range: on the feeding grounds, on the calving grounds, and on the migratory corridors between these areas (Wolman, 1985). And yet, most calves are born in January and February (Rice and Wolman, 1971; Swartz, 1986). However, Darling (1977) noted that females are definitely not present during some of the 'courtship' activities observed while the whales are away from the breeding grounds. Due to the difficulty of distinguishing the females in groups of whales, it is quite possible that many of the observations on the feeding grounds and the migratory pathways involve all-male groups and do not represent true copulatory activity.

Sexual behavior, including groups of males apparently attempting to copulate with a female, has also been observed in right whales on the feeding grounds in late summer (Kraus, 1986). If believed to result in conception, this is inconsistent with the proposed gestation period of 12 months (Klumov, 1962). Payne (1986) commonly observed copulation, with intromission, in right whales on the calving grounds in Argentina. Individually known females return to calve at three-year intervals. However, they usually do not return to this area the year before they give birth. As both delayed implantation, which is not known in any species of cetacean, and a two-year gestation period are unlikely, it seems probable that the copulation that actually results in conception occurs in some other area.

Relative testes weight

The most striking result of our analysis is the relatively enormous testes size in the right whale. The datum point for this species is so far above the line relating testes weight to body weight that those unfamiliar with mysticetes may suspect that it is an error. However, we believe that this value is more likely an underestimate than an overestimate because the testes weights were not obtained from animals on, or migrating towards, the breeding grounds.

The males of some baleen whales are known to have a seasonal reproductive cycle which closely correlates with a main winter estrus in the female (Lockyer, 1984). Testes size can vary appreciably during this seasonal cycle. For example, the average testis weight in minke whales is about 40% greater during the breeding season than during the feeding season (Best, 1982) and the average testes weight in gray whales on the migration to the breeding grounds is about 70% greater than on the return journey (Rice and Wolman, 1971). A seasonal cycle has not been demonstrated in all species and populations of baleen whales and it seems likely that there is no seasonal cycle in some populations. For example, there are coastal populations of Bryde's whale, which do not undertake long-distance migrations, in which equal proportions of conceptions occur at all times of the year (Best, 1977).

Because of the male seasonal reproductive cycle, our combined testes weights for those species not collected on or near the breeding grounds may be underestimates. In addition to the right whale, these species are the bowhead, fin and blue whales. Furthermore, we have data on only two bowhead whales and the testes weight of the larger is very likely below the maximum for the species. However, the right and bowhead whales have relatively large testes in spite of the possible underestimation and the blue and fin whales would still have relatively small testes even if we increased the testes weights in Table 1 by 50%.

Penis length

Smith (1984) discussed various speculations as to why a long penis has evolved in humans. Possible functions include aggressive display, attractive display and the facilitation of a variety of copulatory positions to enhance female sexual stimulation. However, he suggests that the most important function is the delivery of sperm as close as possible to ova.

Right, bowhead and gray whales all have penis lengths, expressed as a percentage of total body length, that are longer than those of the other whales. We provisionally interpret this as additional evidence for the importance of sperm competition in these species.

However, we have been unable to compare penis length with vaginal length across species. Furthermore, a series of complex vaginal folds has been described in many cetaceans (Harrison, 1969). The function of these is unclear; they may form a pseudocervix that could limit the penetration of the penis (Harrison, 1969). There may be six to 12 of these folds in balaenopterids (Harrison, 1969). As we were unable to find quantitative descriptions of these folds in all species of baleen whales, we were unable to consider them in relation to penis length or other factors.

Copulation

Slijper (1938) has suggested that the usual copulation pattern of species with a fibroelastic type of penis is one with rapid intromission, no or almost no friction movements and a duration of only a few seconds. Such rapid copulations are characteristic of many artiodactyls with this type of penis. Slijper (1966) therefore suggests that cetaceans, with their fibroelastic penis, may also be able to copulate very rapidly. It is known that various species of small cetaceans can copulate in only 10 to 30 seconds (Slijper, 1966). If this is true in humpbacks, it may help explain why copulation has never been reliably observed on the breeding grounds in this species.

Theoretical models and baleen whales

The mating systems of many primate species are comparatively well-known and can be classified into three groups: those in which mating occurs between monogamous pairs, those in which it occurs in groups of females with a single male, and those in which it occurs in female groups containing multiple males (Harcourt *et al.*, 1981; Harvey and Harcourt, 1984). Body size dimorphism is greatest in the species with groups of females and a single male, intermediate in those with multiple males, and lowest in those with monogamous pairs. Primate males often use their canine teeth in fighting and relative canine size varies among the three groups in the same way as body size dimorphism (Harvey, Kavanagh and Clutton-Brock, 1978). In contrast, relative testes size is large in the species with groups of females accompanied by multiple males and small in the other two groups.

Unfortunately, our present understanding of sexual size dimorphism provides little insight into the probable mating systems of baleen whales. Females are larger than males in all 10 species (Ralls, 1976; Baker, 1985).

Knowledge of secondary sexual characteristics that might be used in male–male interactions is too limited to be of value. There are a number of candidate structures in various species: different species of barnacles, the callosities of right whales, the peculiar growths found on the anterior ventral surface of the lower jaw in humpback whales and the knobs on their flippers and heads (Payne and Dorsey, 1983) and the series of bumps along the dorsal ridge in gray whales. However, these structures are not comparable across species like the canine teeth of primates and, in any event, their functions and manner of use are poorly known. Although all baleen whales have flippers and flukes, the extent to which these are used in male–male interactions is poorly known.

Males of many species of animals compete with other males to sire as many offspring as possible. There may also be conflict between males and females during breeding, as the costs and benefits of a particular characteristic need not be the same for males and females. Parker (1984) has incorporated both male–male and male–female conflict into a simple model that consists of three inter-dependent parts (Fig. 3). Males can be selected either to prevent second matings by other males or to mate with previously-mated females and displace the sperm of other males. The balance between these two types of selection depends, in part, upon the costs and benefits of various male behaviors to the females. If male attempts to prevent second matings are costly to females, there will be male–female conflict in part 2 of Fig. 3 and if multiple matings are costly to females there will be male–female conflict in part 3 of Fig. 3. If, however, male attempts to prevent second matings are not costly or are even beneficial to females, there will be no conflict in part 2 and males will be selected to guard females and interact aggressively with other males. If, on the other hand, multiple matings are not costly or are beneficial to females (e.g. lions, Davies and Boersma, 1984), there will be no conflict in part 3 and males will be selected to compete through sperm competition.

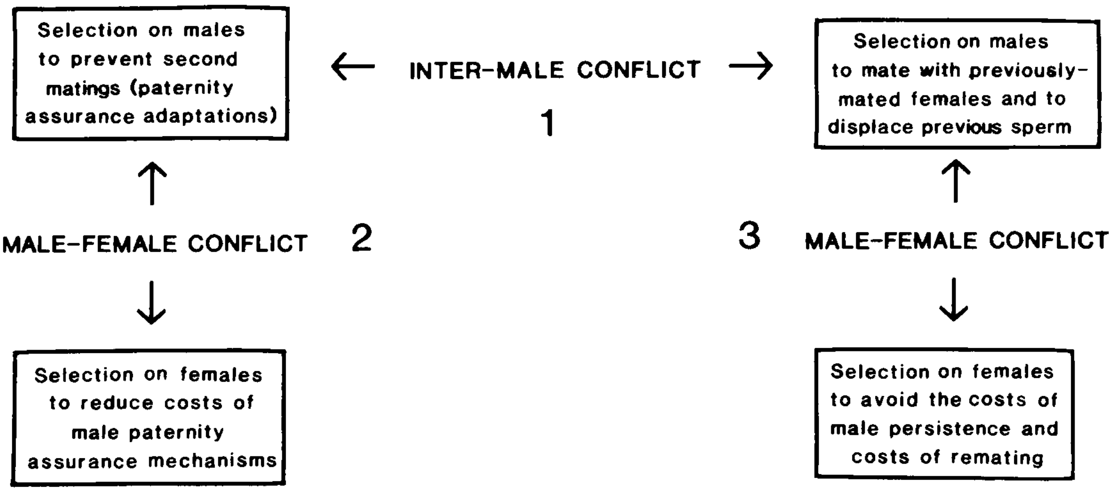

Fig. 3. Model of the evolutionary dynamics of sperm competition systems. See text for details. Modified after Parker (1984).

The available data on humpback and right whales can be interpreted in the light of this model. The relatively small testes of the humpback whale, its shorter penis and the conspicuous and sometimes violent interactions between males in mating groups suggest that males of this species compete primarily by attempting to prevent matings by other males. In contrast, the exceedingly large testes of the right whale, its longer penis and the apparently much less aggressive interactions between males in mating groups suggest that this species has been selected primarily for competition through multiple matings and sperm competition.

The long penis of the bowhead whale, which appears to be relatively as long as that of the right whale, suggests that these two species may be quite similar. If so, interactions between bowhead males may be relatively amicable, and the fact that aggressive interactions have not been reported may not be due simply to insufficient observations.

As gray whales also have relatively larger testes than expected for their body weight and aggressive interactions between males are apparently lacking, it seems probable that males of this species also compete by sperm competition. However, since their testes are relatively much smaller than those of right and bowhead whales, sperm competition in gray whales may be much less intense than in these species. Female right whales tend to calve every three years whereas many female gray whales calve every other year. If other factors, such as survival rates, were the same for the two species, this difference in reproductive cycle length could produce a higher ratio of adult males to estrous females in right whales. However, it remains to be determined whether or not female right whales usually mate with more males than gray whale females do.

The trios of two males and a female sometimes seen in gray whales have been interpreted as a mating couple and an additional 'helper' male (Samaras, 1974). It seems likely that this is a misinterpretation and that multiple males are copulating with the female and competing through sperm competition in mating groups of all sizes.

The mating systems of the pelagic baleen whales and the pygmy right whale are not known. Since these whales all have relatively small testes and short penises, we would predict that they are not selected for sperm competition and that females may not mate with more than one male during a single estrus. It is possible, however, that some males move from female to female during the breeding season. The rorquals are sometimes said to be monogamous (Lockyer, 1984) but the behavioral data are insufficient to determine whether or not this is true. We consider it unlikely, due to the rarity of monogamy in mammals (Kleiman, 1977) and because none of the conditions thought to favor the evolution of monogamy, such as inability of the female to rear her young successfully without male assistance (Kleiman, 1980, Wittenberger and Tilson, 1980), appear to apply to these whales.

RESEARCH NEEDS

We have identified several areas in which additional data are needed to improve our understanding of the potential for sperm competition and mating systems in baleen whales. On the anatomical side, these are additional testes weights and penis lengths for bowhead whales and measurements of the length of the vagina and the vaginal folds in most species. On the behavioral side, these are observations of *Balaenoptera* spp. on the breeding grounds and the development of criteria to separate copulation likely to result in conception from other forms of sexual activity in most species. More careful observations of gray whales on the feeding grounds and migratory pathways should help resolve the question of whether or not most sexual activity in these areas involves groups of males or copulations between males and females that do not result in pregnancy. Steps that might help to answer the question of why so many right whale copulations, between known individuals in the waters off the Valdes Peninsula in Argentina, do not result in pregnancy are far from obvious.

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Fig. 3. Right whale penis from an animal taken off Kodiak Island, Alaska in 1961 under Special Permit. Photo courtesy of H. Omura and H. Kato.

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METHODOLOGY FOR BEHAVIOURAL STUDIES OF CETACEANS: RIGHT WHALE MOTHER–INFANT BEHAVIOUR

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ABSTRACT

Methodology successfully used in studying mother–infant behaviour of right whales at Peninsula Valdes, Argentina, is presented and discussed. In the light of the right whale case study, the application of these methods to other cetacean species is discussed. Finally, the importance of mother–infant behaviour to management issues is identified.

INTRODUCTION

In observational as well as experimental studies of animal behaviour, methodological design largely determines the value and character of the findings. For quantitative studies of mother–infant behaviour in southern right whales, *Eubalaena australis*, methods proven in observational studies of terrestrial mothers and infants were selected (Taber and Thomas, 1982; Thomas and Taber, 1984).

First, I review the methods used and the nature of the results obtained from our right whale studies. The methods are presented in general to specific order, mirroring the development of this and other observational studies of behaviour. The application of this behavioural methodology to other species is then discussed. Finally, specific aspects of the stages of mother–infant development in right whales which have management implications are discussed.

METHODOLOGY

I focus on five aspects of methodology: (1) individual identification and focal animal sampling; (2) uniform categorisation of independent variables; (3) use of ethograms to select significant behaviours to sample; (4) sampling methods: one-zero, instantaneous, counting number of events; (5) specific measures of mother–infant spatial relationships.

Individual identification

In studies of social behaviour it is common practice to focus observations on individuals of age, sex, or reproductive classes of specific interest (Altmann, 1974). Individual identification is thus an integral tool in studies of animal behaviour. Reliable identification methods make it possible to track the movements and reproductive histories of known animals and allow estimation of population size by mark-recapture techniques (Hammond, 1986). This approach has proven useful in studies of right whales, *Eubalaena australis* (e.g. Payne, Brazier, Dorsey, Perkins, Rowntree and Titus, 1983), humpbacks, *Megaptera novaeangliae* (e.g. Glockner-Ferrari and Ferrari, 1984; Katona, Baxter, Brazier, Kraus, Perkins and Whitehead, 1979), killer whales, *Orcinus orca* (e.g. Balcomb, Boran and Heimlich, 1982) and gray whales, *Eschrichtius robustus* (e.g. Swartz, 1986).

We observed mother–infant right whale pairs during two four-month nursery periods, from August to November, in 1978 and 1979. Our observations were made at Golfo San Jose, Peninsula Valdes, Argentina (Taber and Thomas, 1982). Individuals were identified using the callosity identification methods developed by Payne *et al.* (1983). Repeated observations of focal pairs allowed us to document trends common to most pairs. Five clear stages of infant development from birth until weaning were identified (Taber and Thomas, 1982).

Independent variables

One of the methodological decisions which must be made is the choice of independent variables against which to gauge mother–infant development. We used two such variables: date and calf size. On each sighting of a focal pair, the calf's size relative to its mother and to other calves was determined and used to provide a rough measure of calf age (calibrated by the sizes of two calves of known age).

Analysis of our data by date revealed clear development trends. The most significant departure from age-scheduled behavioural development was that just prior to migration, most pairs, regardless of differences in calf age (see below), showed the same restless behaviour and most pairs departed within a few days of each other (Taber and Thomas, 1982).

Ethogram

During our first season of observations at Peninsula Valdes, we developed an ethogram of mother–infant behaviours. We tape recorded observations of behaviour and analysed these tapes to describe behaviours and determine their relative frequencies. The ethogram was hierarchically arranged to include behaviours at the level of Modal Action Patterns (MAP) (Barlow, 1977) such as tail slaps, flipper slaps, breaches, respirations and locomotory behaviour, combinations of MAPs that are frequently repeated such as breaching bouts, and complex play patterns; and a final major grouping of behavioural states that endure for long periods and are mutually exclusive, such as travel, rest, nurse, and play.

We chose those activities from our ethogram that seemed most likely to elucidate general trends in mother–infant activity. These behaviours formed the central focus of our second year of observations. This narrowing of goals was crucial for several reasons.

(1) The simplest measures produced some of the most useful results, as in the case of the leave-approach data described below (and see Taber and Thomas, 1982).

(2) The effectiveness of the observers was increased by limiting the number of behavioural categories considered, and by clearly defining the most important data. In our first year of observations we had a tendency to attempt to record everything that happened, in the hope that the significant behaviours would become obvious; a common approach of people studying rarely sighted animals. This can result in haphazard and inconsistent sampling, since what is perceived to

be important may change with each observation and the observer may be overwhelmed by too much detail.

(3) In the limited hours of observation available on an elusive species, it is important to decide what specific observations must be taken at each sighting. When making observation from the air, for example, it is crucial that the observer record the number of animals in a group and their locations every time animals are seen. In our study of mother–infant behaviour, we sampled the distance of mother from calf and the general activity type occurring at every 30 s interval during the encounter.

General sampling methods

After deciding what behaviours to sample, checksheets were designed with activities arranged from general behavioural states to specific events. The methods of sampling long enduring states and of recording quick events differed. Altmann (1974) has synthesised sampling methods for observational studies of animals in a valuable paper. We chose three sampling techniques described by her, and adapted each for use with a 30 s sampling interval. In one-zero sampling a check indicates that a particular behaviour has occurred at least once during the sampling interval. This method was chosen to record behavioural states unlikely to occur more than once in an interval or likely to continue through several intervals. One problem with one-zero sampling is that it under-represents the occurrence of those behavioural events repeated within the interval (Altmann, 1974; Kraemer, 1979; Leger, 1977; Simpson and Simpson, 1977).

An alternative to one-zero sampling is instantaneous sampling. In instantaneous sampling, a check mark indicates that a behaviour was occurring at the moment of onset of a particular sampling interval. The repeated instantaneous views provide an accurate sample of behaviour (Altmann, 1974). We sampled the distance between mother and calf by this method (Taber and Thomas, 1982).

A simple counting of the number of events of several behaviours during the 30 s interval was also employed. This was most useful for quickly repeated behaviours such as breach, flipper slap and other aerial behaviours.

Using these techniques, behavioural time budgets were determined for right whale mothers and infants (Thomas and Taber, 1984). The time budgets of mothers were different from those of the calves and both changed as the calves grew. The characteristics of calf activity at different ages and seasons gave some power to predict when migration and weaning were about to occur, and provided a basis for estimating calf ages.

Specific measures of mother-infant behaviour

Three measures of mother–infant proximity have been used extensively in studies of how mother-offspring spatial relationships in primates predict changes from birth to weaning (Altmann, 1980; Hinde and Atkinson, 1970; Struhsaker, 1971). These are simple methods requiring minimal previous experience with a study species and they produce clear predictive results (Taber and Thomas, 1982).

The three measures used to document mother–calf spatial relations were:

(1) instantaneous sampling of the shortest distance between mother and ~~calf~~ (in increments of the mother's length) every 30 s;

(2) recording of 'leaves' (when one pair member was orienting away from the other and actively increasing the distance between the two) and 'approaches' (the opposite) every time they occurred;

(3) the proportion of total approaches that were made by the calf minus the proportion of total leaves that were made by the calf. The resulting Proximity Quotient (Hinde and Atkinson, 1970) provides a measure of the calf's and the mother's relative roles in maintaining proximity. If the calf is primarily responsible for maintaining contact, the value of the measure is positive, if the mother is responsible, it is negative.

Each behavioural stage could be characterised by differences in the three measures of proximity (Taber and Thomas, 1982). Stage one, the newborn stage, is characterised by constant closeness. Few 'leaves' and 'approaches' are recorded and pair members seldom separate. Mothers approach their calves more than they leave them and are responsible for maintaining contact. This stage lasts until the calves are about a month old.

Stage two is the calf play stage. It lasts for a few months, from the gradual transition out of stage one until just before the pairs migrate away from the area in November. During this stage the pair members spend decreasing amounts of time within physical contact. Calves become dramatically more active in leaving and approaching the mother in play. Calves leave and approach more than their mothers but mothers continue to approach their calves more than they leave them, thereby maintaining contact between the two.

Stage three is the pre-migration stage. Pairs reunite spatially, spending more than 90% of their time in close contact. 'Leaves' and 'approaches' are few and both mother and calf approach more than leave each other (possible since they often drift apart). Mothers remain more responsible for maintenance of contact than the calves.

Stage four is when the pairs are away from the Valdes region, migrating and feeding. Behaviour of the mother and calf during this period is undocumented.

Stage five begins when the pair returns to Peninsula Valdes the next year. This is the pre-weaning and separation stage. The calves are 12–14 months old and the pair members are still in constant close contact. Rates of 'leaves' and 'approaches' are low, but, in contrast to all previous stages, the yearling calves showed a clear pattern of approaching more than leaving their mothers. The mothers, for the first time, left their calves more than they approached them and calves were clearly responsible for maintaining contact between the two.

This reversal of responsibility for maintenance of contact has been shown in many primate species (Altmann, 1980; Hinde and Atkinson, 1970) and is a good indicator that weaning is imminent. Trivers (1974) predicts that this reversal should occur from his work on parent–offspring conflict.

Researchers designing behavioural studies of cetaceans have several studies to refer to for ethograms and detailed descriptions of behaviour (Martinez and Klinghammer, 1978; Würsig, Clark, Dorsey, Fraker and Payne, 1982) and we are preparing one of right whale mother–infant behaviour. Observational studies can work from, and add to, these descriptions while working on the more crucial question of how populations and species differ from each other behaviourally. This is important since many harvested species are inaccessible to detailed behavioural studies.

The methods described above can be easily adapted to produce comparable results for studies of mother–infant behaviour of humpback and gray whales in all portions of their ranges in the North Pacific, as well as other humpback and right whale populations. The three measures of mother–young spatial relationships can be incorporated into aerial observation methods and used opportunistically in sightings of mother–young pairs of any species encountered. Leave-approach and distance measurements are easy to collect in the field and provide a quick, clear way to identify where a calf is in its progression from birth to weaning (Taber and Thomas, 1982).

It is not necessary in such studies to divide behaviour up into minute detail. The most useful behaviours we sampled which characterised right whale mother–calf activity in a general way were travel, rest, nurse and play. Using only these four categories it was possible to describe the time budgets of the whales (Thomas and Taber, 1984). With the addition of a few more sampling categories, such as feed, socialise and mate, the time budgets can be compared to similar data collected at different times of the year, in other locations, or from animals of different age–sex classes.

ASPECTS OF MOTHER–INFANT BEHAVIOUR RELATED TO MANAGEMENT

Studies of right whales at Peninsula Valdes have been ongoing since 1970 (Payne, 1976; Payne *et al.*, 1983; Clark and Clark, 1980). More than 580 individual right whales have been identified by callosity patterns at Peninsula Valdes (Payne, 1984). Adult females are normally seen in the area with a newborn calf every three years (Payne, 1984) and are occasionally sighted the year after calving with their still nursing yearling calves (Taber and Thomas, 1982). Females of breeding age are not seen in the region the year before calving (Payne, 1984). Adult males come to the area, and yearling and sub-adult animals are also present (Payne, 1980).

The mother–infant bond in right whales lasts up to 14 months. The first three to four months of a calf's life are spent in the protected waters of Peninsula Valdes. In November, pairs migrate away from the area in temporal synchrony with other pairs. During the next six to seven months (when they have not been studied) they migrate and feed. After this period, at least some of the pairs return to the Peninsula Valdes region. These pairs separate after a few weeks there (Taber and Thomas, 1982).

The sightability of the calves in our study changed with age. A combination of factors reduces the likelihood that a newborn calf up to a month old will be seen by aerial or shore based studies. Until about the age of one month, the mother and infant are travelling 89% of the time (SD = 9.06). While remaining in one region of the Peninsula such as Golfo San Jose, the pairs stay in constant forward motion, rarely stopping. They cover many kilometers along the coastline before retracting their path or slowing. This behaviour allows the observer little time for observations as the newborns pass fixed shore points. Newborn calves were submerged during a mean of 85% of the sampling intervals (SD = 18.09) while their mothers were submerged only 39% of the time (SD = 24.66). Even when at the surface, the calves were difficult to see for two reasons; (1) they were often hidden behind the bulk of the mother, and (2) even when in direct view of the observer, very little of the newborn calf breaks the surface when it rises to breathe, and the surfacings are very brief (1–2 seconds). This is clearly important for other species if aerial, ship or shore based surveys are used to obtain estimates of gross recruitment (e.g. see IWC, 1983 with respect to bowhead whales) or infant mortality rates, especially if, for example, numbers of calves in the breeding grounds are compared with numbers during migration or on feeding grounds.

In the second stage (1–3 months of age) calves are more easily visible. They spend up to 40% of their time in active play behaviour (mean = 20.6%, SD = 9.7). They are submerged less than newborns (57% of the time, SD = 17.75), although their mothers are submerged for about the same amount of time as at the first stage (36%, SD = 21.79). In contrast to the pairs containing newborns, these pairs stay in the same place for hours at a time or move slowly along the coast. This makes them ideal subjects for the shore-based observer. They remain very close to shore, preferring water depths of 5 m or less (Payne, 1980).

In the third short stage of mother–infant development (it occurred for about one week in November) pairs began constant rapid travelling movements in preparation for migration. By this time the calves were large enough to be almost as easily visible as their mothers. However, both calves and mothers were submerged more than at the previous stage (calves 78%, SD = 12.23; mothers 46%, SD = 34.44) which made individual identification from callosity patterns difficult as they passed by with their heads submerged. In our particular study this problem was reduced as previous familiarity with the individual pairs who had been present in the area for several months had made us more aware of subtle clues, such as nicks, scars, or unique profiles which facilitated recognition.

Without callosity identification we might have mistaken the yearlings returning to Golfo San Jose with their mothers for infants born out of the normal calving season (June–September). This again has clear implications for studies of gross recruitment rate. These yearlings acted superficially like infants, and did not appear to our eyes to be much larger than the infants we had watched depart six months earlier. Without certain identification, we would have made incorrect inferences about the range of the calving season and about mother–infant behaviour. To avoid such mistakes, a diligent effort must be made to identify individuals each year. Photographs of each mother–calf pair would facilitate identifications and document the relative size of each calf.

Interactions with other whales also varied with calf age. Mother–calf pairs rarely interacted with other whales (11% of the time). Early in stage two, calves were approached by other whales more than at any other time. Single whales approaching them often interposed themselves between the mother and her calf and occasionally succeeded in sequestering the calf away from the mother for a few minutes. Later in the infant period, interactions of this sort were uncommon and most interactions were passive ones with other mothers and calves. Despite occasional close proximity, calves were never observed interacting with one another.

The spacing of right whales in Golfo San Jose suggest that the mothers and calves require separation from the other whales in the area. Similar segregation during breeding, feeding or migration again has implications for estimates of gross recruitment from survey data. The mothers and calves were generally found along one beach, closer to shore than any other whales. Other whales were further offshore, or along more rocky stretches of the gulf. The boisterous activity of socialising animals therefore takes place away from the mothers and calves and when mothers and calves got into the midst of such activity they usually fled. Were the area available to the right whales in a particular area of Peninsular Valdes reduced, one might see effects on the mothers and calves as they came into more contact with the active groups. A further aspect of mother–young behaviour with relevance to management is the importance to the mother of conserving resources during her period of fasting while nursing her calf. This is discussed by Thomas and Taber (1984). This need to conserve energy should be considered when the potential for harassment by humans or even other whales is increased.

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USE OF ACOUSTIC TECHNIQUES IN STUDYING WHALE BEHAVIOR

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ABSTRACT

As research on cetacean vocalizations continues, analysis methods and acoustic equipment improve. Conclusions drawn from marine mammal bioacoustical studies should be based on appropriate data collection, recording equipment, analysis methods and knowledge of the whale's behavior. This paper reports the current 'state of the art' in collecting and analyzing cetacean acoustic data and discusses the potentials for future acoustic research using towed arrays and satellite technology.

INTRODUCTION

Studies by Clark and Clark (1980) on right whales (*Eubalaena australis*), by Watkins (1977) on sperm whales (*Physeter macrocephalus*), and by Payne and McVay (1971) on humpback whales (*Megaptera novaeangliae*), show the utility of acoustics in studying cetacean habits. Underwater sounds can be received over long distances and passive listening need not disturb the animal's normal behavior. Acousticians try to relate variability in vocalizations to biological parameters, e.g. individual, age, pod, sexual or seasonal differences. Most cetacean vocalizations can be used to identify the species. Because vocalization data can be collected even during a brief encounter with a whale, their use in population assessment is growing. As acoustic research on cetaceans continues, methods and equipment improve. This paper is as an update on the 'state of the art' in collecting and analyzing cetacean acoustic data and makes some predictions about the potentials for acoustic research in the future. Our purpose is to provide a background document for evaluating previous acoustic investigations and for designing future acoustic studies.

Virtually all marine organisms, vertebrates and invertebrates alike, produce sounds. Sound production can be *active* or intentional for the purposes of communicating, finding food and, navigating and *passive* or unintentional from activities like swimming or feeding. Oceans have a variety of non-biological sounds (Fig. 1): volcanic rumblings, seismic activity, sea state, ice noise and rain (Albers, 1965; Ganton and Milne, 1964; Ryan, 1977; Payne and Webb, 1971; Corcela and Green, 1968). Human activities such as ship traffic and oil production also produce significant amounts of underwater noise (Payne and Webb, 1971; Myrberg, 1978). A prime objective in acoustic studies of marine mammal sounds is to discriminate background noise from biological signals and maximize the signal-to-noise ratio for marine mammal sounds. Fish and Mowbray (1970), Tavolga (1968), Fish (1967),

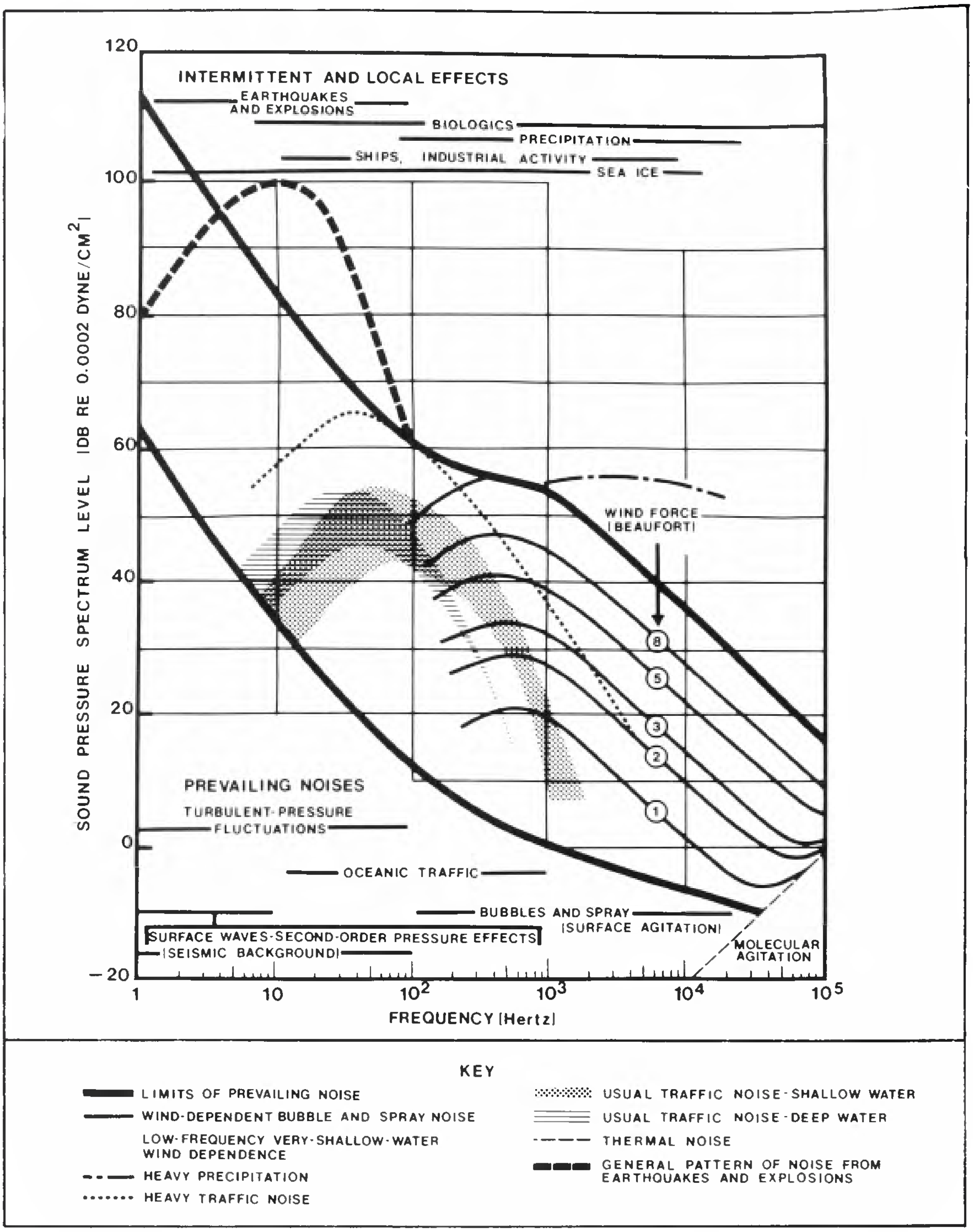

Fig. 1. Composite of ambient noise spectra.

and Cummings and Fish (1971) have compiled sonagrams and descriptions of sounds produced by marine organisms. Cummings (1971) has published a demonstration tape of biological sounds. With practical experience anyone can learn to distinguish cetacean sounds from those of other organisms or non-biological sounds.

The most common mistake that researchers make in studying marine mammal sounds is using inappropriate equipment or analysis techniques. Conclusions drawn from marine mammal bioacoustic studies should be scrutinized based on the data collection regime, recording system, analysis methods and knowledge of the animal's behavior.

DATA COLLECTION

Cetacean sounds have been studied in captivity and in the field; both locations have advantages and limitations. The most important advantage of acoustic studies of captive cetaceans is that the age, sex, individual identity and species of the subject are known. In several cases, the acoustic behavior of captive cetaceans has been studied successfully (Caldwell and Caldwell, 1971; 1973; and Evans, 1973). However, many cetaceans cannot be studied in captivity because of husbandry problems and also because of changes in acoustic behavior in captivity. Some species drastically decrease the number of vocalizations produced in captivity because of overwhelming reverberation in their tank. Partvulescu (1967) discussed acoustic considerations for tanks. In addition, recent evidence from Jeff Norris (pers. comm.) suggests that because of tank reverberation, common dolphins (*Delphinus delphis*) change the duration of their vocalizations in captivity. Reverberation in enclosures may also cause marine mammals to change temporal and amplitude aspects of their vocalizations (Au, Carder, Penner and Scronce, 1985). Lack of environmental stimulation, changes in feeding behavior and artificial social structures may also change the vocal repertoire of captive animals. Careful assessment of the animal's acoustic environment and comparison of captive with wild sounds should be made before conclusions about captive data are made.

In the field, a few resident populations where the identities of individuals are known have been examined acoustically; killer whales (*Orcinus orca*) in Puget Sound and McMurdo Sound, Antarctica dolphins, spinner (*Stenella longirostris*) near Kona, Hawaii and spotted dolphins (*Stenella plagiodon*) near the Bahamas. Unless a researcher studies a resident population, there is little control over the duration of encounters and the behavior of the animal; most acoustic data collected in the field come from chance encounters. However, recordings from the wild do represent the animal's natural acoustic behavior and acoustic environment.

Oceanographic conditions during a recording session affect the amount of background noise, the area sampled, and the transmission characteristics of cetacean sounds (Fig. 1). Each sea state adds about 10 dB to the background noise (Albers, 1965). Except in polar oceans where the water column is nearly isothermal, temperature stratification in the ocean tends to create horizontal sound channels (Ryan, 1977). Sounds produced in the surface mixed layer tend to bounce within this temperature zone and their propogation is enhanced (Fig. 2). Similarly, sounds within the thermocline and deep sound channel tend to propogate horizontally within that temperature layer (Albers, 1965). Unless temperature stratification is known, the distance to a sound source cannot be estimated because spherical spreading might not apply and acoustic shadows may be created by listening in a temperature layer above or below the sound producer.

RECORDING EQUIPMENT

Currently, several recording systems are used to study cetacean acoustic behavior: (1) a manually operated, stationary hydrophone and recorder, (2) an automated hydrophone and recorder, (3) a sonobuoy and receiver, (4) a stationary hydrophone array and (5) a towed hydrophone array. The advantages and limitations of these recording systems and cetacean studies that have employed them are discussed below.

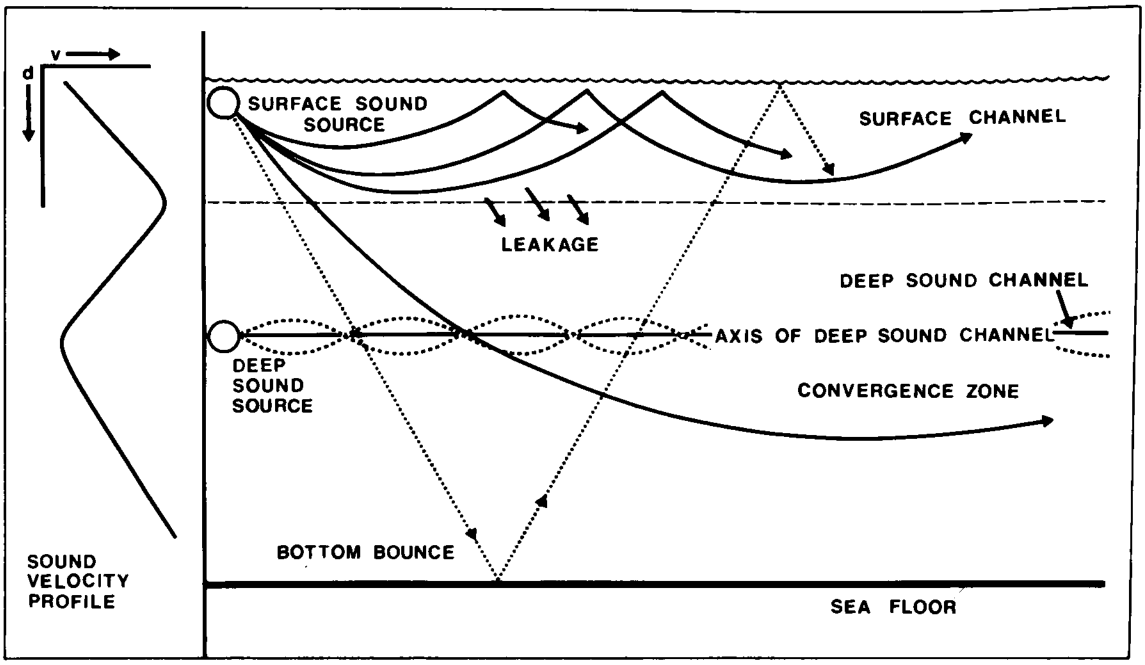

Fig. 2. Modes of underwater sound propagation.

Recorders

Each system stores acoustic data on magnetic tape. Maintenance of recording systems is imperative to accurate data collection, e.g. cleaning, aligning and degaussing recording heads. Field recorders usually are battery operated. The best reel to reel and cassette field recorders have electronic speed regulation. Some will not function when batteries are too low. In others, such as most inexpensive cassette recorders, but including one reel-to-reel recorder that costs over $1,000, tape speed is a function of battery voltage below a certain level. All good recorders have a variable tape bias level that affects distortion and frequency response. Tape bias should be optimized for the specific tape in use. Alternatively, several types of magnetic tape can be tested to find the one that matches best the recorders' frequency response. A few tape recorders have a reference oscillator that produces a known frequency and amplitude sound to calibrate each tape.

Common reel to reel recorders record on one or two channels at 19.5 cm/sec with a frequency response linear to about 20 kHz. Many cetaceans produce extremely high frequency vocalizations, e.g. Dall's porpoise (*Phocoenoides dalli*) produces narrowband pulses between 100 and 200 kHz (Evans, Awbrey, Norris and Hubbard, 1979). Audio tape recorders, and even many instrumentation recorders, cannot register such high frequencies. For high frequency vocalizations, instrumentation recorders running at 152.4 cm/sec with a frequency response good to about 300 kHz are necessary.

Instrumentation recorders that can be battery operated and have 4, 7 or 14 channels, providing a channel for narration, a channel for a time signal and simultaneous collection of data from multiple hydrophones, are ideal. Combinations of 'direct' and frequency modulated (FM) channels provide a frequency range from 0 Hz to as high as 300 kHz, depending upon tape speed. Dynamic range of a channel is about 40 dB, but this can be extended by recording simultaneously on 2 or 3 channels with input attenuators set 20–30 dB apart.

Several review articles are available that discuss recording equipment and techniques (Frings and Frings, 1965; Tavolga, 1965; Eagle, 1980; Worman, 1980; Berger, 1981).

Cassette recorders have been used for recording marine mammal sounds. However, they have serious shortcomings. Non-linear frequency response and poor speed regulation of inexpensive, single channel cassette recorders limit them to such uses as determining general activity levels. All consumer market cassette recorders run at 3.81 cm/sec. The best claim a response that is linear to 20 kHz, but high frequencies require preemphasis to be recorded at slow tape speeds. This can be nearly 20 dB at 20 kHz. The usual sounds recorded on stereo cassettes have little acoustic energy above 8–10 kHz so problems are minimal, although audiophiles are familiar with the 'splatter' that can result from attempting to record trumpet or piano music at normal levels. Cetacean sounds that peak above 10 kHz must be recorded 20 dB below the normal level to avoid tape saturation. Most recorder level meters indicate only to −20 dB. Any dolphin whistle or click that causes such a level meter to deflect has probably saturated the tape, making it useless for determining frequency characteristics of the vocalizations. This is especially true if the meter has 'VU' rather than 'peak' response time constants.

At the other end of the audio spectrum, the extremely narrow record head gap necessary to record high frequencies causes uneven response (head bumps) below about 50 Hz. Within these limitations, high quality stereo cassette recorders can be used to make recordings of marine mammal sounds.

Transducers

A common mistake in studying animal sounds is mismatching of the recorder/transducer system and the animal's sounds. Hydrophones vary in frequency range, transient response, size and cost. The military is a common source of hydrophones (Groves, 1974). Most of these transducers are linear at low frequencies, for measuring vessel noise, but may have one or more major peaks at upper audio frequencies. These peaks are caused by resonances in the transducer elements. They distort any transients, such as broad band pulses or echolocation clicks, that have significant energy at the transducer's resonant frequency. All transducers resonate at some frequency. Calibration is essential for quantitative work.

To ensure documenting the entire vocal repertoire, the bandwidth of the receiving and recording system has to match or exceed that of the animal's sounds. The bandwidth problem is compounded by directionality. Horizontal and vertical variations in frequency response pattern of a hydrophone, can cause the same sounds to differ significantly depending upon the relative location of the subject. Very small and spherical hydrophones have the best omnidirectional responses, but also are the least sensitive. The vertical and horizontal frequency response of a hydrophone should be measured and understood to appropriately interpret recordings. In some cases unidirectional hydrophones are useful to monitor vocal behaviors of animals passing a specific location. The method used to suspend a hydrophone affects its reception field and may introduce cable strumming noise.

For accurate amplitude measurements, the sensitivity of the hydrophone must be known relative to a known sound pressure level. The system's sensitivity and dynamic range must be appropriate for levels to be measured to avoid losing the signal in electronic noise, overloading an amplifier, or saturating the tape. Bobber

(1970) summarized methods for calibrating transducers and measuring source sound pressure levels. Fish and Turl (1967) described methods of measuring sound pressure levels in four species of small whales.

Amplifiers

Broad bandwidth, omnidirectionality, and good transient response in transducers are obtained at the expense of sensitivity. Typical hydrophones with a usable frequency response to 200 kHz generate 5 microvolts or less when receiving a pressure sound level of 100 dB re 1 micropascal. Such low level signals must be amplified to be usable with tape recorders. The same hydrophone might also be used to receive sound pressure levels of 300 dB, its output then would be 1/2 volt. Furthermore, interactions between the high impedance of the transducer and the capacitance of shielded cables causes noise problems and increasingly severe high frequency roll-off as longer cables are used. One way that these problems can be avoided is by using a very expensive charge-coupled amplifier. More commonly, a preamplifier to convert the hydrophone output to low impedance and sometimes to provide voltage gain is placed near the hydrophone. Sometimes this in-line preamplifier provides enough amplification, but often additional amplification and/or signal conditioning is needed between the cable and the recorder. Regardless of where they are placed in the system, amplifiers with suitably low self noise, high sensitivity, broad bandwidth, linearity and dynamic range are expensive. Addition of switchable filters or precision attenuators increases the utility of an amplifier, but also adds to the cost. Some amplifiers have high and/or low roll-off filters allowing the selective elimination of frequencies outside the range of the animal's sounds. Effective dynamic range is increased to enhance the signal-to-noise ratio by placing a variable attenuator ahead of a high gain amplifier. Precision step attenuators used here facilitate accurately measuring source sound pressure levels.

Recording systems

(1) *Manually operated hydrophone and recorder*

The most common method of collecting cetacean acoustic data is a single hydrophone monitored by a researcher with data recorded on a tape recorder (Fig. 3). Studies by Fish and Mowbray (1962) on *Delphinapterus leucas*; by Awbrey, Thomas, Evans and Leatherwood (1982) on *Orcinus orca*; by Ford and Fisher (1978) on *Monodon monoceros*; and by Leatherwood, Thomas and Awbrey (1981) on *Balaenoptera acutorostrata* have successfully used this system on cetaceans. The primary advantage of this system is the first hand observation and narration of background data such as the animal's behavior and ambient conditions. This technique is constrained often by weather or daylight.

(2) *Automated hydrophone and recorder*

Systems to sample and record cetacean sounds can be automated and controlled by a timer or sound powered switch (Fig. 4). This method has the advantage of sampling during daylight and dark, sampling in remote areas, and systematically collecting diurnal or acoustic activity information without the researcher having to be present. If the object of the study is to document diurnal variations in vocalization rates, spectral information is not needed. Often because of the

Fig. 3. Interoceans 605B hydrophone and Nagra IV tape recorder.

precarious environment there is a high risk of equipment loss, so inexpensive cassette players and hydrophones usually are used. Such an automated system has been used to sample vocalizations of leopard (*Hydrurga leptonyx*), crabeater (*Lobodon carcinophagus*), and Weddell (*Leptonychotes weddelli*) seals (Thomas and DeMaster, 1982), but has not been used for any cetacean. The disadvantage of an automated system, in addition to poor frequency response is that other background data such as weather conditions and the animals' behavior probably will be missed.

(3) *Sonobuoy and receiver*

Sonobuoys were developed by the military as a disposable listening device that can be dropped from aircraft to detect ship noise. A military sonobuoy (Fig. 5) is a hydrophone and transmitter housed in a buoyant cylinder with a saltwater activated antennae, battery, hydrophone and scuttle switch. Most of the models available have a low frequency response (below 20kHz) because they are designed for reception of vessel noise. Sonobuoys can be modified to be reusable and more useful for making marine mammal recordings (Ljungblad, Thompson and Moore, 1982) by using different hydrophones, antennae and batteries. Because whale sounds are transmitted from the sonobuoy to a receiver, the signal-to-noise ratio can be higher than direct recordings, which often includes machinery noise or water slapping against a hull.

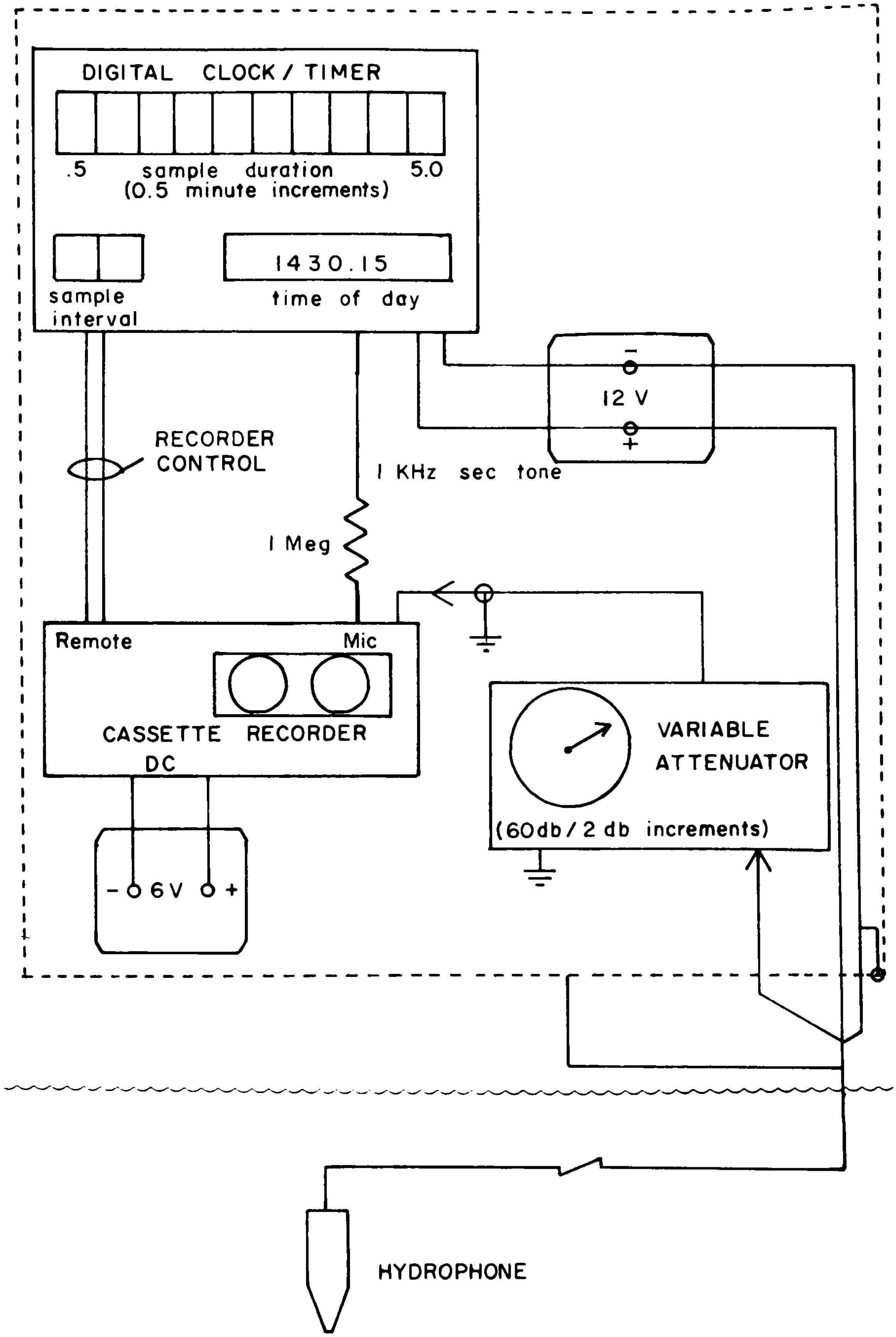

Fig. 4. System used to make automated 24 hour timed interval recordings.

Fig. 5. Disposable, military type sonobuoy.

In spite of their sensitivity to vessel noise, a sonobuoy can be used from a ship by cruising away from the launch point until vessel noise diminishes to a reasonable level. A circumpolar transect around the Antarctic was conducted by Thomas, Awbrey, Leatherwood, Evans and Jehl (1981) using periodic sonobuoy drops to monitor *O. orca* and *B. acutorostrata* vocalizations. This technique proved particularly useful for transects where the ship must remain underway or for night recording sessions where activity in a small boat is not advisable.

(4) *Stationary hydrophone arrays*

A hydrophone array is a group of transducers arranged in a variety of configurations e.g. linear, triangular, grid, to jointly receive acoustic signals in an area (Fig. 6). The array transducers could be simple hydrophones or sonobuoys.

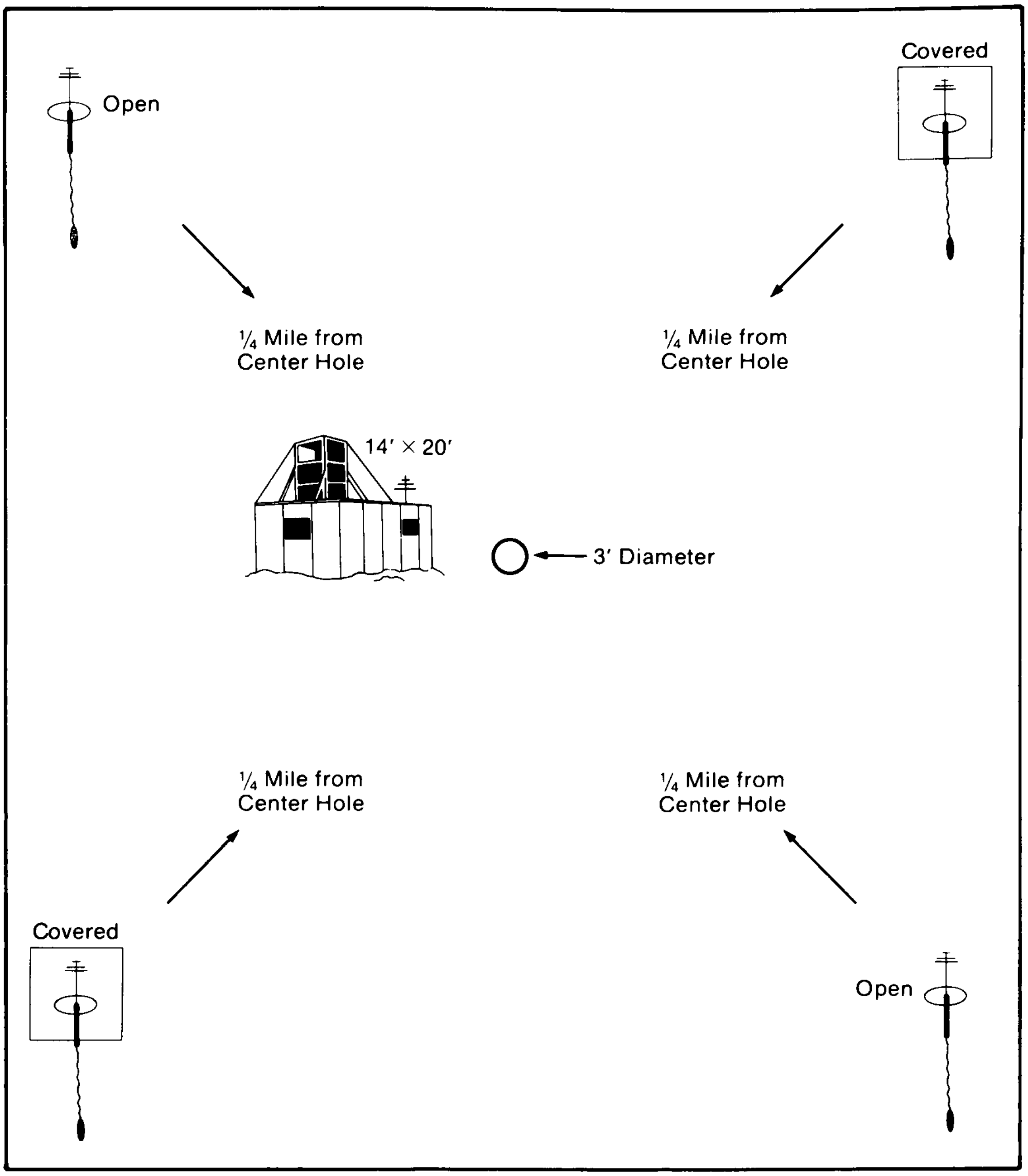

Fig. 6. Grid of sonobuoys used to monitor marine mammal vocalizations in a fast ice area.

An array can be used to locate a whale's position by examining the time delay between reception at the transducers. A linear array can be used to monitor movements of whales along migration corridors as in bowhead whales, *Balaena mysticetus* (Ljungblad *et al.*, 1982). A grid of hydrophones or sonobuoys can be used to monitor movements of whales within a large study area. Studies by Clark and Clark (1980) showed that the location of right whales (*E. glacialis*) should be determined by looking at the difference in time of reception between an array of bottom-mounted hydrophones. A triangular array was used to track movements of sperm whales by Watkins (1977). Hydrophones placed in a vertical array at different depths have been used to study depth usage by Weddell seals (Thomas and Kuechle, ms) and a similar arrangement could be used for cetaceans.

(5) *Towed hydrophone arrays*

An alternative to a stationary listening system is the use of a towed hydrophone array. By using acceleration cancelling hydrophones, a towed array allows movement of transducers through the water behind a vessel, thus keeping pace with the cetacean producing sounds. Fig. 7 illustrates a simple model of the towed array used by Hubbs Marine Research Institute to study acoustic behavior of small cetaceans in the Eastern Tropical Pacific. The linear hydrophone array is directional. It has low fore and aft sensitivity, thus minimizing pick-up of noise from the towing vessel. Sensitivity is maximum perpendicular to the array axis so turning the vessel or electronically scanning the hydrophones determines the direction of the incoming sound source. The distance to a source of known level can be crudely estimated from attenuation constants and assumptions about oceanographic conditions. Depth and temperature sensors on the array allow accurate measurement of thermal gradients and the array can be positioned within a thermocline. Pilot whales (*Globicephala machrorhynchus*), common dolphins (*D. delphis*), spotted dolphins (*Stenella attenuata*), spinner dolphins (*S. longirostris*) and bottlenose dolphins (*Tursiops truncatus*) have been detected and tracked using a towed array (Thomas and Evans, 1982). This tool may be one of the most useful acoustic methods for assessing marine mammal stocks and may become an important method of line transect estimates of cetaceans.

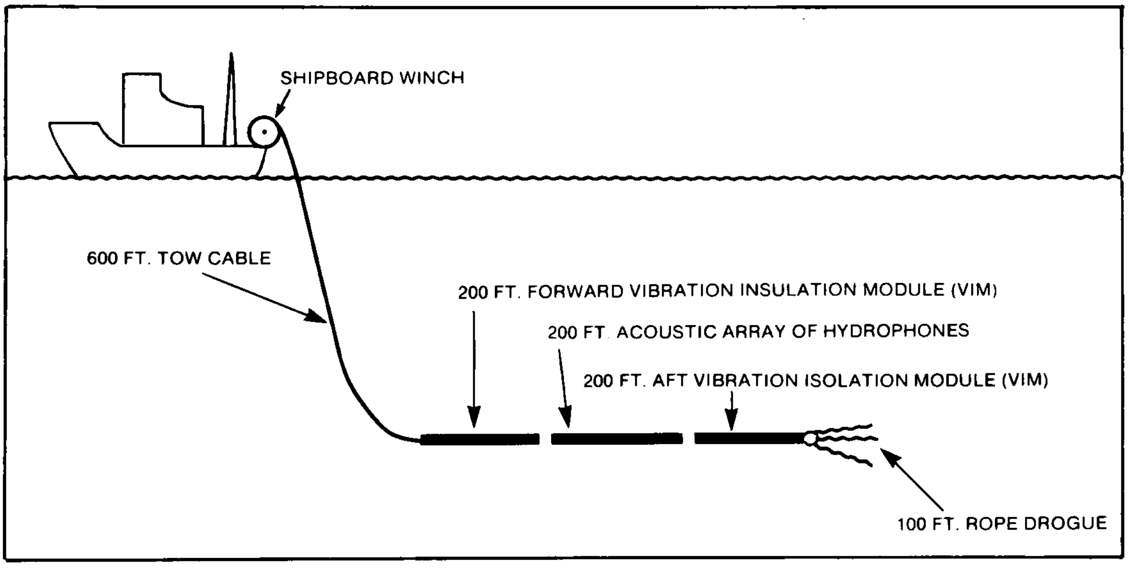

Fig. 7. Towed acoustic array used to monitor marine mammal vocalizations.

DATA ANALYSIS

All sounds can be described by measuring time (seconds), frequency (Hertz), and amplitude (voltage or decibel) relationships. The most common analysis display is the sonagram, which relates frequency on the Y-axis, time on the X-axis, and amplitude in shades of gray (Fig. 8a). The Kay Sona-Graph has been the primary instrument for analyzing marine mammal sounds in the past (Caldwell and Caldwell, 1971; 1973; Fish, Sumich and Lingle, 1974; Tavolga, 1968; and Fish and Mowbray, 1970). The Sona-Graph is a heterodyne instrument. Like all other analysis instruments, it trades off frequency for time resolution and vice-versa.

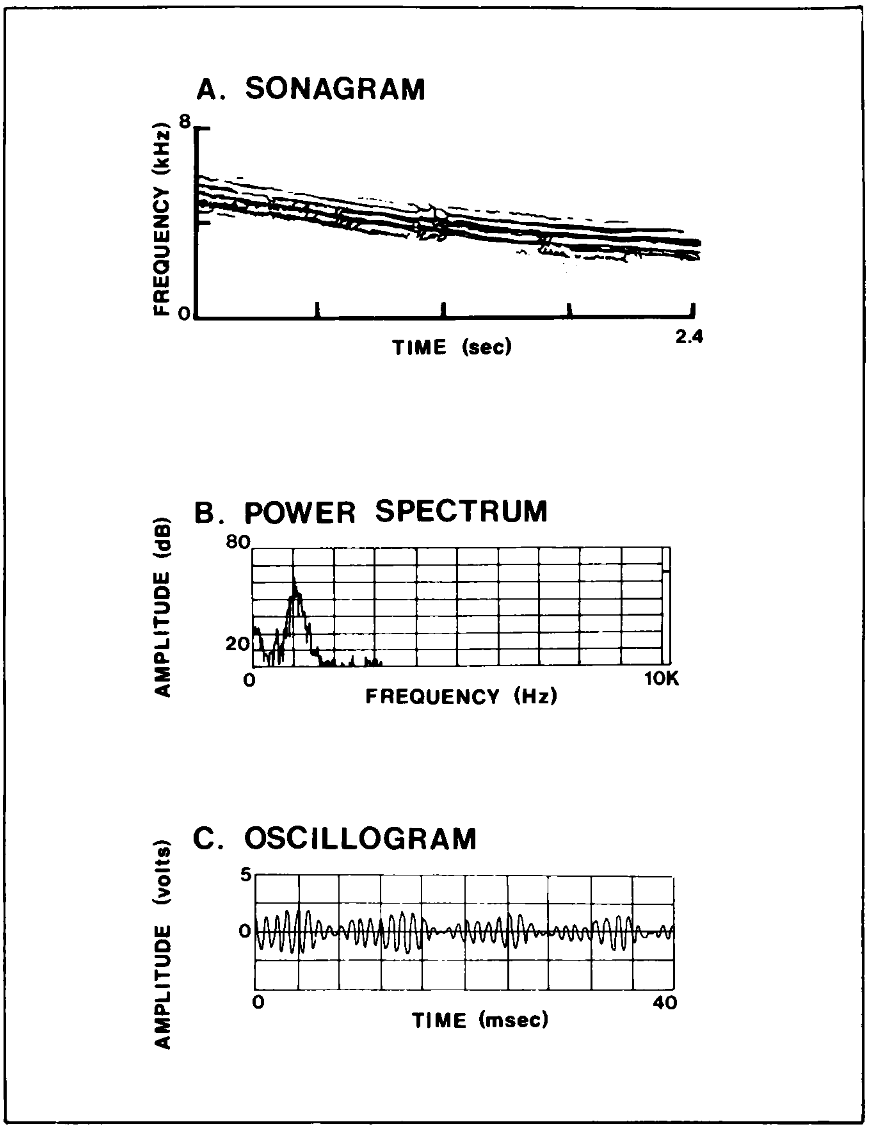

Fig. 8. Analysis methods used on the same Weddell seal vocalization; A. sonogram, B. power spectrum and C. oscillogram. B and C demonstrate the trade off between frequency and time resolution.

Because it uses RC and LC filters that ring when excited by transients (such as delphinid clicks) it is not to be trusted for measuring pulse durations. Pulse rates are fine except when they fall into the uncertainty range near the filter bandwidth. Sampling waterfall displays derived from digital spectrum analyzers are even worse for measuring pulse rates and are hopeless for pulse durations. Oscilloscopes are best for these uses. Davis (1964) reviewed the assets and limitations of the Sona-Graph.

Sonagram analysis is inexpensive and has good frequency resolution (bandwidth selectable to 45 Hz or 300 kHz); however, its major limitations are the short analysis time (1.2 or 2.4 seconds) and low frequency range (8 or 16 kHz). Vocalizations by many marine mammals are longer than 2.4 seconds, e.g. *M. novaeangliae* (Payne and McVay, 1971) and *O. orca* (Awbrey *et al.*, 1982); analysis using this equipment requires partitioning the sound. To solve this time problem, recordings can be played back at faster tape speeds, thus compressing time, but decreasing the frequency resolution. For cetacean vocalizations that exhibit complicated temporal patterns, e.g. humpback whale songs, increasing the playback speed several times facilitates recognition of temporal relationships. Many cetacean sounds are higher in frequency than the 16 kHz maximum of the Kay Sona-Graph, e.g. Dall's porpoise, killer whales, and spotted dolphins. To solve the frequency problem, tapes can be played back at slower speeds, but available analysis time decreases. Especially, for short duration vocalizations, such as pulses, decreasing the playback speed allows more detailed measurements of frequency components.

Several 'real time' digital sonagram/waterfall analysis units are now available to bioacousticians. The important advantage of these analyzers is that near real time fast Fourier transforms can be displayed and copied. Most sonagram analyzers have selectable frequency, amplitude, and time ranges and cursors for specific measurements within a sound. Some analyzers have output capabilities for a computer or plotter, thus facilitating measurements. As with recording systems, digital sonagram analyzers need to cover wide frequency ranges to be useful in studying marine mammal sounds.

Digital spectrum analyzers provide both oscillogram and power spectrum (frequency versus amplitude, Fig. 8b) analysis. Most spectrum analyzers have selectable frequency, amplitude, and time ranges with cursors for precise measurements. Many spectrum analyzers have added mathematical functions that can add, subtract, multiply and divide spectra or average spectra over time. Again, frequency range of some spectrum analyzers may become a limiting factor for analyzing marine mammal vocalizations. Some have frequency ranges to 100 kHz or more, but few of these have actual real time capability above 2–4 kHz. Although real time power spectra and oscillograms can be displayed, a good inexpensive method for continuous copying in real time has not been developed. Some spectrum analyzers have plotter and computer outputs for delayed copying.

Oscilloscopes are used to examine the waveform (amplitude versus time, Fig. 8c) of marine mammal sounds. Multiple channel storage oscilloscopes provide a means of setting an amplitude threshold, capturing, and comparing several signals. Recent digital storage oscilloscopes make these measurements even easier and more accurate because they have cursors that allow very precise time and amplitude measurements. Microprocessors and computer interfaces make these instruments even more versatile.

CETACEAN BEHAVIOR

Some, indeed many, of the problems with using marine mammal sounds for population assessment are associated with the fact that the animal *must* vocalize; and that many factors affect sound production. Cetaceans are not sympathetic to the analysis problems of acousticians. Fig. 9 is a sonagram from a pod of about 500 spotted dolphins (*S. attenuata*). Because cetaceans are social, recordings are often of large numbers of animals, making it difficult to distinguish individual sounds. To further complicate analysis, some (perhaps all) cetaceans can produce at least two sounds simultaneously; e.g. *O. orca, S. attenuata, G. macrorhynchus* (Fig. 10). Attenuation of sounds by distances causes only the highest amplitude and lower frequency portions of a sound to be recorded (see Fig. 11). A researcher must know the harmonic structure and amplitude relationships within a sound in order to recognize the sounds. Many cetaceans may exhibit diurnal variations in the rate of sound production. Therefore, using the rate of sound production as an estimator

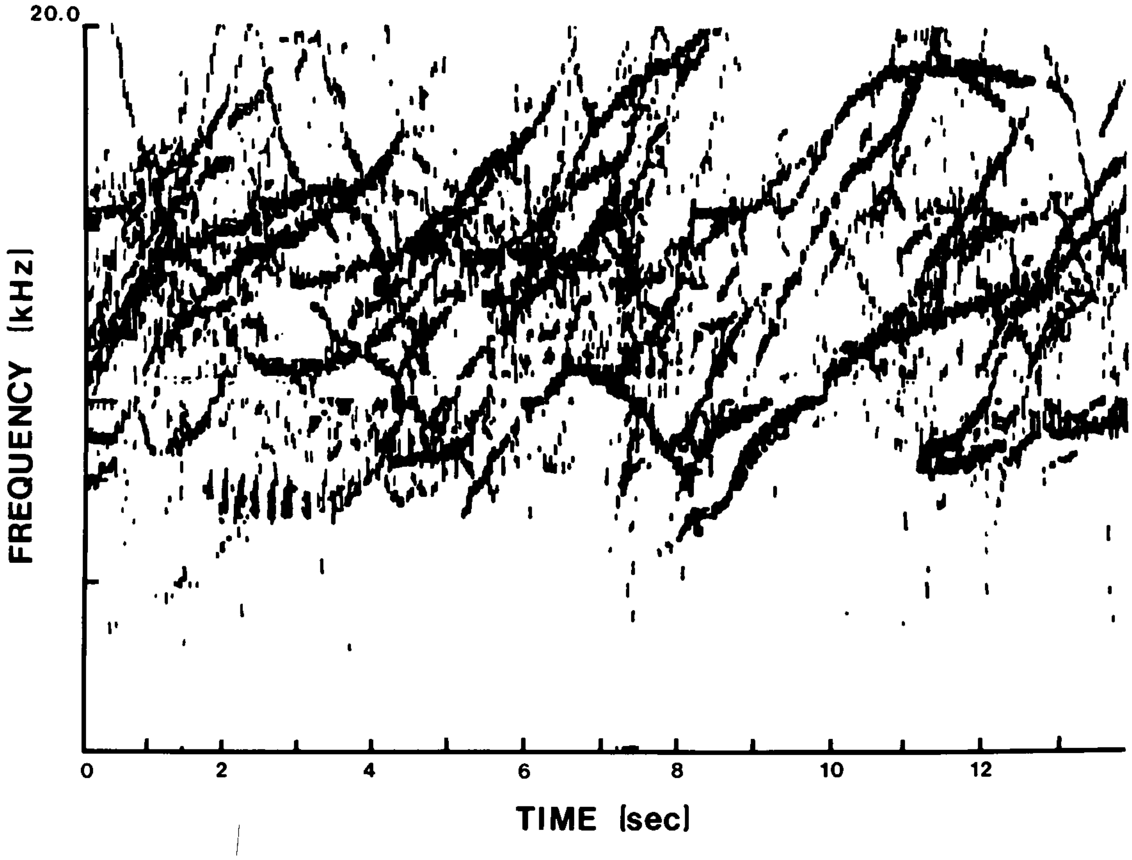

Fig. 9. Sonogram of vocalizations produced by over 500 spotted porpoise.

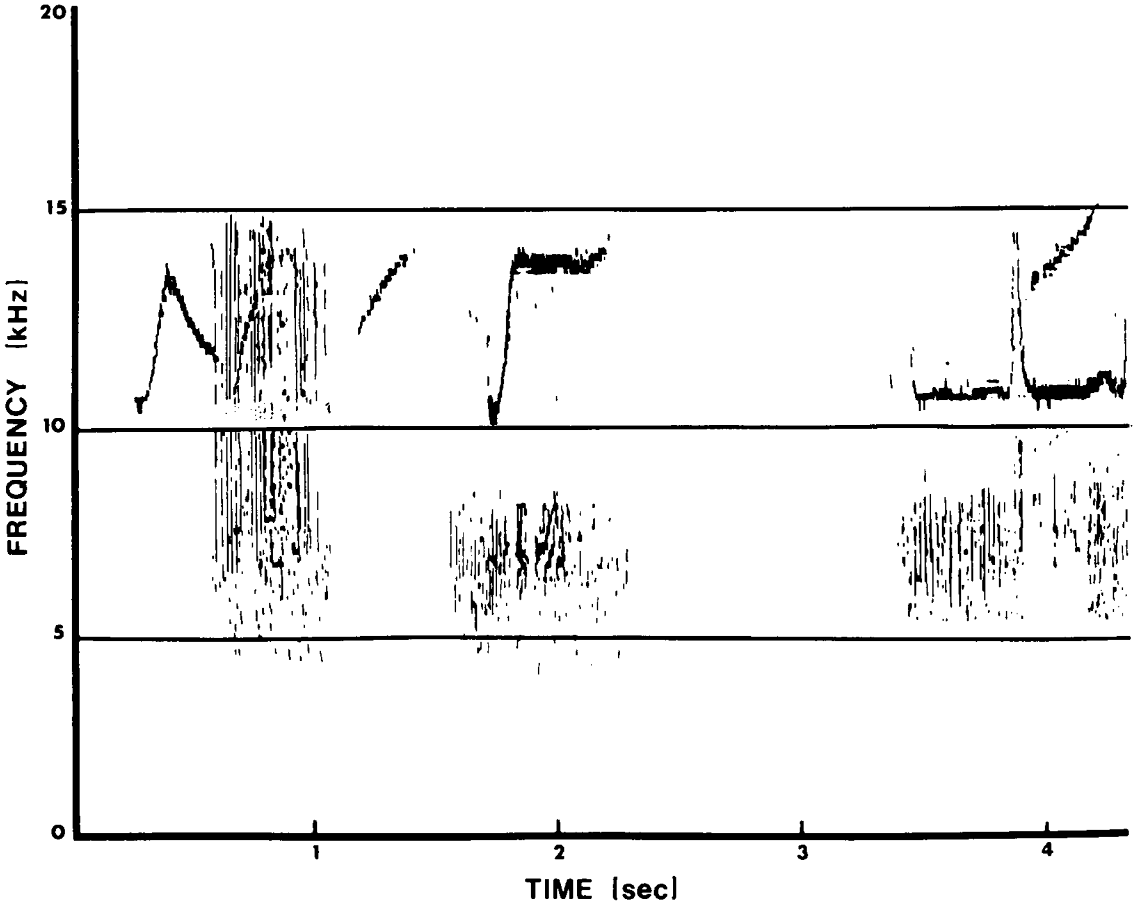

Fig. 10. Sonogram of spotted porpoise simultaneously producing a 'buzz' and a whistle.

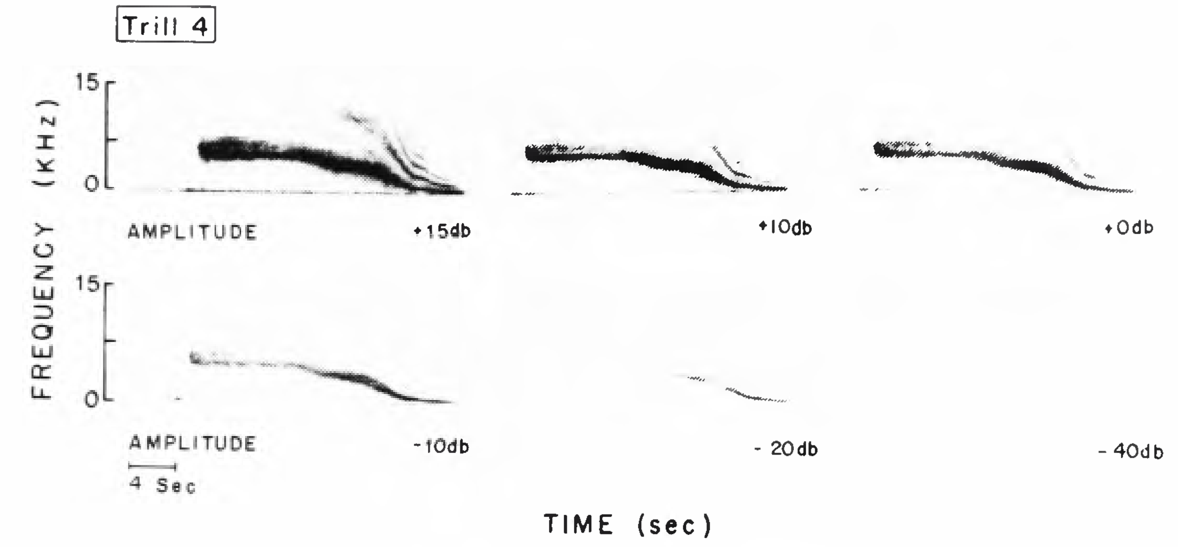

Fig. 11. Sonogram of the same Weddell seal trill attenuated in 5 dB increments on the tape recorder playback.

of abundance must be coupled with a thorough knowledge of the animal's diurnal vocalization rate. Humpback whales vocalize frequently during the breeding season and in the breeding grounds, but their vocalization rates decrease outside the breeding season and in other areas of the world (Payne and McVay, 1971). Acousticians must know the breeding and social habits of a cetacean before making conclusions about their vocal behavior (especially before concluding that they do not vocalize).

Signature whistles of individual dolphins (*Lagenorhynchus obliquidens* and *Stenella plagiodon*), have been documented in captivity (Caldwell and Caldwell, 1971; 1973) and this same individual identifier may or may not exist in wild populations. The age or sex of an individual may affect vocalizations. Geographic variation in vocalizations has been documented in killer whales by Thomas *et al.* (1981) and is suspected in pilot whales by Evans *et al.* (1985). This geographic variation seems to reflect discrete breeding populations. Vocalizations of humpback whales change within a pod from year to year (Payne and McVay, 1971). Long term studies and thorough knowledge of the whale's age, sex and behavior are necessary to interpret these variations in vocal behavior.

With all these analysis methods, hundreds of measurements can be taken from a single sound. In fact, the whole sound can be digitized and synthesized by a computer. Where does a researcher draw the line in measuring sound characteristics? What are the most informative characteristics? Measurements must reflect units of information that are biologically important and applicable to a hypothesis. For example, Fig. 12 illustrates a sound produced by killer whales from two different regions. Is there a geographic difference between these calls? Simply measuring the duration and frequency range of the sounds confirms they do differ. In contrast, to determine whether whales have signature sounds, the frequency, duration and slope of components in addition to the total call duration and frequency range, must be measured from the calls of known individuals.

Classification of cetacean sounds for comparison or discussion also presents a problem. As with any behavioral repertoire, a vocal repertoire can be classified in many ways. Classification is a technique to identify discrete units needed to test a

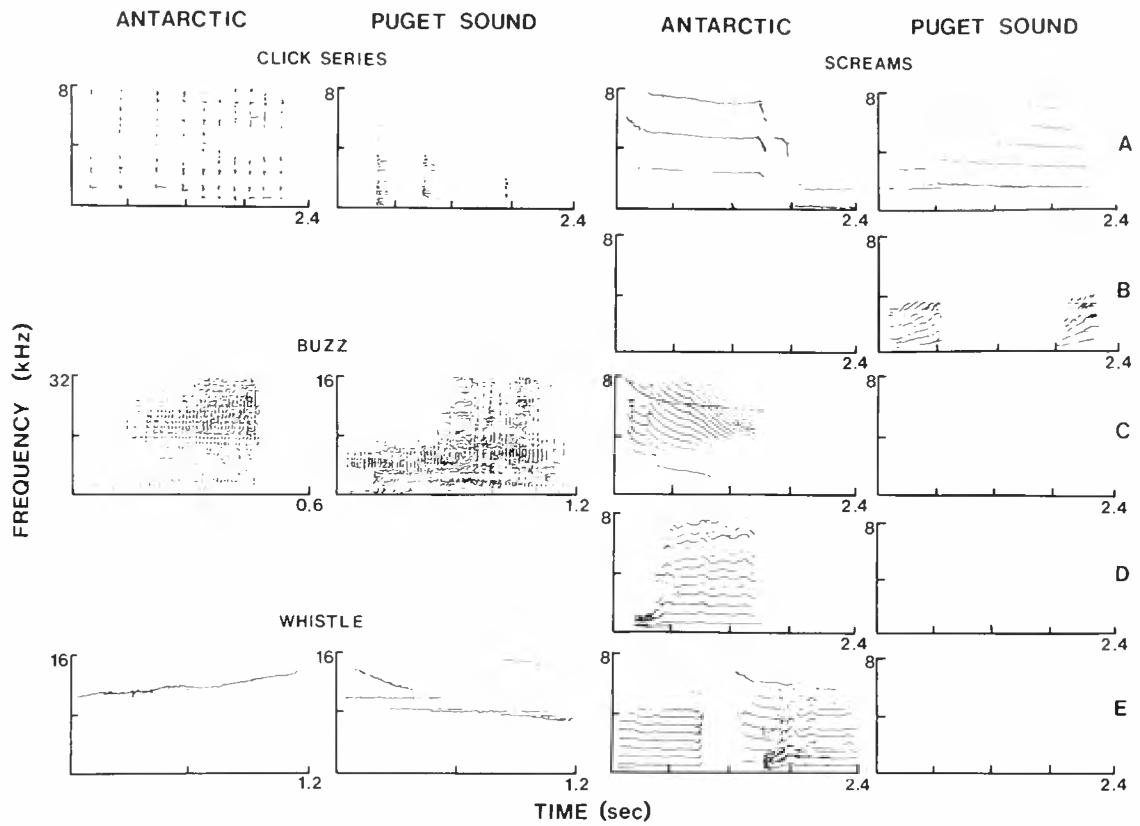

Fig. 12. Vocalizations from killer whales in McMurdo Sound, Antarctica and Puget Sound, Washington.

hypothesis. The number of categories should reflect the biological question to be answered and the fewest categories necessary to answer the question should be used. For example, if the hypothesis is that killer whales feed at a certain time of day, comparing the number of echolocation clicks versus other vocalizations by time of day might answer this question. In contrast, if the hypothesis is that vocalizations are sex related, many more vocalization categories should be scored. Knowledge of a whale's ecology and behavior is essential to interpret acoustic recordings.

FUTURE ACOUSTIC RESEARCH

Acoustic techniques are needed to document individual, age, or sex related differences in cetacean sounds. A potential technique for collecting these data would be to attach to an animal a transducer and recorder that records its vocalizations. A depth/temperature sensor coupled with this system could provide a vocalization profile over depth.

Sonobuoys will probably become more important in future bioacoustic research and such modifications as solar power panels and satellite reception can provide long term remote sensing stations. Theoretically, large and remote expanses of the ocean could be monitored for cetacean sounds throughout the year.

Towed arrays may become a useful tool for assessing marine mammal stocks using line transect techniques and counting densities of vocalizations along the track. Because this is the only existing acoustic method of tracking cetaceans with their vocalizations, towed arrays may help us learn more about movement, feeding and breeding behavior. Acoustic research on cetaceans will become a more important technique for assessing populations throughout the world. The introduction of digital (PCM) recorders into acoustic research is one improvement that will eliminate many of the problems experienced with analog recorders. Digital recorders store periodically sampled voltage levels on magnetic tape in the form of digital words or pulses.

Benefits of digital recorders include increased dynamic range, improved signal-to-noise ratio, flat frequency response, lower distortion, and elimination of wow/flutter speed variations, print-through, amplitude variations due to slight changes in magnetism, and interchannel crosstalk. Digital recordings can be made without the signal degradation that is inevitable for analog recordings.

The major limitation of most digital recorders is a narrow frequency response (20 kHz). This limitation is a design decision, not a technological limitation. Digital recorders will continue to evolve, further increasing their role in marine mammal acoustic research. However, the bandwidth of the Video cassette recorders used is limited to about 6 mHz so that the upper frequency limit or number of bits is also limited; 16 bits at 200 kHz is not possible. Distortion is low then, until the dynamic range of the analog-to-digital converter is exceeded, then distortion is much worse than with analog recorders, which clip gradually. Sampling rate must be very precise to minimize sample uncertainty. The same is true of voltage increments; fewer bits cause greater voltage uncertainty. Recorders must include parity check and duplication to avoid drop-out effects. Regardless of the problems, digital recorders are a lot better than nearly all analog machines.

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ACOUSTIC DETECTION OF CETACEANS USING A TOWED ARRAY OF HYDROPHONES

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ABSTRACT

For the purpose of identifying and locating cetaceans by their sounds, Hubbs Marine Research Institute designed a broadband hydrophone array that is a modified version of low frequency arrays currently used by the military and the geophysical industry. This array was towed from the R/V *David Starr Jordan* during a June 1982 cruise, conducted by the National Marine Fisheries Service to assess the size of dolphin populations in the eastern tropical Pacific. Using this system, we acoustically identified five dolphin and three whale species by their sound signatures. A comparison of visual and acoustic detection data demonstrated that using the array increased our ability to detect cetaceans by 32% overall and significantly enhanced detection during high sea states and inclement weather. Some cetaceans were more difficult to track acoustically because they are less vocal. We advocate using acoustic monitoring in conjunction with visual surveys to produce more accurate estimates of distribution and abundance of vocal species of cetaceans.

INTRODUCTION

Accurate information on distribution and abundance is essential for effective management of cetacean stocks. Such information is often obtained from visual counts made from ships or aircraft moving along line-transects. Although significant improvements have been made in recent years in the application of line-transect techniques to surveys of cetacean populations (see IWC, 1982) it is clear that such methods have their limitations. For example, cetaceans spend a large part of their time underwater unavailable to be sighted. This could result in a violation of the important assumption that all animals are seen on the transect-line itself. This and other aspects of line-transect surveys of cetaceans, such as the tendency of cetaceans to travel in groups, the large areas in which they are found and the high variability in sighting conditions, adversely affect obtaining accurate and precise estimates of population size. A supplemental method for detecting and identifying cetaceans could enhance the accuracy of visual counts and hence population estimates.

Most cetaceans are vocal under water and their sounds have unique, species-specific characteristics (Fish, 1967; Tavolga, 1968; Cummings and Fish, 1971; Thomas, Evans and Fisher, 1982 a, b). Because the sounds are high in amplitude and propagate long distances under water (Fish and Turl, 1976), they are potentially useful for detecting cetaceans at great distances. Acoustic surveys could enhance the accuracy of visual surveys for cetaceans, but for this would require a mobile underwater listening device; most listening devices used by cetacean biologists at present are stationary and depend on vocal animals passing by (e.g. Clark, Ellison and Beeman, 1986).

The military has studied underwater sounds extensively for purposes of passive and active (sonar) acoustic surveillance of vessels. One of its most important passive acoustic tools is a cadre of towed array systems; groups of hydrophones which are towed through the water by a ship and used to monitor underwater sounds. The geophysical industry has drawn from this technology and now uses the echo characteristics received by a towed array when a loud impulsive sound is introduced into the water to describe ocean sediments. Currently, several nations use towed array systems for seismic exploration.

Biologists have used echoes from active sonars to detect schools of fish along survey transects and estimate their density (Smith, 1970; Hewitt, Smith and Brown, 1976). We believed that passive acoustic techniques, namely towed arrays, might be used in a similar manner to assess cetacean stocks. To be useful in biological surveys, a passive listening device must meet several requirements: (i) a broad frequency bandwidth, to detect sounds from a variety of species; (ii) mobility, to monitor sounds along a survey track; (iii) directionality, to determine the animal's position relative to the survey track; and (iv) high sensitivity, to detect sounds from long distances. Towed array systems used by the military and geophysical industry lack the broadband capabilities, but otherwise are well-suited to this task. In this paper we describe how we modified such a towed array system and present some results from a test survey.

MATERIALS AND METHODS

Array description

To modify a towed array for cetacean surveys, we simply replaced the hydrophones used in a geophysical array with broadband hydrophones. The modified array is much shorter (45 m) than military and geophysical arrays with a frequency response that is linear from 20 Hz to 15 kHz (for details see Anderson, 1980).

Fig. 1 illustrates the major components of the array. Three acoustic modules house hydrophones. The 'dead section' (25 m) is a vibration isolating module which reduces noise during towing. The 'tail drogue' (30 m) is a 1.4 cm OD nylon rope that also diminishes noise from towing turbulence. The 2.2 cm OD tow cable (300 m) contains 32 wire pairs and a 6.4 mm inner steel stress member and is used to lower the acoustic modules into the water and to transmit the signal to onboard electronics. All modules are joined using waterproof *Teledyne* 28440 'quick disconnect' connecters.

Hydrophones (*Teledyne* model T-1 and *Benthos* AQ-10) are acceleration cancelling (acceleration sensitivity—35 dB re/v/g), thus fulfilling the mobility prerequisite, and are mounted on their side so that reception is omnidirectional in the XY plane. The acoustic modules contain 16 channels; 8 low frequency channels (14 hydrophones each) centered at 30 Hz, 1 channel (14 hydrophones) centered at 480 Hz, 1 channel (14 hydrophones) centered at 3,840 Hz, 2 channels (20 hydrophones each) centered at 5,000 Hz, 2 channels (10 hydrophones each) centered at 10,000 Hz and 2 channels (6 hydrophones each) centered at 15,000 Hz.

Acoustic modules can be used in various combinations, depending on the sound source. The distance between acoustic modules can be changed using additional 'dead sections'. During the study described in this paper, we used two high frequency modules (hydrophones centered at 5, 10 and 15 Hz) and one low frequency module (hydrophones centered at 30, 48, and 3,800 Hz). Fig. 1 illustrates the most common towing configuration of modules.

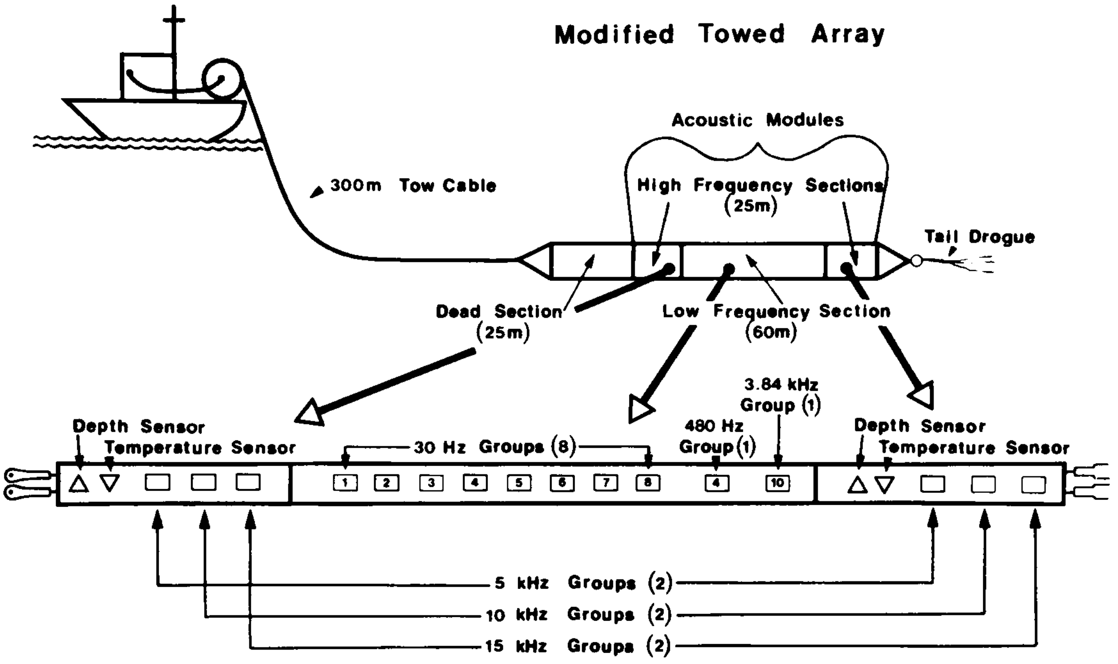

Fig. 1. Above are the major components in the towed acoustic array. Below is the configuration of hydrophones in each acoustic module. Note the broad frequency response of the system (20 Hz to 15 kHz). Depth and temperature sensors provide additional oceanographic data for predicting the thermocline in given areas.

All sections are composed of a 4.8 cm OD urethane tubular sleeve that covers all electronics and are filled with *Shelsol* No. 71 oil. This oil closely matches the acoustic impedance of salt water, protects electronic connections and makes the sections neutrally buoyant censusing it to ride in a level plane while under tow. The depth of tow is determined by the length of two cable deployed and the speed of the vessel (Fig. 2). *Teledyne* digital depth indicators (model 28950) allow the operator to note the depth of forward and aft acoustic modules.

Onboard electronics include instruments for reception, amplification, analysis and storage of data. The summing amplifier (*SIE* model RA-44A) is battery operated, has calibration tones and receives data from 16 channels. The continuity of each channel can be measured. Data from each channel can be amplified up to 60 dB and monitored separately or in combination with other channels. Signals from single or multiple channels can be fed into two analyzers: a spectrum analyzer (*Spectra Dynamics* SD 345) and a real time sonagram analyzer (SCO1 *Unigon*), and then into a recorder (*Racal Store*-4, frequency response 0.02 to 75.0 kHz ± 3.0 dB at 19 cm per second).

Spectra can be averaged over time and stored in memory. A variety of mathematical functions can be performed to compare spectra. Transient signals can be captured and averaged over time. The sonagram analyzer provides a continuous frequency versus time display for identifying sound signatures. Filters can be used to maximize the signal-to-noise ratio for reception of cetacean sounds.

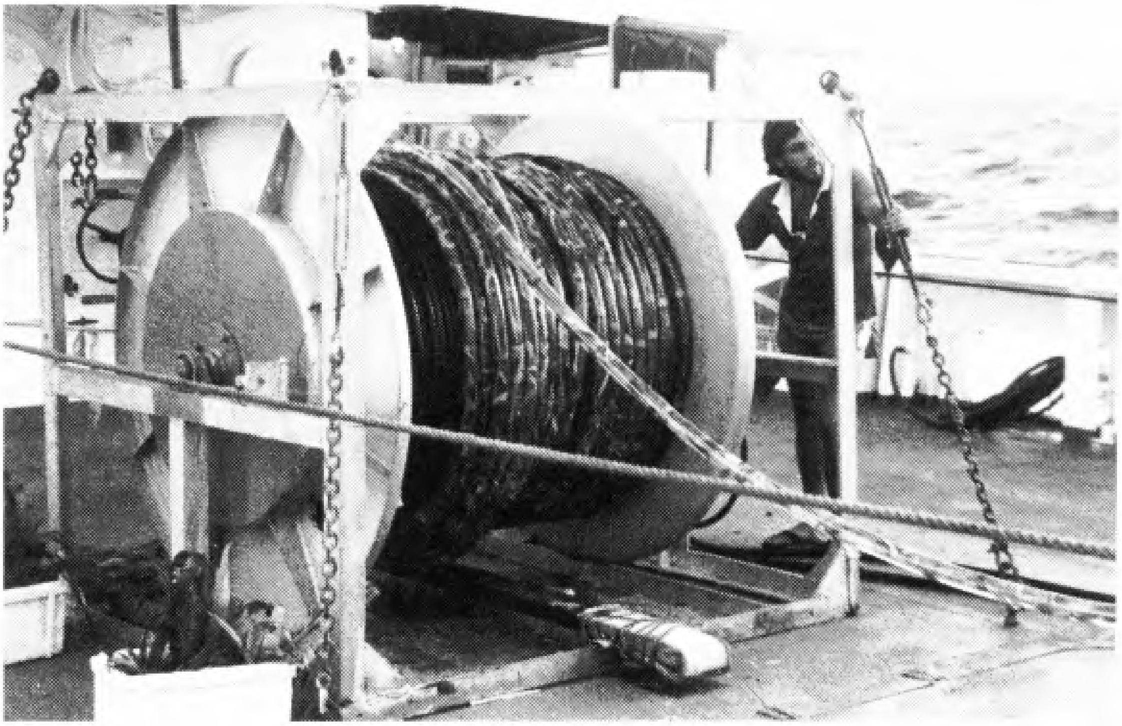

Fig. 2. Winch and towed array system used to detect cetacean sounds in the eastern tropical Pacific.

Survey methods

Onboard the NOAA ship *David Starr Jordan* from 11 June to 8 July 1982, *enroute* from Manzanillo, Mexico to Honolulu, Hawaii, we made simultaneous visual and acoustic surveys for cetaceans along line-transects between 5 and 15°N (Fig. 3). Our objectives were to: (i) record sound signatures from known species; (ii) document the array's ability to detect different species; (iii) compare the rate of detection by observers with that by the array; (iv) determine the array's search angle; (v) determine the influence of sea state and weather on detection by the array; and (vi) determine the effects of time of day on the detection ability of the array.

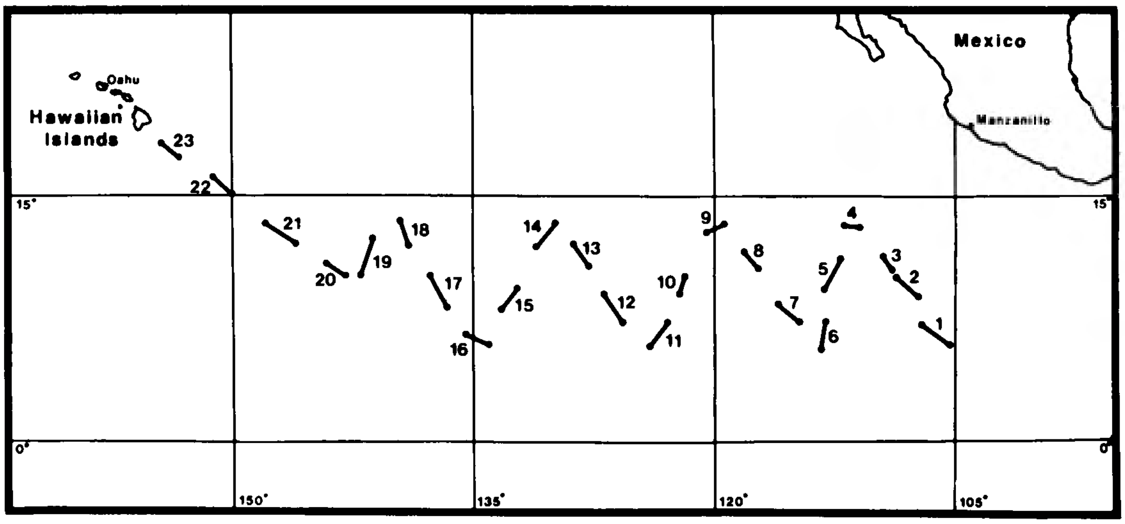

Fig. 3. Site of 23 tows of the array during simultaneous acoustic and visual surveys for cetaceans from 11 June to 8 July 1982.

Two observers, one port and one starboard, maintained continuous visual surveys for cetaceans during daylight hours, searching from the flying bridge using 25 power binoculars. For each sighting, observers independently identified the species, distance and bearing from the ship, herd size, location and time.

Tows of the array coincided with observer effort when possible. Thermoclines were documented using XBTs. The array was generally positioned in the middle of the mixed layer (*ca* 27–34 m) for optimum reception of cetacean sounds. The towed array operator listened simultaneously to the two high frequency channels in a stereo fashion to locate the sound source as aft, abeam or forward of the ship. When cetaceans were heard, we noted the time, sea state, location, postulated species identification, and recorded their sounds on magnetic tape from four channels of the array; usually one low frequency channel, one middle frequency channel and the most forward and the most aft high frequency channels. Thus, recording captured most frequency components of the animals' sounds and continuous data on the animal's position relative to the ship. Visual and acoustic detection data were obtained independently and not compared until the end of each day. A sequential record of sightings by observers and the array was assembled and data were divided into encounters by: observer only, array only, observer first, array first or disqualified because one detection method was not 'on effort'.

RESULTS AND DISCUSSION

During the cruise (23 tows, 237 hours) observers detected 63 cetacean encounters (defined as a single animal or herd) while 74 were acoustically detected. Sometimes only observers detected the animals (18 encounters), sometimes only the array detected them (29 encounters) and sometimes (9 encounters) both techniques detected animals almost simultaneously (within ± 2 minutes). In 21 sightings, the array detected animals first, as long as 83 minutes before the observers. In 15 sightings, observers detected animals first, as long as 65 minutes earlier. Observers and the array scanned somewhat overlapping, but generally different, areas around the heading of the ship. Observers scanned the semicircular area between 270° and 90° relative to the ship. The array's most sensitive region covered a fan-shaped area about 90° on each side, directly abeam of the ship. The technique that detected cetaceans first thus depended partly on the animal's position relative to the ship. For example, one might expect cetaceans approaching from behind or moving parallel to the ship to be detected first acoustically, whereas animals approaching the bow first would probably be detected visually. Fig. 4 shows that not only did the array detect more animals abeam and behind the ship, but it also detected a high number of sightings first when animals were off the bow next to the ship. This simple analysis may be misleading because the array could have detected animals well in advance, but no position could be recorded until an observer saw them. What is clear is that the combination of the two methods provided a better coverage of the transect.

We are able to identify several whales from their acoustic signatures: sperm whales (*Physeter macrocephalus*), pilot whales (*Globicephala macrorhynchus*), false killer whales (*Pseudorca crassidens*), as well as several porpoises; spotted dolphins (*Stenella attenuata*), spinner dolphins (*Stenella longirostris*), common dolphins (*Delphinus delphis*), Risso's dolphins (*Grampus griseus*), and striped dolphins (*Stenella coeruleoalba*). Fig. 5 shows examples of sounds for some species. In some cases, we audibly identified whether a school was homogeneous or a mixed species school. In addition, different stocks of the same species, e.g. eastern and white belly spinners, were audibly distinguished.

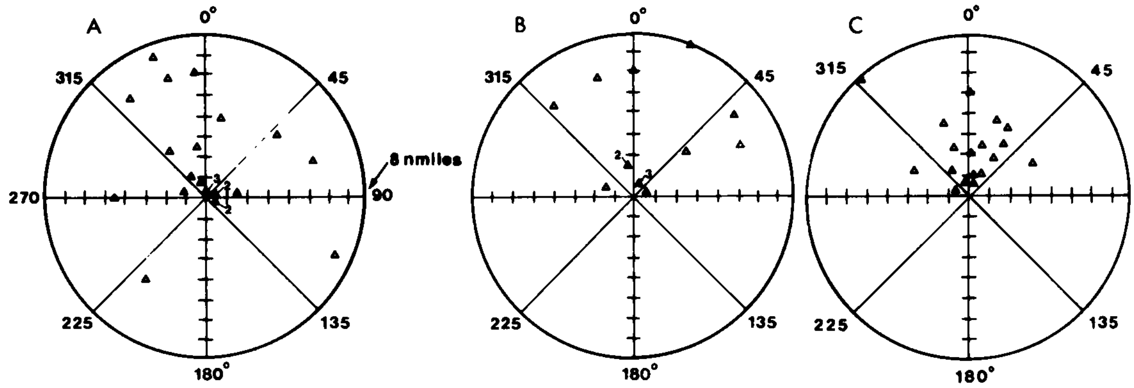

Fig. 4. Directional characteristics of visual versus acoustic detection of cetaceans. Data points are the position of cetaceans relative to the ship (center of circle) when first sighted by observers. Detection data were classified into three categories: (A) array first, (B) observers first and (C) observers only. Data for the 'array only' category are not presented because these encounters were never verified by observers. Note that observers detected more encounters immediately off the bow, ±45°. The array detected more encounters abeam of the ship.

The effects of time of day and sea state on visual versus acoustic detections were tested. A weighted linear regression was conducted using the variables sea state (good = Beaufort 1–2, poor = Beaufort 3–6), time of day (early a.m. = 0700–0900 hr, late a.m. = 1000–1200 hr, early p.m. = 1300–1500 hr, and late p.m. = 1600–1800 hr), and sea state × time. Results of the weighted regression analysis are summarized in Table 1. The F value for entering the variable time into a simple model including an intercept was not significant ($F = 1.222$, $p < 0.005$). However, the inclusion of sea state leads to a significant reduction in the sum of squares ($F = 7.078$, $p < 0.05$). There is thus a significant association between sea state and detection method, but not between time of day and detection method. Although other studies have shown diel vocal behavior of porpoises (Powell, 1966), a time of day effect in array versus observer detection was not apparent.

As observers usually saw animals during good visibility, the animals detected only by the array were probably in small herds or out of visual range because there were generally fewer vocalizations. However, as one would expect, sea state and weather affected the observers' ability to see cetaceans. Under such conditions the use of the array is a distinct advantage as shown by the fact that the array found more cetaceans than did observers at sea states between Beaufort 3–6. Even during heavy rain when observers could not search, the array detected a large herd of spotted dolphins.

Of course, animals must vocalize to be detected by the array. Unlike toothed whales and dolphins, beaked whales were not often detected by the array (Table 2). Beaked whales may be less vocal than other cetaceans: to our knowledge, there are no published accounts of vocal behavior in beaked whales. For such species, visual detection by observers apparently is better.

On several occasions, cetaceans were heard, but reception diminished as the ship slowed and the array dropped below the mixed layer. Under tow, reception of cetacean sounds was restored. Array placement within the mixed layer is essential to detect animals in that layer, just as to hear cetaceans below that layer, the array must also be positioned below it. Thus, an alternative explanation for our inability to hear beaked whales would be that they spend most of their time below the mixed layer. Baird's beaked whales, for example, are thought to dive deeply (Kasuya and Ohsumi, 1984), and our sightings were characterized by brief surfacing.

Our transect width was difficult to estimate, but was probably greater than the visual range of 8 n.miles on each side of the ship. The search path of the array is dependent on the sea state, thermoclines, and weather. Increased sea state and rain increase the ambient noise level, while the depth of the mixed layer influences the distance of sound propagation; a shallow mixed layer enhances sound transmission. These three conditions, and thus the transect width of the array, changes throughout the day. Methods of monitoring these changes and estimating the new search path need to be developed.

Table 1

Summary of data used in weighted linear regression analysis; number of cetacean encounters subdivided by time of day, sea state, and array versus observer detection.

Sea state	Time	Array detected	Observer detected	Hrs. effort	Total sightings
Good (Sea state 1–2)					
Early a.m.	700	0	1	2.60	1
	800	4	4	6.70	8
	900	3	1	6.77	4
Late a.m.	1000	3	5	8.15	8
	1100	2	4	5.73	6
	1200	5	5	5.78	10
Early p.m.	1300	4	5	6.42	9
	1400	1	1	5.16	2
	1500	3	2	6.35	5
Late p.m.	1600	3	3	5.55	6
	1700	0	1	5.38	2
	1800	2	0	3.60	3
TOTALS		30	32	68.19	64
Poor (Sea State 3–6)					
Early a.m.	700	3	1	5.08	4
	800	3	0	7.12	3
	900	1	0	8.89	1
Late a.m.	1000	2	0	8.31	2
	1100	1	1	8.95	2
	1200	2	0	9.08	2
Early p.m.	1300	3	0	9.05	3
	1400	1	0	8.49	1
	1500	2	0	9.52	2
Late p.m.	1600	2	2	10.86	5
	1700	2	2	9.80	4
	1800	1	0	5.77	1
TOTALS		23	6	100.92	30

Table 2

Number of cetacean encounters for various array and observers categories for each species. The number of unidentified species in the 'array only' column is high because no visual identifications were obtained. A large number of beaked whales were seen, but never heard by the array. Other species of cetaceans were readily detected by the array.

	Number of cetacean encounters				
SPECIES	Array only	Observer only	Array first	Observer first	Same time (± 2 min.)
Spotted dolphin	0	0	0	2	0
Mixed herd of Spotted and Spinner dolphin	0	2	5	7	2
Risso's dolphin	0	1	2	1	0
Rough toothed dolphin	0	1	0	0	0
Common dolphin	0	0	1	0	0
Pilot whales	0	0	3	0	2
False killer whales	0	0	1	0	1
Sperm whales	0	0	1	1	0
Killer whales	0	1	0	0	1
Bryde's whales	0	1	0	0	0
Beaked whales	0	8	0	1	1
Unidentified dolphin	25	0	2	1	2
Unidentified small whales	4	2	1	0	0
Unidentified large whales	0	2	0	0	0
TOTAL	29	18	21	15	9

Table 3

Results from a five by five contingency table analysis of the number of marine mammal detections per hour of effort. The array can be used at sea states up to 6, and the number of encounters per hour of effort is approximately the same. Sea state 3 was eliminated from the analysis because no samples were available. $\chi^2 = 2.30$, $F_{0.05,16} = 23$.

		Number of Detections per Hour of Effort (number of encounters)				
Sea State	Number of Hours of effort	Array only	Observer only	Array first	Observer first	Same time (± 2 min)
1	20.45	.05(1)	.24(5)	.10(2)	.10(5)	.20(4)
2	91.00	.12(11)	.13(12)	.15(14)	.08(7)	.04(4)
4	50.68	.20(10)	.02(1)	.04(2)	.02(1)	.00(0)
5	44.32	.11(5)	.00(0)	.05(2)	.05(2)	.02(1)
6	12.43	.16(2)	.00(0)	.08(1)	.00(0)	.00(0)

CONCLUSIONS

The array has several advantages for line-transect surveys of marine mammals: (i) long distance reception, often greater than the 8 n.miles maximum of observers; (ii) operation in any weather conditions and at high sea states; (iii) detection of

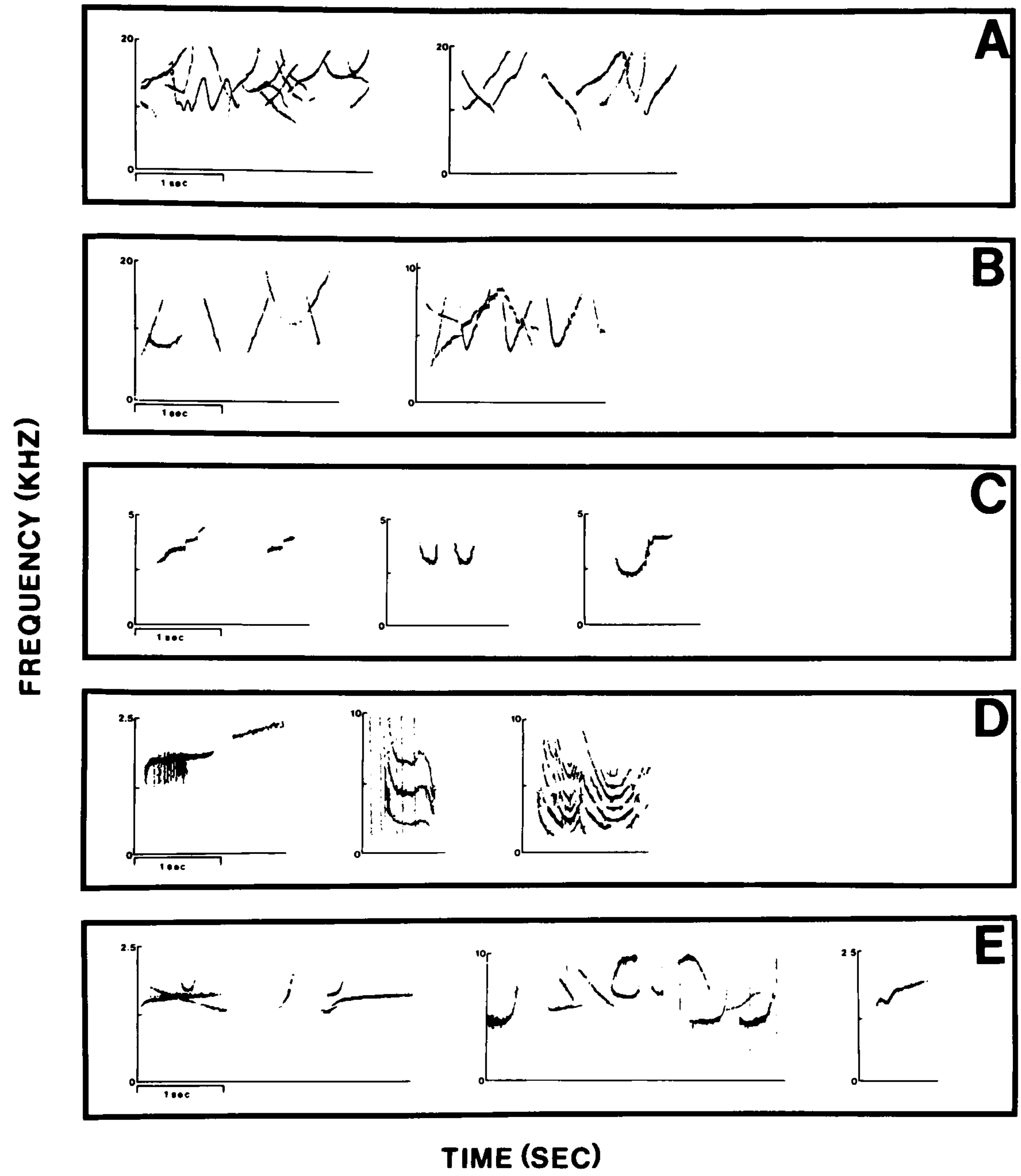

Fig. 5. Selected sonagrams illustrating some species-specific characteristics of the vocalizations of A—spotted dolphins, B—spinner dolphins, C—striped dolphins, D—pilot whales, and E—false killer whales.

small groups; (iv) long-term tracking of acoustically active marine mammals, often seen only briefly by observers; and (v) accurate identification of species. Limitations of the array includes: (i) transect width variability dependent on mixed layer depth and sea state, and (ii) dependence on vocal behavior of animals.

This study has documented the potential use of acoustic surveys as a census technique for cetaceans. In the future, we must develop techniques to determine: (i) the animal's distance and bearing from the ship; (ii) the transect width; (iii) the depth of the mixed layer; and (iv) the number of animals detected. The combination of visual and acoustic surveys may well provide more accurate estimates of the abundance and the distribution of cetaceans and help determine the biases of visual assessment.

Finally, although only cetaceans were detected acoustically in this study, the array may have similar application for assessing acoustically active pinnipeds, fish and invertebrates.

ACKNOWLEDGMENTS

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METHODS OF OBTAINING DATA FOR ASSESSING AND MODELLING SPERM WHALE POPULATIONS WHICH DO NOT DEPEND ON CATCHES

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ABSTRACT

New methods have been developed for obtaining data from living sperm whales which can be used to assess and model their populations. Sperm whale schools can be tracked acoustically for periods of several days from a 10 m boat. The whales' behaviour can be observed and photographed from the boat, and by swimmers. The whales can be identified, sexed, and measured photographically, and squid beaks can be retrieved from their faeces. Acoustic censuses appear promising. Data collected by these new techniques can be used to estimate important parameters required for modelling sperm whale populations, including some that cannot be obtained from catch data. The approximate efficiency with which the parameters can be estimated is calculated. At least 10 months of sea time will be needed to obtain meaningful parameter estimates. The value of the research will increase considerably as the time span is extended, and the effort expanded.

INTRODUCTION

During the past ten years there has been considerable effort devoted to the assessment and modelling of sperm whale (*Physeter macrocephalus*) populations. Early analyses concentrated on catch per unit effort methods, but there were many problems (Cooke and de la Mare, 1983). Recently emphasis has shifted to least-squares estimation of population size from length or age data (Beddington and Cooke, 1981). The estimates produced are contentious, and subject to errors from several sources (IWC, 1983), not the least of which are uncertainties about the underlying social system of the sperm whale, often referred to as the 'Sperm Whale Model'. In particular, the interactions between mature males and schools principally composed of mature females are poorly understood, and have great bearing on the resultant population dynamics. This is despite the examination of hundreds of thousands of carcasses. A new approach in sperm whale research is needed if the assessments are to be improved (Chapman, 1980).

If sperm whaling comes to a halt, the data that the whaling industry did provide will cease. New techniques must be developed if we are to improve our understanding of sperm whale populations, and monitor their response to protection.

Payne (1983) has reviewed the recently developed benign research techniques for studying whales. He concluded that all of the parameters needed for population assessment and modelling can be determined by non-consumptive techniques. Progress in this work has varied from species to species, but particularly important results have been obtained for orcas (*Orcinus orca*) (Balcomb, Boran and Heimlich, 1982; Bigg, 1982), right whales (*Eubalaena australis*) (Payne, in press), grey whales (*Eschrichtius robustus*) (Swartz and Jones, 1980), and humpbacks (*Megaptera novaeangliae*) (Darling, Gibson and Silber, 1983; Whitehead, 1982). Sperm whales, being creatures of the deep ocean, are less accessible to researchers with small boats and budgets. They had therefore attracted very little of this benign research, until recently.

The World Wildlife Fund/International Union for the Conservation of Nature *Tulip* Project was set up in 1981 principally to investigate the feasibility of benign research techniques on sperm whales. During the three years of the project we have had considerable opportunity to evaluate different field methods. In this paper we describe the most successful of them, discuss how they can be used to obtain the data necessary to realistically assess and model sperm whale populations, and consider how the research should be developed.

FIELD METHODS

Vessel, schedule

The research was conducted from the 10 m ocean-going auxiliary sloop, *Tulip*, with a crew of five, in the northern Indian Ocean. The study was divided into four research seasons:

Dec. 1981–March 1982. Djibouti—Oman—Sri Lanka.
Jan. 1983–April 1983. Waters off Sri Lanka.
Oct. 1983–Dec. 1983. Waters off Sri Lanka, Maldives.
Feb. 1984–April 1984. Waters off Sri Lanka.

Information gathered during the last research season is not yet available, and will not be incorporated into this paper.

During each season *Tulip* spent approximately two week periods at sea, with a few days in port between periods.

Following sperm whales

Sperm whales were tracked for hours or days with a passive directional hydrophone. We used a specially built directional hydrophone, which rotated within an acoustically transparent, faired housing, filled with seawater, at a depth of 1.5 m below the surface. This system reduced water noise. The output of the hydrophone was fed through a pre-amplifier and 10 kHz high-pass filter, and monitored with headphones. With this system we could hear clicks from sperm whales at about 3–5 n.miles (determined by sailing fast away from fairly stationary whales, listening regularly), although this varied considerably with sea conditions and the depth of the whale.

When following sperm whales we monitored the sperm whale clicks on hydrophones every 10–20 minutes and adjusted the speed and heading of the vessel accordingly. The maximum speed of *Tulip* under most conditions was about 5.5 knots. This was almost always sufficient to keep up with the whales.

We have found that a single sperm whale clicks regularly, with few pauses, approximately once per second, when at depths greater than about 100 m (as determined by a recording depth sounder). While at or near the surface the sperm whales were most often silent (as in Watkins and Schevill, 1977). Surface times between deep dives were usually 10–15 minutes. During this interval the whales rarely travelled at more than 3 knots. However occasionally a particular whale spent several hours at or near the surface, almost totally silent. During this time they could move several miles. In daylight, with good sea conditions and visibility, the whales could sometimes be followed visually through these silent periods, but they were usually lost at night.

Because of these silent periods, and for other reasons, when tracking single whales we usually lost contact within 36 hours. There was also the problem of confusion with other whales. Although Backus and Schevill (1966) suggest that there are characteristics of sperm whale clicks which can be used to identify individuals, we found this very difficult to achieve in real time at sea.

With cohesive groups of five or more sperm whales our tracking was much more successful. In these groups there are rarely pauses, without any clicks being heard, which last longer than a few minutes, and these usually take place in daytime with the whales at or near the surface.

During the third season of the study, when our techniques were most fully developed, we followed nine of these large groups. The nine watches totalled 14 days, 4 hours, and 47 minutes. Five of the watches were abandoned because of low fuel, low food, approaches to the shipping lanes, or other reasons unconnected with the whales. The other four watches ended when we lost the group. In two of these we became confused, and found ourselves following a nearby, but different, group (confirmed from identification photographs)—thereby ending the original watch. Thus average time before losing the whales, either through confusion with another group or for other reasons, was 3 days, 4 hours, and 12 minutes (14-4-47/4).

The longest watch was 4 days and 9 hours, on 21–25 October 1983. The endpoints of this watch were 172 n.miles apart, and the watch was abandoned because of low fuel. Using our current techniques, and a vessel with the ability to stay at sea for 3–4 weeks, over 10% of the watches would be expected to last a week or more. This estimate, which assumes that the lengths of the watches are negatively exponentially distributed, is conservative, because, as we spend more time following a particular group of sperm whales we become increasingly familiar with their habits, and less likely to lose them.

The durations of the watches could probably be extended by using radio tracking techniques if necessary.

Behavioural observations

While following groups of sperm whales we were able to observe their behaviour both from the deck, a position 8 m above the water surface up the mast, and when in the water towing behind *Tulip* wearing a mask and snorkel. The whales were photographed from any of these positions with still, movie, or video cameras.

As we were usually unable to swim as fast as the whales, and could only see them underwater to a maximum of about 30 m, we were rarely able to view a particular whale underwater for more than about one minute. However amongst our observations underwater have been: nursing, remnants of umbilical cords attached to new-born calves, and afterbirth from a new mother. We have also been able to determine the sex of several whales from observations of the genital area.

From the deck we have seen the birth of a calf; and from the mast remnants of umbilical cords attached to new-born calves, and the expulsion of afterbirth from a new mother.

Individual identification and sexing

We have used photographs of dorsal fins and flukes to identify individuals. To take the photographs we have used 35 mm cameras with 300 mm lenses, and various black-and-white or colour films. In the later seasons we generally used Kodachrome 64 colour film, as this gave good clarity, and could be examined directly under a microscope, without the additional labour and expense of making prints.

Dorsal fin photographs (Fig. 1) are particularly useful for identifying whales amongst the members of a school. Approximately 20% of sperm whales have dorsal fins with visible characteristics which might be recognized within a population of several thousand animals. The fins of the remaining 80% are usually sufficiently distinctive to identify them within the 5–20 other whales seen during the same watch.

Fig. 1. Three sperm whale dorsal fins, showing marks. The closer two whales possess calluses.

Sperm whale flukes have marks, scars, and nicks along their edges (Fig. 2). At least 10% of the flukes that we have photographed have some identifying feature or features that would allow them to be recognized within a population of several thousand animals. Several sperm whale flukes have been identified from each of two photographs taken one year apart.

During the second field season about 50 sperm whales were identified from their flukes (photographed and found to be different), and several hundred from characteristics of their dorsal fins.

Fig. 2. Sperm whale flukes showing distinctive notch.

Occasionally a sperm whale was sighted with other (e.g. albinistic) markings which distinctively identified it. One such is shown in Fig. 3.

We have no information on the persistence of these markings, although on other large whales such features have generally been shown to remain stable over many years (Payne, 1983).

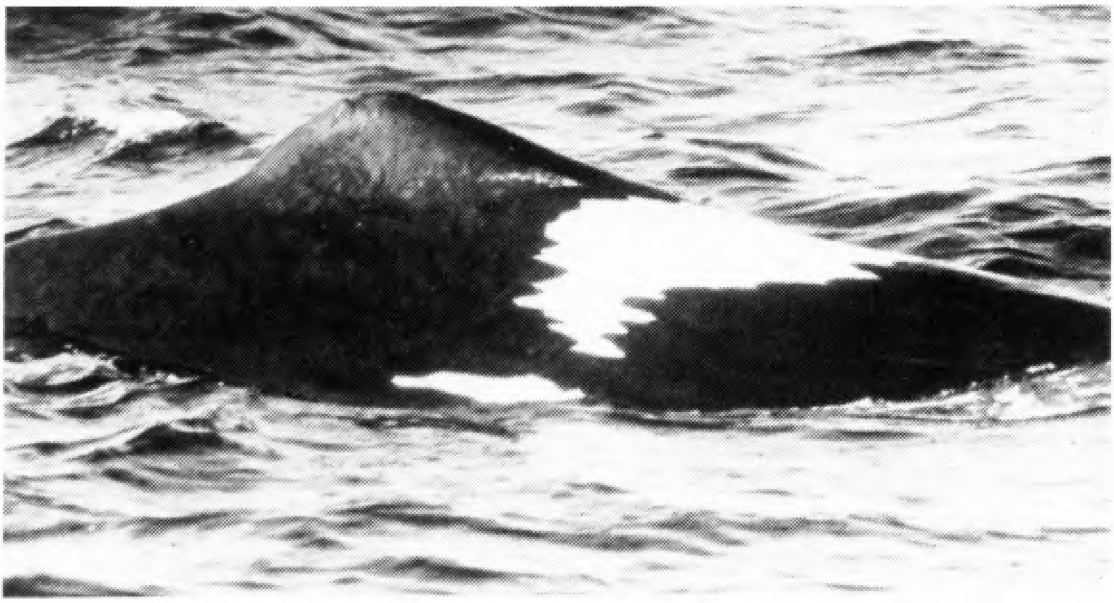

Fig. 3. Sperm whale dorsal area showing distinctive white marks, and notch in fin.

The presence of a callus (whitish patches of hard, thickened tissue) on the upper edge of the dorsal fin (Fig. 1) has been shown to be indicative of females among mature sperm whales (Kasuya and Ohsumi, 1966). On the approximately 5 times that we have sexed animals by underwater observation, and have been able to identify the dorsal fin, the females have all possessed calluses, and the males never have. Thus an identification photograph of a sperm whale's dorsal fin is a strong indicator of sex.

Measuring

We have investigated two methods of measuring living sperm whales. The data have not been fully processed so that we can only give preliminary impressions on the efficiency of the methods. A comprehensive analysis will be presented in due course.

Norris and Harvey (1972) have proposed that the length of a sperm whale may be estimated from the inter-pulse-interval within its clicks. According to this theory, the inter-pulse-interval is the time taken for the initial pulse to travel the length of the sperm whale's oil-filled case twice. It is therefore proportional to the size of the case, and related to the length of the whale.

Analysis of clicks recorded from on board *Tulip* has shown that, for a large proportion of the clicks, no secondary pulse and therefore no inter-pulse-interval could be discerned. Additionally, inter-pulse-intervals measured from the click train of a single sperm whale showed variation. These variations may be the source of useful information on perhaps the whale's orientation, depth, or behaviour. With further investigation it might prove possible to use inter-pulse-intervals for measuring sperm whales, but unfortunately the situation does not seem as clear as Norris and Harvey (1972) had hoped.

One of us (J. G.) has developed a photographic method of measuring sperm whales. Photographs were taken from a fixed height (9 m) above the water surface, with a 35 mm camera and a 50 mm lens, showing the whale lying at the surface parallel to the horizon. The distance between the whale and the horizon on the film enabled the range to the whale to be calculated. This, together with the length of the image of the whale on the film and the focal length of the camera lens, allowed the length of the whale to be estimated. Approximately 50 sperm whales have been measured by this technique, whose resolution appears to be about 5%, or 0.6 m for a 12 m adult female (calculated from comparing photographic measurements of objects of known size with their actual length). Sperm whales, because, when at the surface they often lie with their bodies straight just beneath the surface, so that their blowhole and dorsal fin are both visible from the mast position, are most suitable for this method.

Feeding

Sperm whales frequently defecated when they dived, or when startled by the close approach of the vessel. Samples of the faeces could be collected, using a net, if the boat was at the site of the defecation within about one minute. The identifiable parts of our samples have principally consisted of portions of squid beaks. During the first three field seasons aboard *Tulip* 20 samples were collected, containing about 30 beaks. These are being used to examine sperm whale diet.

Censusing

Sperm whales are not very suitable targets for visual censuses from ships or aeroplanes. They spend little time at the surface, show only a small proportion of their bodies above the water, and have low, and sometimes weak, blows. We found that, even in good conditions, our rate of sighting sperm whales was variable and decreased considerably at distances greater than 0.5 n.miles.

In contrast sperm whales make regular clicks during approximately 1/2 to 2/3 of the day. These clicks can be heard at 3–5 n.miles, in both daylight and at night, and during relatively poor weather conditions. As an example of the increased efficiency of acoustic techniques, on surveys off Sri Lanka, during which sperm whales were simultaneously counted visually and acoustically, we saw 4 sperm whales but heard at least 21.

This indicates that sperm whales might be censused more efficiently by acoustic rather than visual means. L. Hiby of the Sea Mammals Research Unit is currently investigating the technical feasibility of acoustically censusing sperm whales, including methods of assessing range using towed arrays of hydrophones. We have collected considerable data on the variation in sperm whale clicking rates for particular groups with time of day, which will be important in assessing the efficiency of acoustic censusing.

HOW BENIGN DATA COLLECTION TECHNIQUES CAN CONTRIBUTE TO SPERM WHALE ASSESSMENT AND MODELLING

'The Model'

The collection of assumptions about sperm whale social behaviour and natural history, which are used when modelling their population dynamics, are generally referred to as 'The Sperm Whale Model'. The Model makes assumptions about the interactions between mature males and schools of mature females. The nature of these assumptions can have great influence on the resulting population trajectories (IWC, 1983), and there is a lack of data on which to base or test any particular hypotheses.

To clear up some of the uncertainties we need to know:

1. Which males do the mating? In particular, what is the size distribution of 'socially mature' males (those who successfully mate with females)?
2. How long does an individual socially mature male stay with a school of females?
3. How is such a male accompanying a school replaced?

In the previous section we have described a method whereby schools of females can be followed for a week or so, and a single whale for a day or two, while behavioural interactions are observed. We believe that this methodology is the key to answering the important questions about sperm whale behaviour.

Males can be observed entering and leaving schools, and some of their interactions with individual females and other males may be observed. Of key importance to the success of this method is whether mating takes place at the surface, and in daylight. Our work so far, based upon correlations between acoustic and visually observable behaviour, indicates that most complex interactions within schools of females take place near or at the surface, and most frequently in the middle of the day. There are reports in the literature of observations of sperm whale mating (e.g. Tormosov and Sazhinov, 1974).

During the *Tulip* studies, we saw only three large males. Two were sighted during November 1983, and one in April 1984. The first was seen on 9 November for about ten minutes in the middle of a group of four smaller animals lying at the surface. The male was sighted neither during the previous 23 hours nor during the succeeding 30 hours of the watch of the group. The second large male was found alone at 14.55 on 11 Nov. At about 01.00 on 12 November the male (which had a distinctively slow click rate) joined a school of 7 or more animals (as indicated by the clicks). *Tulip* stayed with the school until 23.30 on 12 November, but the large male was not seen again. It probably left the school within a few hours of joining. The third male was alone, and circumstances prevented it being followed.

This paucity of sightings strongly suggests that large males are scarce in the Northern Indian Ocean. However, additional work is needed to confirm this.

We believe that, if we can conduct watches of groups of females lasting five days or more, at times when large males are with them for the purpose of mating, then we can learn a considerable amount about the mating system of the sperm whale.

Stock divisions

Our work suggests several different ways of examining sperm whale stock divisions.

The photographic identifications can be used to trace the movements of individual whales. The more identifications that are collected, the more effective this work becomes. Similar work on the humpbacks in the western North Atlantic (Katona, Beard, Balcomb, Whitehead and Matilla, 1983) and eastern North Pacific (Darling and McSweeney, 1983), the right whales in the South Atlantic (Payne *et al.*, 1983), and the orcas off Washington State and Vancouver Island (Balcomb *et al.*, 1982; Bigg, 1982), have shown stock divisions, or the lack of them, more clearly than any data collected by the whaling industry.

Veinger (1980) has suggested that the morphology of sperm whale flukes can be used to identify stocks. Our photographs of sperm whale flukes can provide data to test this method.

Another benign method of investigating sperm whale stock divisions is satellite radio tracking. This technique is being developed by A. Martin of the Sea Mammals Research Unit.

Lengths

Lengths can be obtained efficiently by the photographic methods described above. The acoustic technique of Norris and Harvey (1972), if it can be validated, would allow large samples of sperm whale lengths to be obtained quickly (as in Alder-Fenchel, 1980).

Ages (age at recruitment, sexual maturity, social maturity)

Ages are hard to obtain using benign techniques. With intensive long-term studies of a segment of the population the ages of particular identified individuals will be known. This has been achieved for some southern right whales (Payne *et al.*, 1983). However the technique is unlikely to age more than a small proportion of the population.

With an age-length key, lengths may be converted into approximate ages (although this would not be very efficient with mature female sperm whales who soon approach asymptotic length). Age-length keys for sperm whales have been constructed (e.g. Ohsumi, 1977). It would also be possible to construct one entirely from a 'benign data base', using measurements of animals of known age, and/or measurements of known animals made one or more years apart. This has been done for southern right whales by Whitehead and Payne (1981).

Such an age–length key would estimate the age at recruitment to the exploitable population (which is defined by a minimum length). This could also come from repeated measurements of individuals of known age.

The age at sexual maturity of females could be deduced from the lengths at which animals are found with dorsal fin calluses (Kasuya and Ohsumi, 1966), or are seen with their own calves. Care must be taken with this latter measure, as we have often observed the same sperm whale calf successively swimming beside several animals (including small males). However, over a few days we found that a calf spent a considerably greater time with a particular female, presumably its mother. Females of known age beginning to show calluses or producing calves can be expected to indicate the age of sexual maturity.

When we have greatly increased our observations of the interactions between large males and schools of females it will be possible to determine which males are socially mature. If these animals are measured, a length at social maturity may be inferred with the aid of an age–length key.

Females per school and pregnancy rate

The parameters 'Females per School' and 'Pregnancy Rate' come from observation of the numbers of animals with calluses per school, and the numbers of small calves per school. We caution against estimating these parameters, except after a thorough analysis of identification photographs, as it is rare for all the animals to be at the surface at any one time. Depending on the size of the school, its behaviour, and the weather conditions, it may take two or more days to photographically identify all members of the school. A knowledge of the calving season would also be necessary to realistically investigate the pregnancy rate. The pregnancy rate could also be estimated by measuring the interval between successive calves of known females.

Harem reserve ratio

A better estimate of the number of socially mature males per school necessary for maximum pregnancy rates will be possible once the dynamics of the interactions between mature males and schools of females have been further elucidated.

Natural mortality

Natural mortality is difficult to estimate, either from living or dead whales. However some estimates can be made, either from longitudinal studies of particular animals, or as a product of mark–recapture analyses based upon individual identifications.

Numbers

Two benign techniques which could be used to estimate populations of sperm whales are:

1. The acoustic census methods being developed by L. Hiby (Sea Mammal Research Unit, UK), in which a vessel tows a hydrophone array over a randomly or systematically determined track, while sperm whale sounds are recorded.
2. Mark–recapture analysis of individual identification photographs, as has been done for humpback whales (Whitehead, 1982), and right whales (Whitehead, Payne and Payne, in press).

Other methods; such as satellite imagery, or high altitude photography, might prove useful in assessing sperm whale populations, but considerable development work would be needed.

EFFORT

In this section we make rough estimates of the effort required to contribute meaningfully to the data base used for sperm whale assessment and modelling. We assume the type of research plan used on board *Tulip*, although, by making changes, emphasis could be shifted from one set of parameters to another. For instance, if less time was spent with each school, but more schools were encountered during each period at sea, there would be more lengths and individual identifications but less information on the intricacies of sperm whale social relationships. It is also likely that, as work progresses and techniques are modified, the necessary data will be able to be collected more efficiently than is suggested here.

The efficiency of our work depends greatly on characteristics of the study area—particularly the weather, sperm whale density, proximity of ports, and facilities on shore. It would considerably assist the efficiency of the operation if periods at sea could be three weeks, rather than two. It would require only minor modifications to the vessel to achieve this, and we make this assumption. Otherwise we base our estimates of the rate of obtaining data on our experiences off Sri Lanka. We assume that during each month:

1. The vessel spends 3 weeks at sea, 1 week in port.
2. During the time at sea, ten days are spent following schools of sperm whales—the other ten days are used searching for whales, returning to port, etc.
3. The ten days spent following whales are divided into three watches, each of a different school, for 6 days, 3 days and 1 day respectively. Our experience off Sri Lanka suggests that data could be obtained from the watches approximately as in the following schedule:

	School Identity			
	A	B	C	Total
Length of watch in days	6	3	1	10
Whales identified from fins	15	15	5	35
Whales identified from flukes	8	4	1	13
Whales measured photographically	12	6	2	20
Whales sexed from fin calluses	15	15	5	35
Whales sexed by diving	3	1	0	4
Squid beaks obtained from whale faeces	6	3	1	10

For the purposes of illustration we assume that we are trying to assess and model the population of sperm whales in the North Atlantic, with a population of about 20,000 mature females (although there is no reliable estimate this is close to the mean of those available), and about 10 females per school, giving about 2,000 schools (IWC, 1982).

We will now consider how much effort would be required to estimate parameters useful in the assessment and modelling of North Atlantic sperm whale populations.

The model, harem reserve ratio

In order to begin to understand properly the interactions between mature male sperm whales and schools of females, we estimate that approximately ten watches of schools of females, each lasting four days or more, would be needed (assuming that large male sperm whales are considerably more abundant than off Sri Lanka). Four days should allow all members of the school to be identified, and patterns of association lasting of the order of several days of large males with such schools to be documented. Ten watches would allow the degree of variation in the behaviour of the associating males to be very roughly estimated. According to the above schedule this would require ten months of sea time. It would also have to be carried out during the mating season, which lasts approximately 3–4 months (Best, 1979). This means that the work would need to be spread over at least three years, or be performed by more than one vessel. It is likely that, with different male/female ratios in different oceans, the patterns of their interactions would vary. It might thus be premature to extrapolate information on these kinds of social interactions from one ocean to another.

Stock divisions

Suppose that we wished to examine the degree of interchange beween female sperm whale schools on the east and west sides of the tropical North Atlantic. A reasonable proportion of whales from each of n schools are photographically identified from each area. We now ask the question: what is the minimum value of n for there to be a reasonable number of expected matches, say five schools, between the two samples, if there were total mixing? n is given by:

$$n^2 = 5 \times 2{,}000 \text{ (the number of expected matches } \times \text{ the estimated number of schools)}$$

$$\text{or: } n = 100 \text{ schools}$$

To photographically identify 100 schools would, according to the schedule at the beginning of this section, take about 33 months of sea time, and this would have to be applied on both sides of the Atlantic. The identification work could be increased, to perhaps ten schools per month, if a vessel concentrated on this work at the expense of long watches and behavioural observations.

Additionally, if no matches were obtained, an estimate of population size would be needed to assess the significance of the failure.

Lengths

Length estimates of whales are usually given to the nearest foot (e.g. in the reports of the Bureau of International Whaling Statistics). The number of length estimates required would depend on the use to which they were to be put. As an example, to obtain reasonable expected numbers throughout the size range 30′–50′, say ten per one foot interval, we would have to measure 200 whales. According to the schedule above, this would take about 10 months of sea time to do photographically. Acoustic measurement is much more efficient, but, as noted above, there are still unresolved problems with the method, and it would be less accurate than the photographic technique.

Ages

The amount of information obtainable on sperm whale ages is closely related to how often known individuals are rephotographed. This, in turn, depends greatly on the movement patterns of the whales. If individuals can be found year after year in particular areas, their ages can be estimated, and age–length keys constructed.

If, on the other hand, schools within a stock mix randomly over a large ocean area, we will expect few resightings of known individuals, and little age data.

Assuming the least favourable case, that little age data can be obtained with a reasonable amount of effort, the age–length keys constructed from information obtained from dead animals would have to be used. These would give the age at recruitment, and, when combined with 200 benignly acquired length measurements of animals of known sex and observed behaviour, estimates of the lengths at sexual maturity for females, and social maturity for males.

In the most favourable circumstances, we might expect an encounter with a particular school, during which we would hope to measure over half the animals in the school, every two months at sea. To construct a realistic age–length key we would need to encounter two familiar schools each year for about five years. This would require about four months at sea each year.

Females per school and pregnancy rate

Data presented by Best (1979) indicate that the standard deviation of the number of females per school is about 7.5. Thus if we wished to estimate the mean number of females per school with a standard error of one animal we would have to examine about $(7.5 \times 7.5)/(1 \times 1) = 56.25$ schools. We would expect that within each month two schools would be followed sufficiently long to identify all the females. It would therefore require 28 months of sea time to achieve the accuracy of a standard deviation of one animal in the number of females per school.

If the probability of a female possessing a first year calf in any year is p and the pregnancy rate in a sample of females is binomially distributed, then p is estimated by:

$$p = f/F$$

where f is the number of females with calves, and F is the number of females examined. The coefficient of variation of the estimate of p is given by:

$$\text{c.v.}\ (p) = \sqrt{((1 - p)/(F \times p))}$$

This means that in order to achieve a coefficient of variation of 0.1, assuming p is about 0.2 (IWC, 1982), F would be about 400 females. According to the schedule, we would expect to examine approximately 20 females per month, and thus to achieve this accuracy would require about 20 months at sea. If schools have significantly different pregnancy rates, then more effort would be required to obtain a given coefficient of variation of the estimate. A knowledge of the seasonal distributon of calving would also be necessary to estimate this parameter.

Natural Mortality

Estimates of natural mortality are very difficult to obtain by any method. However, if circumstances are favourable, an estimate of the natural mortality of females might be obtained as follows.

Under the most favourable conditions envisioned above under 'Ages', a number of particular schools could be identified each year over several years. Suppose W females are identified from these schools, and k years later the schools are reexamined and w of the females are missing. An estimate of the female mortality, M, would then be:

$$M = 1/k \text{ Ln } (w/W)$$

The coefficient of variation of M can be approximated by:

$$\text{c.v.}(M) = ((\exp(M \times k) - 1)/W)^{0.5}/(M \times k)$$

If $W = 30$, $M = 0.06$ (IWC, 1982), and we wish c.v.(M) to be 0.25, then $k = 14$. In other words, even under the most favourable conditions, it would take about 14 years to obtain a high quality estimate of natural mortality. An estimate of female natural mortality obtained by these methods would also be of questionable validity, as females might have left a school, schools might have split, or so many females might have died that the school was unrecognizable.

Using mark–recapture analysis would also require a considerable data set, over a long time period, to produce reasonable estimates of natural mortality.

Numbers

According to the schedule given above, about three sperm whale groups would be identified per month, and therefore, with a four month field season, 12 per year. Using equations given by Seber (1973, pp. 130–33) for a Schnabel mark–recapture census of a closed population of about 2,000 schools, we have calculated coefficients of variation of the estimate of the number of female sperm whale schools in the North Atlantic, for different numbers of years of data collection. The number of schools identified per year was also varied. The results are given in Table 1. It can be seen that if only 12 sperm whale schools are identified per year, it would take 11 years to achieve a c.v. of 0.5, and 50 years to achieve a c.v. of 0.1. However, if the effort is increased, either by using several research vessels, or extending the sea time beyond four months, or by devoting one or more months totally to obtaining identifications (identifying perhaps 10 schools per month), then the time required to achieve a certain precision would be greatly decreased. If schools split and/or merge permanently there would be complications with the assumptions of the Schnabel census, which would have to be considered.

Table 1

Expected coefficients of variation for estimates of the number of female sperm whale schools in the North Atlantic, using a Schnabel mark–recapture census based on identifications of individual schools. Expected coefficients of variation are given for different study durations (3, 5, 10, 15, 20, 30, 50 years), and efforts (12, 24, 36 schools identified per year).

	No. of Schools Identified per Year		
Years of Study	12 per year	24 per year	36 per year
3	2.14	1.06	0.70
5	1.16	0.58	0.38
10	0.55	0.27	0.18
15	0.36	0.17	0.11
20	0.26	0.13	0.08
30	0.17	0.08	0.05
50	0.10	0.05	0.03

Direct acoustic censusing seems to us to be the most feasible technique in the short term for assessing sperm whale populations. Let us suppose that a hydrophone array can be towed from a ship to pick up all sperm whale schools at less than 3 n.miles from the transect line. The area surveyed, a, will then be $6 \times L$

square n.miles, where L is the distance travelled. The coefficient of variation in the population estimate, N, in this kind of survey is approximately given by:

$$\text{c.v.}\ (N) = 1/\sqrt{(n)}$$

where n is the number of schools counted. But $n = N \times a/A$, where A is the area to be surveyed. Substituting we get:

$$L = n \times A/(6 \times N) = A/(6 \times N \times (\text{c.v.}\ (N))^2)$$

From this we find that if we are trying to estimate the number of schools of females in the tropical North Atlantic (very approximately 25×10^5 square n.miles), with a coefficient of variation of 0.1, we would need to survey about 20,000 n.miles. This would constitute about ten transAtlantic voyages. If the schools are not randomly distributed the coefficient of variation for a given amount of effort would be larger.

EVALUATION

The measures of effort required to realistically estimate the parameters used for assessing and modelling sperm whale populations, which were calculated in the previous section, are summarized in Table 2. It is apparent that, using the techniques that we have investigated, a study would need at least 10 months of sea time to substantially assist the data base used for examining sperm whale population dynamics. However, once this level of effort is achieved, meaningful results can be expected. Their value will increase greatly if the time span of the research is extended, and the effort is expanded. Studies on right whales and humpbacks have shown the benefits of longevity in benign studies of large whales (Payne *et al.*, 1983). It is also apparent that if researchers, making studies in different parts of the same ocean, collaborate, then the results are much more powerful than the sum of the individual efforts. This has been shown in the western North Atlantic, where humpback researchers have pooled their photographic data, with the result that the migrations and population sizes of the humpbacks in this area are fairly clearly understood (Katona *et al.*, 1983).

The work on board *Tulip* was largely based on investigating and developing techniques of studying living sperm whales. The data collection was therefore generally less efficient than is estimated to be possible in this paper. This was especially true during the earlier parts of the study. However, we have begun to collect a data base which can be used to assess and model Indian Ocean sperm whale populations.

Our research techniques are based on using relatively small ocean-going vessels. This is a cheap (running *Tulip*, including maintenance, insurance, food, etc, comes to very approximately US$2,000 per month of sea time) and effective manner in which to collect data, but it is not the only way, and is not well suited to those who are not experienced sailors. It is likely that other benign techniques, using aircraft, satellites, acoustic arrays, radio-tags, etc, will make substantial contributions to the collection of data useful for the study of sperm whale population dynamics.

At this stage in the research, we have only been able to sketch the probable uses and efficiency of our benign techniques. Compared with traditional methods using commercial catch data they possess several limitations, particularly the slow rate of data collection. The results will be subject to many of the same difficulties of interpretation that tax IWC scientists working on commercial catch data, such as uncertainties about the stability of marks, and the difficulties of estimating ages and mortalities. However, the benign techniques do have some advantages, in addition to not destroying the subjects of study, particularly for the investigation of behaviour. Benign techniques also allow the construction of carefully designed, seasonally and geographically balanced, surveys, and permit much greater control during the collection of data.

Table 2

Summary of calculations of approximate effort required to obtain estimates of sperm whale population parameters, for schools of females in North Atlantic. Mos = Months, c.v. = Coefficient of Variation.

	Accuracy	Effort—Time at Sea
Nature of Model	Greatly Increased Accuracy	10 Mos, Breeding Season
Harem Reserve Ratio	Greatly Increased Accuracy	10 Mos, Breeding Season
Lengths	200 Whales Measured	10 Mos
Ages	Age-Length Key	>20 Mos, over 5 Years
Females per School	Standard Error = 1 animal	28 Mos
Pregnancy Rate	c.v. = 0.1	>20 Mos
Natural Mortality	c.v. = 0.25	>2 Schools Monitored Over 14 Years (females only)
Population—Mark–Recapture	c.v. = 0.5	11 Years at 4 mos per Year
Population—Acoustic Census	c.v. = 0.1	>20,000 n.miles

We intend to continue our sperm whale research, on the lines indicated in this paper, and we expect that others will join us. It would be of considerable help when planning this research if the IWC, and other organizations, could indicate what they believe are suitable priorities. For instance, by changing the techniques slightly, we can emphasize the collection of identification and length data, useful for assessing populations, over detailed and long-term behavioural observations, which have greater significance for modelling.

We believe that we have shown that benign research can duplicate the kinds of data provided by commercial whaling, as well as investigating some areas of sperm whale biology for which catch data could not provide information. Therefore, maintaining the supply of data is no valid argument for the continuation of sperm whaling. We hope that this paper encourages other scientists to become involved in the work, and funding agencies to allow it to take place.

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SC/A82/BW14

BEHAVIOR OF BOWHEAD WHALES, *BALAENA MYSTICETUS*, SUMMERING IN THE BEAUFORT SEA: A SUMMARY

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ABSTRACT

The behavior of bowhead whales was studied in the Canadian Beaufort Sea during the summers of 1980–83 and this paper summarises more detailed observations published elsewhere. Bowhead whales feed in the water column, at the bottom and at the surface. Surface feeding at times involves the whales moving in an echelon formation which probably is the result of cooperation between animals. Social interactions occur sporadically, but more towards the end of the summer. Respiration, surfacing and dive characteristics change with the different behaviors. Distribution of bowheads in the Beaufort Sea varies between years and it is probable that distribution and relative frequencies of behaviors are in large part determined by food availability.

INTRODUCTION

Although Scoresby (1820), Scammon (1874) and Bodfish (1936) described behavior of bowhead whales under stress during capture, it is only recently that systematic observations of undisturbed behavior have begun. Several investigators measured duration of dives, surface times and swimming speeds for migrating bowheads (Braham, Krogman, Leatherwood, Marquette, Rugh, Tillman, Johnson and Carroll, 1979; Carroll and Smithhisler, 1980; Davis and Koski, 1980; Koski and Davis, 1980; Rugh and Cubbage, 1980; and Reeves, Ljungblad and Clarke, 1983). Everitt and Krogman (1979) described six bowheads interacting sexually during the spring migration past Point Barrow, Alaska, and there are other brief accounts of bowheads engaging in precopulatory behavior in the Bering and Chukchi Seas (e.g. Braham, Krogman, Johnson, Marquette, Rugh, Nerini, Sonntag, Bray, Brueggeman, Dahlheim, Savage and Goebel, 1980; Johnson, Braham, Krogman, Marquette, Sonntag and Rugh, 1981; Ljungblad, 1981). It is

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believed that mating in bowheads of the Western Arctic population occurs during the spring migration or just prior to it (Braham, Krogman and Carroll, 1984). During the present study in the eastern Beaufort Sea during the summers of 1980–83, we observed some socializing and travelling, and a small amount of apparent sexual activity, but bowheads spent most of their time feeding.

This study was prompted by (1) the general lack of knowledge of behavior of bowhead whales, and (2) the need to understand the undisturbed behavior of the species in order to recognize and interpret potential reactions to oil and gas exploration activities in the Beaufort Sea. The present paper was originally prepared as a preliminary summary of results from 1980 and 1981, to be followed by more detailed analyses in later papers. Two detailed papers describing bowhead behavior in 1980–82 were subsequently prepared (Würsig, Dorsey, Fraker, Payne, Richardson and Wells, 1984a; Würsig, Dorsey, Fraker, Payne and Richardson, in press), as was a report on additional data from 1983 (Würsig, Dorsey, Richardson, Clark, Payne and Wells, 1984b). The present paper was updated before publication to provide a brief summary of the behavioral findings from the summers of 1980–83. The reader is referred to the above accounts for more details. Work on reactions of bowheads to industrial disturbance is described by Richardson, Fraker, Würsig and Wells (in press), Richardson, Wells and Würsig (1984) and Reeves *et al.* (1983).

METHOD

The normal 'undisturbed' behavior of summering bowhead whales was observed from an aircraft, a boat, and a shore station during late July–early September of 1980 and 1981; and from aircraft and a boat during August of 1982 and August–early September of 1983 (Würsig *et al.*, 1984a,b; in press; Fig. 1). Most data were gathered by aerial observations from a *Britten-Norman Islander* aircraft based at Tuktoyaktuk, N.W.T., Canada. The systematic observations described here were obtained from the aeroplane while it circled at altitudes of at least 457 m above sea level. When the aircraft remained this high, overt reactions by the whales to the aircraft were infrequent or absent (Richardson *et al.*, 1985; in press).

Behavior of bowhead whales was observed from the aircraft during 61 of 99 flights from 1980 through 1983, and we circled over bowhead whales for 136.1 hours. Flights were generally within 200 km of home base at Tuktoyaktuk. A pilot, three observers, and an equipment operator comprised the crew. Observations of bowhead behavior were dictated onto a comment cassette recorder, and most behavioral sequences were also videotaped for further analysis in the laboratory.

RESULTS AND DISCUSSION

Feeding

Bowhead whales feed at and below the surface, and one often has to rely on indirect cues to judge whether feeding is taking place. We identified three probable modes of feeding: (1) water column feeding, (2) bottom feeding, and (3) skim feeding at the surface.

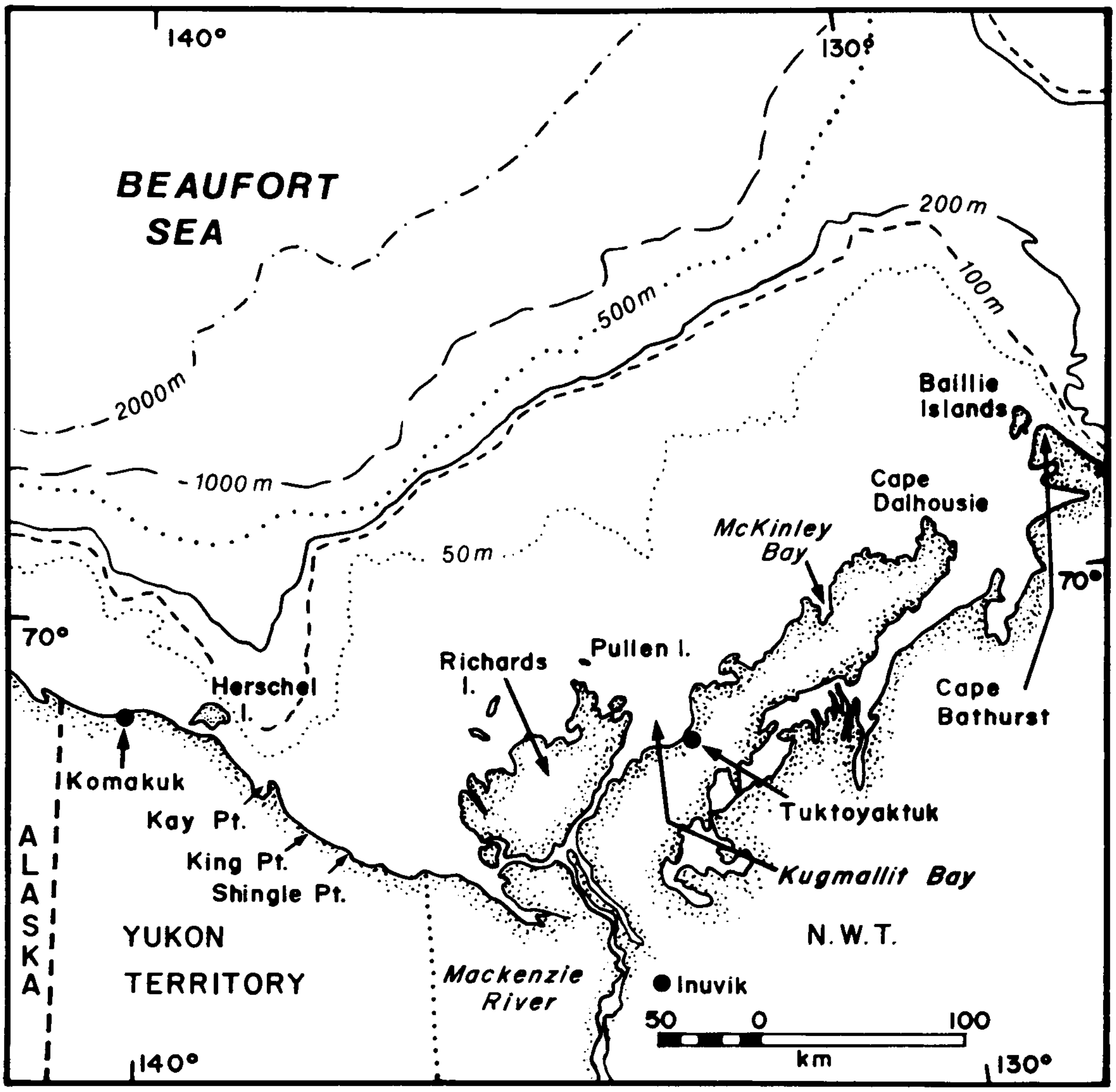

Fig. 1. The eastern Beaufort Sea region, showing bathymetry and locations mentioned in the text.

Whales were presumed to be feeding in the water column when they dove repeatedly in the same area, generally for longer than 10 minutes, and moved forward only slowly during surfacings. At times, much defecation occurred during these surfacings. Whales assumed to be feeding in the water column were generally greater than 75 m from each other, and were thus not socializing actively.

Southern right whales (*Eubalaena australis*) off Argentina sometimes exhibit surface patterns similar to those described above—long dives separated by surfacings during which the whales defecate and swim forward slowly (R. Payne and B. Würsig, pers. obs.). As in bowheads, right whales continue this apparent water-column feeding for hours at a time, and for several days in a row. We hypothesize, but have no direct evidence, that bowheads are feeding in the water column on concentrations of calanoid copepods or euphausiid crustaceans. These are the main types of organisms consumed by bowheads just west of our study area during late summer and early autumn (Lowry and Frost, 1984). Both taxa are abundant (but patchy in distribution) within our study area (Griffiths and Buchanan, 1982).

Bowhead whales sometimes surfaced with mud streaming out of their mouths in 1980 and 1983, indicating that bottom or near-bottom feeding was taking place.

The behavior occurred in water less than 30 m deep. Although apparent near-bottom feeding was first seen by us in 1980, other earlier researchers (Johnson, Fiscus, Ostenson and Barbour, 1966; Durham, 1972; Lowry and Burns, 1980) described pebbles and bottom-dwelling species of invertebrates from bowhead stomachs. These previous indications of bottom feeding usually involved immature whales taken in spring, and in most instances only a few benthic prey items were found in the stomachs (Lowry and Frost, 1984). In contrast, our observations show that feeding at or near the bottom is common at some locations during summer.

In gray whales, *Eschrichtius robustus*, release of mud from the mouth is indicative of bottom feeding. We expect that bottom feeding is quite different in the two species. Gray whales are thought to suck inbenthic invertebrates from the bottom, leaving depressions in the substrate (Nerini, 1984). The modified, short baleen of gray whales is assumed to make it possible for them to feed on inbenthic organisms. In contrast, bowheads have the longest baleen of any species. Although the average biomass of inbenthic animals in the eastern Beaufort sea greatly exceeds that of epibenthic animals, the latter occur in dense swarms in certain places (Griffiths and Buchanan, 1982). Such swarms may be a more suitable source of food for a balaenid whale, and mud may be taken inadvertently along with the epibenthic animals.

When whales moved slowly at the surface with mouths wide open, they were skim feeding. At times, whales skim fed alone and at times they did so in groups of up to 14 individuals. When whales skim fed together, they did so as a coordinated unit, usually in echelon formation with animals staggered to the side and behind the whale at the apex, each separated by 10 to 50 m. The general effect was reminiscent of geese in 'V' formation.

The considerable coordination and cooperation shown by whales while skim feeding in echelon formation means that they probably gain some advantage by it. Whales staggered to the side of the apex may gain an advantage if prey are unable to escape to one side because of the adjacent whale. If this is true echelon feeding is likely of greatest help while whales are feeding on euphausiids, which are capable of avoiding most sampling gear. It is possible that, without this form of cooperative feeding, most euphausiids can avoid the slow-moving bowhead whale.

Social interactions

Social interactions generally consisted of nudges, pushes, movement in close proximity and apparent chases. Social behavior was less predominant in late August–early September than in early August. For example, in the first 10 days of August in 1980 and 1981, we saw 3 or more social interactions per aerial observation hour during 5 of 8 flights when data were collected. After 10 August, this frequency of socializing was observed during only 1 of 17 flights. Rugh and Cubbage (1980) report a high incidence of social interactions during the spring migration around Alaska. The apparent waning of social activity that we observed as summer progressed was probably part of a continuous decrease from the higher spring level.

Some of the social interactions that we saw may have been a part of sexual activity, but social groups were never as boisterous as mating bowheads observed during spring migration (*cf.* Everitt and Krogman, 1979).

During all four years, there was a low level of aerial activity (0.89 aerial bouts/whale-hour of observation of whales at the surface), consisting of breaches, tail slaps, flipper slaps, and associated activity at the surface. These activities were usually carried out by lone whales, but flipper slaps sometimes were associated with socializing whales. Whales also played with logs on three occasions. It is possible that playing with objects is in lieu of social activity, as in spinner dolphins, for example (Norris and Dohl, 1980).

Adult–calf pairs

Calves (young-of-the-year) encountered in the Beaufort Sea in summer are generally 41%–57% of the length of the accompanying adult, assumed to be the mother (length data from Davis, Koski and Miller, 1983; and Würsig *et al.*, in press). Calves usually are within one adult length of the presumed mother. However, when suspected water-column feeding occurs, calves may be at the surface alone while the adult dives for >10 min. In 1982, when there were many long dives by adults, calves spent almost 40% of the time at the surface unaccompanied by an adult. On one occasion, a calf and adult that had been separated for at least 71 min swam toward one another and rejoined after the adult surfaced 1.6 km from the calf. This incident indicates that the mother and calf must have been in contact by acoustic communication. (Indeed, bowhead calls were detected by a sonobuoy dropped near these whales during this incident.)

Apparent nursing usually occurred in bouts lasting <1 min, as the calf dove towards the teat region of the adult's belly. Each bout consisted of one to several brief (about 15 s) dives separated by brief (about 12 s) surfacings with one respiration per surfacing. A nursing calf often changed sides between surfacings; it oriented toward the adult's belly from one side, apparently nursed, swam under the adult, and then surfaced on the other side.

Respiration, surfacings and dives

Intervals between blows, number of blows per surfacing, duration of surfacing, and duration of dive were measured 3,688, 551, 616 and 296 times, respectively, during the four seasons of study. There was more day-to-day and hour-to-hour variability in number of blows per surfacing and duration of surfacing than in intervals between blows. There were strong positive correlations between duration of surfacing and number of blows during that surfacing, and between the durations of consecutive dives. Details are given by Würsig *et al.* (1984a) for 1980–82, and by Würsig *et al.* (1984b) for 1983.

Intervals between successive blows within single surfacings averaged 14.3 ± s.d. 9.99 s (n = 3,688), excluding calves. The mean number of blows per surfacing by 'non-calves' was 4.2 ± s.d. 3.26 (n = 551), and the mean duration of each surfacing was 1.20 ± s.d. 1.204 min (n = 616). The mean duration of dives by non-calves was 4.19 ± s.d. 6.176 min (n = 296). The longest recorded dive was 31.0 min. There was no consistent hour-to-hour pattern in respiration and surfacing characteristics.

In general, calves surfaced and dove for shorter periods than did adults, and mean number of blows per surfacing was lower for calves. Mean blow interval for calves was similar to that for other whales, however.

The most dramatic differences in respiration, surfacing, and dive characteristics occurred between whales skim feeding at the surface and non-feeding whales in 1983. (Although skim feeding was also seen in 1980 and 1981, our 1980–81 data on respiration, surfacing, and dive characteristics during skim feeding were biased by measurement difficulties.) In 1983, skim feeders had longer blow intervals, longer surfacings, more blows per surfacing, and shorter dive times than whales that were not skim feeding. The blow rate, or number of blows per minute, was also higher in skim feeders than in other whales (Fig. 2).

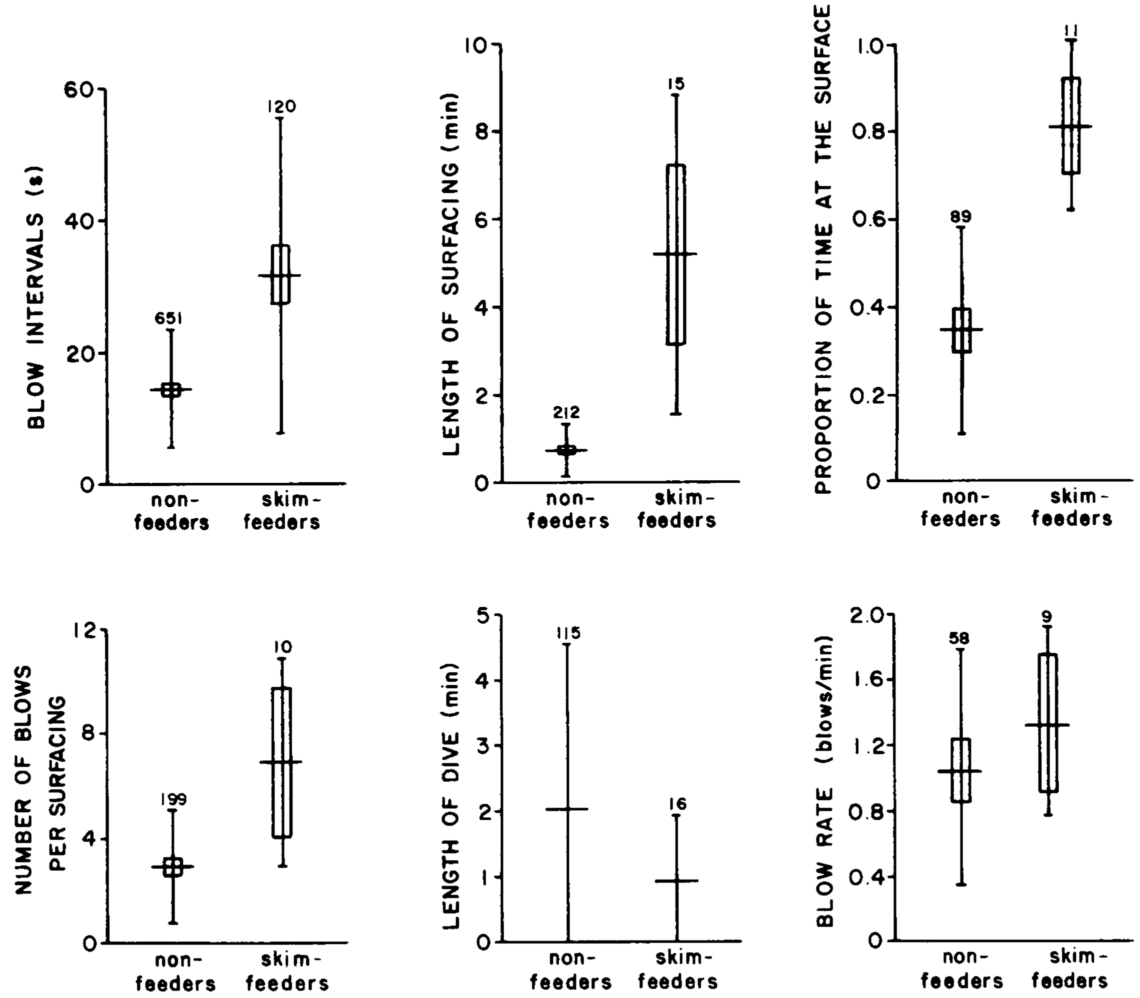

Fig. 2. Comparison of respiration, surfacing and dive characteristics of skim feeding whales and non-feeding whales in 1983. Only presumably undisturbed non-calves are included. In each case, the mean ±1 standard deviation (vertical line) and ±95% confidence interval (rectangle) are shown.

Distribution and general activity

The general locations where whales were sighted changed dramatically from year to year. In 1980, the bowheads that we observed were within 50 km of shore, mainly north of the Tuktoyaktuk Peninsula (Fig. 1) in water only 10–40 m deep. In 1981, they were farther from shore and in >20 m depth. In 1982, bowheads were infrequently encountered close to shore; most of those seen were in water 40–600 m deep. In 1983, many bowheads again occurred close to shore, but mainly off Richards Island and along the Yukon coast southeast of Herschel Island (Fig. 1) rather than off the Tukoyaktuk Peninsula. These concentration areas were not the only locations where bowheads occurred during the summers of 1980–83. However, it was clear that distribution varied markedly among years.

In 1980–82, we noticed some clumping by categories of whales; adults with calves were often found together in some areas, and whales that appeared smaller (possibly subadults) were also seen together at times. Age segregation was more dramatic in 1983. The animals off Richards Island and the Yukon coast were mainly subadults, based on their small size, their lack of prominent white markings (a characteristic of smaller bowheads—Davis *et al.*, 1983), and the absence of calves. Our visual impression of small size was confirmed by photogrammetric data (Cubbage, Calambokidis and Rugh, 1984; W. R. Koski, LGL Ltd, unpubl. data). On a larger geographic scale, Cubbage *et al.* (1984) found a trend for increasing size from west (Mackenzie Bay) to east (east of the Tuktoyaktuk Peninsula) across the summer range in 1983. Calves were not seen with the smaller whales close to shore, but were seen far from shore and in the more easterly areas in 1983. On the other hand, we and others have found numerous bowhead calves (and accompanying mature females) in the western part of the summer range in some other years (e.g., near Herschel Island in August 1982). It therefore appears that bowheads do not show year-to-year fidelity on the summer feeding grounds in the Western Arctic. However, more detailed study of recognizable individuals will be necessary to determine whether some categories of animals return to the same areas on an annual basis, or at some longer interval.

Relative frequencies of some behaviors also changed from year to year. In 1980 we saw indications of bottom feeding, skim feeding and water-column feeding. In 1981 we saw skim feeding and water-column feeding. In 1982 we presumed that most whales were water-column feeding but had little direct evidence for this aside from observations of long dives in deep water. Activities in nearshore waters during 1983 were most like those in 1980, with bottom feeding and skim feeding being common.

We saw some social behavior every year, with a progressive decrease in the rate of socializing from 1980 through 1982 (Table 1). The rate of socializing in 1983 was back up to the approximate level observed in 1981, and was thus intermediate between the 1980 and 1982 levels.

Table 1

Rate of socializing among bowhead whales, 1980–83, calculated according to number of whale-hours of observation of whales at the surface

		1980	1981	1982	1983
A	Number of instances of socializing	42	39	7	27
B	Whale-hours at the surface	5.9	10.1	6.3	7.9
C	Socializing rate (A/B)	7.1	3.9	1.1	3.4

We have wondered whether there might be some cyclicity to the year-to-year changes in distribution and activities. In southern right whales, which are close relatives of bowhead whales, most females bear calves only once every three years and are absent from the winter calving grounds in Argentina during the two years when they do not have calves (R. Payne, in prep.). The calving interval is probably similar in bowhead whales (Davis *et al.*, 1983). It is not known whether summer distribution and behavior of either right or bowhead whales change as a function of stage within the multi-year breeding cycle, but this is a possibility. There is, however, after four years of study, no consistent evidence that the considerable year-to-year variation in behavior of bowheads forms a repeating pattern.

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SC/36/PS1

SEASONAL PATTERNS OF DISTRIBUTION, ABUNDANCE, MIGRATION AND BEHAVIOR OF THE WESTERN ARCTIC STOCK OF BOWHEAD WHALES, *BALAENA MYSTICETUS* IN ALASKAN SEAS

Donald K. Ljungblad,[1] Sue E. Moore[2] and D. Rick Van Schoik[2]

ABSTRACT

The western arctic stock of bowhead whales was studied in Alaskan waters via aerial surveys during spring (April, May) and fall (August, September, October) between 1979 and 1983. A total of 2,605 bowheads were seen in spring with highest annual densities observed north of St Lawrence Island (2.48 whales/km^2), north of Cape Prince of Wales (2.29 whales/km^2) and northeast of Pt Barrow (0.88 whales/km^2). Two peaks in sightings per unit effort (SPUE) were observed northeast of Pt Barrow in early and mid-May each year, except in 1980 when a twenty day delay in SPUE peaks was caused by persistent heavy ice coverage near the Bering Strait. Bowheads were seen in larger groups ($t = 3.68$, $p \leq 0.001$) and exhibited more social behaviors in the northern Bering Sea than in the Chukchi or Beaufort Seas. Swimming direction was significantly clustered about the mean heading of 084°T in the Beaufort Sea. A total of 1,193 bowheads were seen in fall with highest annual densities observed in the Beaufort Sea; northeast of Barter Island in August (0.13 whales/km^2), north of Prudhoe Bay in September (0.27 whales/km^2) and north of Harrison Bay in October (0.58 whales/km^2). Bowhead fall distribution and density across the Alaskan Beaufort Sea appeared to be related to feeding. Whales that seemed to be feeding were observed in shallow water where prey densities are reported to be high. The timing and character of migration observed each fall appeared to be regulated by ice conditions, to the extent that ice coverage affects productivity and limits feeding opportunities. The migration in light-ice years extended over a longer time period, exhibited higher densities and had a later overall SPUE peak than in years of heavy ice. The larger and greater number of SPUE peaks during light-ice years appeared to be related to observed occurrence of bowhead feeding ($\chi^2 = 68.2$, df = 8, $p \leq 0.0001$). Bowhead distribution, density (0.14 whales/km^2) and swimming direction in the northeastern Chukchi Sea in September and October indicates some whales, after migrating around Pt Barrow, disperse across the Chukchi Sea passing roughly over Herald Shoal enroute to the Chukotka peninsula. Estimates of gross annual recruitment rate (GARR), uncorrected for effects of survey type and possible age–class segregation, ranged from 1.7% to 7.6% with highest GARR calculated for mid-August through mid-September, and the first half of October each year. Migrating, resting and feeding behaviors were seen in fall with average group size 2.86 ± 1.55 s.d. Sounds recorded during both seasons were aurally tabulated, but no significant correlations were found between observed surface behavior and call production ratios.

INTRODUCTION

The seasonal distribution, abundance, migration and behavior of bowhead whales (*Balaena mysticetus*) has been investigated via aerial surveys since 1979. Principal areas surveyed included the northern Bering Sea, the eastern Chukchi and the Alaskan Beaufort Sea. Historically, bowheads had a nearly circumpolar

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distribution north of 60°N latitude. However, a long history of exploitation seriously reduced the number of whales in each of five geographically separate stocks (Braham, Krogman and Carroll, 1984; Breiwick, Mitchell and Chapman, 1981). The western Arctic stock, now estimated to contain 3,871 (s.e. = 254) whales (Chapman, 1983), was the population monitored in this study.

The objectives of the study have remained similar over the years and in summary were to:

- determine the distribution and derive estimates of relative abundance and/or absolute density of bowhead whales in the northern Bering, eastern Chukchi and Alaskan Beaufort Seas;
- describe the seasonal migratory timing, habitat and behavioral characteristics of bowheads as observed during their migration; and
- obtain and analyze recordings of bowhead whale sounds.

METHODS AND MATERIALS

Study area and aerial surveys

The study area included the Bering Sea north of St Lawrence Island, the Chukchi Sea east of the International Date Line (IDL), and the Alaskan Beaufort Sea from Pt Barrow to 140°W longitude offshore to 72°N latitude. This area was divided into blocks (Fig. 1) suitable to line transect surveys (i.e. one, or with favorable conditions, two blocks could be surveyed completely on one flight). The bases of operation were Nome, Kotzebue, Pt Barrow, Kaktovik and Deadhorse, Alaska.

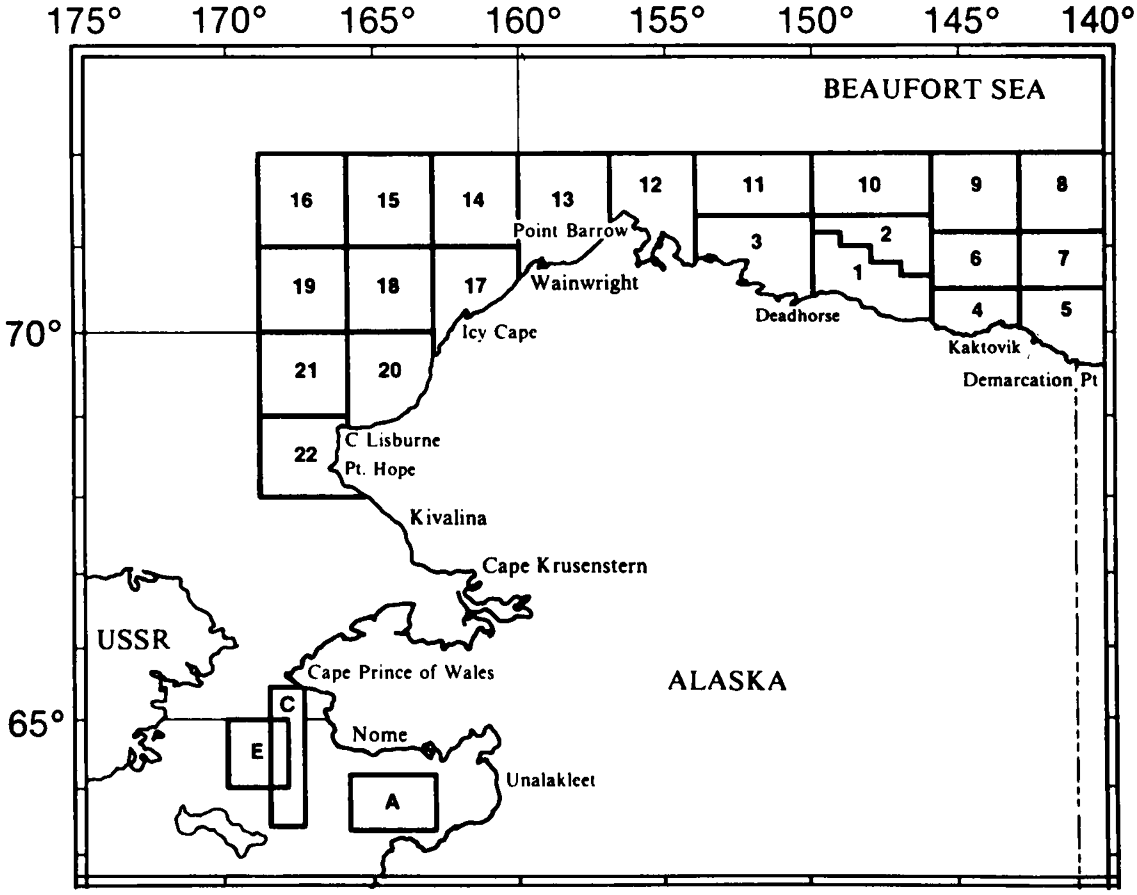

Fig. 1. Overall survey area and survey blocks.

Two types of aerial surveys were utilized to accomplish the objectives listed:

(1) *Line transect surveys* were flown in survey blocks to determine distribution and estimate relative and absolute abundance. Coverage of no less than 10% of the total area of each block was planned. Line transect is one available survey method from which statistical inferences can be made, provided the starting and turning points of the line are selected randomly (Cochran, 1963). Survey blocks were divided into sections that were 30 minutes of longitude in width, and each section marked at top and bottom with 10 equally spaced ticks. Starting and/or turning points were chosen within each section by selecting two numbers between 1 and 10 from a random numbers table and matching them to the numbered ticks. The transect line was then drawn between these two points. The same procedure was followed for each section of the survey block, then all transect lines were linked together with short connecting lines at top and bottom.

(2) *Search surveys* were flown into areas of maximum probability of sighting bowheads and did not follow a preset paradigm. The exact routes of search surveys were dependent upon previous patterns of whale sightings (i.e. number, heading, swimming speed), weather, sea state and ice conditions. Search surveys were flown to locate whales, observe their behavior, follow migrating groups or individuals and record water-borne sounds.

Equipment, data collection and analyses

The methods of data collection and analysis have remained similar throughout all years with the principal exception of the use of a microcomputer aboard the aircraft since 1982 to record, and later analyse, data (Ljungblad, Platter-Reiger and Shipp, 1980; Ljungblad, 1981; Ljungblad, Moore, Van Schoik and Winchell, 1982; Ljungblad, Moore and Van Schoik, 1983; Ljungblad, Moore and Van Schoik, 1984). Surveys were flown in Single and Twin Otter,[1] or Grumman Goose[2] aircraft at 152 to 458 m depending on weather and cloud ceilings. Higher altitudes were maintained when possible to maximize visibility. Airspeed varied between 222 and 296 km/h.

Bowhead behaviors were classified by means of operational definitions, and grossly catalogued into two types for purposes of discussion migratory behaviors, which included swimming and diving; and social behaviors (typically observed in groups) such as milling, feeding, mating, calf nurturing, resting and displaying (Table 1). Displays included breaches, spy-hops, tail and flipper-slaps, rolls and underwater blows. Sonobuoys were dropped near whales whenever possible to record water-borne sounds.

Bowhead distribution was plotted by month and season. Relative abundance and absolute density were derived as sightings per unit effort (SPUE; unit of effort = 1 hour survey time)/block, and strip transect/region, respectively. In the Beaufort Sea, the regions used for absolute density calculation were based upon proposed or existing oil lease areas (A–D), and were further stratified bathymetrically (10 m, 20 m, 50 m, 200 m, 2,000 m). Whale distribution and density patterns, rather than proposed lease area or physical (i.e. bathymetric) features, determined the boundaries of (density) regions in the Bering and Chukchi Seas (see Figs 3 and 7). Calculation of density statistics for each region followed methods reported in Krogman, Braham, Sonntag and Punsley (1979),

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[1] Single and Twin Otter aircraft provided by Naval Arctic Research Laboratory (1979).

[2] Provided by Office of Aircraft Services, Dept. Interior, Anchorage, Alaska (1980–83).

Table 1

Operational definitions of observed bowhead whale behaviors

MIGRATORY:	
Swimming	Forward movement through the water propelled by tail pushes; performed individually or as part of a group.
Diving	Change of swimming direction or body orientation relative to the water surface resulting in submergence; may or may not be accompanied by lifting the tail out of the water; performed individually or as part of a group.
SOCIAL:	
Milling	Whales swimming slowly around one another in close proximity (100 m) at the water surface.
Feeding	Whale/whales diving repetitively in usually cloudy water often accompanied by mud streaming from the mouth and defecation upon surfacing (Würsig *et al.*, 1982); nearly synchronous diving and surfacing has been noted as has echelon formation surface feeding with swaths of clearer water noted behind the whales, and open mouth surface swimming.
Mating	Ventral–ventral orientation of pair of whales often with at least one other whale present to stabilize the mating couple; often within a group of milling whales; pairs appear to hold each other with their pectoral flippers and may entwine their tails.
Nurturing (Cow–Calf)	Calf nursing; proximal swimming to an adult; adults coalescing around a cow–calf pair.
Resting	Whale/whales at the surface with head, or head and back exposed, showing no movement; more commonly observed in heavy ice conditions than in open water.
DISPLAYING:	
Rolling	Whale rotating on longitudinal axis, sometimes associated with mating.
Flipper-Slapping	Whale on its side striking the water surface with its pectoral flipper one or many times; usually seen in groups, often when slapping whale is touching another whale.
Tail-Slapping	Whale hanging vertically in the water head down with tail out of water and waving back and forth striking the water surface; usually seen in groups.
Spy-Hopping	Whale rising vertically from the water such that the head and up to one third of the body is exposed; usually seen in groups.
Breaching	Whale exiting vertically from the water such that half to nearly all of the body is exposed then falling back into the water, usually on its side, creating a large splash and presumably some sounds.
Underwater Blow	Exhalation of breath while submerged.

which were based on the strip transect technique described in Estes and Gilbert (1978).

Migration timing was analysed as SPUE/date. Multiple regression, correlation analysis and t-test were performed on data sets to assess relatedness and difference (Zar, 1974). Directionality of whale headings was analysed using Rayleigh's and Chi square tests (Batschelet, 1972).

Flight effort varied somewhat each year with input from the expanding data base. Such variations in effort from year to year sometimes made comparisons of data between years difficult. The report follows the format of the field season efforts: spring (April, May) and fall (August, September, October). Retaining this format resulted in 26 flights in the Beaufort Sea (June–July 1980) being excluded from review, on which 16 bowheads were seen in June.

RESULTS AND DISCUSSION

Spring (April, May)

Distribution and Density

A total of 2,605 bowheads were sighted over the five spring seasons (Fig. 2). Bowhead spring distribution generally corresponded to open water areas that develop annually during ice breakup such as areas southeast and north of St Lawrence Island, areas north and south of Cape Prince of Wales, the nearshore lead stretching between Pt Hope and Pt Barrow and an easterly directed lead centered roughly along the 71°30′N line between Pt Barrow and approximately 149°W. The plotted distribution corresponds very well with that reported in Braham, Fraker and Krogman (1980) for spring bowhead sighting data collected between 1974 and 1979.

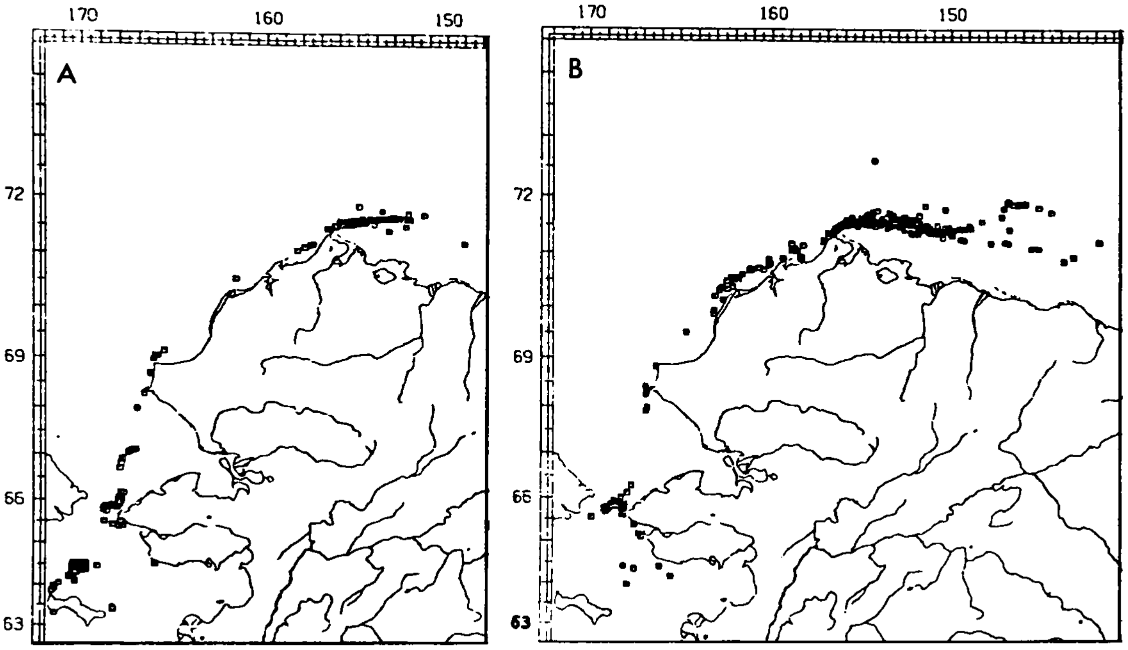

Fig. 2. Distribution of 891 sightings representing 2,605 bowheads plotted by month (April = A; May = B), spring 1979–83.

Highest observed bowhead subregional densities compiled over five years demonstrate that whales are found in greatest abundance in those areas of relatively open water along the migration route (Table 2, Fig. 3). Highest annual densities were calculated for subregions north of St Lawrence Island, north of Cape Prince of Wales and northeast of Pt Barrow.

The distribution and observed densities of bowheads in the Beaufort Sea reflects a migration route that is approximately 25-km wide at Pt Barrow, broadening to about 50 km north of Smith Bay and extending east to Harrison Bay centered approximately on 71°30′N. A predicted 50 to 100-km wide migration corridor east of 149°W to the US–Canadian border is based on only 7% of all the sightings in the Beaufort Sea. Ice is usually very heavy (>9/10) there resulting in few whale sightings (see Fig. 2).

Migration timing and habitat relationships

In spring, bowheads migrate through open water areas in predominantly ice covered seas. Whales seen in the Bering and Chukchi Seas maintained primarily

Table 2

Statistics from aerial surveys of bowhead whales conducted in the northern Bering, Chukchi and Beaufort Seas, April–May 1979 to 1983. Values for each region were summed where appropriate. Region numbers refer to areas depicted in Fig. 3. Number of bowheads observed are those seen on transect lines *only*, not the total number of whales seen on surveys. P = percent of area surveyed; D = density, number/km².

Year Region Number	Area km²	1979 P/D		1980 P/D		1981 P/D		1982 P/D		1983 P/D	
Bering and Chukchi Seas											
1	22,504	0.0	0.0	0.16	0.0	0.26	0.0	0.03	0.0	0.0	0.0
2	19,902	0.0	0.0	2.68	0.0	9.18	0.0	1.80	0.0	0.0	0.0
3	6,918	0.0	0.0	2.97	0.0	11.83	0.0	9.44	0.0	0.0	0.0
4	7,606	0.0	0.0	3.12	0.0	25.45	0.0	14.75	0.01	0.0	0.0
5	2,491	0.0	0.0	1.64	0.0	20.68	0.0	12.86	0.0	0.0	0.0
6	7,957	0.0	0.0	2.73	0.0	49.56	2.48	9.12	0.0	7.15	0.0
7	14,263	0.0	0.0	3.27	0.10	38.68	0.0	17.20	0.0	5.93	0.03
8	15,707	0.0	0.0	14.78	0.01	42.19	0.0	12.95	0.0	2.48	0.0
9	24,981	0.0	0.0	4.31	0.0	12.28	0.0	3.19	0.0	0.0	0.0
10	12,645	0.0	0.0	20.24	0.05	25.77	0.01	21.46	0.02	4.83	0.02
11	2,638	0.0	0.0	35.84	0.02	39.38	0.0	32.85	0.0	5.17	0.0
12	21,276	0.0	0.0	7.57	2.29	17.33	0.09	9.58	0.14	1.89	0.0
13	14,242	0.0	0.0	3.74	0.0	0.10	0.0	0.0	0.0	0.0	0.0
14	8,493	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
15	19,838	0.0	0.0	0.35	0.0	2.22	0.0	2.48	0.10	0.81	0.07
16	5,174	0.0	0.0	12.78	0.0	5.31	0.22	9.82	0.05	3.85	0.59
17	17,530	7.12	0.0	16.01	0.21	10.18	0.12	15.54	0.03	9.61	0.08
Beaufort Sea											
Total	98,415	8.45	0.02	11.18	0.29	19.27	0.17	17.13	0.10	21.51	0.11
A	13,044	10.79	0.12	36.05	0.44	33.51	0.27	31.15	0.22	56.22	0.20
A1	2,250	9.49	0.0	12.68	0.0	0.74	0.0	4.62	0.0	5.70	0.0
A2	1,648	13.05	0.0	7.13	0.0	1.39	0.0	7.05	0.0	18.29	0.0
A3	2,714	13.58	0.0	47.12	0.54	83.77	0.22	61.67	0.11	84.44	0.23
A4	5,222	9.88	0.30	54.49	0.49	38.24	0.31	38.81	0.35	77.69	0.23
A5	1,321	3.58	0.0	12.81	0.0	5.07	0.88	10.78	0.0	42.98	0.0
B	19,157	8.41	0.0	14.40	0.25	38.25	0.24	25.24	0.13	33.60	0.13
B1	2,542	4.37	0.0	6.12	0.0	7.57	0.0	0.0	0.0	0.0	0.0
B2	3,712	19.05	0.0	2.35	0.0	15.60	0.0	9.38	0.0	2.93	0.0
B3	2,728	20.46	0.0	3.06	0.0	16.74	0.0	17.44	0.0	16.30	0.0
B4	3,072	7.58	0.0	42.80	0.22	87.22	0.25	65.66	0.17	76.31	0.27
B5	5,033	0.0	0.0	22.15	0.35	68.10	0.32	31.99	0.16	58.45	0.07
B6	2,267	0.0	0.0	0.0	0.0	5.33	0.10	16.93	0.03	26.29	0.0
C	26,491	19.55	0.0	7.28	0.15	19.38	0.03	21.68	0.01	15.18	0.0
C1	2,009	80.45	0.0	14.90	0.0	2.64	0.0	11.15	0.0	4.82	0.0
C2	1,816	88.28	0.0	10.64	0.0	15.41	0.0	20.23	0.0	7.59	0.0
C3	6,570	27.51	0.0	5.76	0.0	12.67	0.0	26.36	0.0	11.87	0.0
C4	1,672	0.89	0.0	10.77	0.0	26.95	0.0	19.48	0.0	16.40	0.0
C5	4,211	1.57	0.0	9.13	0.03	50.94	0.03	22.31	0.04	30.16	0.0
C6	10,561	1.25	0.0	4.66	0.55	12.90	0.06	20.33	0.02	15.56	0.0
D	39,990	0.26	0.0	4.07	0.08	5.37	0.04	5.58	0.0	7.98	0.0
D1A	537	0.0	0.0	2.31	0.0	2.96	0.0	0.0	0.0	1.78	0.0
D1B	423	0.0	0.0	0.0	0.0	12.26	0.0	0.0	0.0	1.59	0.0
D2A	884	1.26	0.0	8.50	0.0	2.11	0.0	0.0	0.0	0.16	0.0
D2B	533	0.0	0.0	2.33	0.0	24.88	0.0	1.26	0.0	4.82	0.0
D3	6,870	0.69	0.0	7.30	0.0	4.79	0.0	5.99	0.0	2.81	0.0
D4	3,502	0.0	0.0	1.64	0.0	5.26	0.0	6.48	0.0	3.17	0.0
D5	9,663	0.0	0.0	3.16	0.04	8.32	0.10	4.00	0.0	6.98	0.0
D6	1,542	0.0	0.0	3.65	0.18	3.34	0.02	6.57	0.0	11.37	0.0

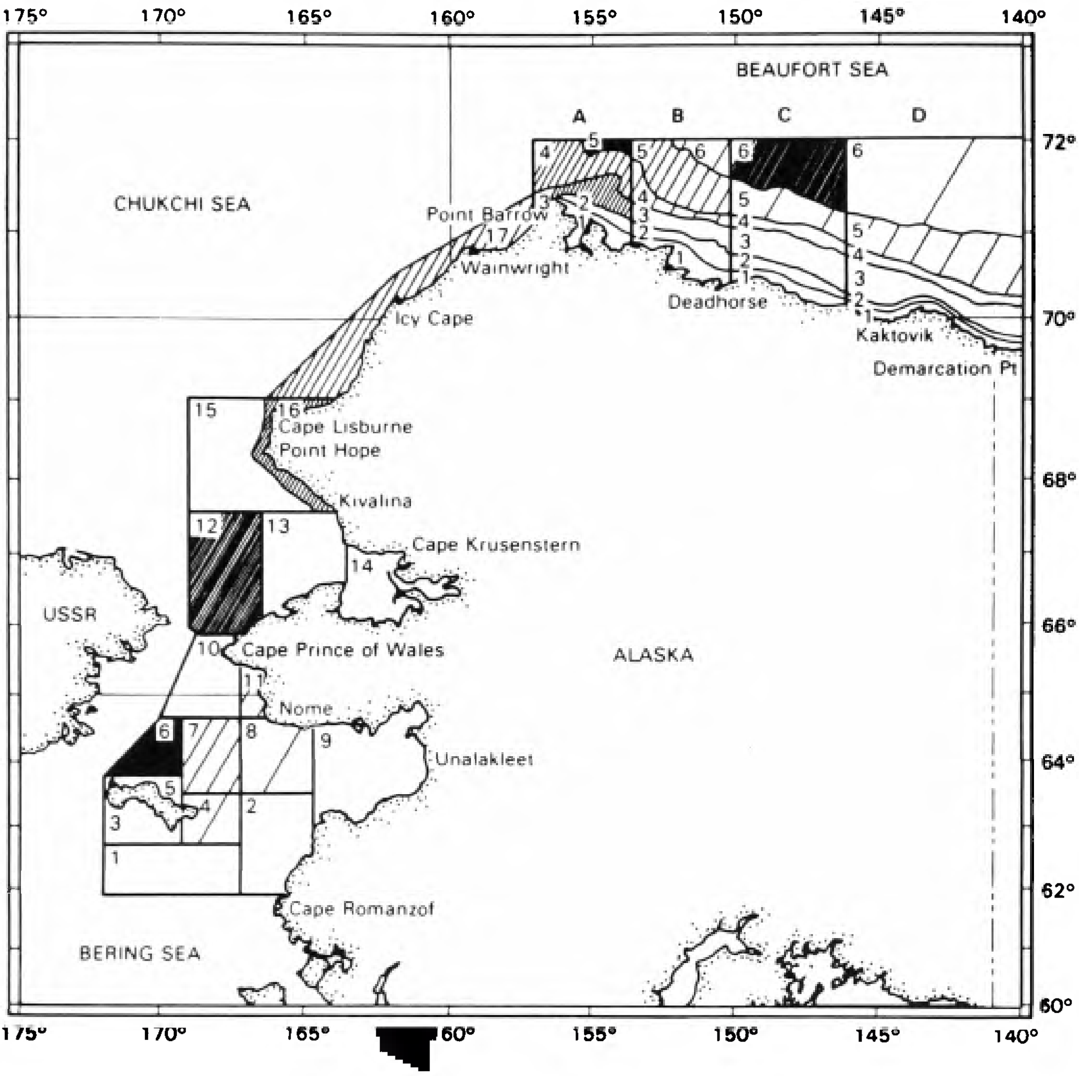

Fig. 3. Highest observed bowhead subregional densities, spring 1979–83. Shading varies from all white (representing 0 density) to all black (representing 2.48 whales/km^2 density). Data based on annual subregional densities presented in Table 2.

northerly headings, although significant clustering about the mean of 100°T was found only in the Chukchi Sea ($z = 39.6$, $p \leq 0.001$) (Fig. 4). Bowheads seen northeast and east of Pt Barrow in the Beaufort Sea were significantly clustered about a mean of 084°T, and 94% of all whales were headed within 30° of due east.

The timing of the northward migration through the northern Bering and eastern Chukchi Seas appears to be regulated in part by the seasonal breakup of the sea ice. Overall, 80% of the bowheads were found in over 7/10 ice coverage, 10% were found in ice coverage ranging from 6/10 to 2/10, and 10% were seen in less than 2/10 coverage. The predominant ice coverage where whales were found varied with sea and year ($\chi^2 = 118.5$, $p \leq 0.10$; Table 3). In 1980, ice remained heavy in the southern Chukchi Sea and appeared to delay at least some bowheads in the open water area north of Cape Prince of Wales through mid-May (Johnson, Braham, Krogman, Marquette, Sonntag and Rugh, 1981). In 1981 through 1983 ice conditions were not as heavy and few bowheads were seen in the northern Bering–southern Chukchi area after the third week of April. Large numbers of bowheads seen north of St Lawrence Island on surveys conducted in early through mid-April 1981 indicate that open water areas in the northern Bering and southern

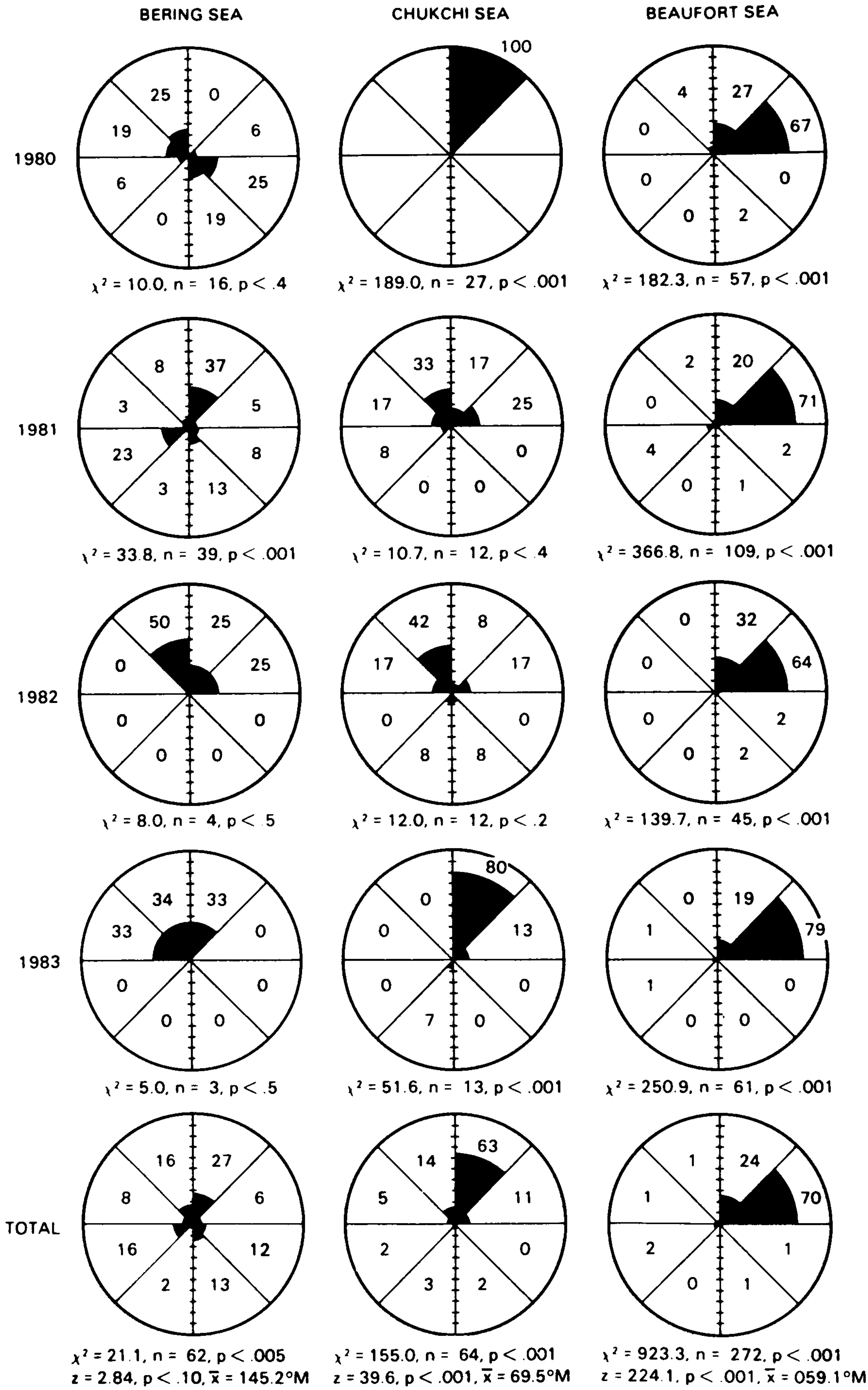

Fig. 4. Swimming direction of bowheads in the northern Bering, Chukchi and Beaufort Seas, spring 1980–83. Numbers in 45° octants represents percentages of whales exhibiting headings within that range.

Table 3

Ice coverage (in tenths) in which bowheads were sighted by Sea, spring 1981–83

	1981			1982[1]		1983[1]		Total			Grand Total
Ice	Bering No. (%)	Chukchi No. (%)	Beaufort No. (%)	Chukchi No. (%)	Beaufort No. (%)	Chukchi No. (%)	Beaufort No. (%)	Bering No. (%)	Chukchi No. (%)	Beaufort No. (%)	No. (%)
0	23(16)	2(6)	0(0)	0(0)	0(0)	0(0)	0(0)	23(15)	2(2)	0(0)	25(4)
1	0(0)	0(0)	0(0)	9(23)	16(17)	0(0)	5(6)	1(1)	9(10)	21(7)	31(6)
2	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	2(3)	0(0)	0(0)	2(1)	2(0)
3	0(0)	0(0)	2(1)	0(0)	0(0)	0(0)	1(1)	0(0)	0(0)	3(1)	3(1)
4	0(0)	0(0)	16(11)	4(10)	0(0)	0(0)	5(6)	0(0)	4(5)	21(7)	25(4)
5	0(0)	1(3)	0(0)	8(21)	0(0)	0(0)	14(18)	0(0)	9(10)	14(4)	23(4)
6	0(0)	0(0)	2(1)	1(3)	0(0)	0(0)	1(1)	0(0)	1(1)	3(1)	4(1)
7	14(10)	3(8)	60(40)	3(8)	8(9)	1(9)	7(9)	14(9)	7(8)	75(23)	96(17)
8	79(55)	0(0)	26(17)	2(5)	10(11)	8(73)	10(13)	81(54)	10(12)	46(14)	137(25)
9	28(19)	30(83)	45(30)	12(33)	58(63)	2(18)	34(43)	30(21)	44(52)	137(42)	211(38)
TOTAL	144	36	151	39	92	11	79	149	86	322	557

[1] In the Bering Sea 1 whale was seen in 1/10 cover and 2 in 8/10 cover, in 1982 and 2 whales seen in 9/10 cover in 1983; these are included under 'Total' and 'Grand Total' columns.

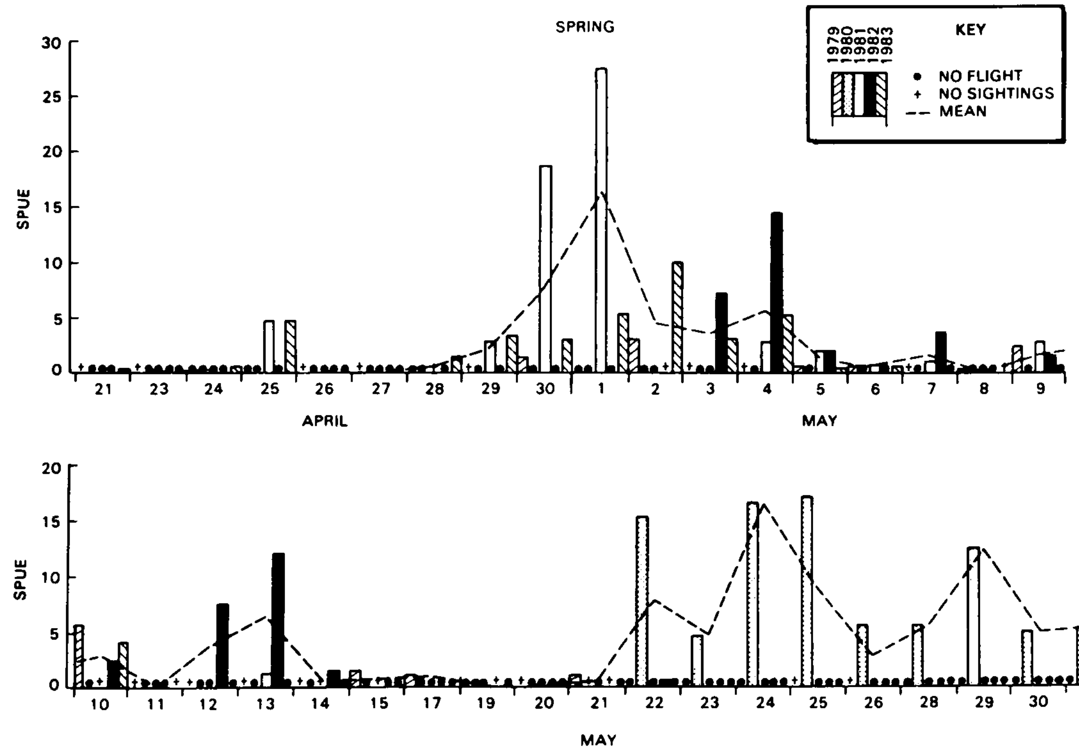

Fig. 5. Bowhead sightings per unit effort (SPUE) by date, spring 1979–83.

Chukchi Seas may be important aggregation points for bowheads as they commence their northward migration (Brueggeman, 1982). No flights were made in the Bering or Chukchi Seas in 1979.

The timing of the migration in the Beaufort Sea northeast and east of Pt Barrow fluctuated somewhat over the five years, but generally was observed to have a pulse-like character as described in Braham *et al.* (1980) with two observed peaks in sighting per unit effort (SPUE) interrupted by seven to nine day periods of relatively low SPUE (Fig. 5, Table 4). These SPUE peaks generally agree with NMFS census camp peaks (Zeh, Ko, Krogman and Sonntag, 1983). Brueggeman

Table 4

Timing of pulses in bowhead spring migration past Pt Barrow, as determined by SPUE/date, 1979–83 and NMFS census counts

Year	First Pulse	Interval (days)	Second Pulse	Census Peak(s)
1979	2 May	8	10 May	—
1980	22 May	7	29 May	25 May
1981	1 May	8	9 May	29 Apr, 22 May
1982	4 May	9	13 May	3 May, 12 May
1983	2 May	8	10 May	28 Apr

(1982) hypothesized that the location of ice fronts in the southern and central Bering Sea may account for 'spacial and temporal separation of whale congregations' seen along the migration route, and the observation of pulses at Pt Hope and Pt Barrow. Notably, the SPUE migration peaks in the heavy ice year of 1980 were approximately twenty days later than those observed in any other year; thus another indication that ice conditions influence migration timing.

Behavior and sound production

Bowhead behavior observed each spring along the migration route included swimming, diving, resting, milling, mating and displaying (Table 5). Not surprisingly, migratory behaviors (swimming and diving) comprised 71.4% of all behavior seen in spring. Resting was the most common social behavior (14.7%), with milling, mating and displaying combined to account for 13.9% of all social behaviors. Although occurrences of each behavior were seen in all seas, with the exception of displays in the Chukchi Sea, there were significant differences in the rates of observed occurrence by sea ($\chi^2 = 451.1$, df = 16, $p \leq 0.001$). Migratory behaviors were strongly associated with the Beaufort Sea, while social behaviors were associated with the Bering Sea. Occurrence of behaviors in the Chukchi Sea were intermediate to these two extremes.

Average size of groups of two or more whales was over twice as large in the Bering Sea as in the Chukchi or Beaufort Seas ($t = 3.68$, $p \leq 0.001$; Table 6). This, combined with the lower observed proportion of solitary whales (31%, $\chi^2 = 6.62$, $p \geq 0.05$), the higher observed occurrence of social behavior there, and the large aggregations seen north of St Lawrence Island in early April 1981, indicates that socially active whales may coalesce in the northern Bering Sea prior to or in the early stages of the northward migration. An overall review of bowhead directionality, behavior and group size observed in spring may be summarized by sea as follows:

- in the northern Bering Sea, 60% of all whales seen were resting, 35% were involved in active social behavior and 5% were migrating. Whales were seen alone 31% of the time or in groups of up to about six, and 57% of all whales maintained northerly headings;
- in the southern and coastal Chukchi Sea, 73% of all whales seen were migrating, 22% were resting, and 5% were involved in active social behavior. Whales were seen alone 49% of the time or in groups of up to about three, and 94% of all whales maintained northerly headings; 74% of these northeasterly headings;

Table 5

Summary of bowhead behavior in the Bering, Chukchi and Beaufort Seas, spring 1979–83

Behavior	Year	Bering Sea No./%	Chukchi Sea No./%	Beaufort Sea No./%	Total No./%
SWIM	1979	—	—	17/100	17
	1980	0/0	11/41	54/44	65
	1981	0/0	18/56	140/68	158
	1982	3/100	23/39	139/70	165
	1983	3/100	19/90	143/74	165
	Total	6/3.9	71/51.1	493/66.9	570/55.4
DIVE	1980	0/0	16/59	64/52	80
	1981	2/4	2/6	38/19	42
	1982	0/0	13/22	11/6	24
	1983	0/0	0/0	18/9	18
	Total	2/1.3	31/22.3	131/17.8	164/16.0
REST	1980	77/83	0/0	5/4	82
	1981	14/26	12/38	9/4	35
	1982	0/0	18/31	16/8	34
	Total	91/59.9	30/21.6	30/4.1	151/14.7
MILL	1980	12/13	0/0	0/0	12
	1982	0/0	2/3	21/11	23
	Total	12/7.9	2/1.4	21/2.8	35/3.4
MATE	1981	26/49	0/0	0/0	26
	1982	0/0	3/5	9/5	12
	1983	0/0	2/10	24/12	26
	Total	26/17.1	5/3.6	33/4.5	64/6.2
DISPLAY	1980	4/4	0/0	0/0	4
	1981	11/21	0/0	18/9	29
	1982	0/0	0/0	3/2	3
	1983	0/0	0/0	8/4	8
	Total	15/9.9	0/0	29/3.9	44/4.3
GRAND TOTAL		152/100	139/100	737/100	1028/100

Table 6

Bowhead average group size in the Bering, Chukchi and Beaufort Seas, spring 1979–83

Year	Bering Sea x̄ ± s.d. (n)	Chukchi Sea x̄ ± s.d. (n)	Beaufort Sea x̄ ± s.d. (n)	Total x̄ ± s.d. (n)
1979	—	—	4.15 ± 2.91 (13)	4.15 ± 2.91 (13)
1980	8.64 ± 14.96 (58)	2.33 ± 2.00 (15)	2.61 ± 0.91 (49)	5.44 ± 5.84 (122)
1981	7.95 ± 21.99 (116)	3.26 ± 1.82 (19)	1.82 ± 0.93 (62)	5.57 ± 3.47 (197)
1982	2.0 ± 0.0 (3)	2.43 ± 0.51 (14)	2.88 ± 1.49 (52)	2.74 ± 1.34 (69)
1983	2.0 (1)	6.0 ± 4.24 (2)	3.50 ± 2.19 (48)	3.57 ± 2.27 (51)
TOTAL	8.04 ± 7.87 (178)	2.86 ± 1.74 (50)	2.74 ± 3.92 (224)	4.84 ± 5.17 (452)

(n) = number of groups of two or more whales.

- In the Beaufort Sea, 85% of all whales seen were migrating, 4% were resting and 11% were involved in active social behavior. Whales were seen alone 56% of the time or in groups of up to about three, and 94% of all whales maintained northeasterly headings.

In general, larger groups of loosely directed, resting or socially active whales were seen in the northern Bering Sea. In the Chukchi and Beaufort Seas active social behavior fell off as whales exhibited increasingly directed, migratory behavior.

Quantitative and qualitative description of sounds recorded near bowheads (Ljungblad, Thompson and Moore, 1982), and similar descriptions of bowhead calls by others (Würsig, Clark, Dorsey, Fraker and Payne, 1982) precedented aural (i.e. subject to listener's hearing) bowhead call analysis and tabularization for 1982 and 1983 data (Moore, Ljungblad and Schmidt, 1984). Sounds recorded in 1979–81 have not been similarly analysed due to time constraints. The preliminary tabularizations indicate some differential call production rates, but as yet no statistically significant correlations with observed surface behavior have been found. Clark (1982, 1983) has reported some success in identifying discrete southern right whale (*Eubalaena australis*) calls using multivariate statistical methods, and in correlating calls with observed surface behaviors. In Würsig *et al.* (1982), these correlations were used in an attempt to infer biological significance of recorded bowhead calls. Such intraspecies comparisons, if done carefully, coupled with further quantitative analysis of recorded bowhead calls may yield a more specific guide to these sounds and thereby enhance their value as a behavioral assessment tool.

Fall (August–October)

Distribution and density

A total of 1,193 bowheads were sighted over the five fall seasons (Fig. 6). The distribution, plotted by month, shows that in August bowheads were generally found in the northeast Alaskan Beaufort Sea between 146° and 139°W, north of 70°N (Fig. 6A). In September bowheads were found across the Beaufort Sea, generally along the continental shelf break, and into the northern coastal Chukchi Sea (Fig. 6B). A similar distribution was found in October, with more whales seen in the Chukchi Sea (Fig. 6C). This distribution corresponds well with Beaufort Sea monthly bowhead catch data of the late 19th and early 20th century summarized in Sergeant and Hoek (1974).

Highest observed bowhead subregional densities compiled over five years depict westward shifting abundance indices in the Beaufort Sea from August through

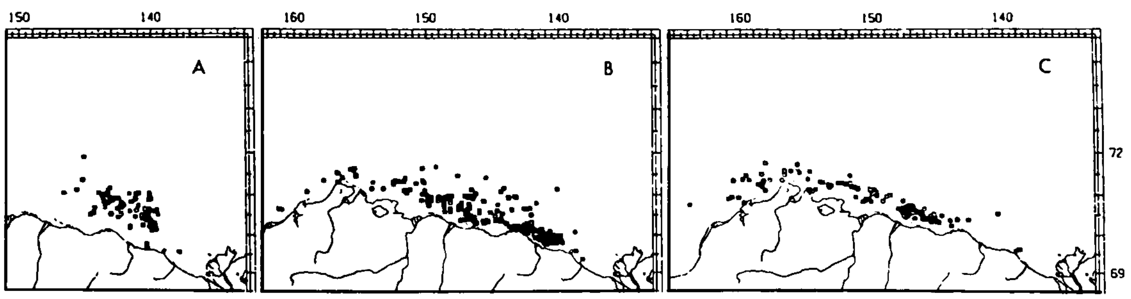

Fig. 6. Distribution of 660 sightings representing 1,193 bowheads plotted by month (August = A; September = B, October = C), fall 1979–83.

Table 7

Statistics from aerial surveys of bowhead whales conducted in the Beaufort Sea; August, September, October 1979–83. Values for each region were summed where appropriate. Region numbers refer to areas depicted in Fig. 7. Number of bowheads observed are those seen on transect lines *only*, not the total number of whales seen on surveys. P = percent area surveyed; D = density, number/km².

Region Number	Region Area km²	1979 P/D		1980 P/D		1981 P/D		1982 P/D		1983 P/D	
August											
Total	98,415	14.43	0.01	8.29	0.0	6.66	0.0	26.94	0.03	36.18	0.01
A	13,044	0.0	0.0	1.94	0.0	5.72	0.0	0.0	0.0	21.67	0.0
A1	2,250	0.0	0.0	3.38	0.0	8.20	0.0	0.0	0.0	24.31	0.0
A2	1,648	0.0	0.0	3.37	0.0	5.56	0.0	0.0	0.0	33.17	0.0
A3	2,714	0.0	0.0	4.25	0.0	9.76	0.0	0.0	0.0	26.67	0.0
A4	5,222	0.0	0.0	0.15	0.0	4.00	0.0	0.0	0.0	16.45	0.0
A5	1,321	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	11.23	0.0
B	19,157	0.0	0.0	16.36	0.0	7.87	0.0	0.0	0.0	33.21	0.0
B1	2,542	0.0	0.0	36.89	0.0	10.96	0.0	0.0	0.0	38.64	0.0
B2	3,712	0.0	0.0	31.23	0.0	10.22	0.0	0.0	0.0	65.24	0.0
B3	2,728	0.0	0.0	20.23	0.0	19.62	0.0	0.0	0.0	50.90	0.0
B4	3,072	0.0	0.0	12.59	0.0	6.71	0.0	0.0	0.0	19.12	0.0
B5	5,033	0.0	0.0	1.90	0.0	2.12	0.0	0.0	0.0	12.40	0.0
B6	2,267	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	15.55	0.0
C	26,491	30.37	0.0	12.53	0.0	9.09	0.0	17.77	0.0	31.52	0.0
C1	2,009	134.66	0.0	32.67	0.0	28.30	0.0	45.68	0.0	65.32	0.0
C2	1,816	68.95	0.0	31.04	0.0	41.87	0.0	22.62	0.0	53.72	0.0
C3	6,570	54.34	0.0	29.67	0.0	10.12	0.0	24.20	0.0	35.07	0.0
C4	1,672	8.69	0.0	8.49	0.0	2.06	0.0	23.70	0.0	24.39	0.0
C5	4,211	7.83	0.0	0.24	0.0	2.90	0.0	21.41	0.0	20.34	0.01
C6	10,561	2.58	0.0	0.0	0.0	2.44	0.0	4.68	0.0	23.48	0.0
D	39,990	15.40	0.01	3.45	0.0	4.71	0.0	54.57	0.04	45.28	0.01
D1A	537	15.04	0.0	11.44	0.0	0.0	0.0	140.15	0.0	36.62	0.0
D1B	423	0.0	0.0	4.93	0.0	3.93	0.0	57.24	0.0	66.13	0.0
D2A	884	111.90	0.0	2.85	0.0	17.43	0.0	109.20	0.0	68.66	0.0
D2B	533	9.68	0.0	8.11	0.0	7.22	0.0	123.46	0.0	57.30	0.0
D3	6,870	44.65	0.0	17.48	0.0	21.82	0.0	80.48	0.0	65.32	0.01
D4	3,502	31.73	0.04	0.74	0.0	0.0	0.0	84.05	0.01	55.45	0.0
D5	9,663	7.05	0.05	0.0	0.0	1.83	0.0	67.16	0.13	53.55	0.01
D6	1,542	0.0	0.0	0.0	0.0	0.0	0.0	23.14	0.01	28.08	0.01
September											
Total	98,415	18.84	0.01	28.10	0.01	25.23	0.07	29.30	0.05	46.69	0.02
A	13,044	1.58	0.0	5.88	0.0	1.48	0.0	20.81	0.01	45.24	0.03
A1	2,250	1.86	0.0	12.56	0.0	0.98	0.0	23.84	0.0	40.06	0.0
A2	1,648	7.71	0.0	15.72	0.0	3.02	0.0	33.80	0.02	63.68	0.0
A3	2,714	1.48	0.0	8.12	0.0	4.38	0.0	31.85	0.0	48.72	0.10
A4	5,222	0.0	0.0	0.14	0.0	0.06	0.0	13.44	0.03	38.54	0.02
A5	1,321	0.0	0.0	0.0	0.0	0.0	0.0	4.43	0.0	47.32	0.0
B	19,157	1.28	0.0	27.61	0.0	12.49	0.0	43.90	0.07	58.66	0.02
B1	2,542	0.0	0.0	47.16	0.0	5.26	0.0	52.93	0.0	47.84	0.0
B2	3,712	5.28	0.0	51.75	0.0	27.66	0.0	68.27	0.02	51.78	0.0
B3	2,728	1.80	0.0	40.71	0.0	27.82	0.0	63.41	0.01	59.92	0.07
B4	3,072	0.0	0.0	28.35	0.0	13.00	0.0	46.94	0.01	71.80	0.04
B5	5,033	0.0	0.0	4.03	0.0	1.41	0.0	22.95	0.0	60.22	0.01
B6	2,267	0.0	0.0	0.0	0.0	0.0	0.0	8.94	0.0	53.34	0.01
C	26,491	38.33	0.01	58.23	0.01	36.14	0.01	19.01	0.17	64.33	0.01
C1	2,009	139.42	0.0	190.54	0.01	112.97	0.0	60.77	0.0	97.34	0.0

Table 7 continued

Region Number	Region Area km²	1979 P/D		1980 P/D		1981 P/D		1982 P/D		1983 P/D	
C2	1,816	78.13	0.0	154.06	0.01	148.46	0.0	46.59	0.02	61.87	0.0
C3	6,570	72.99	0.01	111.24	0.01	66.92	0.01	37.58	0.27	79.74	0.01
C4	1,672	22.13	0.0	30.81	0.0	11.13	0.0	20.85	0.03	75.25	0.02
C5	4,211	14.47	0.0	12.39	0.0	0.37	0.0	6.34	0.0	65.45	0.02
C6	10,561	1.45	0.0	4.72	0.0	0.0	0.0	0.46	0.0	44.52	0.01
D	39,990	19.95	0.01	15.42	0.01	31.59	0.14	30.97	0.05	29.59	0.02
D1A	537	39.70	0.0	65.06	0.03	75.12	0.0	38.50	0.0	17.02	0.0
D1B	423	24.07	0.0	83.16	0.0	71.77	0.0	65.79	0.0	3.49	0.0
D2A	884	140.52	0.01	96.88	0.0	121.26	0.0	46.16	0.0	17.16	0.0
D2B	533	47.99	0.0	78.36	0.09	152.46	0.07	101.45	0.0	17.80	0.0
D3	6,870	52.93	0.01	45.30	0.01	114.76	0.22	59.77	0.14	32.40	0.0
D4	3,502	44.12	0.0	5.93	0.0	9.21	0.04	46.39	0.0	58.91	0.01
D5	9,663	10.41	0.01	5.55	0.0	11.81	0.0	28.64	0.0	46.24	0.05
D6	1,542	0.0	0.0	1.78	0.0	3.99	0.0	13.55	0.02	14.52	0.01
October											
Total	98,415	24.02	0.07	22.24	0.01	17.70	0.03	14.91	0.02	18.87	0.01
A	13,044	19.33	0.02	14.06	0.0	4.92	0.0	32.04	0.03	43.78	0.02
A1	2,250	6.59	0.0	13.12	0.0	12.34	0.0	15.23	0.17	20.67	0.0
A2	1,648	18.86	0.0	18.75	0.0	11.74	0.0	39.58	0.07	50.24	0.0
A3	2,714	26.99	0.02	32.01	0.0	6.39	0.0	37.33	0.01	43.77	0.06
A4	5,222	22.71	0.04	7.15	0.0	0.0	0.0	34.40	0.02	51.15	0.01
A5	1,321	10.68	0.0	0.0	0.0	0.0	0.0	28.09	0.0	42.49	0.0
B	19,157	11.84	0.21	44.80	0.01	30.14	0.02	18.17	0.03	26.47	0.01
B1	2,542	0.64	0.0	74.43	0.0	34.01	0.0	7.02	0.0	17.69	0.0
B2	3,712	23.54	0.0	81.18	0.0	65.23	0.0	12.39	0.05	28.83	0.0
B3	2,728	30.52	0.58	75.15	0.02	59.32	0.06	12.57	0.24	24.67	0.05
B4	3,072	10.51	0.0	41.84	0.0	21.86	0.0	24.41	0.0	33.69	0.0
B5	5,033	4.45	0.0	8.55	0.0	3.85	0.0	22.84	0.01	24.32	0.0
B6	2,267	0.0	0.0	0.0	0.0	0.0	0.0	27.23	0.0	26.96	0.0
C	26,491	62.93	0.06	34.38	0.01	24.28	0.03	12.18	0.01	14.26	0.0
C1	2,009	258.45	0.0	94.01	0.0	50.89	0.0	25.16	0.0	29.11	0.0
C2	1,816	139.58	0.03	79.70	0.0	67.71	0.01	26.33	0.0	34.31	0.0
C3	6,570	119.69	0.11	77.48	0.01	58.35	0.04	25.82	0.07	22.05	0.0
C4	1,672	23.31	0.0	22.51	0.0	28.93	0.02	9.08	0.0	14.81	0.0
C5	4,211	19.97	0.0	5.54	0.0	0.53	0.0	6.07	0.0	10.68	0.0
C6	10,561	2.52	0.0	0.76	0.0	0.0	0.0	1.18	0.0	4.01	0.0
D	39,990	5.65	0.09	5.92	0.0	11.16	0.06	9.52	0.01	10.19	0.01
D1A	537	3.98	0.0	4.96	0.0	6.26	0.0	14.81	0.0	24.19	0.0
D1B	423	0.0	0.0	0.0	0.0	35.17	0.0	9.20	0.0	8.37	0.0
D2A	884	46.27	0.0	32.94	0.0	36.71	0.0	28.50	0.0	23.29	0.0
D2B	533	0.0	0.0	42.15	0.0	36.65	0.0	15.55	0.0	17.01	0.0
D3	6,870	16.11	0.19	26.12	0.0	31.99	0.12	27.87	0.02	20.96	0.01
D4	3,502	8.54	0.0	0.81	0.0	13.09	0.0	13.89	0.0	20.04	0.0
D5	9,663	1.03	0.0	0.0	0.0	10.61	0.0	4.14	0.0	13.45	0.0
D6	1,542	0.02	0.0	0.0	0.0	0.28	0.0	3.01	0.0	0.93	0.0

October (Table 7, Fig. 7). Highest annual density observed in August was in subregion D-5 (0.13 whales/km²; Fig. 7A), although adequate coverage (>10% of area) was only accomplished in 1982 and 1983. In September highest density was calculated for subregion C-3 (0.27 whales/km²; Fig. 7B), and in October for subregion B-3 (0.58 whales/km²; Fig. 7C). A relatively high bowhead density (0.14

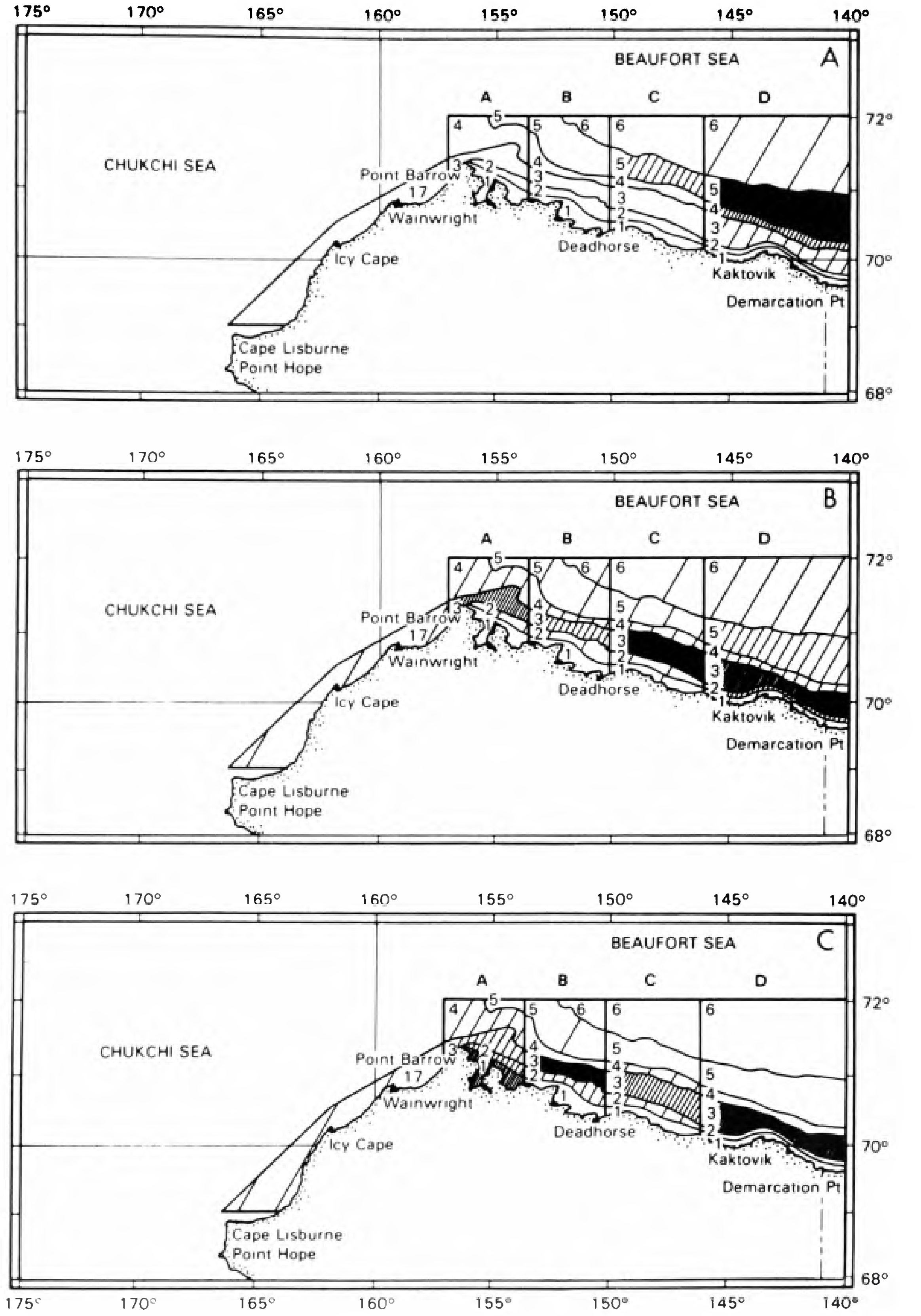

Fig. 7. Highest observed bowhead subregional densities calculated by month, fall 1979–83. August (7A): Shading varies from all white (representing 0 density) to all black (representing 0.13 whales/km^2 density). September (7B): Shading varies from all white (representing 0 density) to all black (representing 0.27 whales/km^2 density). October (7C): Shading varies from all white (representing 0 density) to all black (representing 0.58 whales/km^2 density). Data based on annual subregional densities presented in Table 7.

whales/km^2) was also calculated for subregion 17 along the coastal Chukchi Sea for September and October from data gathered in 1982 and 1983.

Bowhead fall distribution and density may be directly related to feeding opportunities. Bowheads feed primarily on pelagic arthropods including euphausiids, amphipods, copepods and mysids (Lowry, Frost and Burns, 1978) and have been classified as bottom, water-column and surface skim feeders (Nemoto, 1976). Würsig *et al.* (1982) suggests bowheads feed from surface waters and through the water column, as well as near or at the bottom in order to take in sufficient food. Stomachs of bowheads taken near Barter Island between 20 September and 11 October 1979 were found to contain primarily copepods and euphausiids (Lowry and Burns, 1980). Although the great majority of prey items found were pelagic species, the presence of pebbles and some bottom dwelling species indicated that the whales taken near Barter Island did some feeding near the sea floor (Lowry and Frost, 1984).

Whales that appeared to be feeding have been seen from August to mid-October (Table 8) in water 11 m to 62 m deep; depths reported to have stable megaepibenthos assemblages and highest zooplankton densities (Carey, Ruff, Castillo and Dickerson, 1974; Hopkins, 1969; Grainger, 1965; Griffiths and Buchanan, 1982). A plot representing 26 locations where bowhead feeding has been observed over five years (Fig. 8) is similar to that of overall bowhead distribution seen during the fall migration (see Fig. 6). Further, the area between Barter Island and Demarcation Bay, and the area between Smith Bay and Pt Barrow have been identified as important bowhead feeding areas (Lowry and Frost, 1984). Bowhead groups (numbering >100) that appeared to be feeding have been seen 'near' Smith Bay in September 1974 (Ray and Wartzok, 1980) and between Pt Barrow and Smith Bay in September 1976 (Braham *et al.*, 1980).

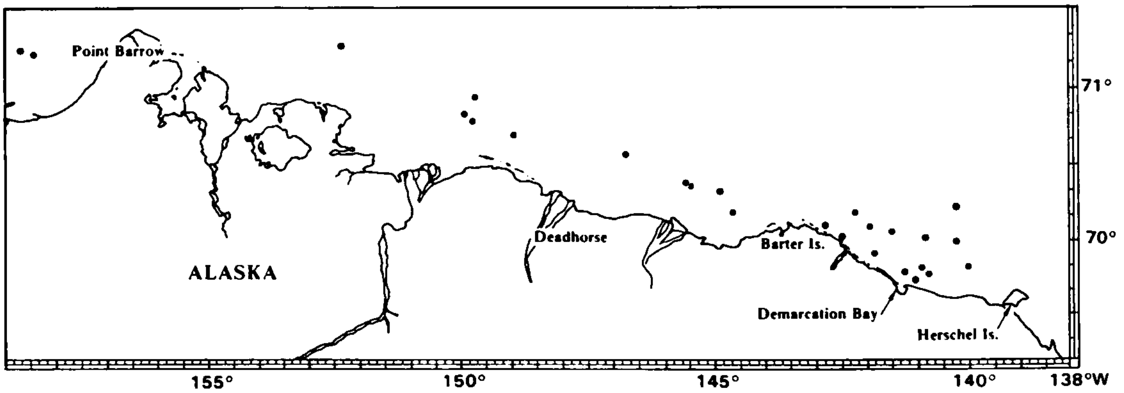

Fig. 8. Distribution of bowheads that appeared to be feeding, fall 1979–83.

Migration timing and habitat relationships

The swimming direction of bowheads in the Beaufort Sea through October was primarily westerly (Fig. 9), although significant clustering around mean headings was noted in all years only in late September and October. Headings of whales seen in August and early September near the Canadian border north of 71°30′N varied over the years.

The timing and character of the bowhead migration across the Alaskan Beaufort Sea and into the Chukchi Sea appears related to the extent of ice coverage and its

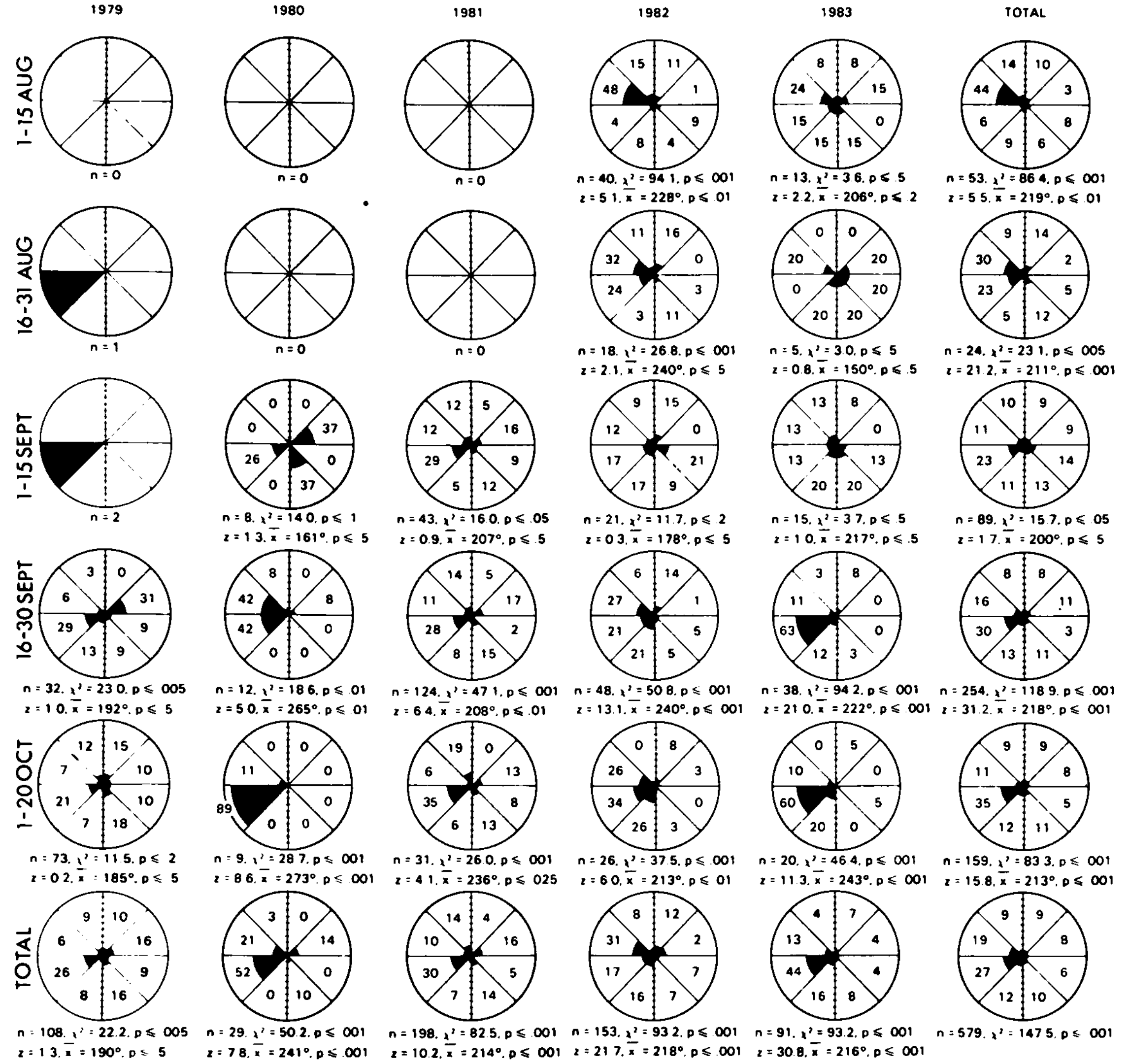

Fig. 9. Swimming direction of bowheads in the Beaufort and Chukchi Seas, fall 1979–83. Numbers in 45° octants represent percentages of whales exhibiting headings within that range.

effect on prey availability. During the fall migration, bowheads were often found in 1/10 or less ice coverage (51%), or in 7/10 or greater ice coverage (30%) (Table 9). The predominant ice coverage where they were found changed each year (χ^2 = 235.5, p ≤ 0.05). Ice coverage limits primary, and therefore secondary productivity (i.e. bowhead prey) in the Alaskan Beaufort Sea by deflecting and diffusing incident light (Schell, Ziemann, Parrish, Danton and Brown, 1982). Ice coverage remained heavy in the Beaufort Sea, throughout the fall of 1980 and 1983, while in 1979, 1981 and 1982 waters were relatively ice free through September and into early October. Sightings of bowheads that appeared to be feeding in Alaskan waters (per hour of survey effort) increased each year in September as bowheads entered the Alaskan Beaufort Sea (see Table 8). Notably, feeding was observed much less often in the heavy-ice years (1980, 1983) than in the light-ice years (1979, 1981, 1982). In the light-ice years, 71 sightings comprising 199 feeding whales were noted, while only 11 sightings, representing 19 whales, exhibited feeding behavior in the heavy-ice years (Table 9). The average observed migration period was approximately 10 days longer during light-ice years, with the SPUE peak occurring approximately eight days later than in

Table 8

Sightings of bowheads that appeared to be feeding per hour of survey effort by two week interval, fall 1979–83

Year	1–15 Aug	16–31 Aug	1–15 Sept	16–30 Sept	1–20 Oct	Total
1979	—	0	0	4.69	0.05	1.04
1980	—	—	0.50	0	0	0.04
1981	—	0	0.94	1.33	0.54	0.85
1982	0	0	0.61	2.34	0	0.64
1983	0.09	0	0	0	0.14	0.05
Total	0.05	0	0.35	1.15	0.12	0.40

Table 9

Ice coverage in which bowheads were sighted, fall 1981–83

Tenths of Ice Coverage	1981 No. (%)	1982 No. (%)	1983 No. (%)	Total No. (%)
0	0(0)	118(53)	23(20)	141(20)
1	98(66)	6(3)	3(3)	107(22)
2	11(7)	6(3)	0(0)	17(3)
3	5(3)	5(2)	7(6)	17(3)
4	2(2)	2(1)	15(13)	19(4)
5	7(5)	7(3)	4(4)	18(4)
6	1(1)	16(7)	9(8)	26(5)
7	5(3)	15(7)	18(16)	38(8)
8	17(11)	15(7)	18(16)	50(11)
9	2(2)	32(14)	19(16)	53(11)
Total	148(100)	222(100)	116(100)	486(100)

heavy-ice years. Average SPUE in heavy ice years was 1.56 whales/h, while for light ice years it was 15.56 whales/h. During the heavy-ice years, few groups or aggregations of bowheads were seen as indicated by lower relative number of whales seen and by all SPUE peaks ≤ 5 (Table 10, Fig. 10). In contrast, five to eight SPUE peaks >5 were noted in the light-ice years of 1981 and 1982. Surveys in 1979 were concentrated very near shore and thus affect SPUE comparisons for that year. The larger and greater number of SPUE peaks during light-ice years appeared to be related to the higher incidence of observed bowhead feeding in those years ($\chi^2 = 68.2$, df = 8, $p \leq 0.0001$).

The bowhead aggregations found offshore, which resulted in early August SPUE peaks in 1982 and 1983, may also be related to feeding. Schell *et al.* (1982) reported primary production peaks occur in June offshore, and in August nearshore in the Alaskan Beaufort Sea. Theoretically, bowheads may encounter a bloom of secondary producers offshore in July–August. In 1982 and 1983 bowheads were found primarily offshore in deep (>2,000 m) water in August and early September, and in transitional (50–2,000 m) or shallow depths (<50 m) in later September and October (Table 11). In 1979–81 little or no effort was dedicated to offshore surveys which limits available comparisons. If whales

Table 10

Summary of bowhead migration, timing, character and habitat relationships in the Alaskan Beaufort Sea, fall 1979–83

						Summary of data by General Ice Habitat	
Year	1979	1980	1981	1982	1983	Light	Heavy
Average September Ice Coverage	0/10–1/10	6/10–9/10	0/10–1/10	0/10	6/10–9/10	0/10–1/10	6/10–9/10
Feeding Bowheads (Sightings/Whales)	16/50	3/5	24/41	31/108	8/14	71/199	11/19
Migration: Period	20 Aug -20 Oct	4 Sept -9 Oct	7 Sept -20 Oct	2 Sept -17 Oct	3 Sept -17 Oct	31 Aug -19 Oct	3 Sept -13 Oct
Length (Days)	(61)	(35)	(43)	(45)	(44)	(49.7)	(39.5)
SPUE: Peak	7.33	1.25	15.75	23.60	1.86	15.56	1.56
Date	14 Oct	18 Sept	28 Sept	16 Sept	24 Sept	29 Sept	21 Sept
Number of Bowheads Sighted:	197	46	288	490	172	975	218

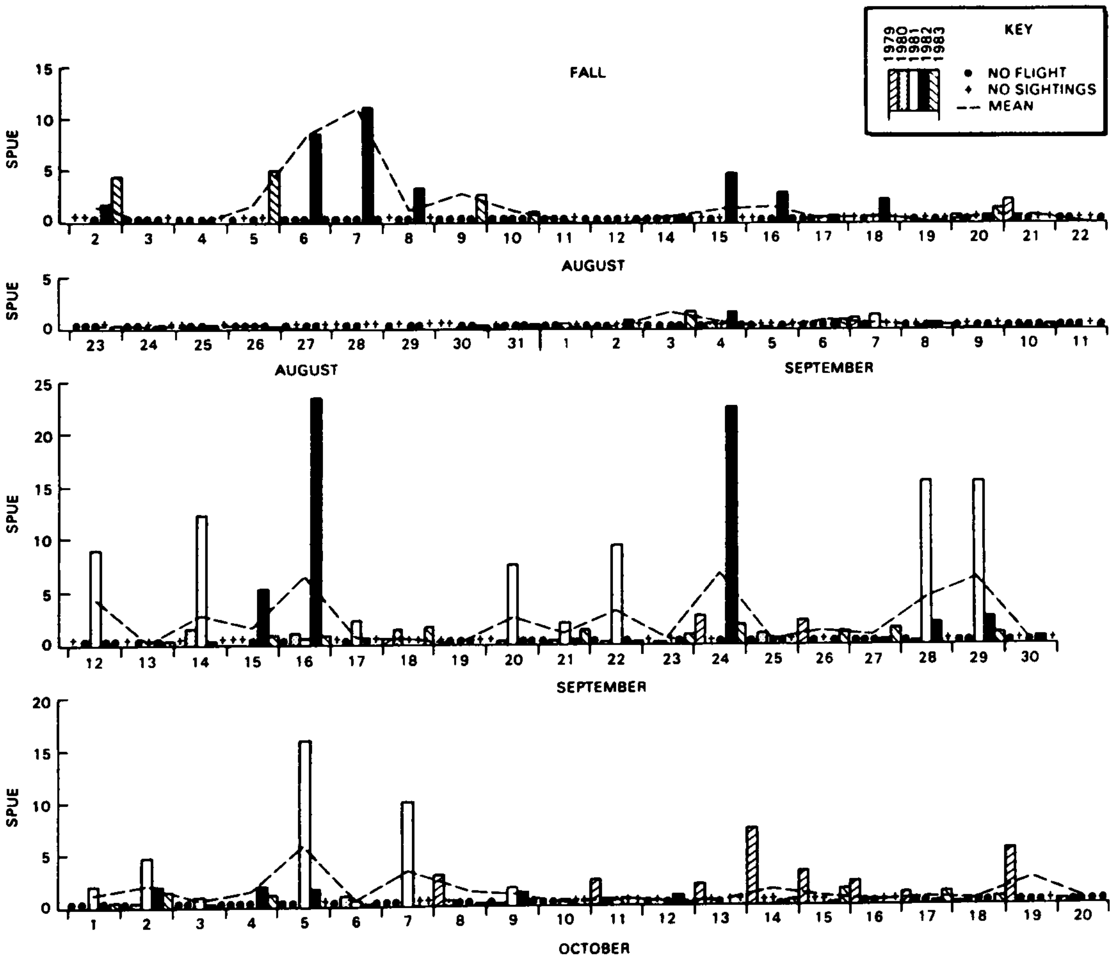

Fig. 10. Bowhead sightings per unit effort (SPUE) by date, fall 1979–83.

migrating east past Pt Barrow in late May and early June encounter an offshore food source in the eastern Alaskan Beaufort Sea, they may swim no further than approximately 140°W. When offshore food sources are reduced in availability in August and early September, these same whales may be the first ones to move west

Table 11

Number (percent) of bowhead sightings in deep (over 2000 m), transitional (50 m to 2000 m) and shallow (less than 50 m) water, fall 1979–83

	1–15 Aug No. (%)	16–31 Aug No. (%)	1–15 Sept No. (%)	16–30 Sept No. (%)	1–20 Oct No. (%)	TOTAL No. (%)
1979						
Deep	—	0(0)	0(0)	0(0)	0(0)	0(0)
Transition	—	1(25)	2(100)	1(4)	0(0)	4(3)
Shallow	—	3(75)	0(0)	26(96)	108(100)	137(97)
Total	—	4(100)	2(100)	27(100)	108(100)	141(100)
1980						
Deep	—	—	0(0)	0(0)	0(0)	0(0)
Transition	—	—	0(0)	0(0)	0(0)	0(0)
Shallow	—	—	9(100)	15(100)	9(100)	33(100)
Total	—	—	9(100)	15(100)	9(100)	33(100)
1981						
Deep	—	0(0)	0(0)	0(0)	0(0)	0(0)
Transition	—	0(0)	0(0)	0(0)	1(2)	1(1)
Shallow	—	1(100)	26(100)	80(100)	40(98)	147(99)
Total	—	1(100)	26(100)	80(100)	41(100)	148(100)
1982						
Deep	2(3)	2(9)	0(0)	0(0)	0(0)	4(2)
Transition	49(86)	19(86)	6(24)	11(12)	4(14)	89(40)
Shallow	6(14)	1(5)	19(76)	78(88)	25(86)	129(58)
Total	57(100)	22(100)	25(100)	89(100)	29(100)	222(100)
1983						
Deep	1(4)	4(57)	4(21)	0(0)	0(0)	9(8)
Transition	24(96)	3(43)	15(79)	21(51)	8(33)	71(61)
Shallow	0(0)	0(0)	0(0)	20(49)	16(67)	36(31)
Total	25(100)	7(100)	19(100)	41(100)	24(100)	116(100)
TOTAL						
Deep	3(4)	6(18)	4(5)	0(0)	0(0)	13(2)
Transition	73(89)	23(68)	23(28)	33(13)	13(6)	165(25)
Shallow	6(7)	5(14)	54(67)	219(87)	198(94)	482(73)
TOTAL	82(100)	34(100)	81(100)	252(100)	211(100)	660(100)

and initiate the fall westerly migration or south toward shallower coastal waters. In short, late arrivals to the Beaufort Sea in spring may be the first westward migrants seen in fall.

To summarize, as whales migrate west into the Alaskan Beaufort Sea from summer feeding grounds in the Canadian Beaufort Sea in light-ice years they aggregate and appear to feed in areas where dense prey is likely. In years when heavy ice limits productivity, bowheads may remain on Canadian feeding grounds longer and upon moving west (and finding insufficient prey abundance in the Alaskan Beaufort Sea) may simply continue swimming west. A multiple regression of date, longitude, depth and ice cover at bowhead sighting, for 1982–83 data found the strongest correlation to be between date and longitude ($r^2 = 0.758$) indicating a strong westward progression with time. Correlation between depth and longitude ($r^2 = 0.351$) and depth and date ($r^2 = 0.197$) indicated whales were seen in shallower water as they moved west and with time. The relative number/percent of bowheads seen in shallow, transitional and deep depth regimes

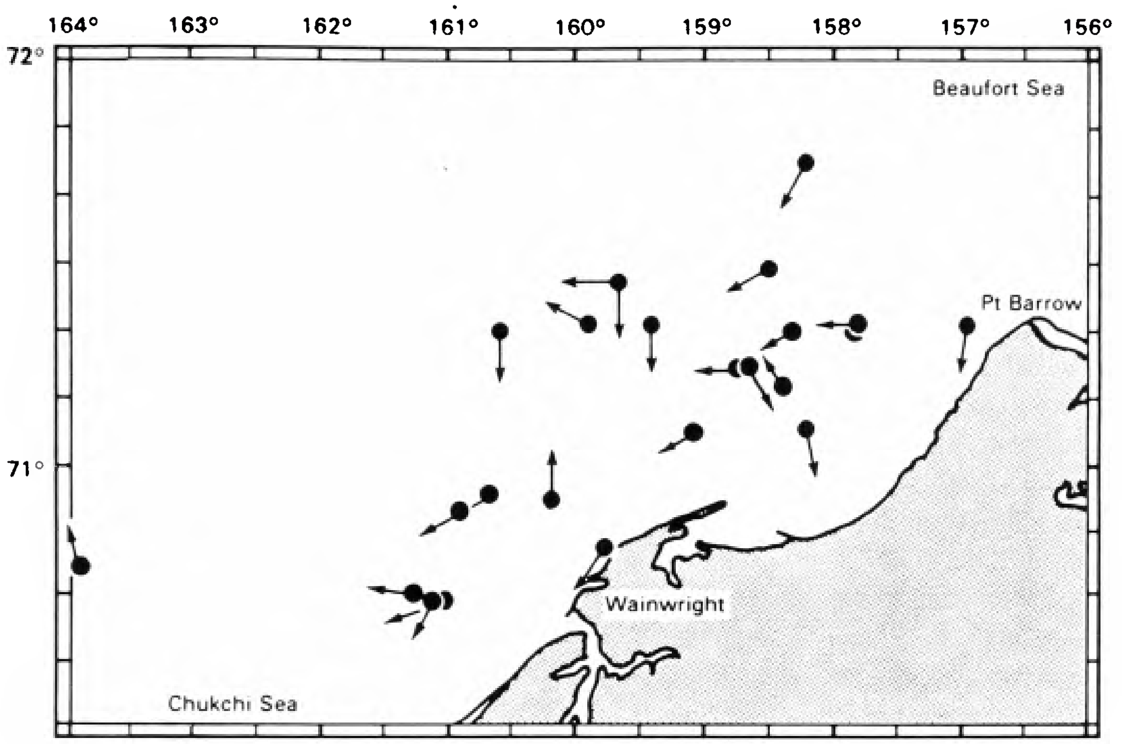

Fig. 11. Bowhead sightings in the Chukchi Sea, fall 1982–83.

supports this trend (see Table 11). There was disparity in the proportion of bowheads found in each depth zone between 1982 and 1983 ($\chi^2 = 33.4$, df = 4, $p \leq 0.001$) that may reflect the difference between the years in ice coverage. In 1982, a relatively light-ice year, most sightings were in shallow water, and a majority of whales were sighted in shallow water as early as the beginning of September. In 1983, a heavier ice year, most sightings were in transitional depths, and it was October before a majority of whales were sighted in shallow water.

Thirty-seven bowheads were seen in the Chukchi Sea during September and October, 1982–83 from 0.5 to 40 km from shore (Fig. 11). These whales exhibited mostly southwest headings ($\chi^2 = 33.1$, $p \leq 0.001$) with clustering about a mean heading of 242°T ($z = 14.1$, $n = 23$, $p \leq 0.001$). Fall bowhead sightings in the Chukchi Sea can be encompassed by a rectangle bounded by latitudes 71°45′N to 70°44′N and longitudes 156°58′W to 164°00′W. If an average southwesterly heading of 252°T is applied to that rectangle, a hypothetical picture of bowheads dispersing across the Chukchi Sea develops with some crossing roughly over Herald Shoal (70°30′N, 171°30′W). This pattern of a southwestward dispersion of bowheads across the Chukchi Sea in fall complements, yet diverges from, the currently held model that suggests bowheads primarily travel along the ice front west to Herald and Wrangel Islands before following the Chukotka peninsula south and through the Bering Strait (Braham *et al.*, 1980). Ray and Wartzok (1980) reported five bowheads slightly west of Herald Shoal on 11 October 1975. Johnson *et al.* (1981) reported 104 bowheads sighted along the Siberian coast between Tenkergin and Cape Onman (68°N–69°N, 174°W–178°W) between 16 and 18 October 1979, whereas only three bowheads were observed northeast of Wrangel Island in the same time frame. Bogoslovskaya, Votrogov and Krupnik (1982) reported 274 bowheads along the mainland coastline between early September and mid-October, with only four to 12 whales seen off Herald Island in October 1980.

Additionally, Bogoslovskaya *et al.* (1982) report that neither the inhabitants of, nor the scientists working on Wrangel Island have ever observed bowheads there in fall. Marquette, Nerini, Braham and Miller (1981) reported 227 bowheads sighted along the Siberian coast between 21 and 23 September 1980, with no bowheads seen near Wrangel or Herald Island. Miller, Johnson and Rugh (1983) concluded that bowheads seen along the Siberian coast in September and October 1979 to 1982 were early returnees from the western Arctic stock, and not whales that had spent the summer in the Chukchi Sea. Our data, in conjunction with these published accounts, support the hypothesis of a dispersion of at least some bowheads south and west across the Chukchi Sea after they round Pt Barrow in the fall. Migration patterns in the Chukchi Sea may be more dispersed, compared with those seen in the Beaufort Sea, due to the differences in the bathymetry and ice (i.e. the Chukchi Sea lacks the shelf break, and usually the ice coverage, pertinent to discussion of the bowhead migration across the Beaufort Sea).

The timing and observed distribution of bowheads in the Beaufort and Chukchi Seas during the fall migration can be depicted by a westerly directed, continuous distribution of whales in a general trapezoid shape. The population moves west across the Beaufort Sea and disperses southwest across the Chukchi Sea from August through October (Fig. 12). The following observations support this hypothesis:

- in August 1982–83, bowheads were seen offshore in the west and closer to shore to the east;
- peak subregional abundance estimates (and depth regimes) by month were D5 (>200 m) in August with 82% of all sightings, C3 (20–50 m) in September with

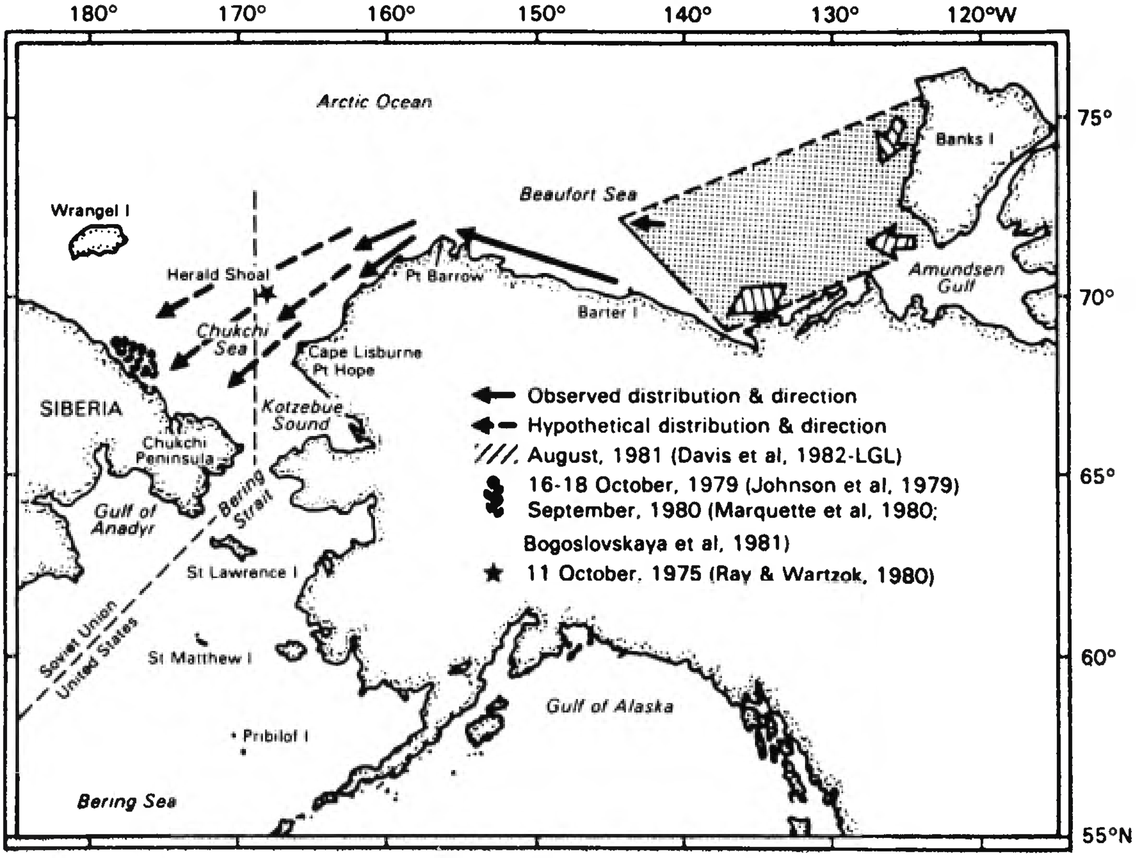

Fig. 12. General representation of likely fall bowhead migration showing approximate distribution in August, September and October, 1979–83.

84% of all sightings and B3 (20–50 m) in October with 46% of all sightings, respectively;

- the strongest correlate with bowhead sighting longitude was date ($r^2 = 0.758$) in 1982 and 1983;
- the direction of the bowheads remained westerly (see Fig. 9) from August through October, with significant clustering about the predicted migration route of 248°T and 243°T in late September and October, respectively;
- correlation between longitude and depth ($r^2 = 0.351$), and depth and date ($r^2 = 0.197$) indicated whales were seen in shallower water as they moved west in time;
- ice coverage was not significantly correlated with longitude ($r^2 = 0.060$) nor with depth at sighting ($r^2 = 0.067$) indicating ice may not be the major factor in determining whale location in fall; and
- bowheads seen in the Chukchi Sea in September and October were 0.5 km to 40 km from shore and clustered about a mean heading of 242°T.

In this model, the bowheads seen offshore in early August are the leading edge of a much larger westerly moving population and suggest that initial migratory movements could occur that early in the Alaskan Beaufort Sea. By the first part of September, whales are seen near Demarcation Bay and Barter Island as the population shifts to the west. Continued westward movement brings the majority of the population through the Alaskan Beaufort Sea along the shelf break where continued feeding may be optimized in September and early October. In late September and early October, bowheads disperse across the Chukchi to the Siberian coast.

Calf sightings and recruitment

Calves were seen with migrating bowheads from August through October (Table 12). In 1979 and 1980 calves were seen only in October. In 1981, calves were seen in September and October, and in 1982 and 1983, when a greater flight effort was directed offshore, calves were seen from August through October.

Estimates of gross annual recruitment rate (GARR = no. calves/total no. bowheads including calves) ranged from 1.7% in 1981 to 7.6% in 1983. Highest GARR was seen between mid-August and early September ($\chi^2 = 5.29, p \leq 0.10$). Estimates of bowhead GARR have until recently been low relative to other mysticetes. Estimates derived from studies since 1976 over a variety of seasons, geographical areas and survey platforms range from 0.0 to 12.4% (Nerini, Braham, Marquette and Rugh, 1984) with an accepted point estimate, corrected for type of survey, of 7.2% (1.4% = s.e.) (Chapman, 1984).

Although within each year there was one or several peak calf sighting date(s), when the ratio of calves to total number of bowheads seen per one hour of survey effort was plotted, there was no cumulative peak for all years (Fig. 13). The periods of peak calf sightings in 1982 and 1983 may be generally correlated to sightings of whales offshore and nearshore. Calf sighting peaks in mid August were associated with those whales seen offshore near the Canadian border, while the peaks seen in September and early October were associated with whales seen near shore. Their distribution both spatially and temporally matches the general distribution.

Evidence of segregation of bowhead age-classes in the eastern Beaufort Sea has been suggested via photogrammatic length frequency studies (Cubbage,

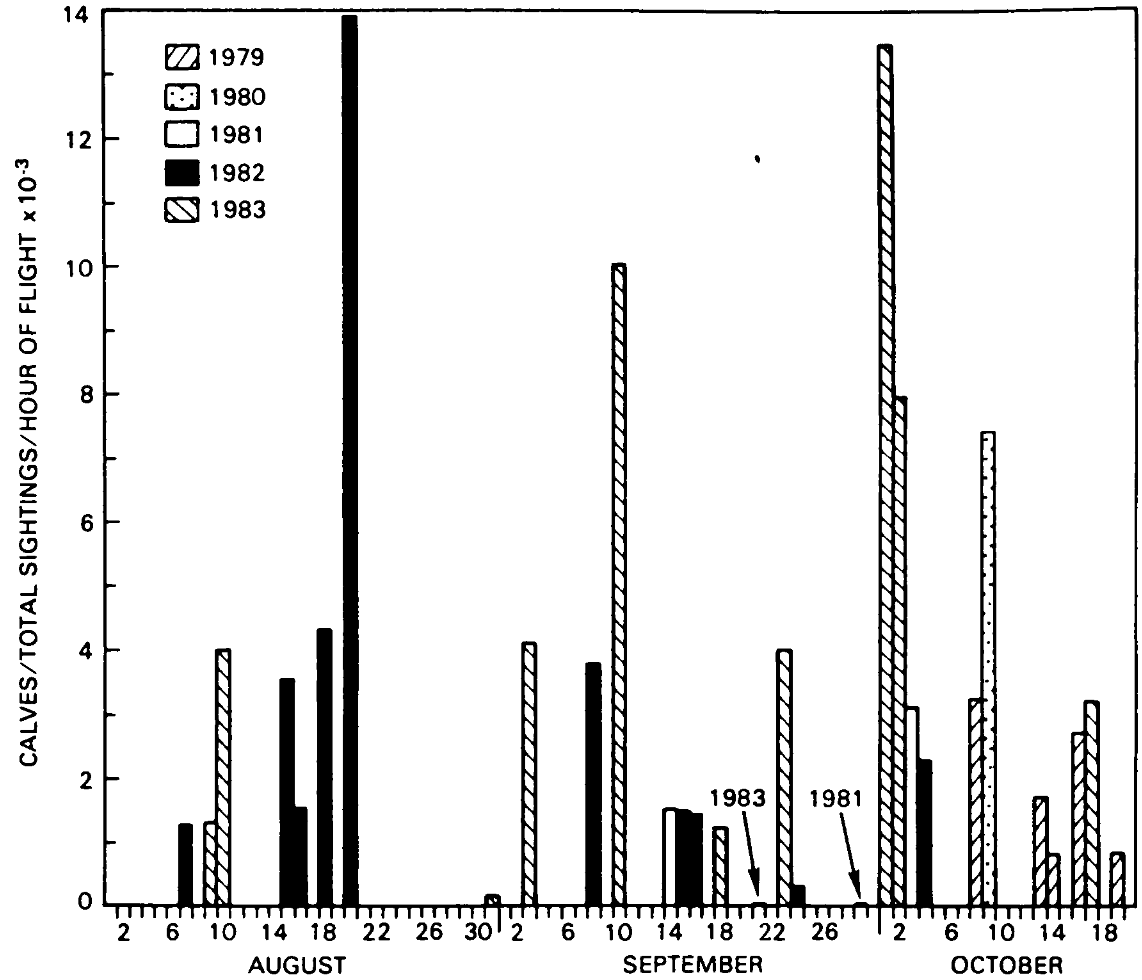

Fig. 13. Ratio of bowhead calves/total number of bowheads seen by survey hour, fall 1979–83.

Table 12

Sightings and recruitment estimate (%)* of bowhead calves by two week interval, fall 1979–83

Year	1–15 Aug	16–31 Aug	1–15 Sept	16–30 Sept	1–20 Oct	Total
1979	0	0	0	0	6(3.9)	6(2.5)
1980	0	0	0	0	1(8.3)	1(2.2)
1981	—	0	1(3.2)	1(1.1)	1(2.0)	3(1.7)
1982	5(4.6)	6(16.2)	4(7.4)	7(2.8)	1(2.2)	23(4.7)
1983	2(4.1)	1(10.0)	3(12.5)	3(5.6)	4(11.4)	13(7.6)
Total	7(4.6)	7(13.0)	8(6.5)	11(2.2)	13(4.4)	46(4.1)

(%) * GARR = Number Calves/Total Number Bowheads.

Calambokidis and Rugh, 1984; Davis, Koski and Miller, 1983). Differences in age-class were found between locations each year, and age-class location seemed to vary between years. The GARR provided here was not corrected for such segregation. Chapman (1983) noted that to derive an accurate GARR, given the existence of segregation, all components of the population must be sampled and then combined, weighted by the number of whales comprising each component. Because survey effort is directed toward the Alaskan Beaufort Sea, the components of the population sampled is not known with certainty for any year.

Table 13

Bi-monthly summary of bowhead behavior, fall 1979–83

Behavior	Year	1–15 Aug	16–31 Aug	1–15 Sept	16–30 Sept	1–20 Oct	Total (%)
SWIM	1979	—	4	2	6	57	69(35)
	1980	—	—	7	5	2	14(30)
	1981	—	2	38	70	19	129(45)
	1982	76	18	9	117	29	249(51)
	1983	27	8	6	38	16	95(55)
	Total	103	32	62	236	123	556(47)
DIVE	1979	—	3	0	3	7	13(7)
	1980	—	—	0	17	8	25(54)
	1981	—	0	5	20	8	33(11)
	1982	5	5	7	21	3	41(8)
	1983	2	0	4	5	1	12(7)
	Total	7	8	16	66	27	124(10)
REST	1979	—	0	0	0	2	2(1)
	1980	—	—	0	0	0	0(0)
	1981	—	0	17	22	6	45(16)
	1982	18	7	2	10	8	45(9)
	1983	8	0	3	1	0	12(7)
	Total	26	7	22	33	16	104(9)
FEED	1979	—	0	0	43	7	50(25)
	1980	—	—	5	0	0	5(11)
	1981	—	0	8	22	11	41(14)
	1982	0	0	23	85	0	108(22)
	1983	4	0	0	0	10	14(8)
	Total	4	0	36	150	28	218(18)
CALF	1979	—	0	0	0	4	4(2)
	1980	—	—	0	0	2	2(4)
	1981	—	0	0	2	2	4(1)
	1982	8	5	6	0	2	21(4)
	1983	0	2	4	3	6	15(9)
	Total	8	7	10	5	16	46(4)
DISPLAY	1979	—	0	0	0	1	1(0)
	1980	—	—	0	0	0	0(0)
	1981	—	0	0	0	0	0(0)
	1982	0	2	7	12	1	22(4)
	1983	8	0	7	7	2	24(14)
	Total	8	2	14	19	4	47(4)
NONE	1979	—	0	0	6	52	58(29)
	1980	—	—	0	0	0	0(0)
	1981	—	0	2	26	8	36(13)
	1982	0	0	0	4	0	4(1)
	1983	0	0	0	0	0	0(0)
	Total	0	0	2	36	60	98(8)
TOTAL	1979	—	7	2	58	130	197(17)
	1980	—	—	12	22	12	46(4)
	1981	—	2	70	162	54	288(24)
	1982	107	37	54	249	43	490(41)
	1983	49	10	24	54	35	172(14)
Grand Total (%)		156(13)	56(5)	162(13)	545(46)	274(23)	1193(100)

Thus, the derived GARR (Table 12) and the GARR/survey hour (Fig. 13) represent only the observed portion of the bowhead population in the Alaskan Beaufort Sea during the stated time period.

Behavior and sound production

The predominant behavior of bowheads throughout the fall was active migration 57% (Table 13). Approximately 9% of all whales seen were resting, 18% were feeding, 4% exhibited cow–calf behavior and 4% were displaying. None were observed mating in the fall season. The highest proportion of feeding whales were seen in mid to late September. Observation of cow–calf interactions coincided with peak sighting periods of mid to late August and early October. Displays and resting behaviors were seen across all time periods.

The average group size, excluding solitary whales, was 2.86 ± 1.55 s.d. ($n = 249$; Table 14). There was no difference in group size among the time intervals ($t = 0.81$, $p \leq 0.5$) except between late September ($\bar{x} = 3.62 \pm 2.51$ s.d.) and October ($\bar{x} = 2.52 \pm 1.02$ s.d., $t = 3.43$, $p \leq 0.001$). Large groups of socializing or feeding whales were noted in September while smaller, more migrational groups were encountered in October. Solitary whales were observed relatively equally throughout the season and in all years.

Table 14

Bimonthly summary of bowhead average group size, fall 1979–83

	1–15 Aug $\bar{x}$ ± s.d. (n)	15–31 Aug $\bar{x}$ ± s.d. (n)	1–15 Sept $\bar{x}$ ± s.d. (n)	16–30 Sept $\bar{x}$ ± s.d. (n)	1–20 Oct $\bar{x}$ ± s.d. (n)	TOTAL $\bar{x}$ ± s.d. (n)
1979	—	1.50 ± 0.71 (2)	—	3.70 ± 2.36 (20)	2.50 ± 1.02 (24)	3.00 ± 1.81 (46)
1980	—	—	2.50 ± 0.71 (2)	2.75 ± 0.96 (4)	2.00 ± 0.0 (3)	2.44 ± 0.73 (9)
1981	—	2.0 (1)	3.70 ± 2.6 (20)	2.42 ± 0.72 (24)	3.00 ± 1.47 (14)	3.00 ± 0.81 (59)
1982	3.13 ± 2.05 (24)	2.89 ± 2.32 (9)	3.07 ± 1.73 (14)	4.67 ± 3.08 (43)	2.45 ± 0.69 (11)	3.68 ± 2.57 (101)
1983	3.67 ± 1.0 (9)	2.50 ± 0.71 (2)	2.25 ± 0.50 (4)	2.30 ± 0.67 (10)	2.10 ± 0.32 (10)	2.60 ± 0.91 (35)
Total	3.27 ± 1.82 (33)	2.77 ± 1.92 (14)	3.28 ± 2.14 (40)	3.62 ± 2.51 (101)	2.52 ± 1.02 (62)	2.86 ± 1.55 (250)

(n) = number of groups of two or more whales.

The only significant differences in group size among years were between 1982 ($\bar{x} = 3.68 \pm 2.57$ s.d.), a light-ice year with a relatively high mean group size, and the heavy-ice years 1980 ($\bar{x} = 2.44 \pm 0.73$ s.d., $t = 3.44$, $p \leq 0.001$) and 1983 ($\bar{x} = 2.60 \pm 0.91$ s.d., $t = 3.60$, $p \leq 0.001$). More whales were actively migrating and not aggregated in groups in the heavier ice years.

Sounds recorded near bowheads in fall 1982 and 1983 have been aurally analysed as described for spring samples (Moore *et al.*, 1983). As in spring samples, this initial analysis has indicated some differential call production when data from different recording circumstances are compared, although significant correlation with observed surface behaviors has not been found. Some intriguing results of aural analysis have been the identification of several call sequences and notation of several unusual, rarely recorded calls. A complete analysis of all bowheads sounds recorded between 1979 and 1983 might yield a classification scheme that would enhance the utility of bioacoustic data as a behavior monitoring and population assessment tool.

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GRAY WHALE MIGRATORY, SOCIAL AND BREEDING BEHAVIOR

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ABSTRACT

The recovery of the Chukchi-California stock of gray whales from depletion and the species unique coastal habits make it relatively accessible for study, and numerous studies of living whales have contributed new behavioral information from various portions of the gray whale's range. This paper reviews the findings of recent demographic and behavioral studies regarding gray whale migration, natural history, social behavior and mating system. Their annual polar-to-semi-tropical migration occurs along the eastern Pacific coast of North America and brings the whales in contact with a variety of prey species which is reflected in the diversity of the whale's diets. During the fall southward migration the whales travel 7,602 km between the Arctic and Baja California in approximately 66 days at a rate of 4.8 km/hr. Their migration rate between the Arctic and Monterey is approximately 7.1 km/h, while their rate between Monterey and the breeding lagoon of San Ignacio is approximately 2.2 km/h or 31% as fast as the first leg of the migration. An apparent overlap of southward and northward migrating whales may account for this slowing and suggests that only a proportion of the population occupies the coastal waters of Baja California at any time while the remainder are distributed throughout the Southern California Bight and elsewhere. The departure of whales from the southern range appears to be segregated according to age, sex and reproductive condition, and is bimodal. Whales without calves lead the spring northward migration and travel more rapidly than females with calves. The majority of females with calves depart later in the spring and their northward migration is more protracted; thus, female whales spend more time in the winter range in years in which they give birth to calves, and they would spend less time on the summer feeding grounds. Courting whales were most abundant in San Ignacio lagoon in January and February, and there was a rapid exchange of these animals with lengths of stay between 1 and 4 weeks. Females with calves remained up to 13 weeks in the lagoon and some circulated between different lagoons both within and between years. Female-calf pairs avoided courting whales in San Ignacio resulting in a spatial and temporal segregation between these two groups. Courting activities were primarily concentrated in the area nearest the inlet, while females and calves utilized the interior areas farthest from the sea as nurseries. With the departure of courting whales, female-calf pairs abandoned the lagoon interior and shifted their distribution to the inlet areas. The calving period ranged approximately 66 days with a mean birth date around 27 January. Calving periodicity for 30 females ranged from annual to two years between calves, and their mimimum birth rate weas 0.50 to 0.55 calves/females/yr. Given that most females reproduce biennially, they would alternate between a longer period on the summer range feeding when newly pregnant and a shorter period on the summer range when lactating. The logic and evidence for opportunistic feeding by late migrating whales to compensate for less time spent on the summer range is discussed. The segregation of gray whales into two groups, females with calves and other whales, is suggestive of their behavioral incompatibility and appears prominent during migration, on the winter grounds, and apparently on the Arctic summer grounds. The early development of calves in San Ignacio lagoon included imprinting on their mothers, mimicry of adult behaviors, and socialization with other calves and adults. Adult gray whales demonstrated epimeletic or care giving behavior toward unrelated calves. Mating groups were fluid and involved up to 32 individual animals. These groups were characterized by high speed chases interrupted by mating bouts that lasted up to four hours. Adult males and females mated with more than one partner during the same season, and males did not appear to compete for females. Sperm competition in gray whales may account for the lack of obvious male–male competition and sexual selection in this species.

INTRODUCTION

During the past four decades, the eastern Pacific or Chukchi-California stock of gray whales (*Eschrichtius robustus*) has demonstrated a remarkable recovery from severe depletion by modern whalers (Reilly, 1981) and has become the best studied group of baleen whales. This population makes an extensive migration each year between its major summer feeding grounds in the Bering, Chukchi and Beaufort Seas and its winter breeding grounds in the near-shore waters, bays and lagoons of Southern California, Baja California and to some extent the Gulf of California. Compared to more pelagic species, the gray whale's unique coastal habits throughout most of its range make it relatively accessible for study. Consequently, more is known about these whales than any other mysticete. Until relatively recently, however, information on gray whale distribution and behavior was based on observations of a depleted stock, and many important aspects of gray whale migratory, social and breeding behavior remained little known.

The first description of the migration and natural history of the gray whale was written by the American whaling captain Charles M. Scammon (1874) and based on his observations of the whales on their summer feeding grounds, along their migration routes and during their winter occupation of the breeding lagoons. Not until 1947 and with the slow recovery of the stock from depletion did scientists begin to show interest in this cetacean. A series of short-term aerial surveys to monitor the winter abundance of whales in Baja California was conducted by Gilmore (1960), Hubbs and Hubbs (1967) and Gard (1978). These studies clearly showed that the gray whale population was increasing, and prompted additional investigations.

Between 1959 and 1969 Rice and Wolman (1971) examined 316 gray whales taken by whalers along the central California coast. Their analysis of these specimens contributed to the study of gray whale reproductive physiology and migration timing. Within the past decade detailed non-consumptive studies of the winter abundance and behavior of gray whales have been conducted in Laguna San Ignacio (Swartz and Jones, 1979; 1980; 1981, 1983; Jones and Swartz, 1984a), Laguna Ojo de Liebre (White, 1975; Rice *et al.*, 1981; Fleischer and Carlson, 1981; Fleischer *et al.*, 1984), Laguna Guerrero Negro (Bryant, 1980 Bryant *et al.*, 1981, 1984), Bahia Magdalena (Norris *et al.*, 1977, 1983; Lawson, 1984; Fliescher *et al.*, 1984) and the Gulf of California (Findley and Vidal, 1982). Additional studies by Soviet scientists on the summer feeding grounds (e.g. Zimushko and Ivashin, 1980; Blokhin, 1984, 1986; Yablokov and Bogoslovskaya, 1984) and by Canadian and American investigators along the migration route (Jones *et al.*, 1984) have contributed new information that enables a preliminary synthesis of gray whale migration and behavior following the recovery of the stock.

In this paper I review the findings of recent demographic and behavioral studies of gray whales (*Eschrichtius robustus*) in the breeding lagoons of Baja California along with observations of gray whales throughout their range, and present a preliminary synthesis of their natural history, migration, social behavior and mating system in light of recent theories on the evolution of the social structure of mysticetes.

MIGRATION

The migrations of mysticete whales are thought to have arisen as an evolutionary response to the seasonal production of prey in the Antarctic and Arctic seas (Lipps and Mitchell, 1976). The paleontological records indicate that the relatively mild temperatures of the world's seas changed radically with the breakup of the super-continent of Pangea and the resulting changes in the circulation patterns of the oceans. The creation of mountain ranges radically affected regional temperatures, wind patterns and rainfall on a world wide scale. When temperatures dropped and seasons became more pronounced in the late Miocene and early Pleistocene, marine organisms such as plankton, fish and squid must have changed both qualitatively and quantitatively. Predators on these organisms, for example the early cetaceans, were also affected. Presumably, early cetaceans were able to exploit local perennial sources of prey. However, coincident with these geologic changes, their prey species became seasonal and their distributions more specific. Thus, seasonal movements of certain marine mammals tracked those of their prey, and may have been the origins of today's migration routes (Scheffer, 1976).

Seasonally predictable sources of food shaped the life history of baleen whales into two periods: summers when animals feed in the higher latitudes when food is abundant and the weather reasonable for an aquatic mammal; and winters when whales migrate to the lower latitudes to escape inclement weather and to reproduce in warmer waters that are more conducive to the rearing of calves and mating. These lower latitudes, however, generally do not afford the high standing crop of prey found in the polar seas, and thus baleen whales also evolved an energy storage strategy whereby they fast during their reproductive period and survive on stored energy reserves in the form of body fats accumulated during summer feeding (Slijper, 1976; Matthews, 1978). Although the gray whale's migration is typical of baleen whales, its coastal habits have resulted in some modifications of the general mysticete life history pattern which appear unique to this species.

Gray whales participate in an annual polar-to-semi-tropical winter migration, but, unlike the more pelagic species that migrate across vast deep ocean basins which offer little food, they migrate along the coast of North America where upwellings of nutrient rich waters drive some of the world's most productive marine ecosystems. Thus, except perhaps in the southernmost portion of their range, the gray whale's migration brings them into contact with a wide variety of prey species. Analysis of stomach contents confirms that gray whales consume numerous kinds of prey (Nerini, 1984), and that they are capable of feeding off the bottom, in the water column and by surface skimming (Rice and Wolman, 1971, Swartz and Jones, 1981; Oliver *et al.*, 1984; Wursig *et al.*, 1984). The gray whales' association with the rich coastal ecosystems along the Pacific coast of North America that provide a variety of resources throughout virtually the entire year has no doubt contributed to their resiliency as a species and their remarkable recovery from depletion (e.g. see Reilly, 1984b).

The coastal migration of the gray whale in the eastern North Pacific has been described by numerous investigators including Scammon (1874), Gilmore (1960), Pike (1962) and Rice and Wolman (1971), and is one of the best known movements of all the large cetaceans. Recent studies throughout the range of this, the Chukchi-California, stock have provided detailed information on the timing of the fall (southerly) and spring (northerly) migrations at specific locations along the migration route (Jones *et al.*, 1984). Shore based censuses provide daily counts of the number of whales passing each location, and from these the distribution and rate of movement of the population during migration may be inferred. The distribution of the gray whale population during migration may be visualized as a bell-shaped curve that moves along the migration route at a particular rate. For the purposes of describing the timing of the migration, I have chosen to use the day with the greatest number of whales counted at a census station as an index of the average date that the population passes that location. In cases where more than one year of counts were available, I have used the mean day of the peak counts as the average date of passage.

Fall southward migration

Gray whales are commonly found in the Bering and Chukchi Sea feeding grounds between June and October (Rice and Wolman, 1971) with some remaining in feeding areas off the Soviet Coast of Chukotka as late as November (Blokhin, 1984; 1986). By mid-August gray whales seen near Barrow, Alaska are predominantly moving south (Braham, 1984; Moore and Ljungblad, 1984), and by late October southward migrating whales begin to arrive at Unimak Pass where they leave the Bering Sea (Fig. 1). The mean date of the peak counts of whales passing through Unimak Pass, Alaska, between 1977 and 1979 was 5 December (Rugh, 1984). From Alaska, southbound gray whale migrants pass Vancouver Island, British Columbia from November to late January with peak numbers passing during the last two weeks in December (Darling, 1984).

The first southward migrants past Newport, Oregon are observed in early December with maximum numbers passing during the first week in January. The average mean day of the southward migration between 1978 and 1981 was 6 January, after which counts declined until by early February few whales were seen until the onset of the northward migration (Herzing and Mate, 1984). During this first leg of their southerly migration the population travels approximately 4,815 km between Unimak Pass and Newport in 32 days (based on dates of peak counts)—an average rate of 6.3 km/h.

Southward migrating gray whales begin to pass Monterey, California as early as late-November, although these early arrivals may represent animals that spend the summer along the Pacific coast of Canada (Darling, 1984), Washington (Braham, 1984), Oregon (Herzing and Mate, 1984) and northern California (Dohl, 1979), and reach central California in addition to those that have travelled from the Bering Sea through Unimak Pass. Censuses conducted at Monterey by the National Marine Fisheries Service between 1967 and 1980 obtained peak numbers of passing whales during the second week in January (Reilly *et al.*, 1983). The mean peak count date for the southward migration during these 13 consecutive censuses was 9 January, after which counts of southbound whales declined until the first northward migrants were observed during the first week in February (Reilly, 1981). Gray whales begin to arrive at the breeding lagoons in December, and reach maximum abundance there in early February. Peak counts of whales were obtained around 10 February in Laguna Guerrero Negro between 1980 and 1982 (Bryant *et al.*, 1984), around 15 February in Laguna Ojo de Liebre between 1980 and 1981 (Rice *et al.*, 1981; 1983), around 15 February in Laguna San Ignacio between 1978 and 1982 (Jones and Swartz, 1984a), and between 7 and 10 February in northern Magdalena Bay between 1982 and 1985 (Lawson, 1983; Fleischer *et al.*, 1985). If 9 February is used as an index of the average date of maximum counts at the lagoons, it appears that the whales travel the 1,657 km between Monterey and Baja California in approximately 31 days at 2.2 km/h, or about 31% as fast as their migration rate between Unimak Pass and Monterey. The reason for this reduced migration rate through southern and Baja California is not understood. The whale's overall southward migration rate between Alaska and the breeding grounds would be 4.8 km/h, or 7,602 km in approximately 66 days.

Fig. 1. Range and migration route of the Chukchi–California stock of gray whales along the eastern Pacific coast of North America.

The timing of the gray whale migration south of Point Conception raises some interesting points that have yet to be adequately studied. For example, between Alaska and Monterey the population is travelling at approximately 7 km/h and passes during a period of 4 to 6 weeks. Travelling at this rate, the population would be distributed over approximately 4,700 to 7,100 km of coastline, the majority of the west coast of North America. As the whales move south they apparently slow down, and by the time the last of the southward migrants reach the central California coast in early February, they begin to overlap with the first of the northward migrants leaving the southern range (Reilly, 1981; Poole, 1984; Herzing and Mate, 1984). This overlap suggests that only a proportion of the migrating whales are in Mexican waters during the winter while the remainder are distributed throughout the Southern California Bight and to some extent the migratory corridor along the Central California coast.

Evidence in support of this mixing of southward and northward migrants in the Southern California Bight comes from several sources. As early as 1950 the late Carl L. Hubbs reported three female–calf pairs in the kelp off Isla Guadalupe in April (Gilmore, 1955). Rice (1965) discussed the offshore southward migration of gray whales off Southern California and noted that an undetermined proportion of the population migrated beyond sight of the Point Loma (San Diego) census station. Gilmore (1969) concluded that south of Point Conception, California, the migration divided with some whales taking the 'inter-island leg', and later returning to the coast below Ensenada, Mexico. The most convincing evidence that significant numbers of gray whales occur in the Southern California Bight during the winter comes from aerial surveys conducted by Leatherwood (1974) and Dohl (1979) who observed migrating gray whales 80 to 160 km from shore with the same relative frequency as within 80 km of shore. Finally, the discrepancy between the National Marine Fisheries Service population estimates from shore based counts in 1980 of approximately 16,000 whales (Reilly *et al.*, 1983) and estimates of 7,600 whales counted in the breeding lagoons and coastal waters of Baja California in mid-February of the same year (Rice *et al.*, 1981) could be the result of more migrating whales being distributed north of the Mexican border than had been previously assumed. The difference between these estimates, approximately 8,400 whales, is probably a reasonable estimate of the proportion of the population in the Southern California Bight in February.

The spring northward migration

The departure of gray whales from the southern range appears to be segregated according to age, sex and reproductive condition. Vessel censuses and aerial surveys of the breeding lagoons indicate that the departure of females with calves occurs after the departure of whales without calves, and is more protracted. For example, although maximum counts of female-calf pairs were obtained in mid-February in Laguna Guerrero Negro (Bryant *et al.*, 1984), Laguna Ojo de Liebre (Rice *et al.*, 1981; 1983), and in northern Bahia Magdalena (Lawson, 1983; Fleischer *et al.*, 1985), counts of female-calf pairs in Laguna San Ignacio increased steadily throughout the winter and reached peak numbers in late-March or early-April with a 5-year mean peak day of 19 March (Jones and Swartz, 1984a). Vessel counts in San Ignacio between 1978 and 1982 indicated that after mid-March the lagoon is occupied by female-calf pairs alone, and that some of these remain until late-April and early-May of some years. From these data, Jones and Swartz (1984a) estimated that female-calf pairs may remain in the lagoon 1 to 1.5 months longer than whales without calves.

Rice and Wolman (1971) also found that in both the southward and northward migration, mature females migrate earlier than males, and adults migrate earlier than sexually immature animals. Near-term pregnant females lead the southward migration, but following the birth of their calves, these females are the last group of whales to leave the winter range. Newly pregnant females comprise the first northward migrants past central California in mid-February, and they are followed approximately two weeks later by adult males, anestrous females and immatures of both sexes (Rice and Wolman, 1971).

In 1980 and 1981 a shore based census was taken of northward migrating gray whales at Pt Piedras Blancas, California (Poole, 1983) which indicated the northward migration to be bimodal, consisting of two distinct pulses of whales temporally spaced and comprising two distinct groups: whales without calves and female–calf pairs. The first pulse, Phase A, occurring during February and March, comprised whales without calves passing 1 to 2 km offshore, and had a mean peak passage date of 1 March. This suggests that these whales travelled the 1,472 km in 20 days following their 9 February mean peak day in the lagoon at an average rate of 3.1 km/h.

The second pulse, Phase B, occurring from late March to mid-May, consisted primarily of females with calves of the year passing within 1 km of shore, and had a mean date of peak passage of 26 April. If maximum counts of female-calf pairs occur in the lagoons from mid-February to mid-March, their rate of migration to Piedras Blancas would range from 0.9 km/h (15 February departure) to 1.6 km/h (19 March departure). Compared to single whales, this slower rate of movement is undoubtedly due to the presence of the calf, its need to nurse, and probably opportunistic feeding by the female as she encounters food along the migratory route. There are a few scattered reports of female–calf pairs feeding during the northward migration (Mate and Harvey, 1984; Malme *et al.*, 1984; Leatherwood, pers. comm.), but additional data will be required to verify the utilization of food resources by females with calves during their northward migration, and to determine to what extent lactating females rely on food resources in this portion of their range.

The first northward migrants to pass Newport, Oregon (between 1978–79 and 1980–81 winters) were seen during the last week in February, just a few days after the last of the southward migrants were counted (Herzing and Mate, 1984). The first group, or Phase A, was composed entirely of whales without calves and counts of these whales peaked around 15 March, declining to zero by the end of April. Phase A whales had thus travelled the 2,787 km from the lagoons in 34 days averaging 3.4 km/h. The second group of northward migrants was primarily females with calves of the year, Phase B, and were first seen passing in late March. Maximum counts of these whales were obtained by 10 May, declining to near zero by June, and thus suggesting that Phase B female–calf pairs travelled the distance from the lagoons to Oregon in 52–84 days at average rates of 1.4–2.2 km/h.

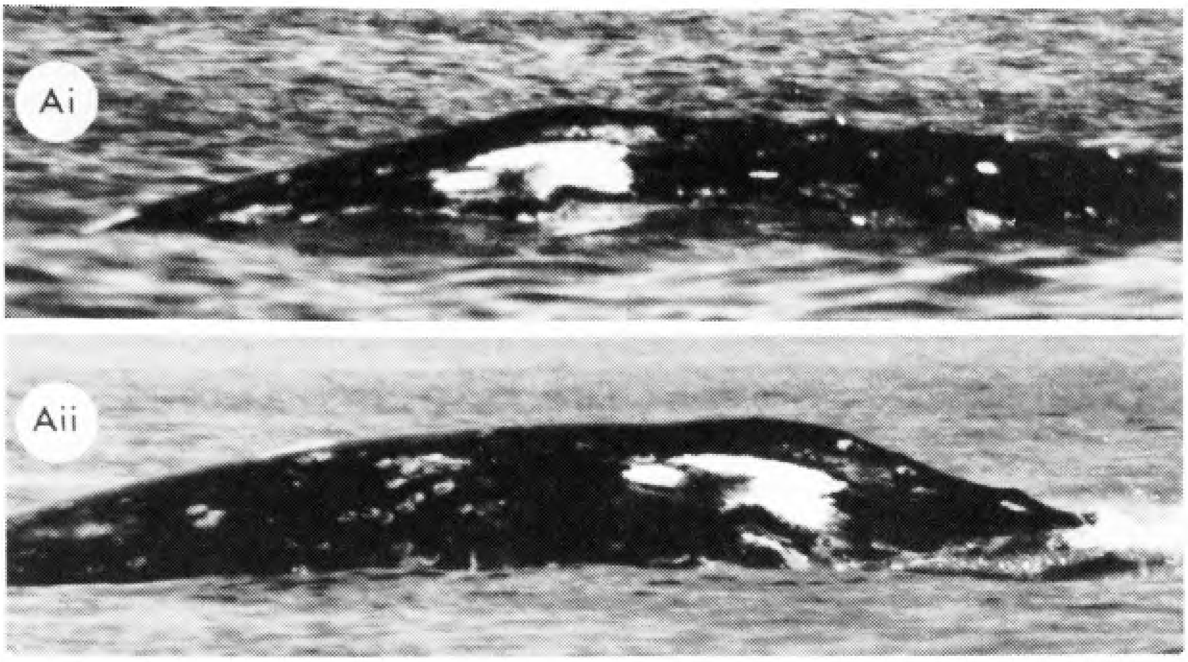
If the two groups of whales maintained their northward migration rates, the peaks of Phase A whales would reach Unimak Pass, Alaska on 13 May, approximately 59 days after they passed Newport, Oregon, and Phase B female–calf pairs around 9 August, approximately 91 days after passing Newport. These estimated rates are corroborated by the following field observations. First, a single whale without a calf radio-tagged in Laguna San Ignacio reached Unimak Pass, Alaska 95 days after its radio signal was last received in the lagoon (Mate and Harvey, 1984), and thus averaged 3.4 km/h for 3.2 months during its northward migration. In addition, the arrival of northbound spring migrants at Unimak Pass begins in late March and reaches its peak around 5 May. Hessing (1981) observed two phases to the northward migration of gray whales through Unimak Pass between 23 March and 17 June in 1981. Although all sizes of whales were observed throughout her study, no females with calves were seen until May, and female–calf pair counts continued to increase until mid-June when her study was terminated. The duration of the female-calf pair spring migration thus remains unknown.

The segregation between Phase A and B northward migrating gray whales supports the concept that gray whales behave as two distinct groups, with females alternating between two migration timetables. Females with calves travel more slowly than females without calves (anestrous and newly pregnant) during the northward spring migration, and subsequently have less time to spend feeding on the summer grounds. Based on the migration rates estimated above, the interval between summers on the Arctic feeding grounds would be approximately 5.1 months for newly pregnant females (as well as males and juveniles) and 8.5 months for females with calves that remain in the lagoons longer and whose departure from the southern range is more protracted than that of the single whales. This yields a summer feeding period of 6.9 months for newly pregnant females and only 3.5 months for females that had given birth to a calf the previous winter.

OCCUPATION OF BREEDING LAGOONS

The overall seasonal abundance of gray whales within the breeding lagoons of Baja California, Mexico can be divided into two periods. The first is the period of maximum gray whale abundance in the lagoons and occurs during the first half of each winter. At this time the population is composed of courting whales without calves (males, mature females, and immatures) and females with newborn calves. The second period occurs during the latter half of the winter after the departure of whales without calves from the lagoon when the lagoon populations are composed entirely of female–calf pairs. In this section I will describe the timetable of occupation for Laguna San Ignacio as being representative of the occupation of other major breeding lagoons.

The abundance of courting whales (whales without calves) increases rapidly during a six week period from the last week in December through the second week in February. Maximum counts of these animals in the lagoon occur in mid-February, after which their numbers decline as they begin their spring northward migration. Courting whales are encountered in the lagoon for approximately three months, but there appears to be a substantial turnover rate. Evidence for a rapid exchange of courting whales through the lagoons during each season comes from a photographic identification study between 1977 and 1982 (Jones and Swartz, 1984a) (Fig. 2), and shore-based observations of the main entry channel of San Ignacio lagoon in 1982. The photographic identification results revealed that 81% of the courting whales photographed in Laguna San Ignacio remained there for one week or less (Jones, 1985). In addition, the fact that two of these whales photographed by D. Withrow (National Marine Mammal Laboratory, pers. comm.) in Laguna Ojo de Liebre were re-sighted approximately one week later in Laguna San Ignacio suggests the possibility of a relatively rapid circulation of courting whales between breeding areas (Jones and Swartz, 1984a). Finally, counts of whales moving through the inlet of San Ignacio demonstrated that substantial numbers of single whales enter and exit the lagoon every day. For example, at the time of the maximum counts in 1982, when 270 whales were counted within the lagoon, a minimum of 341 others entered and 185 left the lagoon during a seven hour daylight period. Because the majority of the adult



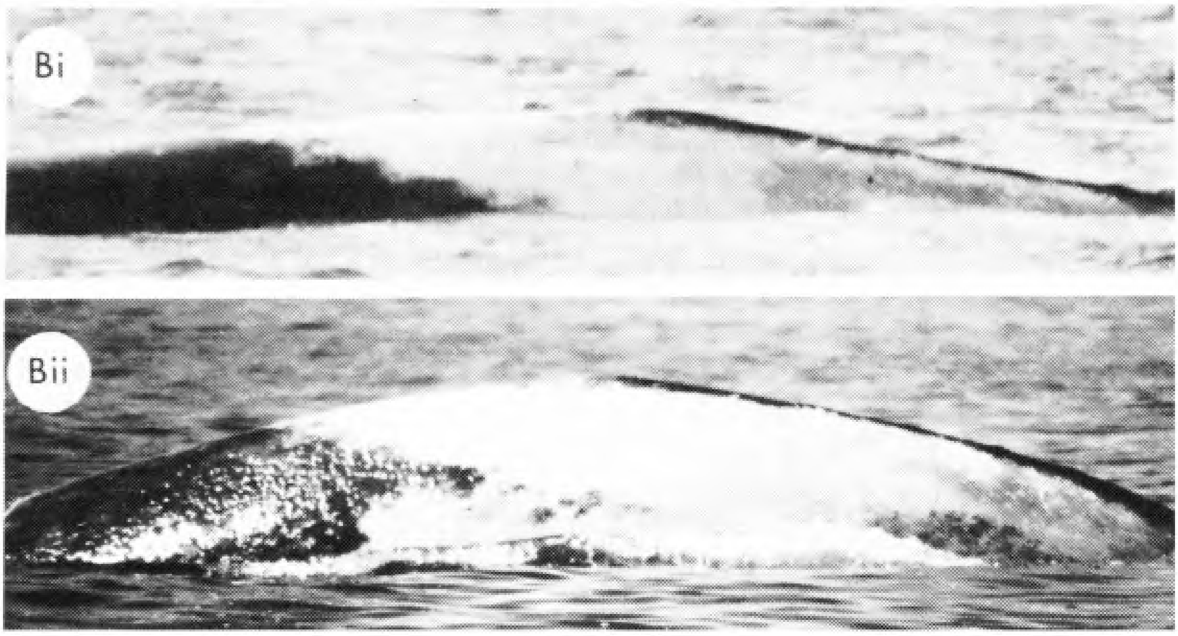


Fig. 2A. A female gray whale photographed during the 1976–77 winter in San Ignacio lagoon (i), and again during the 1978–79 winter (ii). This whale was re-photographed on 12 January 1986 during the southward migration off Monterey, California.

Fig. 2B. A female gray whale with extenhsive white areas on her tail. This whale was first photographed during the 1976–77 winter in San Ignacio Lagoon (i), and re-photographed each winter until 1981–82 (ii). During this six year period she produced three calves.

whales present in the inlet throughout the winter were actively transiting and their movement was independent of the tides, counts of these whales through the inlet were indicative of a real exchange of animals rather than being repeat counts of the same individuals passively moving into and out of the lagoon with the tide.

The pattern of female–calf pair abundance is more complex and they remain longer in the lagoon. The abundance of females with calves of the year increases continuously between early January and mid-February as whales arrive in the lagoon and as calves are born. Following the end of the birth period, some females circulate with their calves between the breeding lagoons prior to departing from the winter range (Jones, 1985). Although arriving at about the same time as the courting whales in the lagoons, the departure of cow–calf pairs is more protracted than that of the courting whales, and continues all spring with some females and their calves remaining within the southern range until the end of April and early May of some years (Jones and Swartz, 1984a). Thus, the duration of the female–calf season in the lagoon can be as long as 4 to 4.5 months.

In San Ignacio, but apparently not in other lagoons, numerous females and calves congregate and reach peak abundance in March and April, indicating that this lagoon may serve as a staging area for female–calf pairs prior to their departure from the southern range. There are two sources of evidence supporting this idea. First is the observation that this late season influx is not due to continued births, for these late season females have calves that are approximately two to three months old (Swartz and Jones, 1981). Second, the results of the six year photographic identification study, in combination with a three year program in Laguna Guerrero Negro by Bryant and co-workers, a two year study by the National Marine Fisheries Service in Laguna Ojo de Liebre, and a one year project in Boca de Soledad by Lawson (1983), revealed that some female with older calves were immigrating to Laguna San Ignacio after leaving these breeding areas (Jones, 1985; pers. comm.).

Prior to the extension of photographic identification studies to other breeding areas, investigators had speculated that the late season influx of whales consisted of females with calves that were moving northward from areas south of San Ignacio, e.g. Bahia Magdalena (Swartz and Jones, 1979; Rice *et al.*, 1981). This is only partly true. In addition to northbound immigrants, some females with calves photographed early in the season in more northerly lagoons (e.g. Laguna Guerrero Negro and Laguna Ojo de Liebre) vacated these areas and moved south to Laguna San Ignacio late in the season (Jones, 1985). Some females radio-tagged in Laguna San Ignacio (Harvey and Mate, 1984) and in Bahia Magdalena (Norris *et al.*, 1977) also moved south after leaving the areas in which they were tagged.

DISTRIBUTION WITHIN THE BREEDING LAGOONS

Although the lagoons of Baja California are important areas for both courting whales and females with calves, these two groups utilize them quite differently. As whales enter Laguna San Ignacio, they become segregated spatially and temporally such that their distribution, gross movement and timetable of occupation differs. Courting whales are found at highest densities near the lagoon inlets and their density then decreases with increasing distance from the inlet. The courting whales' preference for the lower lagoons may be related to ease of access to (1) the relatively deep and wide channels that characterize these areas and remain unrestricted even at low tides or, (2) to the open ocean, or (3) both. While in these areas, these whales are predominantly engaged in social activities associated with courtship and mating. Most female–calf pairs are concentrated in the inner lagoon nurseries farthest from the open sea (Swartz and Jones, 1981; Jones and Swartz, 1984a). Mothers and calves in the inner lagoon are primarily engaged in the tranquil activities of resting, nursing and moving about with the changing tides. Moreover, the nursery furthest from the inlet provides an area of relative solitude for the females following parturition and during early calf development.

This localization of courting whales in the inlet and outer lagoon region of San Ignacio and the preponderance of female–calf pairs within the lagoon is a feature found in other breeding areas. Scammon (1874) wrote '. . . the cows enter the lagoons on the lower (Baja) coast to bring forth their young, while males patrol outside along the sea shore'. Gilmore (1960) reported that lone adults, courting adults and juveniles predominate at the entrances to Laguna Ojo de Liebre and Bahia Magdalena, and suggested that courting and mating are the primary activities of the whales in these areas. In addition, Samaras (1974) stated that adult male and female gray whales use the inlet of Laguna Ojo de Liebre as a staging area for precopulatory behavior, while pregnant females occupy the inner lagoon calving area. Norris *et al.* (1983), who studied lagoon entrance aggregations of gray whales at La Entrada (the main entrance to Bahia Magdalena) and Canal Rehusa (the entrance of the southernmost calving lagoons at Bahia Almejas and Santa Maria), reported that they were composed entirely of males, nonparturient females and juveniles, whose primary behaviors appeared to be courtship, mating and possibly feeding. Although, Bryant *et al.* (1984) described Laguna Guerrero Negro as hosting very few courting whales with no apparent aggregations in the area nearest the inlet, they noted that this lagoon did not have any deep-water areas comparable to those in the larger breeding lagoons. They further remarked that a large number of courting whales were observed in the deep-water area just offshore. This finding, then, is similar to the distribution of courting whales seen in other breeding areas.

Following the period of combined maximum counts, and with the gradual departure of courting whales from the lagoons, females and calves gradually shift their distribution to the outer lagoons and inlets, essentially abandoning the nurseries. The trend for female–calf pairs to occupy the area nearest the sea following the end of the birth period and the departure of courting whales from the lagoons suggests that females prefer these areas when their calves are 2–3 months old. Scammon (1874) and Norris *et al.* (1977) interpreted this shift as being the first stage of the migration preparatory to leaving the lagoons.

FEMALE BREEDING STRATEGIES

Photographic records of 30 females and 15 whales of unconfirmed sex (but presumed to be males) collected between 1977 and 1982 provided data on reproductive behavior and vital rates of females in Laguna San Ignacio. In her analysis of these photographs, Jones (1985) found a range of birth dates from 26 December to 1 March, suggesting a 66-day minimum calving period with a mean birth date of 27 January (Rice and Wolman, 1971). Calving periodicity ranged from annual (one instance) to a two year resting period between calves. Overall, 30 females produced 55 to 58 calves over the six year study to yield a minimum realized birth rate of 0.50 to 0.55 calves per female per year. Thus, most females produce a calf every other year, which is comparable to estimates of the pregnancy rate of 0.46 per year (Rice and Wolman, 1971) and 0.467 (Reilly, 1984a) from studies of whales taken by the Soviet whale fishery.

Jones (1985) analysis of photographs from Laguna San Ignacio confirmed that adult female gray whales alternate between two behavioral strategies; longer stays in the lagoon when nursing, and shorter visits as courting whales in non-calving years. The longest period between first and last sightings within one season of a known female without a calf was three weeks, and of a female-calf pair was 13 weeks. Her data suggested a minimum of three patterns of lagoon occupation for breeding females: 'residents' consisted of females which were photographed for long periods during calving years, and for short periods early in the season in non-calving years; 'transients' included females with older calves which emigrated to the lagoon from other areas late in the season for a short period, and were responsible for the late-season maximum female-calf pair counts in this lagoon; and the third pattern (a combination of resident and transient) was of females photographed with a calf during a long period throughout a season in calving years, for a short period early in the season in non-calving years, and with an older calf for a short period late in the season in calving years. Finally, re-sightings in other breeding lagoons of whales photographed in Laguna San Ignacio demonstrated that some females utilized different calving lagoons in different years, some females changed lagoon areas within the same year (as with late season immigrants) and that males visited more than one breeding lagoon within a winter.

If gray whales cease feeding when they leave the Arctic, courting females would not feed for approximately five months between the beginning of their southern migration in November and their return, as pregnant females, to the summer range in May. They would spend approximately seven months on the summer grounds feeding extensively to develop food reserves in the form of body fat. For newly pregnant females these 'stores' would nurture the developing fetus and provide energy reserves for lactation and body maintenance of the female following the birth of her calf. After giving birth, mothers would spend only four months feeding on the summer range, in contrast to newly pregnant females. Having left the summer grounds in November as near-term females, they would have given birth sometime during January and February, remained in the winter range until April or May when they would have migrated northward with their calves and reached the summer range in August, approximately nine months after their departure the previous fall (Fig. 3).

The duration of stay of gray whales in the lagoons has important implications in terms of their energetic requirements, particularly for lactating females. Because courting whales leave the breeding areas approximately one month earlier than the majority of the female–calf pairs, they presumably arrive on the summer feeding grounds earlier and spend more time there than females that give birth to calves during the same year (Rice and Wolman, 1971). Given that gray whale females normally reproduce biennially, this suggests that adult females would alternate between a longer period on the summer range feeding when newly pregnant and a shorter period on the summer range when lactating. Males, however, would be able to spend the same amount of time feeding on the summer range each year. For newly pregnant females, this extra summer feeding time is of obvious energetic significance related to their need to acquire more fat reserves for the gestation of a calf and a 6 to 8 month lactation peiod. Females with calves, on the other hand, would have to feed more extensively during a shorter period of time to meet both their own energetic maintenance cost and that of their calves.

It is possible that females that do not feed outside the summer range may be energetically stressed following their southern migration, parturition and lactation during the northward migration. Opportunistic feeding during the spring northward migration could serve to augment their reduced feeding period on the

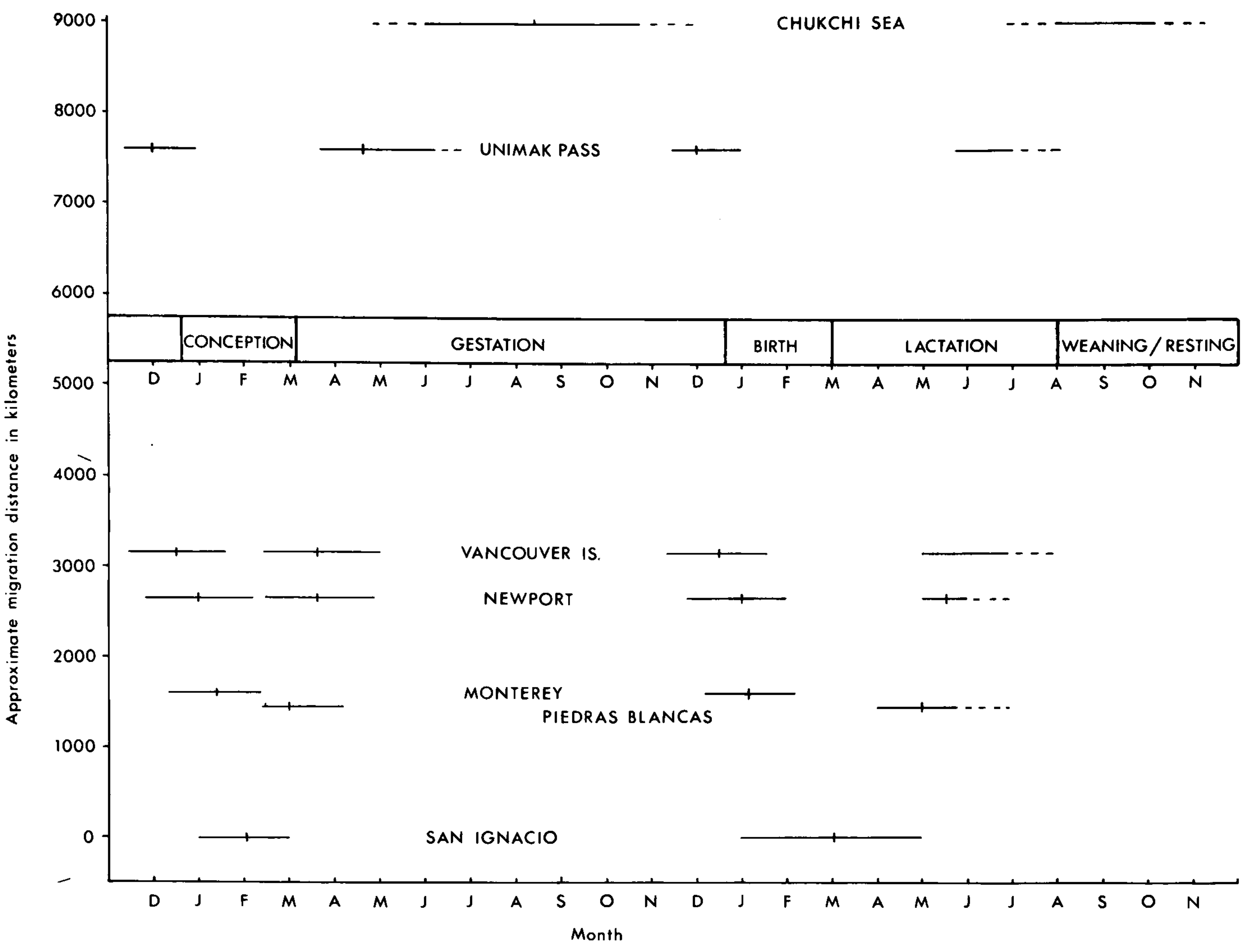


Fig. 3. The distribution of female gray whales of the Chukchi–California stock during their two year reproductive cycle. Horizontal lines represent the range of sighting dates during southward (fall) and northward (spring) migration for each location. Vertical bars indicate mean date of passage at a specific location. Broken lines indicate probable occurrence.

summer range in calving years and could help to explain the protracted departure of these whales from the southern range, and their slow rate of movement through the Southern California Bight. Evidence of opportunistic feeding by gray whales has been obtained by Swartz and Jones (1981), Norris *et al.* (1983), Mate and Harvey (1984) for Baja California; by Darling (1977, 1984), Murison *et al.* (1984) and Oliver *et al.* (1984) for Vancouver, British Columbia; and by Braham *et al.* (1984), Rough (1984) and Rugh and Braham (1979) for Southeast Alaska. Additional field studies are required to determine the extent that females with calves feed during their northward spring migration, and whether this feeding is critical to the survival of their calves.

SEGREGATION BY AGE AND SEX

It is clear from the discussion so far that the most prominent feature of gray whale behavior is the temporal and spatial segregation of the population into females with calves and whales without calves (including mature females and males, juveniles). This segregation exists during both the fall southward and the spring northward migrations of the California-Chukchi population. Andrews (1914) and Mizue (1949) also reported temporal segregation in the Okhotsk–Korean population of gray whales as they migrated past Uslan, Korea. Their records of whales taken in the Korean fishery indicated that the first southbound migrants past Uslan were near-term pregnant females, and that following the birth of their calves, these females migrated north apart from the herd.

This segregation according to age, sex and reproductive condition appears to exist to the Arctic feeding grounds, although relatively few studies have been conducted in this portion of the species range. Ljungblad *et al.* (1985) noted that female–calf pairs were distributed in specific near-shore portions of the northern Bering and eastern Chukchi Seas during the summer months while few calves were seen in more offshore areas and on the feeding grounds around St Lawrence Island. Krupnik's (1984) analysis of numerous archaeological sites along the Chukotka Peninsula reveals that 1st Century AD native whalers concentrated on young gray whales, particularly calves, as the bones of these animals were found in large numbers in the ancient middens. Because aboriginal hunters did not have the ability to travel far offshore, the predominance of gray whale calf bones in the excavations suggest that these whales were taken near-shore.

In their review of the Soviet literature on gray whale distribution in the Bering and Chukchi Seas, Yablokov and Bogoslovskaya (1984) described the age differentiation of the stock, with young animals congregating around the Koryak coastline from Glubokiv Bay to Cape Navarin, and groups of adults found in more northern waters. Soviet whaling records further indicated that small animals predominated in the catches from specific coastal areas (Bogoslovskaya *et al.*, 1982), and that females with young were mainly distributed in shallow coastal waters while larger whales were found further offshore at depths of 50 to 60 m (Votrogov and Bogoslovskaya, 1980). The segregation of gray whales by age and reproductive condition, thus, appears to be a behavioral characteristic that prevails throughout the species range.

The segregation of courting whales from females with calves is indicative of the behavioral incompatibility of these two groups and appears to be the primary mechanism behind their spatial distribution within the breeding lagoons. Harassment by courting whales is probably a major factor in the female–calf pair avoidance of courting whales inhabiting the outer lagoon areas. Females with calves avoid courting groups; despite this, they are occasionally pursued by groups of single whales that appear to harass and attempt to mate with them (Jones and Swartz, 1984a). Mating bouts appear to be very disruptive events and may involve groups of a dozen or more individual whales thrashing at the surface and throwing their flukes and flippers about as they jocky for mating position. It is certainly reasonable to think that a calf might be separated from its mother or could sustain injuries or even be killed in these circumstances. Norris *et al.* (1977) studied reproductive behavior in the Boca de Soledad area north of Bahia Magdalena, and remarked that 'courting-mating aggregations are almost certainly disruptive places for mother–calf pairs'.

Additional evidence for this interaction comes from observations in Laguna San Ignacio of females and calves passing through areas in the outer lagoon where courting whales are concentrated. In January and February females with calves occupied the lagoon with courting whales, and although female–calf pairs routinely travel the entire length of the lagoon, only 23% of the female–calf pairs passing through areas with courting whales utilized the center of the lagoon channel while courting whales were concentrated there. The remaining 77% hugged the sides of the channel while travelling through areas occupied by courting whales. By early March and with the departure of courting whales from the lagoon this condition reversed. Now 75% of the female–calf pairs utilized the central channel, suggesting that central deeper portion of the lagoon channel was preferred by all whales, but as in other areas throughout the lagoon, females with calves avoided mixing with whales without calves (Swartz and Jones, 1981).

CALF DEVELOPMENT

Quantitative studies of gray whale calf behaviour and development have yet to be conducted; however, observations of female-calf pairs behavior in Laguna San Ignacio between 1978 and 1982 suggest that gray whale calves progress through various developmental stages during their first few months of life in the lagoon, and that these stages are similar to the activity stages of southern right whales (*Eubalaena australis*) described by Thomas and Taber (1983) and Thomas (1986).

Although concentrated in the inner lagoon nursery at peak season, gray whale mothers remain mostly alone with their calves while they rest, nurse and move with the tides during the first few weeks of the calf's life. For example, 90% of all female–calf pairs encountered during lagoon censuses were solitary pairs. Eighty percent of those in the inner lagoon nursery were not moving, while in the lower lagoon nearest the inlet 40% were actively swimming (Swartz and Jones, 1981), suggesting that females with calves behave differently in different portions of the lagoon, and that their least active periods occur while they are within the nursery.

Shortly after birth, the calf's coordination is erratic and it lacks endurance for prolonged swimming. During this period the calf remains close to its mother while she rests and often 'rides' just above or to the side of the female when she travels. As the season progresses, females abandon the nursery and occupy the outer lagoon and inlet with their calves, where the channels are deeper and currents stronger. Here, females position themselves into the ebbing tides, swimming just enough to match the speed of the water and thereby remain stationary in the channel. Their calves swim rapidly in these situations as if on a treadmill, and no doubt develop strength and swimming endurance from the experience.

Calves and mothers do interact with other whales in female–calf social groups characterized by intense physical contact (Jones and Swartz, 1984a). Group members cavort, rolling and rubbing against each other, wheeling and diving at the surface and below as if chasing each other in play. Multiple bubble bursts often mark their location while submerged, and whale calls are frequent (Dahlheim, 1986). The size and duration of these groups vary, but can involve up to 20 mother–calf pairs at a time, and can last from a few minutes to over three hours. The groups are fluid, with pairs coalescing and exchanging continually. These activities may erve as a 'socializing' mechanism to expose the young whales to the behavior of their conspecifics, as compared to the imprinted behavioral attraction to their mothers which characterized their previous development period.

The calves, although still nursing, mimic adult foraging behavior and are frequently seen filtering bottom sediments through their baleen, gulping mouthfulls of sea water, and skimming eel grass pattys from the water surface. These activities appear to prepare the calf for its eventual life at sea, particularly the mimicry of foraging behavior that presumably will aid the calf in learning to locate prey after weaning. The development of social behavior through play and metacommunication in immature mammals has been widely discussed e.g. by Beckoff (1972) for canids and by Kummer (1971) and Poirier (1972) for primates. In his study of play in Steller sealions (*Eumetopias jubatus*), Gentry (1974) identified adult-like behavioral patterns in 2 week old animals, and concluded that play experience was a vehicle by which the frequency, intensity and combination of behavioral patterns present in the young are changed over time and ultimately manifest themselves in the adult as behavior with entirely new functions other than play.

CARE GIVING OR EPIMELETIC BEHAVIOR

Beyond the female–calf bond, courtship and mating and their migration, gray whales (and mysticetes in general) have been presumed to lack complex social behavior described for the social odontocetes (IWC, 1986). Reports of care giving or epimeletic behavior are, however, widespread throughout the Cetacea, and examples from studies of Odontoceti and Mysticeti have been reviewed by Scott (1958), Caldwell and Caldwell (1966) and Connor and Norris (1982). Examples include observations by Soviet biologists who describe 'supporting' and 'standing-by' behavior of gray whales toward injured companions (and see Bogoslovskaya, this volume). Bogoslovskaya *et al.* (1982) reported that on the Arctic feeding grounds it was common for a second whale to remain with a harpooned one. In one instance, a harpooned pregnant female was supported at the surface by a second pregnant female that put her head and tail under the animal.

On two occasions in different years interactions were observed that were suggestive of 'reciprocal altruism' between presumably non-related individuals (two adults) as described by Connor and Norris (1982). In both instances the scenario was similar and began with a calf swimming out of a channel and over the shallow sand bar toward shore until it grounded itself. In no more than a meter of water, the calf began frantically rolling and thrashing. Within moments, an adult, probably the mother, surged out of the channel and lunged up onto the sand bar beaching itself next to the calf. A second adult followed behind the first and positioned itself on the opposite side of the calf. Sandwiching the young whale between them, both adults rocked their bodies in the shallow water, pivoted while lifting the calf, and slid back into the deep channel and disappeared. Each time, the rescue maneuver was performed within fifteen to twenty seconds, and appeared as deliberate and coordinated activity on the part of both adults. It seemed as though the whale helping the mother knew what was required and how best to offer assistance. For this it appears that gray whales have achieved a level of social organization and communication necessary to coordinate the assistance between conspecifics (Jones and Swartz, 1984b).

COURTSHIP AND MATING SYSTEM

The principal activities of whales without calves within the lagoon are courtship and mating. In contrast to the solitary nature of female–calf pairs, 50% or more of the courting whales without calves counted each year in Laguna San Ignacio were in groups of two or more animals. The proportion of these whales that were actively travelling and those involved in social interactions and courtship were about equal, 57% and 43% respectively (Swartz and Jones, 1981).

Courting whales engage in high speed chases where group members (presumably males) appear to pursue a lead animal (presumably a female). These groups lunge through the water creating spectacular bow-waves, and sometimes travel 3–4 km before beginning a mating bout.

The principal gray whale mating group has been described by Gilmore (1960) and Samaras (1974), amongst others, as a 'mating-trio', consisting of a mating pair and a third animal who has been implicated as a helper. Given the 1 : 1 sex ratio of gray whales at birth (Rice and Wolman, 1971; Swartz and Jones, 1983), equal mortality rates for mature males and females (Reilly, 1984a), and a female breeding cycle of two or more years, there necessarily would be a surplus of adult males within a breeding season. Reports of 'mating-trios' are likely oversimplifications, as observations in Laguna San Ignacio confirm that mating groups were not limited to trios, but ranged from pairs up to groups of 18 animals of mixed sexes and sizes (except calves). Courting bouts lasted for two or more hours with some group members departing while other passing whales joined in as if stimulated by the sexual activity of the core group. On one occasion a mating bout lasted over four hours and in the end involved at least thirty individuals. Females appear to control the duration of the mating bouts by either accepting the advances of males or rejecting them by lying ventral side up at the surface or fleeing. Females are promiscuous and repeatedly copulate with more than one male during the same mating bout.

While social odontocetes invest energy in calf rearing as a reproductive strategy (Caldwell and Caldwell, 1966; Wursig, 1978; Wells *et al.*, 1980; Connor and Norris, 1982; Best *et al.*, 1984), mysticetes apparently invest energy in calf bearing with little or no parental care beyond the mother–calf relationship. In this context, the mating system of gray whales appears polygynous with males breeding with more than one female and females being predisposed for the care of the offspring (Wittenberger, 1981). In gray whales, however, important departures from classic mammalian polygyny are that males do not appear to be able to monopolize females, they lack the male–male aggressive displays that may determine which males mate (Krebs and Davies, 1981), and that females are also promiscuous.

In gray whales, female breeding is relatively synchronous. The effective mating period lasts at least as long as the birth period of approximately 66 days compared to 3 to 5 months in humpback whales (*Megaptera novaeangliae*) (Dawbin, 1966; Darling, 1983). During this time gray whales are dispersed along the Pacific coast of North America as they migrate south for the winter. Their compressed breeding season and dispersed geographical distribution limits, and may even preclude, the monopolization of available females by males. Thus, male defense of mates in 'harems' or other similar aggregations that give dominant males exclusive access to females, as seen in other polygynous mammals with compressed breeding seasons [e.g. ungulates like the red deer, *Cervus elaphus*, (Vlutton-Brock *et al.*, 1982), mountain sheep, *Ovis canadensis*, (Geist, 1971); or marine species such as the elephant seal, *Mirounga angustirostris*, (Le Boeuf, 1981); or as proposed for the sperm whale, *Physeter macrocephalus*, (Best, 1979)] may not exist in gray whales.

Given a two year breeding cycle (Rice and Wolman, 1971), the unavailability of half the mature females for breeding each season skews the operational sex ratio 2 : 1 toward males, and as a season progresses the number of females available for mating further declines as they are mated (Emlen and Oring, 1977). Thus, competition between gray whale males for mates would be expected. At this time, evidence for male–male competition for available mates, such as social displays, dominance hierarchies, the defense of territories or the aggressive behavior seen in humpback whales (Darling, 1983), has yet to be identified in gray whales. Females of some species presumably utilize criteria such as these to select the most 'fit' mate in terms of his genetic superiority (Partridge, 1980) or territory offering superior resources (Barash, 1982).

Emlen and Oring (1977) describe 'male dominance polygyny' as occurring in situations where mates are not economically monopolizable. Under these circumstances males aggregate during the breeding season and females 'select' their mates. There is little evidence that female mammals are able to detect genetic superiority in males (Bateson, 1983). In most cases of female choice, it appears that females are choosing males that are likely to be good fathers or males with territories that provide superior resources (Krebs and Davies, 1981). Because gray whale males do not assist with the rearing of offspring, or defend territories, it is unlikely that females select mates on these criteria. Rather, observations in San Ignacio lagoon suggest that females control mating bouts, but repeated copulation with different partners suggest that they, like males, are promiscuous.

Emlen and Oring predict that promiscuity will occur in what they term 'explosive breeding assemblages' where both sexes converge for a short-lived, highly synchronized mating period—as seen in gray whales. One apparent function of the gray whale migration is to bring sexually mature animals together when they are receptive for mating. Because sexual activity occurs during their migration and lagoon occupation (Gilmore, 1960; Pike, 1962; Fay, 1963; Rice and Wolman, 1971; Baldridge, 1974; Hatler and Darling, 1974; Jones and Swartz, 1984a) rather than in one specific portion of their range, the timing of reproduction may be more important than a specific breeding location. Although the lagoons are important core areas for females with calves, mating activities of breeding animals do not appear restricted to particular locations. A 'core time' rather than area might be the important factor in assuring fertilization in gray whales, particularly if female breeding is highly synchronized. Terrestrial analogues for the occurrence of effective breeding during migration include the barren ground caribou (*Rangifer sp.*) and the blue wildebeest (*Connochaetes sp.*) (Wilson, 1975).

Finally, Emlen and Oring (1977) predict that communal displays will be frequent in any species in which the male is totally emancipated from parental care and where the environment provides little potential for resource (mate) control. In these situations, male–male dominance competition will drive the evolution of social displays, such as those seen in polygynous birds and mammals. For example, the songs of the humpback whale have been implicated as secondary sexual characteristics in the form of acoustic displays between breeding males (Darling, 1983).

The lack of direct evidence for male–male competition in gray whales, such as extreme sexual dimorphism, male territorial defense and communal displays, suggests that competition and sexual selection may occur at some level other than that of the individual. In species where females mate with more than one male, sperm competition may determine male paternity (Parker, 1984). Dewsbury (1981) found that in golden hamsters (*Mesocricetus auratus*) the order of mating, differential fertilizing capacity and sperm competition all affected individual male mating success in situations where females subsequently mate with different males. Landino (1985) and Payne and Bird (1985), reviewed the literature on sperm competition and sexual selection theory which indicated that relative testes-to-body weight ratio was indicative of breeding systems in primates. On the basis of testes-to-body weight ratios, they predicted that cetacean mating systems would be either unimale (monogamous or polygynous) or multimale (promiscuous or polyandrous). According to this idea, in multimale breeding systems, a male has to provide enough sperm to compete with the sperm of other males and should have large testes. In unimale polygynous systems, the male can presumably be secure in assuming paternity and must produce only enough sperm to service the females in his harem. The unimale systems, then, would not necessarily require large testes. The testes-to-body weight ratio in gray whales predicted a multimale breeding system, which is consistent with the breeding behavior seen in this species.

Brownell and Ralls (1986) reviewed the literature on baleen whale testes size, penis length and mating system. They reasoned that in species with sperm competition large testes that produce large amounts of sperm per ejaculation would serve to dilute and displace the sperm of rival males, and that longer penises would deliver the sperm closer to the ova. They reported that species without obvious male–male competitive behavior (right, gray and bowhead whales) possessed both large testes-to-body weights and penis-to-body lengths. Because gray whales had testes that were smaller than those of right and bowhead whales, they concluded that sperm competition may be less intense than in these species. The relatively smaller testes of the humpback whale, together with its shorter penis and the conspicuous interactions between breeding males suggest that this species has been selected to compete to a greater extent by preventing matings of rival males than by sperm competition.

If sperm competition exists in gray whales, either by displacement due to differential volume delivered to the female (Dewsbury, 1981) or by physiological deactivation (Whittenberger, 1981), it may account for the lack of obvious male–male sexual displays. Future long-term studies, particularly individuals which can be repeatedly recognized in the field over periods of several seasons, should make significant contributions to our understanding of the evolution of gray whale social behavior and the life history of this unique mysticete.

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ANNUAL PATTERNS OF GRAY WHALE (*ESCHRICHTIUS ROBUSTUS*) DISTRIBUTION, ABUNDANCE AND BEHAVIOR IN THE NORTHERN BERING AND EASTERN CHUKCHI SEAS, JULY 1980–83

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ABSTRACT

A total of 1,543 gray whales were seen on aerial surveys conducted in the northern Bering and eastern Chukchi Seas during July 1980–83. Highest observed annual subregional densities ranged from 0.26 to 1.70 whales/km^2, and were positively correlated with the proportion of gray whales observed feeding in subregions of the north-central Bering Sea, coastal areas south–southeast of St Lawrence Island and the coastal Chukchi Sea between Pt Hope and Pt Barrow, Alaska ($r_s = 0.94$, $p \leq 0.025$, $n = 6$). Estimated gross annual recruitment rate (GARR) ranged from 0.1% to 6.0%, with evidence of segregation of cow–calf groups along the coastal Chukchi Sea supported by significant differences in GARR by sea ($t = 6.9$, $p \leq 0.005$). Swimming and feeding were the predominant behaviors observed in all years. Series of short duration amplitude-modulated (AM) signals were the most prevalent (90%) sounds recorded near feeding gray whales, with occasional moan-like and belch-like sounds interspersed. No function was inferred to any of the recorded sounds.

INTRODUCTION

The annual distribution, abundance and behavior of the California–Chukotka stock of gray whales (*Eschrichtius robustus*) has been investigated via aerial surveys each July since 1980. Principal areas surveyed were the central feeding grounds in the northern Bering and southern Chukchi Seas (Rice and Wolman, 1971; Bogoslovskaya, Votrogov and Semenova, 1981; Nerini, 1984), and the coastal Chukchi Sea between Pt Hope and Pt Barrow, Alaska. Although dense infaunal amphipod assemblages have been sampled from the feeding grounds in the northern Bering Sea, similar concentrations have not been found along the coastal Chukchi Sea (Stoker, 1981), and the extent of gray whale distribution and density along this coast is uncertain.

The objectives of the study were to:

- determine the distribution and derive abundance estimates of gray whales in the survey area,
- utilize estimated abundance to describe spacial and temporal distribution patterns, and
- describe gray whale behavioral characteristics and sound production as possible.

MATERIALS AND METHODS

Study area and aerial surveys

The study area included the Bering Sea north of 62°N and the Chukchi Sea east of the International Date Line (IDL). Except for the northern Chukchi Sea, this area

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was divided into blocks (Fig. 1) suitable to line transect surveys (i.e. one, or with favorable conditions, two blocks could be surveyed completely on one flight). The bases of operation were Nome and Kotzebue, Alaska.

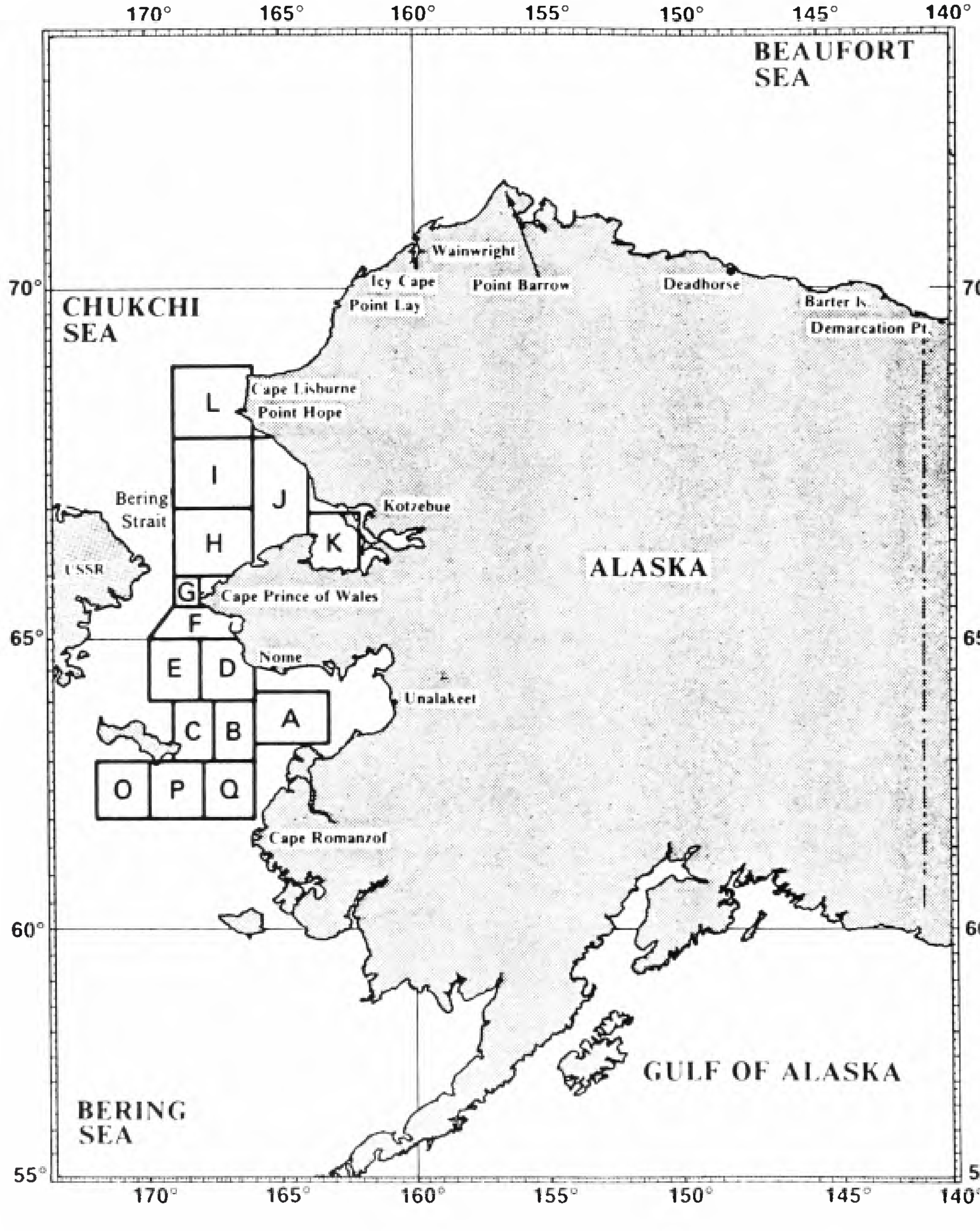

Fig. 1. Survey area and survey blocks.

Two types of aerial surveys were utilized:

(1) *Line transect surveys* were flown in survey blocks to determine distribution and estimate relative and absolute abundance. Coverage of no less than 10% of the total area of each block was planned. Line transect is one available survey method from which statistical inferences can be made, provided the starting and turning

points of the line are selected randomly (Cochran, 1963). Survey blocks were divided into sections that were 10 minutes of latitude wide, and each section marked with 10 equally spaced ticks. Starting and/or turning points were chosen within each section by selecting two numbers between 1 and 10 from a random numbers table and matching them to the numbered ticks. The transect line was then drawn between these two points. The same procedure was followed for each section of the survey block, then all transect lines were linked together with short connecting lines at top and bottom.

(2) *Search surveys* were flown into areas of maximum probability of sighting gray whales and did not follow a preset paradigm. The exact routes of search surveys were dependent upon previous patterns of whale sightings (i.e. number, heading, swimming speed), weather, sea state and ice conditions. Search surveys were flown to locate whales, observe their behavior and record water-borne sounds.

Data collection and analyses

The methods of data collection and analysis have remained similar throughout all years (Ljungblad, 1981; Ljungblad, Moore, Van Schoik and Winchell, 1982; Ljungblad, Moore and Van Schoik, 1983; Ljungblad, Moore and Van Schoik, 1984). Surveys were flown at 152 to 458 m altitude, at 222 to 296 km/h. Higher altitudes were maintained when possible to maximize visibility. The aircraft was equipped with a Global Navigation System 500 that provided continuous position updating (5.83 km position precision) and transect turning point programming. Data routinely logged at the time of sighting included: aircraft altitude, time, latitude and longitude, sea state, visibility range (subjective), number observed, initial heading and behavior of surfaced whales.

Gray whale behavior classifications included resting, swimming, feeding, nurturing and displaying. Nurturing was defined as proximal (<20 m) swimming or apparent nursing exhibited by cow–calf pairs, while displays included tail and flipper-slaps, rolls and underwater blows. Gray whales seen with mud plumes were assumed to be feeding. Mud plumes are conspicuous, large billows of sediment brought to the surface by bottom-feeding whales. Such plumes aid sightability because they attract feeding birds (Harrison, 1979) and in calm waters (Beaufort sea state 00 to 02) they may retain their identifiable shape and sub-surface discoloration for five to ten minutes. Sonobuoys were dropped near whales to record water-borne sounds.

Gray whale distribution was plotted for July 1980 through 1983. Calculation of subregional density statistics followed methods described in Krogman, Braham, Sonntag and Punsley (1979), based on the strip transect technique described in Estes and Gilbert (1978). Directionality of whale headings was analysed using Rayleigh's and Chi square tests (Batschelet, 1972); correlation and comparison of data sets was analysed via Spearman's rank correlation and Student's t-test (Zar, 1974).

Surveys on which gray whales were seen in the study area were conducted as early as 17 May (1981), and as late as 4 November (1980), but July was the only month in which surveys were flown in all years, and therefore the only month across which comparisons were made in this review. Gray whale distribution and bioacoustic data, collected between July and November 1980, and between June and August 1981 were reviewed in Moore and Ljungblad (1984).

Table 1

Total number of flights (FLT), sightings (SI) and gray whales (GW) seen in the northern Bering Sea and Chukchi Sea, July 1980–83

	N. Bering Sea		Chukchi Sea		TOTAL	
Year	FLT	SI/GW	FLT	SI/GW	FLT	SI/GW
1980	0	—	1	8/10	1	8/10
1981	9	42/84	6	40/102	15	82/186
1982	6	115/200	3	31/121	9	146/321
1983	7	435/1005	1	15/21	8	450/1026
Total	22	592/1289	11	94/254	33	686/1543

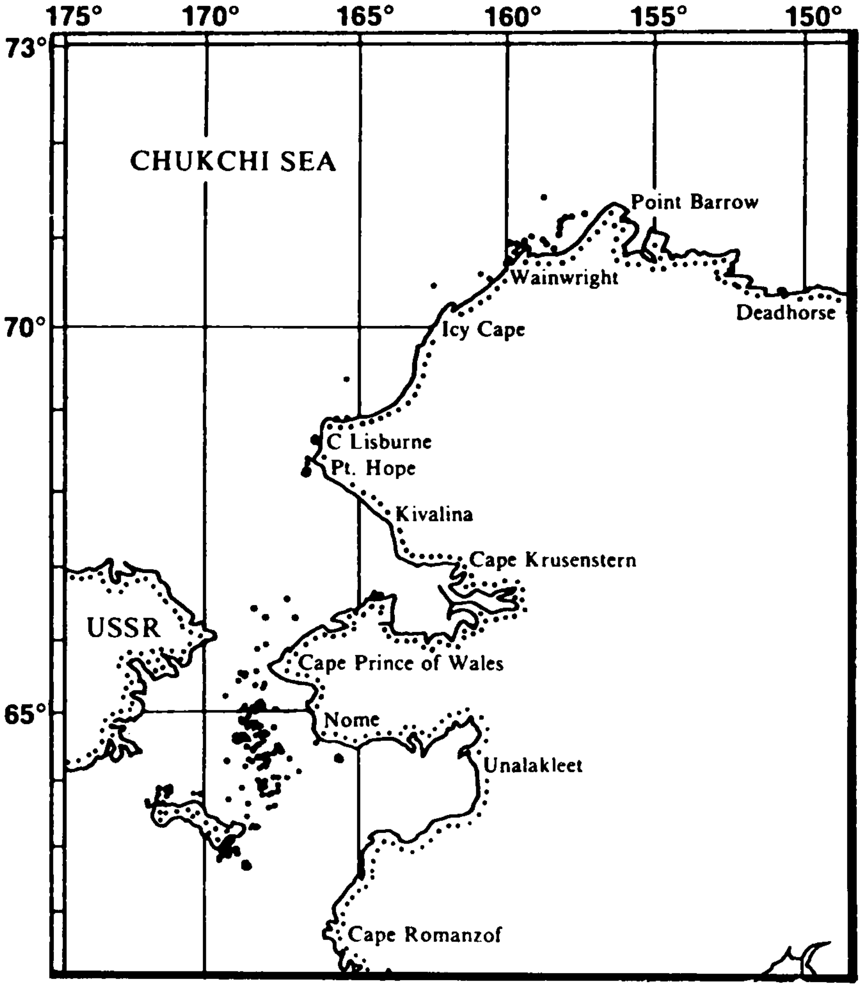

Fig. 2. Distribution of 686 sightings of 1,543 gray whales, July 1980–83.

RESULTS AND DISCUSSION

Distribution and density

A total of 1,543 gray whales were seen during the month of July 1980–83 (Table 1; Fig. 2). The plotted distribution in the central northern Bering Sea and along the eastern coast of the Chukchi Sea is similar to that reported in Votrogov and Bogoslovskaya (1980) and Berzin (1983), respectively, for areas where survey efforts overlapped.

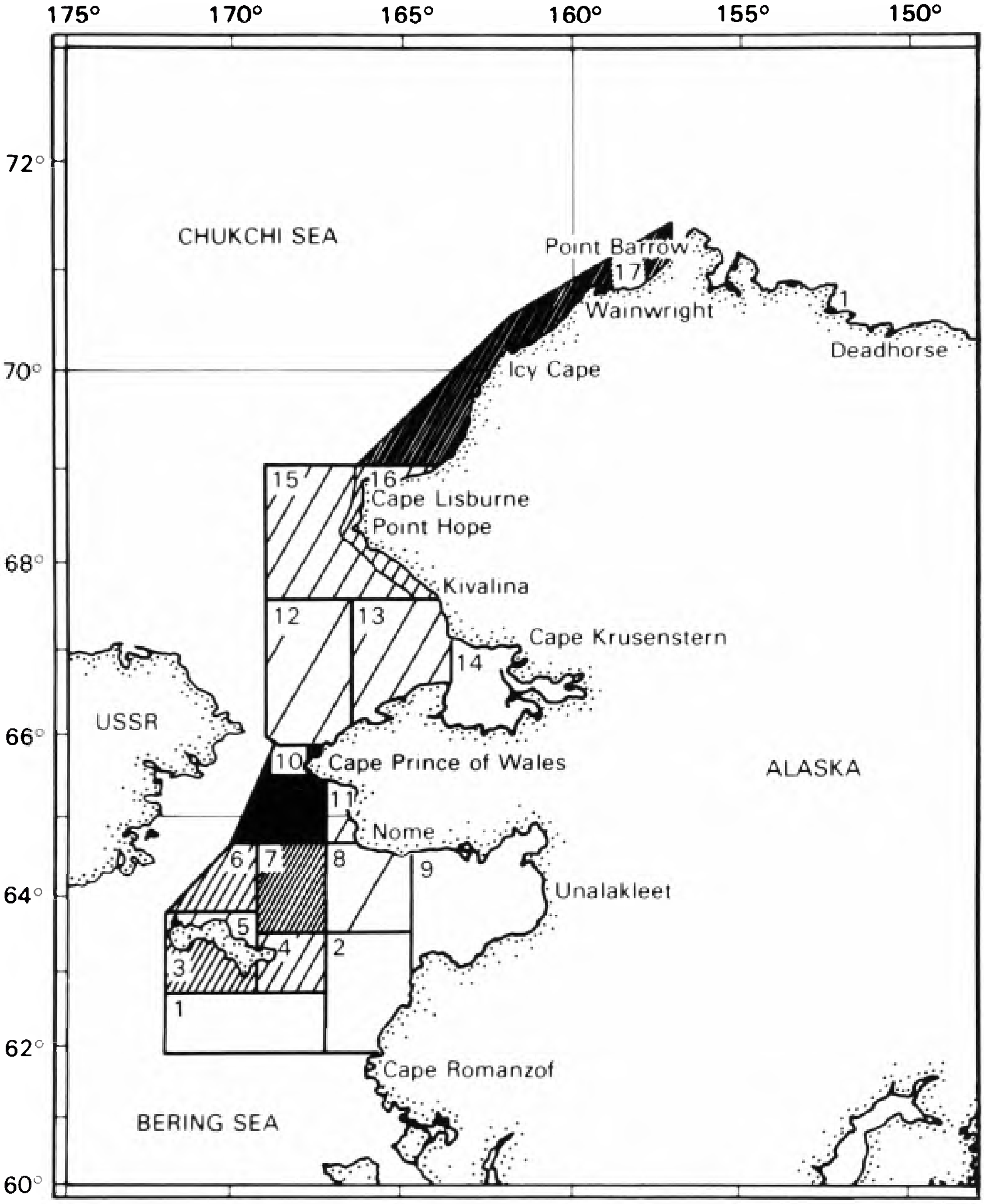

Fig. 3. Highest observed gray whale subregional densities, July 1980–83. Shading varies from all white (representing 0 whales/km^2 density) to all black (representing 1.70 whales/km^2 density). Data based on annual subregional densities presented in Table 2.

In the northern Bering Sea, gray whale distribution was clustered north of St Lawrence Island between 167°W and 169°W, and along the island's southeast and northwest coast each year. The center of the major distribution cluster north of St Lawrence Island shifted only slightly to the northwest from 1981 to 1983. In 1981, the center of this cluster was approximately 63°55′N, 167°30′W. In 1982 the center was about 64°25′W, 167°30′W, and in 1983 the central point was approximately 64°45′N, 168°45′W. Highest annual densities in the northern Bering Sea ranged from 0.361 whales per km^2 in 1981 to 1.70 whales per km^2 in 1983 (Table 2; Fig. 3). Notably, highest annual gray whale densities were not calculated for the same subregion in consecutive years. In 1981, highest density was observed in subregion 7,

Table 2

Statistics from aerial surveys of gray whales conducted in the northern Bering and Chukchi Seas, July 1980–83. Values for each region were summed where appropriate. Region numbers refer to areas depicted in Figure 3. Number of gray whales observed are those seen on transect lines *only*, not the total number of whales seen on surveys.

	Region Name	Region Area km²	Percent of Total Area	Percent of Area Surveyed	Survey Time Hr : Min	Percent of Total Time	Number of Transects Flown (= n)	Number of Grays Observed	Density as Number per km²	Percent of Area Surveyed	Survey Time Hr : Min	Percent of Total Time	Number of Transects Flown (= n)	Number of Grays Observed	Density as Number per km²
				1980						1981					
N. BERING SEA	1	22,504	10.08	0.0						0.0					
	2	19,092	8.56	0.0						2.23	1:01	2.53	7	0	0.0
	3	6,918	3.10	0.0						0.0					
	4	7,606	3.41	0.0						8.20	1:14	3.07	7	0	0.0
	5	2,491	1.12	0.0						0.0					
	6	7,957	3.56	0.0						0.0					
	7	14,063	6.30	0.0						10.74	3:23	8.42	14	46	0.361
	8	15,707	7.04	0.22	0:06	2.03	2	0	0.0	18.21	6:34	16.34	34	0	0.0
	9	24,981	11.19	1.39	0:06	14.92	2	0	0.0	7.86	4:44	11.78	26	0	0.0
	10	12,645	5.67	1.23	0:29	9.83	2	0	0.0	13.65	4:14	10.54	17	14	0.096
	11	2,638	1.18	3.69	0:13	4.41	1	0	0.0	16.54	2:37	6.51	29	5	0.062
CHUKCHI SEA	12	21,276	9.53	1.52	0:59	20.00	1	0	0.0	7.09	4:25	10.99	16	9	0.072
	13	14,242	6.38	0.46	0:09	3.05	1	0	0.0	10.23	3:03	7.59	18	0	0.0
	14	8,493	3.81	0.0						8.29	1:24	3.48	8	0	0.0
	15	19,838	8.89	0.50	0:13	4.41	1	0	0.0	4.73	2:15	5.60	7	12	0.151
	16	5,174	2.32	3.51	0:44	14.92	3	4	0.261	25.79	3:11	7.92	11	28	0.248
	17	17,530	7.86	3.74	1:18	26.44	2	4	0.072	5.02	2:06	5.23	12	21	0.282
				1982						1983					
N. BERING SEA	1	22,504	10.08	0.11	0:04	0.17	1	0	0.0	0.0					
	2	19,092	8.56	0.0						1.71	0:40	2.69	7	0	0.0
	3	6,918	3.10	1.73	0:14	0.58	2	11	1.090	0.0					
	4	7,606	3.41	17.66	3:21	8.30	18	40	0.351	9.56	1:34	6.32	12	0	0.0
	5	2,491	1.12	22.81	1:31	3.76	8	6	0.124	0.0					
	6	7.957	3.56	12.18	2:09	5.32	8	7	0.086	11.55	1:55	7.73	13	65	0.884
	7	14,063	6.30	30.55	9:55	24.56	48	56	0.155	30.26	8:31	34.35	55	429	1.194
	8	15,707	7.04	6.02	2:14	5.53	9	1	0.014	67.76	2:22	9.54	13	0	0.0
	9	24,981	11.19	0.0						2.67	1:18	5.24	7	0	0.0
	10	12,645	5.67	23.18	6:53	17.04	37	37	0.148	19.00	5:04	20.43	33	346	1.703
	11	2,638	1.18	15.73	1:06	2.72	11	0	0.0	5.00	0:17	1.14	4	0	0.0
CHUKCHI SEA	12	21,276	9.53	13.85	6:25	15.89	28	5	0.021	0.62	0:17	1.14	1	1	0.089
	13	14,242	6.38	7.30	2:12	5.45	18	1	0.010	2.24	0:35	2.35	1	4	0.148
	14	8,493	3.81	6.05	1:06	2.72	7	0	0.0	0.0					
	15	19,838	8.89	0.0						0.46	0:09	0.60	1	0	0.0
	16	5,174	2.32	7.75	1:05	2.68	6	24	0.709	3.72	0:25	1.68	3	6	0.368
	17	17,530	7.86	3.83	2:08	5.28	5	84	1.479	3.65	1:41	6.79	12	0	

Table 3

Highest subregional density and percentage (%) of gray whales/subregion seen with mud plumes in the northern Bering Sea and Chukchi Sea, July 1981–83

Year	N. Bering Sea density*(%**)	Chukchi Sea density*(%**)
1981	0.36(14)	0.28(4)
1982	1.09(45)	1.48(41)
1983	1.70(56)	0.37(17)

* density = No. whales/km^2. ** seen with mud plumes.

in 1982 subregion 3 had highest density (1.09 whales/km^2) and in 1983, subregion 10 supported the highest observed gray whale density with observed densities in subregions 6 and 7 of 0.88 and 1.19 whales per km^2, respectively, that year. Such shifts in relative whale abundance may imply similar shifts in the densities of the benthic biota supporting the whales. If so, foraging gray whales may play an important role in structuring the benthic community as has been suggested by Nerini and Oliver (1983). Nerini (1984) has estimated that gray whales may turn over 9% to 27% of the northern Bering Sea benthos each year. If whales feed extensively in a small area one year, the structure of the benthic community may be so altered that the same area cannot support as many gray whales the next year.

In the Chukchi Sea, gray whale distribution was clustered north of Cape Prince of Wales to 66°40′N, and about coastal promontories between Pt Hope and Pt Barrow. Highest annual densities in the southern Chukchi Sea (subregions 12–15) were relatively low each year, ranging from 0.02 to 0.15 whales per km^2. The coastal Chukchi Sea (subregions 16 and 17) supported relatively high whale densities (0.71 and 1.48 whales/km^2) in 1982, but relatively low peak densities (0.26, 0.28 and 0.37 whales/km^2) were observed there in 1980, 1981 and 1983. As in the northern Bering Sea, highest annual densities were not observed in the same Chukchi Sea subregion in consecutive years, although highest calculated densities for the coastal subregions were generally at least double those observed in the southern subregions.

The highest annual subregional densities[1] in both seas were significantly correlated with feeding ($r_s = 0.94$, $z = 2.11$, $p \leq 0.025$, $n = 6$), as represented by the percentage of whales seen with mud plumes (Table 3). Between 1981 and 1983, highest subregional densities in the northern Bering Sea were associated with feeding ratios of 14% to 56%. In the Chukchi Sea, highest subregional densities were associated with feeding ratios of 4% to 41%. The highest observed density along the Chukchi coast in 1982 (1.48 whales/km^2) when 41% of the whales were seen feeding was over five times greater than in 1981 (0.28 whales/km^2) when 4% of the whales were seen feeding. In 1983, 17% of the grays seen along the coastal Chukchi were feeding, and the calculated density was median (0.37 whales/km^2) to that observed in 1981 and 1982. It appears the coastal Chukchi Sea may be a peripheral feeding ground and when food is abundant there, as indicated by a relatively high proportion of whales with mud plumes (i.e. 1982, relatively high whale densities are observed there.

[1] Because only one flight was made through the study area in July 1980, all density-feeding comparisons are for 1981–83 data only.

The data associating gray whale density and feeding should be interpreted with caution due to the reliance of the aerial observer on mud plumes to infer feeding. Although it appears that whales are likely to suck in some plume producing sediment when feeding on infaunal species (Ray and Schevill, 1974), they may not create plumes if feeding on epibenthic fauna. Nerini (1984) points out that gray whales exhibit a high degree of dietary flexibility and are 'generalist' feeders. Further, whales investigating or otherwise disturbing the bottom while not feeding might create a sediment cloud that could be mistaken for a mud plume. Lastly, we are uncertain as to the effect of mud plumes on gray whale sightability. As previously mentioned, mud plumes are excellent sighting cues and as such may positively bias data toward 'feeding' whales.

Calf sightings and estimated recruitment

No calves were seen among the ten gray whales sighted in 1980. Between 1981 and 1983 the number of calves seen in July ranged from one to nineteen (Table 4). All calves seen in the Chukchi Sea were found in coastal subregions 16 and 17. Estimates of gross annual recruitment rate (GARR = no. calves/total no. gray whales including calves) ranged from 0.1% in 1983 to 6.0% in 1982.

Segregation of cow–calf groups from other whales was indicated by a significant difference in GARR estimates by sea (Table 4; $t = 6.9$, $p \leq 0.005$). In the northern Bering Sea, GARR ranged from 0.1 to 0.5%, with a three year average of 0.2%. Along the coastal Chukchi Sea, GARR ranged from 4% to 16%, with a 9% average derived over three years. The best single example of cow–calf segregation was seen in 1982 when a GARR of 16% was calculated for the coastal Chukchi Sea. That year eighteen calves were among the 111 grays distributed between Cape Lisburne and Wainwright, while only one calf was seen in a total of 210 whales between St Lawrence Island and 50 km southwest of Pt Hope (approx. 68°N) in the Chukchi Sea. There was roughly 150 km separation between the first sighting of the 111 gray whales and the most northerly gray whale sighting prior to that date in 1982. Similarly, Würsig, Wells and Croll (1983) reported that they saw no whales that were identified as calves in the course of 158 behavioral observations conducted from a vessel in the Bering Sea north of St Lawrence Island in July 1982, although they noted that calves may have been missed or misidentified. Although Blokhin (1982) reported that female grays taken off Chukotka in 1980 tended to be found in pregnant and nonpregnant groups and segregation of 'small' whales and calves has been reported for the coastal waters of the southern Chukotka Peninsula

Table 4

Number of gray whales calves seen and recruitment estimate (%)* in the northern Bering and coastal Chukchi Seas, July 1981–83

Year	N. Bering Sea	Coastal Chukchi Sea	Total
1981	—	4(4)	4(2)
1982	1(0.5)	18(16)	19(6)
1983	1(0.1)	—	1(0.1)
Total	2(0.2)	22(9)	24(2)

* GARR = number calves/total number gray whales including calves.

(Votrogov and Bogoslovskaya, 1980; Krupnik, Bogoslovskaya and Votrogov, 1983), segregation of cow–calf and/or female gray whale groups in Alaskan arctic waters has not been documented as a common occurrence as it has in the breeding lagoons (Swartz and Jones, 1984), and along the migration route (Herzing and Mate, 1984; Poole, 1984). Specifically, Poole (1984) reported that gray whale cow–calf pairs constituted a second phase of the northward migration weeks after the first phase of large whales passed north. Similarly, Hessing (1983) noted that calves were not seen among large northbound grays migrating past Unimak Island, Alaska between 23 March and 7 April, but were seen with a 'second wave' of whales counted after 9 May in 1981. Additionally, cow–calf pairs were observed to closely follow the coastline with 96% to 99% seen between 10 m to 200 m from shore. Poole suggested such a nearshore migratory path may be the result of food availability (see Nerini, 1984) and for protection from killer whales (*Orcinus orca*).

Although coastal segregation of cow–calf groups on the feeding grounds may be expected as an extension of parturition and migratory segregation, it was somewhat surprising to find such groups which enter the northern feeding grounds later in the season than other 'large' whales, on the more northerly peripheral feeding area of the coastal Chukchi Sea.

Predator avoidance may be a contributing factor to this extreme northerly distribution. Killer whales are known gray whale predators and have been observed chasing gray whales in the northern Bering Sea (Ljungblad and Moore, 1983). Although killer whales have been reported in low numbers along the coastal Chukchi Sea (Frost, Lowry and Burns, 1983), gray whales may encounter fewer killer whales there than in the Bering Sea (Dahlheim, 1981). In a similar scenario, Edwards (1983) reported that cow–calf moose (*Alces alces andersoni*) pairs on Isle Royale, Michigan were found on sub-optimal peripheral feeding areas that were wolf-free, while solitary adults and yearling moose were found in the presence of wolves (*Canis lupus*) in areas of optimal forage.

Alternatively, nurturing behaviors between cow–calf pairs and the inability of calves to dive for long periods in deep water might also be a causal factor in relegating cow–calf groups to coastal peripheral feeding areas all along their feeding range. A peripheral feeding ground near Bamfield, British Columbia has been reported, and observations were made there on the respiration pattern of a 'small' (6 m) feeding whale (Oliver, Slattery, Silberstein and O'Connor, 1984). Because killer whales are common in coastal waters near British Columbia (Dahlheim, 1981), the physiologic requirements for foraging in deep versus shallow water, rather than predator avoidance might be important correlates in finding young whales there. Cows with calves may prefer to forage in shallow coastal waters to avoid predators and to maintain closer physical contact through the avoidance of protracted feeding dives.

Behavior and sound production

Swimming and feeding were the behaviors noted most often in all years (Table 5). Swim direction headings in the Bering and Chukchi Seas showed no significant clustering, indicating feeding whales were not highly directed in their movements (Fig. 4). There was no consistent predominant heading across years, nor between seas within the same year, except 1982 when headings between 225°–270°N were dominant in both seas.

Table 5

Summary of gray whale behavior in the northern Bering and eastern Chukchi Seas, July 1980–83

Behavior	Year	N. Bering Sea No. Whales (%)	E. Chukchi Sea No. Whales (%)	Total No. Whales (%)
SWIM	1980	—	8(80)	8(80)
	1981	39(46)	72(70)	111(60)
	1982	100(50)	34(28)	134(42)
	1983	482(48)	17(81)	499(49)
FEED	1980	—	2(20)	2(20)
	1981	35(42)	20(20)	55(30)
	1982	70(35)	46(38)	116(36)
	1983	462(46)	3(14)	465(45)
REST	1981	10(12)	—	10(5)
	1982	27(13)	5(4)	32(10)
	1983	56(6)	1(5)	57(6)
COW-CALF	1981	—	8(8)	8(4)
	1982	2(1)	36(30)	38(12)
	1983	2(0.2)	—	2(0.2)
DISPLAY	1981	—	2(2)	2(1)
	1982	1(1)	—	1(0.3)
	1983	3(0.3)	—	3(0.3)

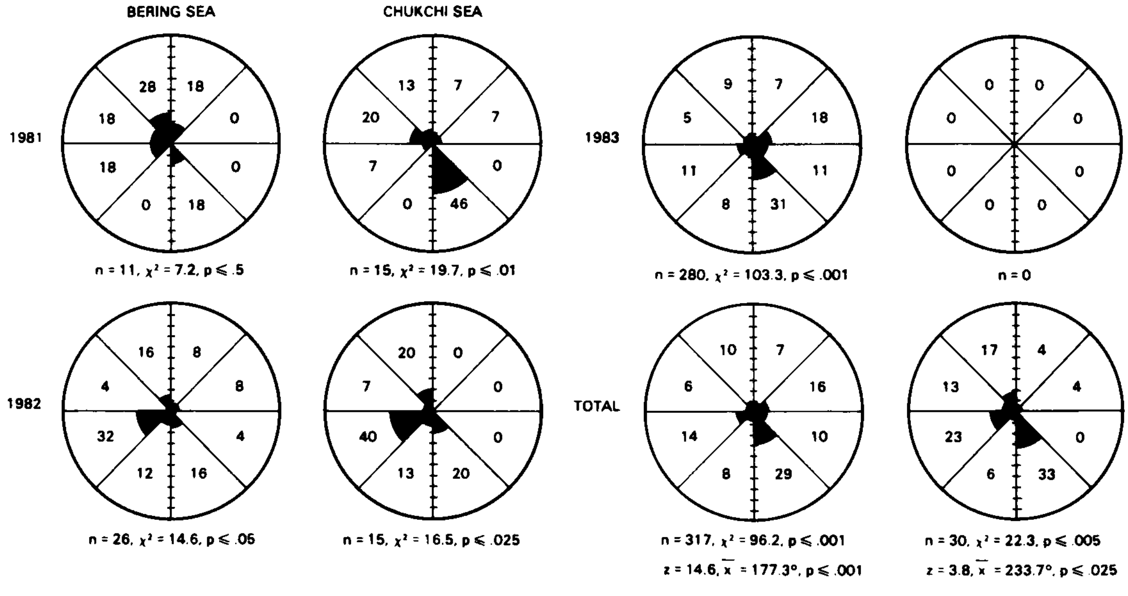

Fig. 4. Swimming direction of gray whales in the northern Bering and Chukchi Seas, July, 1981–83. Numbers in 45° octants represent percentages of whales exhibiting headings within that range.

Grays not swimming or feeding were usually resting. Whales very near shore sometimes appeared to be resting on the bottom. Six displays were seen over four years. In 1981 two whales swimming together and touching were observed as they rolled and flipper-slapped four times over a five minute period. In 1981 and 1983, underwater blows were seen on one and three occasions, respectively, among groups of whales in which feeding was the predominant activity.

Sounds recorded near feeding gray whales in the northern Bering Sea and Norton Sound were analysed and categorized into three types (Moore and Ljungblad, 1984). The most prevalent sounds (90% of sample) were amplitude modulated (AM) signals, termed N_1-type, that to the ear sounded like metallic knocks. These sounds were usually emitted in series with approximately 12 knocks/series at a repetition rate of about 7 knocks/second. N_1-type sounds showed great variation in repetition rate, series duration and frequency of maximum amplitude. Other sounds recorded near grays were moan-like (N_3), or belch-like (N_4). Both sound types showed amplitude and frequency modulation (FM), were in roughly the 100 to 750 Hz frequency band and were about 0.25 to 1.5 s long. A sound that may have been associated with an underwater blow (N_6-type) was recorded in 1983. Function was not ascertained for any of the recorded sounds. A concise review of gray whale sound production and further explanation of the sound category scheme adopted here may be found in Dahlheim, Fisher and Schempp (1984).

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SC/36/PS5

ON THE SOCIAL BEHAVIOUR OF GRAY WHALES OFF CHUKOTKA AND KORYAKA

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ABSTRACT

A summary and synthesis of information on the behaviour of gray whales obtained mainly from whaling operations in their northern feeding grounds between 1977 and 1983 is presented. In an attempt to overcome some of the obvious difficulties with data collected in this manner, additional studies involving the use of a helicopter, land-based observations and observations from the catcher boat outside whaling operations were carried out. Individual identification, group structure, acoustic communication and the distribution of animals within a season are discussed.

INTRODUCTION

This paper is an attempt to collate and summarise material collected between 1977 and 1983 concerning the social behaviour of gray whales (*Eschrichtius robustus*) in their northern feeding grounds. Most of the data were obtained from on board the catcher boat *Zvezdny*, which takes gray whales on behalf of the native people of Chukotka (Ivashin and Mineev, 1981). The assistance of the late Captain L. M. Votrogov, who made a valuable contribution to the study of gray whale biology, and the help of the Chukotkan walrus and seal hunters is acknowledged.

Experience revealed that observations made from the catcher boat or other non-dedicated boats are somewhat limited, as there is no real possibility of following the same animals for any length of time. For this reason, it was decided in 1983 to supplement this work and to cover not only Chukotka but also the lagoons and fiords of Koryaka, where, according to Zenkovich (1934; 1954) and Tomilin (1937), gray whales are found in great numbers.

From 18–27 July 1983, 487 gray whales were sighted during helicopter surveys in five areas along the Kamchatka and Koryaka coastlines (from Mys Afrika in Kamchatka to Gavrilla Bukhta in the southern Gulf of Anadyr, Fig. 1). From 19 July–15 August 1983, 2–4 day long stationary observations were concluded at certain points along the Koryaka Coast, namely: (1) a southern lagoon in Machevna Bukhta, (2) a gulf lying to the North of Mys Wittgenstein, (3) a lagoon to the south of Mys Pyatnitsa, (4) a river estuary near Mys Hyidin and (5) in the Pikk river estuary near Mys Navarin. This last area was also investigated from 20–21 July 1979 by L. M. Votrogov and the author, from the *Zvezdny*.

INDIVIDUAL IDENTIFICATION

Unlike killer whales and some dolphins, gray whales have no dorsal fin or obvious colour patterns which can be used to identify individuals and unlike humpback

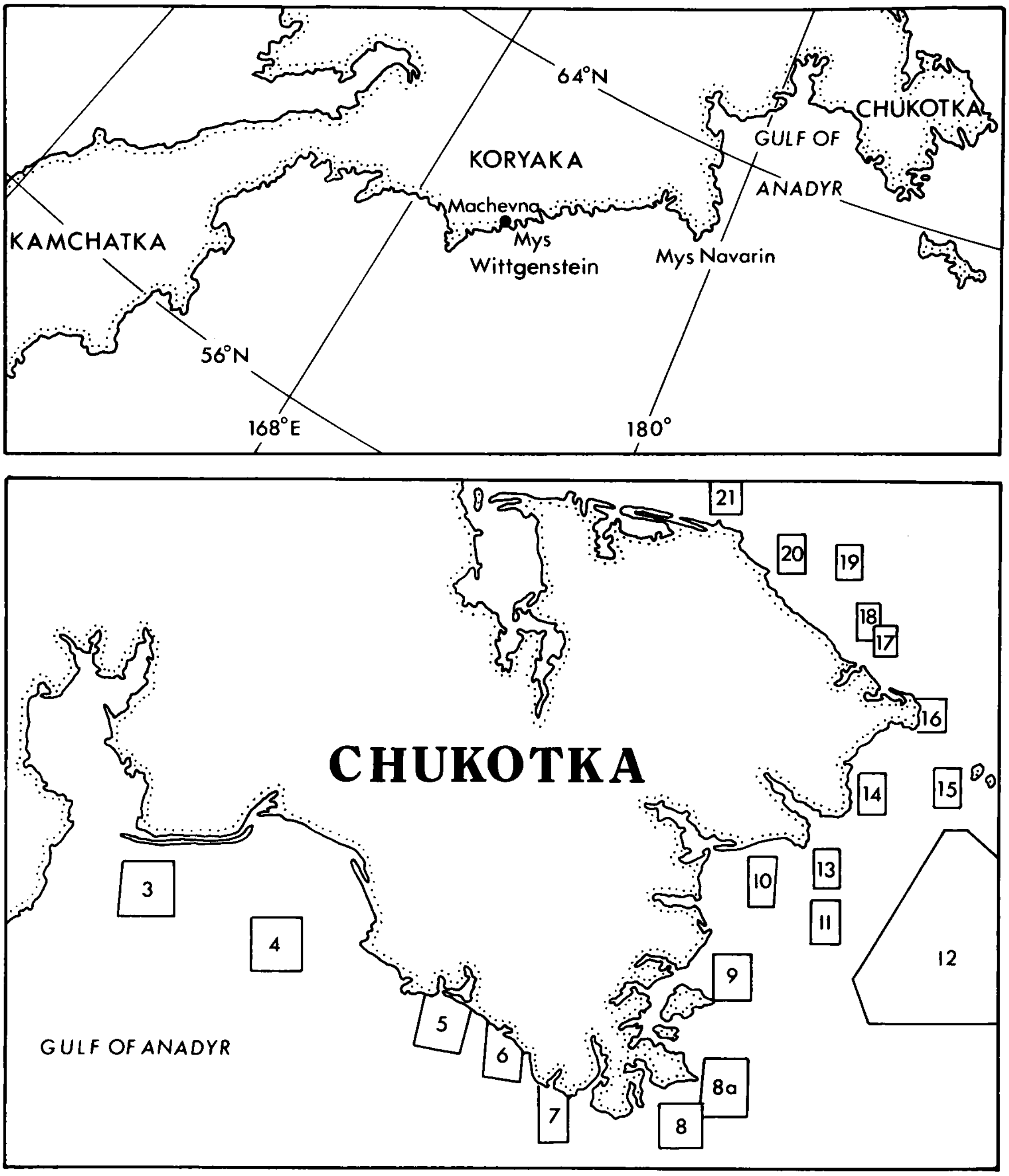

Fig. 1. Map showing the study area and the divisions referred to in the text and tables.

whales they have no unique fluke patterns which can often be used to distinguish between individuals in a group, even before photographs have been analysed.

Although studies of individuals based on photographs have been used in the breeding grounds (Darling, 1984; Swartz, 1986), this approach is more difficult to follow under the field conditions prevalent on the feeding grounds. In any event the subtleties of the differences make it difficult to identify individuals during field observations of groups, even if photographs can be analysed later in the laboratory. The general colouration of gray whales is uniform, with a slightly mottled appearance, ranging from light grey to almost black. This is usually broken by numerous, randomly distributed whitish areas and scars resulting from colonies of ectoparasites or areas they had once occupied. Generally the heads of most whales appear white during their brief appearance at the surface to blow, but it is rare for the whole head to be visible at such times. During all the years of observing gray whales therefore we have only been able to identify in the field some twenty animals which have either been almost all white due to a high ectoparasite burden or have possessed clearly distinguishable fluke outlines due to injury. Even for these animals it was necessary to wait for long periods before the particular distinguishable features became visible. However, when observing small groups, general features such as size can be sufficient to distinguish individuals within the groups.

GROUP STRUCTURE

Bogoslovskaya, Votrogov and Semenova (1981; 1982) noted that over half of the gray whales observed during whaling operations in Chukotka waters were single animals. Table 1 summarises the group size data for the seasons 1980–82. Tables 2–5 summarise daily and monthly variations for 1981 and 1982. Berzin (1984) reported similar results for both aerial and vessel surveys carried out during Soviet–American cooperative cruises in 1979 and 1980.

Table 1

Distribution of group sizes (number of whales), 1980–82

			Group size					
Year	Observations	Total	1	2	3	4	5	6
1980	29 June–28 Oct.	2,220	1,021	686	297	152	40	24
1981	24 Aug.–9 Nov.	1,438	940	370	87	36	5	—
1982	25 July–30 Oct.	1,804	1,068	486	162	52	—	36

These data suggest that singles and pairs are the most stable social units on the feeding grounds; groups of three animals which persist for any length of time seem rare, while associations of 4–6 animals appear unstable.

Large groupings (comprising anything from six to over one hundred animals), which can best be termed ‘herds’, are seen in all areas although they are most common in Divisions 4, 12 and 14 (Bogoslovskaya *et al.*, 1981). These herds can arise over a period of a few hours and can disappear almost as quickly (e.g. see Table 5, 28 July) or (occasionally) persist for 3–4 days. They have their own internal structure of small groups and in this respect the situation is not dissimilar to that observed in a stable large school of Atlantic bottlenose dolphins, *Tursiops truncatus*, by Irvine and Wells (1972) and Wells, Irvine and Scott (1980).

Although the above data suggest that the most stable groups seem to be singles or pairs, there appears to be a second level of association, of groups of up to ten or more, during migration between feeding areas. This level of association can be easily missed during short-term observations from a catcher boat, as typified by the following example. On 27 July 1983, ten whales were observed from 0900–2100 hrs from an observation point on the coast near Mys Pyatnisty. The whales were scattered over a wide area (the blows of some of the animals were only visible with binoculars); an observer from a vessel or an aeroplane passing through the area would have recorded them as 'single' animals (this may also partially explain the predominance of 'single' animals recorded by the catcher boat during its operation and by other vessels and aerial surveys). However, long-term observations revealed that all the animals were in fact moving northwards. In the evening they formed three groups of two animals and one of four. All the animals then moved quickly and purposefully north, each group blowing synchronously with its own respiratory rhythm.

Table 2

Numbers of groups of whales of different group sizes by month (A = August to N = November) and Division seen by the *Zvezdny* during the 1981 season. [1] November, [2]5 animals

	One whale				Two whales				Three				Four		
Divn	A	S	O	N	A	S	O	N	A	S	O	N	A	S	O
3	—	1	3	—	—	—	—	—	—	—	—	—	—	—	—
4	—	2	—	—	—	1	—	—	—	—	—	—	—	—	—
5	—	—	—	2	—	—	—	—	—	—	—	—	—	—	—
6	—	—	—	3	—	—	—	—	—	—	—	—	—	—	—
7	3	—	6	4	2	1	—	2	—	—	—	1	—	—	1[1]
8	2	3	—	—	—	—	—	—	—	1	—	—	—	—	—
8a	—	53	1	—	—	19	—	—	—	1	—	—	—	—	—
9	40	85	147	—	8	29	26	—	2	6	2	—	1	—	2
10	34	75	18	—	4	21	1	—	—	2	—	—	—	—	—
10/13	12	—	13	22	4	—	2	—	—	—	—	—	—	—	—
11	—	13	34	—	—	2	5	—	—	—	2	—	—	—	—
12	—	111	44	—	—	16	9	—	—	3	4	—	—	1	4
12/13	—	—	28	—	—	7	—	—	—	1	—	—	—	—	1[2]
13	4	18	112	7	1	3	9	—	—	—	2	—	—	—	—
13/14	—	5	—	—	—	—	—	—	—	—	—	—	—	—	—
14	19	11	—	—	4	1	—	—	—	—	—	—	—	—	—
15	2	—	—	—	—	—	—	—	—	1	—	—	—	—	—
16	—	—	3	—	—	1	3	—	—	1	—	—	—	—	—
All	114	376	412	38	23	101	55	6	2	16	10	1	1	1	8

Table 3

Number of whales (percent) encountered by group size during seasons 1981 and 1982 by the *Zvezdny*

	1981				1982			
	1	2	3	4+	1	2	3	4+
Jul	114(67)	46(27)	6(4)	4(2)				
Aug	376(60)	202(32)	48(8)	4(1)	311(66)	96(20)	45(9)	20(4)
Sep	412(71)	110(19)	30(5)	29(5)	418(57)	206(28)	69(9)	36(5)
Oct	38(67)	12(21)	3(5)	4(1)	156(49)	116(36)	30(9)	18(6)
Nov					183(65)	68(24)	18(6)	14(5)
Sum	940(65)	370(26)	87(6)	41(3)	1,068(59)	486(27)	162(9)	88(5)

Table 4

Variation in numbers and group sizes within the same Division on consecutive days during the 1982 season. N = no. of whales. Data from the *Zvezdny*

Divn	Date	N	1	2	3	4	Divn	Date	N	1	2	3	4	5
4	19.08	8	6	1	—	—	10/13	18.09	12	6	3	—	—	—
	20.08	4	4	—	—	—		19.09	12	6	3	—	—	—
7	31.08	10	2	2	—	1		20.09	5	5	—	—	—	—
	1.09	9	6	—	1	—	11	11.08	24	10	4	2	—	—
	6.10	2	—	1	—	—		12.08	5	3	1	—	—	—
	7.10	1	1	—	—	—		23.10	31	20	4	1	—	—
8a	22.09	10	5	1	1	—		24.10	12	12	—	—	—	—
	23.09	25	3	8	2	—	13	18.09	3	3	—	—	—	—
	26.09	27	4	10	1	—		19.09	3	3	—	—	—	—
	27.09	0	—	—	—	—		27.09	8	4	2	—	—	—
	6.10	10	6	2	—	—		28.09	41	10	4	1	1	1
	7.10	2	—	1	—	—		29.09	8	4	2	—	—	—
9	21.08	19	15	2	—	—		30.09	9	3	3	—	—	—
	22.08	18	6	3	2	—			1	1	—	—	—	—
	24.08	15	5	3	—	1		29.10	1	1	—	—	—	—
	25.08	10	3	2	1	—		30.10	3	—	—	1	—	—
	26.08	7	5	1	—	—			1	1	—	—	—	—
	27.08	7	5	1	—	—			2	—	1	—	—	—
10	21.08	11	5	3	—	—	14	1.10	10	8	1	—	—	—
	22.08	36	20	8	—	—		2.10	2	2	—	—	—	—
	27.08	8	6	1	—	—	14/18	11.10	14	12	1	—	—	—
	28.08	9	4	1	1	—		12.10	3	3	—	—	—	—
	5.09	5	5	—	—	—		16.08	16	10	3	—	—	—
	6.09	5	5	—	—	—		17.08	30	26	2	—	—	—

Table 5

Variation in the numbers and group sizes of gray whales within a day during the 1982 season. N = no. of whales. [1] = incl. two groups of 4 and one of 6; [2] = incl. one group of 6; [3] = incl. one group of 4

Divn	Date	Time	N	1	2	3	Divn	Date	Time	N	1	2	3
9	26.7	0600	10	6	2	—	3	31.7	0600	3	—	—	1
		0900	3	1	1	—			0900	9	—	—	2[2]
		1100	31	21	5	—			1000	2	—	1	—
10	27.7	0900	20	16	2	—	4	01.8	0700	3	1	1	—
		1100	5	3	1	—			0930	1	1	—	—
		2100	5	5	—	—			13–1800	20	14	3	—
13	27.7	1400	4	4	—	—	9	03.8	0600	8	2	—	1[2]
		1600	10	6	4	—			0800	5	2	—	1
		1800	6	6	—	—	11/12	03.8	0900	3	3	—	—
8a	28.7	0500	20	18	1	—			1000	14	6	2	1[3]
		14–1700	100	51	10	19[1]			13–1600	11	5	3	—
8	28.7	0700	4	2	1	—	16	04.8	0900	8	8	—	—
		1200	5	1	2	—			1400	10	5	1	1
8a	29.7	0600	21	—	—	7	13	13.8	0700	10	10	—	—
		1700	9	7	1	—			0830	5	—	1	1
8		1200	6	4	1	—			1000	20	8	6	—

Some characteristics of grouping behaviour

Acoustic communication

As far back as 1979, Captain Votrogov and myself were curious to know why single whales appeared to be most common during feeding, although they appeared to move between feeding areas in larger groups. We speculated that some acoustic communication may occur between these apparently single feeding animals.

In 1980, in Division 6, we observed what appeared to be a pair of whales and, about 1.5 km away, a 'single' whale, whilst simultaneously monitoring the area using hydrophones. No other whales were seen within a radius of some 15–20 km. Double signals were received from the pair of whales; the intervals between signals were 1–3 seconds and those between pairs of signals from 3–10 minutes. It was of course not possible to determine whether one or both whales were calling. No signals were heard from the 'single' animal. This pattern continued for about 1.5 hours after which the 'single' animal suddenly disappeared, to be resighted 10 minutes later alongside the pair. It adopted their respiratory pattern (surfacing about every 2 minutes, whereas it had previously surfaced about every 3.5 minutes); no more signals were recorded. It seems clear that these three animals comprised a group and also clear that had they been observed for a short period of time, either from a vessel or an aeroplane, they would have been recorded as a pair and a 'single' animal, not a group of three.

In 1982 and 1983, we performed seven observations of feeding gray whales (in Divisions 6, 8a and 12) while simultaneously monitoring them with a hydrophone. On each occasion, the whales were silent when in small 'close' groups of 2–3 animals and respiring in synchrony. However, as soon as they separated to distances of over about 800–1,200 m, short, occasional low frequency sounds were picked up on the hydrophone, suggesting that they were keeping in acoustic contact with each other. The seven cases can be summarised as follows:

> on one occasion an animal was shown to be a true single whale—it paid no attention to the signals of a pair of animals and eventually left the area;
>
> on one occasion, similarly to the 1980 case discussed above, a 'single' animal joined a pair of whales;
>
> on two occasions, 'single' animals which had been 1–1.5 km apart joined to form pairs, after they had been signalling every 5–12 minutes over 2–2.5 hour periods (on both occasions, the signals from each whale were monitored by separate boats, each with their own hydrophones);
>
> on three occasions (twice for two and once for three 'single' whales) when signals had ceased after periods of from 1.5–6 hours, the animals left the area at the same time and moving in the same direction, gradually coming closer together.

In summary then, it appears that stable groups may split up during feeding but that they keep in acoustic contact when they reach distances of over about 800 m. At distances less than this few sounds are heard. Moore and Ljungblad (1984) reported on sounds recorded near feeding gray whales but could attribute no function to them. It seems likely that one of the reasons for that was their short period of observation/recording (three observation periods totalling 4.5 hrs of which only 2 hrs of recording were suitable for analysis).

The above examples, and the case of the ten animals discussed in the previous section, show that considerable caution should be applied when inferring information about group sizes and in particular 'stable' group sizes, from short-term observations from sea or air.

Respiration patterns

In these waters, small groups of feeding or migrating gray whales exhibit certain synchronous patterns of respiration. When feeding at depths of 25–40 m, they usually surface together, or almost together, after dives of 2–4 minutes (Bogoslovskaya *et al.*, 1981).

The precise order of surfacing appears to be somewhat predictable: for example on one occasion when observing a group of five animals, at each surfacing the 'second' whale always appeared first, followed by the 'third', then the 'first' and 'fourth' together and then finally the 'fifth'. Each animal remained on the surface for no more than 2–3 seconds before diving again in the same order.

On many occasions when single animals were observed to join groups of 3–6 whales, this was seen to disrupt the respiratory rhythm of the group, usually with the animals remaining submerged for a longer time. Following this the 'single' animal would leave the group, accompanied by one of its members. The remainder of the group would then normally resume its earlier respiratory pattern, while the newly-formed group adopted its own pattern.

It seems clear that, as suggested by Pryor (1975), synchronous respiration is indicative of social closeness. It is also interesting to note that it is probably not easy for groups of more than three animals to remain in respiratory synchrony for long periods of time.

Cow–calf pairs

Cow–calf relationships are clearly different in nature to those between adults. In July and August, the calves generally leave their mothers and assemble together in certain areas. Some mothers remain with their calves for much longer periods, usually if the calf is weak (either through ill health or if it was born late in the season).

On one occasion, I observed a female bring an evidently weak calf into a small, shallow, sheltered bay near Mys Wittgenstein. She positioned it in a shoal in such a way that its blowhole was only slightly covered with water. The mother then moved out to sea, returning some hours later. Normally a calf swims under the mother and suckles from below, but this female positioned herself so that the calf only had to move a little from the position she had left it in to suckle. This it did for periods of about half a minute to a minute with breathing periods of 15–20 seconds. After about 10 minutes she began to push the calf with her head into deeper waters. The calf tried to position itself over its mother's back, while she dived and tried to swim next to it. After about half an hour, the calf again began to suckle for some 7–10 minutes. The pair then remained almost motionless near to each other for 1–1.5 hours. The calf then suckled for the last time before the mother, after staying with it a short time before pushing it into the shallows, moved out to sea. Observations of suckling were made over a three day period and suckling occurred as follows:

day 1—0500–0700 hrs, 1300–1540 hrs, 2035—dark;
day 2—0430–0600 hrs, 1400–1600 hrs and a third time, as suggested by her high respiratory rate, in darkness;
day 3—0527–0700 hrs, 1600–1700 hrs and, as on day 2, in darkness.

An interesting incident occurred on the third day. Three adult whales entered the bay at 1100 hrs, and one drove the calf from the shoal. The calf swam in deep water for about three hours, but did not leave the bay. As soon as the mother returned to suckle her calf, she understood the situation and twice struck the 'offending' animal in the upper jaw near the eye before swimming underneath it and forcing the back half of its body out of the water. The whale did not resist and afterwards the three adults remained in the bay for only a short while before leaving, heading north and breathing synchronously. As soon as they left, the mother went in and out of the bay three times before beginning to feed her calf.

Behaviour during hunting

The behaviour of groups during hunting can often reveal truly single animals. These animals may unexpectedly change their swimming direction during chasing and dive for long periods at great depth directly under the catcher-boat. Animals in groups of 2 or 3 are less mobile as they retain their synchronous swimming behaviour. Several authors have noted that when one animal had been harpooned, others in the group often stay with their wounded or killed partner. Zimushko and Ivashin (1980) noted such behaviour in groups of two and three whales, including pairs of the same sex and 'troikas' (trios) of two males and a female and vice-versa. In common with Bogoslovskaya *et al.* (1982), they noted that it was more common for a male not to leave a female than a female a male. Groups of more than three whales are usually not stable (Bogoslovskaya *et al.*, 1982) during chasing.

A group of four whales will divide into a single whale and a troika or into two pairs; a group of three may sometimes divide into a pair and single whale but a pair will seldom part. It is not clear why some whales remain together until one of them is killed while others do not. As noted above there appears to be no consistent pattern in terms of size or sex composition of the group.

ATTITUDES TO DIFFERENT AREAS

We have already noted the occurrence of large 'herds' of gray whales in Divisions 4, 12 and 14 when up to 2,400 animals may assemble in a restricted (and not particularly rich feeding) area. Such large groups unexpectedly forming away from the feeding grounds can also be observed in other species. For example, the blackheaded gulls, *Larus ridibundus*, behave in a similar fashion. Kharitonov (1983) found that after staying for a few days in an area rich in food, a group of birds would suddenly leave and assemble with many other birds in another area, possibly but not always rich in food and where of course the competition was extremely high. He also showed that the gulls tended to change their feeding areas from time to time even when they were still rich in food, as has been observed in whales and dolphins.

The regular presence of some gray whales in certain small areas at specific times of day has also been observed. In August 1980, a close troika of animals of similar size was seen from Mys Kygynin on Ostrov Arakamchechen for a five day period. The group emerged every day at 0900 hrs from the northern side of the Cape within 400–600 m of a walrus rookery. The whales always appeared in the same area regardless of the presence or absence of the walruses. The group then slowly moved around Mys Kygynin to Jarvy Lake on the southern shore of the Cape. At 1230 hrs, they moved in a southeasterly direction. The group consistently blew every 2–2.5 minutes during observations over the five days, and always in the same order with the 'middle' whale emerging the first, followed almost immediately by the second whale and then by the third, smallest animal which always kept 2–3 m from the two larger, darker animals.

CONCLUSION

The social structure of the Chukotka–California population of gray whales in the waters off eastern Chukotka is characterised by the considerable diffusion of their groups and the peculiar 'washing away' where one individual joins a group and 'steals' a member of it. Observations independent of whaling operations reveal that both true and false 'single' whales occur, the latter using acoustic one-or-two-way communication with their partners, enabling them to coordinate their behaviour at quite large distances. However, further work is needed to study and discover the meaning of many aspects of gray whale behaviour and distribution on the feeding grounds.

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ESTIMATING THE SIZE OF NATURALLY MARKED WHALE POPULATIONS USING CAPTURE-RECAPTURE TECHNIQUES

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ABSTRACT

The method of estimating population size from the capture and recapture of animals is reviewed with respect to populations of naturally marked whales. The paper is divided into three main sections dealing with (i) using natural markings to 'mark' an animal, (ii) the basic models, and (iii) the effect on population estimates of variation in the characteristics of individual animals. The two main populations of whales discussed are the North Atlantic humpback whale and the southern right whale. Suggestions are made concerning the sampling of naturally marked whale populations and the analysis of data from such experiments.

INTRODUCTION

The recognition of individual whales from photographs of natural markings is best known from the long-term studies of North Atlantic humpback whales (Katona, Baxter, Brazier, Kraus, Perkins and Whitehead, 1979; Katona and Whitehead, 1981), southern right whales off Peninsula Valdes, Argentina (Payne, Brazier, Dorsey, Perkins, Rowntree and Titus, 1983) and killer whales off British Columbia/Washington (Bigg, 1982; Balcomb, Boran and Heimlich, 1982). Photo-identification has also been used to recognise individuals from several additional species/stocks including minke whales off Washington State (Dorsey, 1983), eastern Pacific gray whales (Hatler and Darling, 1974), North Pacific humpback whales (Darling, Gibson and Silber, 1983; Darling and McSweeney, 1985; Baker, Herman, Perry, Lawton, Straley and Straley, 1985), North Atlantic right whales (Kraus and Prescott, in press), North Atlantic fin whales (M. L. Pratt, pers. comm.), blue whales in the Gulf of St Lawrence (Sears, 1984) and in the Indian Ocean (A. Alling, pers. comm.), sperm whales in the Indian Ocean (J. Gordon, pers. comm.) and bowhead whales (D. J. Rugh, pers. comm.).

Some of these studies have produced data which are potentially useful for providing information on population size through the application of capture-recapture analyses. The North Atlantic humpback data have been used fairly extensively for this purpose (e.g. Perkins and Whitehead, 1977; Whitehead, 1982; Whitehead, Chu, Perkins, Bryant and Nichols, 1983; Balcomb and Breiwick, 1984; Perkins, Balcomb, Nichols and De Avilla, 1984; Perkins, Balcomb, Nichols, Hall, Smultea and Thumser, 1985). Population size has also been estimated from the data for Peninsula Valdes right whales (Whitehead, Payne and Payne, in press). For the most part, violations of the assumptions of the various capture-recapture models have received little detailed discussion and in 1984 the

Scientific Committee of the International Whaling Commission recommended that a full review be undertaken of the applicability of these techniques to naturally marked whale populations. This paper was written partly in response to that recommendation.

There is a large body of literature on many aspects of capture-recapture techniques including discussion of the different models which are available, examination of model assumptions and the application of the models to particular field studies. The reader is referred to Cormack (1968; 1979), Otis, Burnham, White and Anderson (1978), and Seber (1982) for reviews of a statistical nature and to Cormack (1972), Begon (1979), Pollock (1981a) and White, Anderson, Burnham and Otis (1982) for reviews more suitable for the biologist. The purpose of this paper is to assess the applicability of capture-recapture techniques to estimating the population size of naturally marked whale populations by discussing how the assumptions of the models may be violated, how such violations affect estimates of population size and what can be done in practical terms to minimise the problems.

To do this I have divided the body of the paper into three sections. The first section deals with the consequences of using natural markings to 'mark' an animal and includes discussion of changes in markings with time, markings not being unique and recognising a 'marked' whale. The second section deals with the basic population models and a discussion of the different ways in which these models have been used in previous analyses. The third section deals with variation in the characteristics of individual animals and its effect on estimates of population size. This section largely comprises discussion of individual variation in survivorship and catchability. Catchability is divided into three processes for the purposes of this discussion: sighting a whale, photographing its natural markings, and treatment of the photograph. The section includes discussion of some theoretical studies which give an indication of how unequal catchability can affect population estimates.

USING NATURAL MARKINGS TO RECOGNISE INDIVIDUAL WHALES

Capture-recapture studies are usually conducted by altering the physical appearance of the captured animals in some way. This can be done by attaching an artificial tag, such as the banding of birds, by applying an indelible substance, such as painting insects, or by removal or alteration of part of the animal itself, such as toe clipping in small mammals. The method of marking is chosen to fit the animal being studied and the conditions of the experiment. Seber (1982, pp. 93–4, 487–8) gives a summary of marking methods.

Although the recognition of individual animals from natural markings is a common practice in behavioural studies, these data are rarely used for the estimation of population size. Apart from a study of alligators (Thompson and Gidden, 1972), I know of no others of this kind except for those on whales discussed in this paper. However, mention should be made of the use of capture-recapture methods on 'populations' of taxi-cabs (Bishop and Bradley, 1972; Carothers, 1973b), the latter reference being to an important study.

If the animals in a population can be recognised from their natural markings there are some obvious advantages to using this method to 'mark' them rather than one of the procedures stated above. Perhaps the most important of these is that the animals do not have to be physically handled because they are neither captured nor marked in the usual sense. Another advantage of appropriate markings is that they are permanent and not liable to fall or wear off as are tags or artificial marks. Being natural they do not affect the animals' behaviour in any way so that probabilities of capture and survival are unaffected and the experiment involves no discomfort to the animals. Payne *et al.* (1983) have discussed these and some other advantages with respect to southern right whales.

Countering these points are some disadvantages. It takes longer to recognise individuals from natural markings than from tags or artificial marks because photographs are essential if the markings contain a lot of information, as in whales. It is easier to make mistaken identifications using natural markings because the 'mark' is a pattern, possibly indistinct, and not, for example, a numbered or colour-coded tag. There is the possibility that natural markings change with time so that a 'marked' animal may not be recognised in a later sample. There is also the possibility that two or more individuals possess markings that are so similar that they are indistinguishable. The remainder of this section discusses some of the disadvantages and advantages and the effects that they have on estimates of population size.

Natural Markings Changing with Time

The natural markings chosen to recognise individuals in a population should be permanent and unchanging throughout the duration of the capture-recapture experiment. If they are not, an animal that has been 'marked' by recording the pattern of these markings may cease to be recognisable in later samples. This is equivalent to the problem of tag-loss in tagging experiments. The effect is to overestimate population size because fewer recaptures occur than should be the case. If the markings change quickly and extensively they are, of course, effectively useless for capture-recapture studies, but it is clear that this is not the case for those populations of whales that have been extensively studied in this way.

In studies of tagged animals it is common to estimate tag-loss rates by double-tagging a sample of the population. With natural markings a similar experiment can be conducted if some animals in the population can also be recognised by a different kind of natural mark. If these animals are recaptured two or more times the extent of any changes in either of these markings can be investigated and, if necessary, quantified. Payne *et al.* (1983) have conducted such an experiment on southern right whales using dorsal markings as a means of searching for changes in the pattern of callosities on the head. Although slight apparent changes were found, these did not affect the identification of the individual. The colouring did change from year to year but not in such a way that the patterns were unrecognisable. In addition, they found that the apparent slight changes in callosity patterns were distributed throughout the length classes sampled. The evidence therefore suggests that patterns of callosities in southern right whales remain recognisable throughout life.

Kraus and Prescott (in press) are more cautious in their assessment of changes in the patterns of callosities on the heads of North Atlantic right whales. They found that visible callosity patterns can change by movements of cyamids, by high peaks breaking off (important if identification is from a photograph taken from a boat) and by darkening over time. This study was over only three years and the authors recommend the long-term monitoring of callosity patterns to investigate their stability. Many of the callosity patterns on North Atlantic right whales are continuous (and thus contain less information) making them more difficult to define than the right whales off Peninsula Valdes, Argentina.

Perkins *et al.* (1984) address the problem with respect to North Atlantic humpbacks. They cite a sighting of a whale off West Greenland in 1982 which has been matched with a sighting off Bermuda in 1968 as 'a prime example of the retention of fluke patterns for at least that length of time' and consider any resulting bias in population estimates to be minimal. There are two flaws with this reasoning. Firstly, there is no independent evidence, such as other natural markings, that the two sightings in Bermuda and West Greenland are of the same whale. Secondly, even if they were, this does not preclude the possibility of the pattern changing on other individuals. C. A. Carlson and C. A. Mayo (pers. comm.) have shown that the patterns can change in young humpbacks. Darling and McSweeney (1985) state that the same is true in North Pacific humpbacks. What is needed is a comprehensive study of humpbacks that can be identified in more than one way (fluke patterns and dorsal fins) to try to quantify the effects, if any, on estimates of population size of any changes in patterns on the ventral surface of the flukes.

Uniqueness of Natural Markings

When the animals are identified by natural markings there is a possibility that two or more individuals are marked so similarly that they are effectively indistinguishable. As Pennycuick (1978) states 'there is no way to be absolutely certain that an individual with particular markings is the only one so marked in the population'. Pennycuick goes on to relate the probability that a given pattern will not be unique to the amount of information in the pattern and the population size. In other words, if the amount of information in the pattern can be quantified and population size can be approximated, the likelihood that a pattern is repeated in the population can be estimated. Payne *et al.* (1983) have estimated the number of distinguishable callosity patterns from photographs of the heads of southern right whales to be about 10^{14}. Even if this figure is reduced to half the number of orders of magnitude (10^7) and population size is estimated optimistically high at 10,000 animals, the probability that a pattern is duplicated is approximately one in two million. Clearly, this is an acceptable level in any field study. Payne *et al.* (1983) also calculated from their data the probability of not finding even one set of 'twins' in photographs of several whales together and in photographs of whales taken too far apart to be the same animal if 25 sets of 'twins' exist in the population. This probability is quite high (0.034) relative to the previous calculation but, as noted by the authors, will become lower as more information becomes available for analysis, providing of course that no sets of 'twins' are found.

No studies of this kind have been published for other species but in the case of humpback whales it should be a relatively straightforward task to estimate the amount of information in the shape of a fluke and its pattern, and hence to estimate the probability that a pattern is not unique. Because humpback fluke patterns clearly contain a large amount of information, comparable to southern right whale callosity patterns, it is reasonable to assume that the probability of a duplicate fluke pattern is very small. If duplicate animals did exist, this would result in an underestimate of population size because more apparent matches would be recorded than actually exist.

Other Considerations

'Marking' animals by taking photographs of their natural markings does not involve physically restraining them or altering their appearance so that it would seem reasonable to assume that 'marked' animals have the same probability of capture at any given sampling occasion and of survival from one sampling occasion to another as do 'unmarked' animals. Possible violation of this assumption could occur if the aircraft or boats used to take the photographs frightened the animals in such a way that after being photographed once, they then tried to avoid the vessels at future sampling occasions thus reducing their probability of being photographed. Alternatively, whales could become more 'friendly' after having been photographed once so that their probability of being photographed increased thereafter. Although these possibilities have not been investigated to my knowledge, it seems unlikely, based on published accounts of whale behaviour, that they are a problem. Payne *et al.* (1983) have documented the reactions of southern right whales to the presence of aircraft and boats. In response to the aircraft from which the photographs were taken, most whales demonstrated no change in behaviour. The exceptions were (i) whales which were milling or still, which seemed actively to avoid the aircraft and (ii) a very few whales (less than 2%) which took fright as the aircraft came overhead. Overall, Payne *et al.* (1983) felt that the aircraft caused a minimum of disturbance. If behavioural observations have been recorded for each whale photographed it would be a simple matter to examine the behaviour of whales at the time they were first sampled and on subsequent occasions. This would also apply to the behaviour of humpbacks being photographed from a boat.

The advantages of this technique of 'capture' and 'marking' without handling the animals with respect to population estimates should be stressed. In studies where animals are restrained and their appearance altered it is common for survivorship and/or catchability to be changed following first capture. For example, small mammals can become 'trap-shy' or 'trap-happy' once they have been captured, so that the probability of capture for animals trapped once or more is smaller or greater, respectively, than for those not yet captured. Another well documented problem is that of decreased survivorship of tagged fish. Although models have been developed to incorporate these problems and estimators of population size are available for certain cases (e.g. Pollock, 1975; Otis *et al.*, 1978), it is clearly better if they can be avoided in the first place. As discussed above, the photographing of natural markings of whales seems to be satisfactory in this respect.

One of the assumptions of the Jolly–Seber model (see 'Open population models', below) is that all animals which are captured have an equal probability of being returned to the population. This is necessary because in some studies, such as tagging fish, some animals are killed accidentally as a result of the capture and marking process, and this mortality should be a random variable. For studies in which the sample data are photographs of natural markings, this assumption is unnecessary because the animals are neither physically restrained nor handled in any way.

Making errors in identification of animals is possible in any capture-recapture study but is more likely to occur when looking at photographs of natural markings. S. K. Katona (pers. comm.) has pointed out that the number of errors in identification may be an increasing function of the number of photographs being handled. This is a potentially serious problem if, for example, relatively fewer matches were made as the number of photographs increased. In this case, a Jolly–Seber analysis would produce population estimates which increased with time. Analyses using a series of independent Petersen estimates e.g. Balcomb, Katona and Hammond's (1986) analysis of North Atlantic humpback data would not be affected because each estimate is calculated from data collected in one year only. Preliminary analyses of these data by the author using the Jolly-Seber model show that one data set did show an increasing trend whilst others did not. Further analyses are continuing.

A final consideration in this section is that of the time and facilities needed to deal with the photographs of natural markings. In studies using this method of marking animals the costs of camera equipment and film replace the costs in other studies of physically capturing the animals, marking equipment and application of the mark. In addition, in order that an animal be considered 'marked' its photograph must be processed and each one needs to be checked against all existing photographs to determine if it is a new animal or a recapture. Clearly, processing these photographs is a skilled and time-consuming task compared to the processing of, for example, numbered tags or patterns of mutilation. However, the field technique of taking a photograph is simpler and less time-consuming than capturing, marking or mutilating an animal. One facility which can aid the processing of photographs of natural markings is the computer. This could be at the level of cataloguing individuals by types of markings or at the more sophisticated level of storing a digitised version of the photograph in a computer. Using a computer in this way could greatly reduce the amount of time spent in processing each new photograph. K. C. Balcomb (pers. comm.) uses a relatively simple computer program to select North Atlantic humpback fluke photographs, stored on a video disk, which possess similar attributes to a new photograph in need of processing.

BASIC MODELS

This section presents the commonly used capture-recapture models and is divided into three sub-sections describing (1) models where the population is closed to birth, death, immigration and/or emigration, (2) models where the population is open to these processes and (3) what use has been made of these models in previous analyses. No attempt is made here to present the models as following on logically from one another; rather, they are included for reasons of background and reference.

Closed Population Models

(i) Two samples (Petersen estimator)

This estimator of population size is based on the simple argument that the proportion of marked animals recaptured in a sample of the population is equivalent to the proportion of marked animals in the total population, N. So if n_1 animals are marked in the first sample and m_2 of these are recaptured in a second sample of size n_2 we have the relationship

$$\frac{m_2}{n_2} = \frac{n_1}{N} \quad \text{and} \quad \hat{N} = \frac{n_1 n_2}{m_2}.$$

The assumptions of this model have been stated and discussed in many texts and are here listed after Seber (1982, p. 59) for reference.

(1) The population is closed.
(2) All animals have the same probability of being caught in the first sample.
(3) Marking does not affect the catchability of an animal.
(4) The second sample is a simple random sample.
(5) Animals do not lose their marks.
(6) All marks are reported on recovery.

As Seber notes, these assumptions are not mutually exclusive. If assumptions 1, 4, 5, and 6 hold, the estimate $\hat{N}$ above is the maximum likelihood estimate of the resulting hypergeometric model. $\hat{N}$ is asymptotically unbiased whether sampling is without replacement (Chapman, 1951) or with replacement (Bailey, 1951). However, if sample sizes are small, Chapman's (1951) modified estimator for sampling without replacement

$$N^* = \frac{(n_1 + 1)(n_2 + 1)}{m_2 + 1} - 1$$

is exactly unbiased if $n_1 + n_2 > N$. Bailey's (1951) modified estimator for sampling with replacement

$$N_1 = \frac{n_1(n_2 + 1)}{m_2 + 1}$$

has bias of order e^{-m_2}. Seber (1982, pp. 59–70) discusses these models, their estimated variances, confidence intervals and desired minimum sample sizes. For studies utilising photographs of naturally marked whales, Bailey's modified estimator, N_1, is the most appropriate because sampling is with replacement in these studies.

The Petersen estimator can still give an appropriate estimate of population size even if certain of its assumptions are not met. One such case is that of the assumption of population closure. If mortality alone occurs between samples, the Petersen estimator gives a valid population estimate at the time of the first sample. If birth, or recruitment, alone occurs, the estimate is valid at the time of the second sample. However, if both are occurring, population size will be overestimated at the time of both samples, as shown neatly by Seber (1982, p. 73).

We can extend Seber's equations to obtain an expression for approximate bias resulting from both death and recruitment in the Petersen estimator. Let marked and unmarked animals have the same average probability of survival, φ, from the first to the second sample and let recruitment to the population between these two times be a proportion, α, of initial population size, N. Then the expected proportion of marked animals in the second sample is approximately

$$E\left[\frac{m_2}{n_2} \,\middle|\, n_1\right] \approx \frac{\varphi n_1}{N(\varphi + \alpha)}.$$

Replacing the expected proportion by that observed we have

$$\frac{\varphi n_1 n_2}{m_2} = N(\varphi + \alpha) \quad \text{and} \quad \hat{N}\frac{n_1 n_2}{m_2} = \frac{N}{\varphi}(\varphi + \alpha) = N\left(1 + \frac{\alpha}{\varphi}\right).$$

Thus, the Petersen estimate, $\hat{N}$, is biased upwards for population size at the time of the first sample, N, by the proportion α/φ, and at the time of the second sample, $N(\varphi + \alpha)$, by a factor $1/\varphi$. In general, the higher the recruitment rate and the lower the probability of survival (that is, the greater the rate of turnover of the population) the greater the positive bias. Values for these parameters are difficult to estimate but taking educated guesses at extreme values of about $\alpha = 0.1$ and $\varphi = 0.9$ per year we obtain an approximate bias of +11% over one year, +23% over two years and +37% over three years. These figures apply to both first and second samples because the parameter values chosen correspond to a population at equilibrium.

Another case is that of the assumption of random sampling. If assumption 2 holds and the first sample is a random sample, then assumption 4 (that the second sample be random) can be violated without biasing the population estimate if (i) there is uniform mixing between samples, (ii) if mortality is occurring, marked and unmarked animals have the same probability of surviving from the first to the second sample and (iii) all animals at each sampling location have the same probability of capture whether marked or not. If these three further assumptions can be made, Robson (1969) has suggested that 'the most effective plan for the 2-sample experiment consists of a determined effort to obtain a random sample for marking and then, exploiting the habits of the creature, to obtain a large, if selective, sample in the recapture stage'.

(ii) *Multiple samples*

Taking multiple samples from a closed population is widely known as a Schnabel census after Schnabel (1938). The maximum likelihood estimators of population size for these experiments cannot be written in simple closed form and estimation must be done by numerical solution of the appropriate equation. Otis *et al.* (1978) have given a number of models for closed populations which differ by relaxation of the assumption of equal catchability in various ways, where catchability may be defined as the probability of an animal being captured and identified. They presented models for three ways in which catchability could vary; from one sampling occasion to another, as a result of a response to capture and/or marking, or because of inherent differences in individual animals, often referred to as heterogeneity. Estimators of population size were derived for each of these three cases, the case where catchability varies as a result of both the latter two and the case where catchability is constant over all the variables. The estimator for the case where catchability varies from one sampling occasion to another is the standard Schnabel estimator. No estimator was derived for an extension of this case to include variation due to inherent differences in individual animals, potentially the most useful case in many studies. Assumptions for these models are the same as for the Petersen estimator except that random sampling and equal catchability (if appropriate) must occur at each sampling occasion.

In a recent analysis of North Pacific humpback whales, Darling and Morowitz (1983) proposed a model to estimate population size which is simply a description of binomial sampling. This model treats animals as being sampled one at a time. Craig (1953) and Seber (1982, pp. 136–8) have discussed this special case of the Schnabel estimator, where the number of animals in each sample is set to one. The number of samples is then the number of photographs taken. The model assumes that each time a photograph is taken, it is equally likely to be any whale in the population. This assumption must be impossible to satisfy in practice because the population cannot possibly mix completely between the taking of successive photographs. Consequently, this is not an appropriate model for whale populations. An alternative might be to divide the data up into units of time, a unit could equal a day's work, for example, and to use the Schnabel estimator or one of Otis *et al.*'s (1978) models.

Otis *et al.* (1978) discuss tests for population closure and conclude that, because the available tests have little chance of rejecting the null hypothesis of closure without a large sample or a marked departure from closure, a biologist should rely mainly on his/her knowledge of the experiment to determine whether or not the population is closed. Furthermore, tests for closure assume that capture probabilities are equal for all animals within a sampling occasion so that rejection of the null hypothesis may mean that the population is closed but that capture probabilities are unequal.

Open Population Models

The most widely used open population model is that proposed independently by Jolly (1965) and Seber (1965), and usually referred to as the Jolly–Seber model. The model provides estimates of population size for each sampling occasion except the first and last, and estimates of survivorship and recruitment for each sample except the first and last two. The estimators of the Jolly–Seber model have been presented in a simple way by Cormack (1973).

The estimator for population size is based on two equations: an estimate of the total number of marked animals in the population at the ith sampling occasion, M_i, and a general form of the Petersen estimate for the ith sampling occasion, $\hat{N}_i = M_i n_i / m_i$, where n_i is the number marked and m_i is the number recaptured in the ith sample. The estimate $\hat{M}_i$ is obtained by assuming that two groups of animals, those marked at time i, the s_i, and those marked up to but not including time i, the $(M_i - m_i)$, will be recaptured in the same proportion subsequent to time i. Thus, if z_i of the $(M_i - m_i)$ and r_i of the s_i are recaptured after time i, we have the relation

$$\frac{z_i}{M_i - m_i} = \frac{r_i}{s_i} \quad \text{and} \quad \hat{M}_i = \frac{s_i z_i}{r_i} + m_i.$$

Substituting the above into the generalised Petersen estimate, we obtain

$$\hat{N}_i = n_i \left[1 + \frac{s_i z_i}{r_i m_i} \right] .$$

The assumptions of the Jolly–Seber model have been widely discussed and are listed here after Seber (1982, p. 196) for reference.

(1) Every animal in the population, whether marked or unmarked, has the same probability of being caught in the ith sample, given that it is alive and in the population when the sample is taken.

(2) Every marked animal has the same probability of surviving from the ith to the (i + 1)th sample and of being in the population at the time of the (i + 1)th sample, given that it is alive and in the population immediately after the ith release.

(3) Every animal caught in the ith sample has the same probability of being returned to the population.

(4) Marked animals do not lose their marks and all marks are reported on recovery.

(5) All samples are instantaneous.

As with closed population models, small sample size can result in substantial bias in the Jolly–Seber estimator of population size. Gilbert (1973) found that when the assumption of equal catchability holds, a severe negative small sample bias results if the probability of capture is less than about 0.2. When heterogeneity of capture probabilities was present, however, small-sample bias was generally rendered insignificant by bias resulting from unequal catchability (see below). Seber (1982, p. 204) suggests changes to the above equations to reduce small sample bias which lead to a modified estimator

$$N_i^* = \frac{n_i + 1}{m_i + 1} \left[\frac{z_i(s_i + 1)}{r_i + 1} + n_i \right] .$$

Manly (1971), in a simulation study of the robustness of Jolly's (1965) variance formulae, found that for small sample sizes estimates of the variance of $\hat{N}_i$ were highly correlated with the estimates themselves. Consequently, overestimates appear less precise than they really are and, more importantly, underestimates appear more precise than they really are. However, if confidence limits (which are asymmetric) are considered instead of standard errors and coefficients of variation, there is no problem (J. G. Cooke, pers. comm.). Carothers (1973a) has suggested that estimates subject to a large small-sample bias will also be characterized by a large estimated variance so that there is little value in devising estimates with lower small-sample bias because such estimates are of limited use due to their poor precision. Roff (1973a) looked at sampling intensities necessary to achieve coefficients of variation which are reliable indices of the actual error. His theoretical and numerical results support those of Manly (1971) and also show that to achieve a coefficient of variation of 5% or less (the level determined by Manly at which an estimate can be considered reliable) the population must be greater than 500 and the probability of capture greater than 0.5. Roff concludes that, because such sampling intensities are unlikely to be achieved in practice, capture-recapture estimates are of limited use. More recently, Manly (1977) has proposed a method of estimating confidence intervals using a modified version of the jackknife procedure which he considered reasonable if at least 20 sub-samples are used.

Cormack (1980, 1981, in press a, b) has proposed the use of a log-linear model which assumes that recaptures of marked animals are Poisson distributed rather than according to the usual multinomial distribution. Sandland and Cormack (1984) discuss the statistical basis for these models. The maximum likelihood estimator for population size for the general open population model is the same as for the standard Jolly–Seber model but the estimates of variance are different. Cormack's application of the log-linear model, through the GLIM statistical computer package, allows variations on the standard Jolly–Seber model. Sampling effort may be set constant among all samples, births may be set to zero and survivorships set to unity, or both (a closed population model), and specific capture histories may be given zero weight to investigate the effects of removing outlying observations. This application is mentioned here because the model can vary in form from the standard Jolly–Seber open population model to a closed population model.

Previous Analyses

Two extensive data sets of photographs of natural markings on whales have been used to estimate population size through the application of capture-recapture techniques. These data sets are for North Atlantic humpback whales and southern right whales in the region of Peninsula Valdes, Argentina.

North Atlantic humpback whales are known to migrate between winter breeding grounds in the Caribbean and summer feeding grounds in northern latitudes (Katona, Harcourt, Perkins and Kraus, 1980). This knowledge is the result of studies undertaken by several research groups involving photography of the ventral surface of the tail flukes from which individual animals can be recognised (Katona *et al.*, 1979). Analysis of the photographs, some of which were taken as early as 1968, has shown that whales seen in the Caribbean can be matched with whales seen in Newfoundland/Labrador, the Gulf of Maine (Katona and Whitehead, 1981), West Greenland (Perkins *et al.*, 1984; 1985) and Iceland (Martin, Katona, Matilla, Hembree and Waters, 1984). Current published data show that generally no whale photographed in one feeding area is photographed in another, but that whales from all feeding areas mix together on the breeding grounds (Balcomb, 1984). There have been some whales photographed in the Gulf of St Lawrence which have previously been seen either in Newfoundland/Labrador or in the Gulf of Maine, but not both (Katona, Beard and Balcomb, 1985). Recently, a photograph taken in the Gulf of St Lawrence has been matched with one of a calf taken in West Greenland (IWC, 1986).

Analyses of these data have put the samples together in different ways using different models. Whitehead (1982), Whitehead *et al.* (1983), Perkins *et al.* (1984; 1985), Hammond and Larsen (1985) and Whitehead and Glass (1985) have analysed data collected from the same site at the same time each year. Whitehead (1981), Balcomb and Breiwick (1984) and Balcomb, Katona and Hammond (1986) have calculated a series of Petersen estimates by treating animals photographed on the feeding grounds as the first sample and animals photographed on the breeding grounds, approximately six months later, as the second sample. Perkins and Whitehead (1977) and Whitehead *et al.* (1983) divided the data collected during one season on a daily basis and calculated a Schnabel estimate. Whitehead and Glass (1985) also did this and, in addition, used the Jolly–Seber model on daily data.

Treating the population in one season as closed and taking days (or whatever) as sampling units in order to use a multi-sample model such as the Schnabel estimator or one of the models proposed by Otis *et al.* (1978) is appealing. The length of the experiment is short relative to the life span of the animal, with associated low mortality and absence of births, and population closure can be approximated to a high degree. However, with this sampling scheme there is a greater chance that the population will not be sampled randomly because of the very short time available for the animals to mix between samples and the difficulty in conducting a random survey of the entire population in a short time. In addition, sample sizes per sampling unit would be smaller with this method than if the sampling unit were the whole seasonal period, with consequently fewer recaptures.

Taking the inter-sampling period as six months or one year does result in much larger samples and numbers of recaptures, but the longer period between samples results in a poorer approximation to population closure. In particular, animals are dying throughout the year and, if samples are taken annually at the feeding grounds, calves will be born between samples. With a six-month interval between samples and no births, the Petersen estimator gives a valid population estimate at the time of the first sample, as noted earlier in this section. With annual samples the situation suggests the use of an open population model such as the Jolly–Seber. However, all the above-mentioned analyses, with the exception of Whitehead (1981), Hammond and Larsen (1985) and Whitehead and Glass (1985) have utilised only closed population models, largely series of Petersen estimates. One reason for this in the past has been the small number of samples which have been taken, but there should now be sufficient data in several areas for Jolly–Seber estimates of population size to be calculated. The author has undertaken some preliminary analyses of these data using the Jolly–Seber model and variations on it and this work is continuing.

The southern right whales at Peninsula Valdes, Argentina have been sampled regularly since 1970, as described by Payne *et al.* (1983). Sampling has taken the form of aerial photographs of the callosity patterns on the heads of the whales taken on flights at altitudes of 200 m or less and within 2 km of the shore line. The flights took place mostly in September, October and November when the whales were most abundant. The whales were concentrated along three lengths of coastline at Valdes but many flights were unable to cover all three regions because of time and/or weather. Whitehead, *et al.* (in press) have estimated the population size of these whales using the Jolly–Seber estimator on data collected from 1970 to 1977 and treating all the flights in a year as the sample for that year. When the data collected from 1978 to 1984 have been analysed, it should be possible to increase the precision of the population estimate because of the longer series of samples.

Analyses of the North Atlantic humpback and southern right whale data suggest a choice between a series of Petersen estimates and a Jolly–Seber estimate. In terms of bias due to violation of the assumption of population closure, the Jolly–Seber estimator is more desirable. However, the Petersen estimator gives more precise results because of the less restrictive assumptions and so may be more appropriate if bias due to the population not being closed can be safely ignored or estimated as described above.

VARIATION IN THE CHARACTERISTICS OF INDIVIDUAL ANIMALS

The commonly applied capture-recapture models described above are all based on the general assumption that each individual in the population has the same characteristics and behaves in the same way. Thus, all animals must have an equal probability of being captured (assumptions 2, 3 and 4 for the Petersen model, assumption 1 for the Jolly–Seber model) and all animals must have an equal probability of surviving from one sample to the next (implicit as unity for the Petersen model, assumption 2 for the Jolly–Seber model). Just as there are general models which allow catchability and survivorship to change following first capture (see above), there are also general models allowing these parameters to vary from individual to individual. Otis *et al.* (1978) have derived an estimator of population size based on the jackknife procedure for closed populations which allows for heterogeneity of capture probabilities. Unfortunately, no estimator has been derived if capture probabilities are also allowed to vary from sample to sample. For open populations, the models of Robson (1969) and Pollock (1975) allow catchability and/or survivorship to vary among individual animals but there are no suitable estimators of population size.

Given that there may be no estimator of population size for the particular model that best describes the circumstances of a specific capture-recapture experiment, it is worth looking in some detail at how the assumptions of equal survivorship and equal catchability are violated by inherent differences among individuals and how such violations effect estimates of population size which are based on these assumptions.

Equal Probability of Survival

Estimates of survivorship or rates of mortality are extremely difficult to obtain for whale populations. Thus it is not possible to say with any confidence whether or not mortality rate is a function of age or sex or any other characteristic of the population. However, one would expect that whales would be similar to other long-lived mammals and be characterised by relatively high juvenile mortality rates, lower rates during middle age followed by a steady increase to higher rates for old animals. Recently, de la Mare (1985) has examined several sets of data obtained by ageing whales killed in commercial operations. Although there are problems in the interpretation of these data, there is strong evidence of age-dependence in mortality rates of a type to be expected of a large mammal, at least for post-juveniles. De la Mare (1985) also found slight differences between sexes in some populations.

Unfortunately, although it may be reasonable to assume that whale mortality rates are age-dependent, and there are estimators of population size which allow for age-dependent survivorship (Pollock, 1981b; Stokes, 1984), this is of little practical use if the sampled animals cannot themselves be aged. This will usually be the case for photographed whales, except for calves or individuals that have been seen as calves in previous samples. It becomes important, therefore, to assess the effects that age-dependent mortality may have on estimates of population size. This has been addressed by Manly (1970) who investigated the behaviour of three different open population models using computer simulation. Manly looked at several different mortality regimes and found that when mortality increases with age the Jolly–Seber method tends to underestimate population size but that when juvenile mortality was high and then decreased with age the method overestimated population size. This is intuitively obvious if one considers that marked animals are on the average older than the population as a whole, because the older an animal is, the more chances it has had to be captured and marked. Hence, because survival rates are estimated only from marked animals, these rates will be positively biased when mortality is less for old animals than for young animals and negatively biased when mortality is greater for old animals than for young animals. Population estimates will be biased in the same directions because marked animals with a positively biased rate of survival will appear to remain in the population longer than they really do, and vice versa. Manly (1970) also found that a survivorship regime characterised by relatively high mortality rates for both young and old animals but being lower in middle age led to no definite pattern in the estimates. Overall, his results suggest that the Jolly–Seber method of estimating population size will provide estimates which are not greatly biased, as long as mortality rates are not strongly age-dependent.

Seber (1982, p. 232) notes that if survival is independent of whether or not an animal is marked and the probability of capturing an animal is independent of its age, then the Jolly–Seber method will not be greatly affected by age-dependent mortality because the two groups of marked animals, the $M_i - m_i$ and the r_i, will have much the same age distributions so that

$$\frac{z_i}{M_i - m_i} \approx \frac{s_i}{r_i}.$$

The age-dependence demonstrated by de la Mare (1985) is characterised by mortality increasing with age for animals recruited to the catchable population. From Manly's (1970) results we would expect, therefore, a negative bias in estimates of population size. However, because mortality rates in young animals are widely held to be relatively high, we might expect that this negative bias would be reduced. Certainly, the age-dependence demonstrated by de la Mare (1985) does not appear to be strong when compared to the most appropriate of Manly's (1970) regimes of survivorship, which produce estimates of mean bias in Jolly–Seber population estimates mostly in the range ±3%. Consequently, it is with some confidence that we can dismiss age-dependent mortality as a minor problem in the use of capture-recapture data to estimate the population size of whale populations. If a very long data series were to be analysed, age-dependent mortality could become more of a problem.

Equal Probability of Capture

It is probably true to say that in most populations of animals inherent differences exist in the characteristics and behaviours of individuals such that capture probabilities are heterogeneous, regardless of the method of sampling. Roff (1973b) provides a list of over 40 studies where equal catchability was investigated. Less than a quarter of these indicated equal catchability to be the case, and the tests used had little power to reject this null hypothesis (see below). If this is the case, the assumption of equal catchability, central to all the commonly-used models such as the Petersen, Schnabel and Jolly–Seber models, is violated. It is important therefore, to look at generalised models, which allow heterogeneity of capture probabilities, to be able to test for deviations from equal catchability and to investigate the robustness of the more restrictive models to violations of their assumption of equal catchability.

As noted above, estimators of population size are not available for all forms of the generalised models developed to allow the relaxation of the assumptions of the commonly used models. More specifically, when capture probabilities are allowed to vary because of inherent differences among individuals, there is no suitable estimator of population size for open population models (Pollock, 1975) nor for closed population models if capture probabilities are also allowed to vary among samplings (model M_{th} of Otis *et al.*, 1978). More recently, Pollock (1981b) and Stokes (1984) have proposed generalised forms of the Jolly–Seber model which allow catchability (and survival) to be age-dependent. Stratifying by age (and sex) would make good sense biologically and statistically, as noted by Bishop and Sheppard (1973), and these models may be useful if animals can be assigned to age-classes when captured. It should be stressed, however, that such stratification would be likely to deal with only part of the problem of heterogeneity of capture probabilities.

Pollock (1982) has also proposed a method of analysis which combines the use of both open and closed population models in an attempt to eliminate bias resulting from heterogeneity of capture probabilities. He suggests dividing the data in each major sampling period into several sub-samples and using Otis *et al*'s (1978) closed population model M_h (which allows heterogeneity of capture probabilities) on the sub-samples to estimate population size at each major sampling occasion, and then using the usual Jolly–Seber open population model to estimate survival rates. The argument for this is that estimators of population size are sensitive to heterogeneity of capture probabilities but estimators of survivorship are not. This model could be useful if a sufficient number of sub-samples could be taken during each major sampling period. The problems in many studies would be ensuring that each sub-sample were representative and obtaining enough recaptures from sub-sample to sub-sample. Pollock and Mann (1983) combine the above two ideas to present a design for the use of sub-samples where catchability can vary within an age-class.

A method which can be used to test for deviations from the assumption of equal catchability is that of P. H. Leslie, presented as an appendix to Orians (1958). This method is discussed in detail by Seber (1982, pp. 161–2, 226–8). It is a test that sampling is random within the marked population only, i.e. that all marked animals have the same probability of capture. If marked and unmarked animals are assumed to mix uniformly between samples or if there is a random sampling, this can then be taken as a test of equal catchability for the whole population. Whitehead *et al.* (in press) have used this test on their southern right whale data, and found that for all animals except calves there was a significant departure from the null hypothesis of equal catchability.

Leslie's test only utilises a proportion, possibly small, of the available data, but Carothers (1971) has proposed an extension which overcomes this drawback, the only restriction for the test being that there should be at least 20 contributing animals for each sample. These need not be the same animals in each sample as is the case in Leslie's original test. However, in an application of this test on data collected from a 'population' of taxicabs, Carothers (1973b) found that the null hypothesis of equal catchability was not rejected even though heterogeneity was present as determined by a more powerful test utilising the known number of taxi-cabs. Thus, even the best test available for real populations may not always detect the presence of heterogeneity of capture probabilities. Roff (1973b), in a simulation study of several tests of equal catchability, but not including Carothers', came to the same conclusion. More recently, Carothers (1979) used his test to show a highly significant departure from the assumption of equal catchability in an analysis of a fulmar population.

The robustness of capture-recapture models which assume equal probability of capture to violation of this assumption in the form of inherent differences among individuals has been investigated in a number of studies. Carothers (1973a) used analytical and simulation methods to investigate relative bias resulting from heterogeneity of capture probabilities for open populations. He found relative bias in population size to be negative, and less for intermediate sampling occasions than for those at the beginning and end of the sequence. The estimated variance of population size was likewise a minimum for the middle marking occasion. The reason for the negative bias in population estimates can be seen intuitively from the fact that animals captured more times in previous samples have higher probabilities of being captured in subsequent samples, causing a positive dependence between samples. We have already seen that estimated variances are correlated with the estimates of population size themselves, as shown by Manly (1971) and Roff (1973a). This results in the group of all marked animals, the M_i, having a higher average probability of recapture than the population as a whole, the N_i, which also contains unmarked animals. Thus, $m_i/M_i > n_i/N_i$ and N_i is underestimated by n_iM_i/m_i. Carothers (1973a) also showed that relative bias increased with the coefficient of variation of mean capture probability, a result which supports the intuitive feeling that the greater the range of capture probabilities, the greater the bias.

A similar study by Gilbert (1973) also found the negative relative bias in population size to be minimized at the middle of the series of samples. He used a number of different specific distributions of capture probabilities in his simulations and found that little negative bias results from those distributions where mean probability of capture was greater than 0.5 and concludes, therefore, that experimenters should aim to ensure that most animals have a high probability of capture rather than trying to ensure equal probability of capture. This may be good advice but unfortunately would be impossible in practice in many studies because of restrictions on time, funding and personnel.

Although not mentioned by him, Gilbert's (1973) results also corroborate Carothers' (1973a) observations that the distribution of capture probabilities has an important bearing on the size of the relative bias. Take, for example, distributions XVI and XVII from Gilbert's Table 1 (p. 502). The probabilities of capture are distributed as follows:

		Probability of Capture									
		0.05	0.15	0.25	0.35	0.45	0.55	0.65	0.75	0.85	0.95
Percent of	XVI	4	4	4	4	4	4	8	8	20	40
distribution	XVII	0	0	0	0	4	10	18	24	28	16

The mean capture probabilities are very similar for the two distributions (0.734 for XVI, 0.760 for XVII) but their coefficients of variation are quite different (0.375 for XVI, 0.181 for XVII, taking sample size as 100 in each case). This results in a relative bias in population size estimated from distribution XVI which is 7 to 16 times that for population size estimated from distribution XVII, depending on the length of the experiment (Gilbert, 1973, p. 514, Table 2). The approximation suggested by Seber (1982, p. 507) that relative bias in population size is roughly equal to the square of the coefficient of variation appears to hold true for Gilbert's (1973) results.

Carothers' (1973b) study of taxicabs is interesting as an example of an experiment in which total 'population' size is known so that bias in estimates of population size could be quantified and, as mentioned above, the power of the best available test for unequal capture probabilities be investigated. Carothers (1973b) found that there was indeed heterogeneity in capture probabilities and that, using Chapman's (1951) modification of the Petersen estimator, population estimates were biased downwards by up to 30%. Even when a sampling scheme which was specifically designed to try to ensure equal probability of capture was used, heterogeneity was still present resulting in a negative bias of 15%. Carothers (1973b) cites this as 'further evidence that equal catchability is an unattainable ideal in natural populations'.

The messages from these studies are that equal probability of capture is unlikely in practice but that negative bias resulting from heterogeneity can be reduced by making capture probabilities as equal and as high as possible. Unfortunately, these goals may be difficult to achieve in practice for populations of whales.

More recently, Jolly and Dickson (1983) have discussed the problem of heterogeneity of capture probabilities and its effect on estimates of population size calculated from the Jolly–Seber open population model. As well as providing a clear description of the effects of heterogeneity, Jolly and Dickson suggest that the method of Carothers (1979) for reducing bias resulting from heterogeneity in estimates of survival rate could also be applied to the estimation of population size.

This method relies on the assumption that the effect of unequal catchability is dependent only upon the variance of its distribution. As discussed above, Carothers (1973a) found relative bias in population estimates to increase with the coefficient of variation of mean capture probability.

Another approach to the problem is to examine the experimental circumstances of each particular study to try and assess the extent of the problem of heterogeneity of capture probabilities and to look for ways in which it may be reduced. For naturally marked populations of whales this is rather different from other situations such as setting traps for small mammals or taking a sample of fish from a net, and it is worth discussing in some detail.

In investigating whether or not naturally marked whales have equal probability of being captured by photographs, it is convenient to divide the process of 'capture' and 'marking' into three component parts. Firstly, the whales must be sighted by conducting a sample survey of some kind, usually from a boat or an aeroplane. Secondly, once a whale has been seen it must present itself in such a way that a photograph of its natural markings can be taken. Thirdly, once the best photograph of a particular whale has been selected, a decision must be made concerning how it should be treated. 'Capture' and 'recapture' are identical processes. For all whales to have equal probability of capture they must all have the same probability of being sighted and of presenting their natural markings. Strictly this need not be true if the product of these probabilities were the same for all animals but we can ignore this in practice. In addition, the photographs must all be treated in the same objective manner. These three stages of the 'capture' and 'marking' process are now discussed.

(i) Equal probability of sighting

For all whales to have an equal probability of being sighted in a given sampling period we must either assume that the probability of a whale occurring at any given location in the area occupied by the population is the same for each whale, i.e. uniform mixing occurs in the population, or we must sample the area randomly. If the whales truly mix uniformly, there is no problem in assuring equal probability of sighting. However, as noted by Seber (1982, pp. 82–3) it is advisable to aim for a random sample rather than rely on uniform mixing. A random sample can be achieved by designing the sample survey such that each point in the area occupied by the population has an equal probability of being sampled. In practice, a stratified random sample may be more appropriate.

We are here assuming that all animals in the population are present in the survey area for the duration of each sampling occasion. In fact, this is unlikely to be the case for a number of reasons. A random sample of whales may be absent from the survey area at each sample. This could occur if there were uniform mixing of the population but the survey area did not cover the entire area inhabited by the population, or if a random selection of animals did not migrate to the survey area. Alternatively, a specific group of individuals may consistently spend less time in the survey area or may consistently be less likely to be present or sighted than the rest of the population. This could occur if individuals in the population always segregated in the same way during migration and sampling overlapped the periods when whales were still arriving or still leaving, or if a certain section of the population returned less often to the survey area or was always more difficult to sight than the rest of the population. Finally, an extreme case, a part of the population may never be available to be sampled. This could occur if segregation occurred during migration or on the study area and sampling consistently excluded a section of the population, or if some animals never migrated to the survey area.

These three circumstances have different effects upon the probability of sighting whales. The absence of a random sample of whales from each sampling occasion does not introduce heterogeneity into the capture probabilities because each whale has the same probability of being present in the survey area and the same probability of being sighted given that it is in the area. However, if some individuals are consistently less available to be sampled, heterogeneity is present because this group of animals will have a lower average probability of being sighted than the rest of the population. If some individuals are never available to be sampled, these animals will simply be excluded from any population estimate.

The way in which the samples from the North Atlantic humpback population can be put together has been discussed above under Previous Analyses in the Basic Models section of this paper. The question of equal probability of sighting concerns the ways in which the whales have been sampled within sampling periods. Are all whales equally available to be sighted or are there sections of the populations which are consistently less available or not available at all? The situation differs quite markedly among the different feeding and breeding areas.

All photographs from the West Greenland feeding area were taken in the summers of 1981, 1982 and 1983 on cruises specifically designed to survey humpback whales in that area (Perkins, Bryant, Nichols and Patten, 1982; Whitehead *et al.*, 1983; Perkins *et al.*, 1984; 1985). Although cruise tracks were not selected randomly, they were chosen to provide a good overall coverage of the area in each year. The area surveyed was similar in all three years except that in 1983 it was possible to search the waters off Fredrickshaab. Ice had made them unnavigable in 1981 and 1982. Perkins *et al.* (1985) believe that the West Greenland humpbacks 'comprise a single and unified feeding aggregation'. If this is true and uniform mixing occurs between sampling occasions, the three samples of humpbacks off West Greenland should be representative of the population. However, it is not possible to be certain that this is true from such a small sample. Hammond (1985) has shown that there is evidence to suggest incomplete mixing but further analyses and, ideally, more data are needed to clarify this point.

Equal probability of sighting is unlikely to be the case for samples taken in the Gulf of Maine feeding area. Because of the accessibility of this area, photographs have been taken not only by researchers, but also by individuals from the public on an opportunistic basis. Humpbacks are known to return to the same areas of the Gulf year after year and many of the data have been collected on Stellwagen Bank where whales have been found to exhibit strong preferences for sites within the area of the Bank itself (C. A. Mayo, pers. comm.). That the data collected from the Gulf of Maine are a random sample of the population returning there each summer seems unlikely. Preliminary analyses by the author of the data from 1980 to 1983 show strong evidence of heterogeneity in this feeding area.

In the Newfoundland/Labrador feeding area, many more whales have been identified than in all other feeding areas combined. In 1978, 1979 and 1980, data were collected in June and July off Newfoundland by H. P. Whitehead and J. Lien. The whales were migrating generally northwards at that time (Whitehead, 1981). In 1978 and 1979, data were also collected in August off Labrador where Whitehead, Silver and Harcourt (1982) demonstrated site fidelity and a general mixing of animals. In 1982 and 1983, Whitehead and Glass (1985) showed that humpbacks on the Southeast Shoal of the Grand Bank are a fairly discrete sub-group of the Newfoundland/Labrador feeding aggregation.

On the breeding grounds, the majority of the data have been collected from regular surveys of two areas over the past several years. Off Puerto Rico, sampling is conducted from small, shore-based inflatable boats, with crews going out each day, weather permitting (D. K. Matilla, pers. comm.). On Silver Bank, sampling is from a larger vessel, formerly the *Regina Maris* and latterly the *Rambler*, operated by the Ocean Research and Education Society, Gloucester, Massachusetts. Up until 1981, Silver Bank was surveyed in a systematic way (Balcomb and Nichols, 1982) but in recent years sampling has taken the form of traversing an area of the Bank each day, the size and position of which are determined primarily by the weather, and attempting to photograph all the whales encountered. It is extremely unusual for a whale to be photographed on more than one day so we are led to the conclusion that the humpbacks are migrating through the area rather than arriving, staying for a certain period of time and then leaving. If this is the case, this method of sampling should result in a representative sample providing that the entire period of the migration is sampled and there are not specific social groups which are consistently less available because, for example, they inhabit unnavigable waters. In fact, sampling has typically taken place from the end of January until mid-April (K. C. Balcomb, pers. comm.), the period when humpbacks are present on the Bank (Balcomb and Nichols, 1982; Whitehead, 1982), and humpbacks do not seem to possess particular movement patterns, preferred ranges or territories within the Bank (Whitehead and Moore, 1982). Consequently, we can be reasonably confident that samples of the whales which do visit Silver Bank are not greatly biased as a result of non-random sampling.

Katona *et al.* (1985) have tested the hypothesis that a constant proportion of humpbacks migrate from each of the northern feeding areas to Silver Bank by performing a Chi-squared test of observed resightings against those expected based on the number of whales identified in each feeding area. None of the tests were significant at the 5% level indicating not only that constant proportions from each feeding area travel to Silver Bank but also that the samples taken on Silver Bank are representative of the entire population. However, Whitehead and Glass (1985) have shown that the whales found on the Southeast Shoal of the Grand Bank in the Newfoundland/Labrador feeding area show a preference for Puerto Rican waters on the breeding grounds.

Unfortunately, Katona *et al.*'s (1985) test does not tell us whether or not the entire North Atlantic population migrates through Silver Bank. If the whales occurring at Silver Bank in each year are a random selection from the whole population, no bias will result. At the other extreme, if there are individuals which consistently never go to the Bank, they will be excluded from any population estimate. If some individuals are consistently less likely than others to go to Silver Bank, estimates of population size will be negatively biased.

At Peninsula Valdes, Argentina, where photographs of the callosities of southern right whales have been taken regularly since 1970, the problems of population definition and of whether or not a representative sample can be obtained are particularly interesting. Payne (1984) has demonstrated that mature females tend to return to Valdes only in years in which they calve, usually every three years. In addition, as noted by Whitehead *et al.* (in press), whales which are seen at Valdes in any one year may be 'resident' for a long time or present only for a short period ('transients'). Furthermore, the three different areas at Valdes are characterised by different social groups of whales: a high proportion of cow/calf pairs at one area, mostly males in another, all groups well represented in the third. Photographic flights did not cover all areas in all years. Clearly, achieving a representative sample from the population resident at Valdes is not a simple task.

Whitehead *et al.* (in press) have analysed the data collected from 1970–77 to give population estimates of (i) total population excluding calves, and (ii) mature females. Most of the data were collected between September and November when right whales are most abundant at Valdes. In testing the assumption of equal probability of capture they found no departure from this assumption for mature females only but did find a significant departure for the total population excluding calves. This trend is as expected because the total population excluding calves contains two groups of animals with known different probabilities of capture (mature females present approximately every third year, others present every year) but mature females may all have the same average probability of capture. In using this test, however, it should be recalled that its power to detect heterogeneity is not strong, as demonstrated by Carothers (1973b). An additional factor is that mature females with calves are easier to find and photograph than other whales because they tend to stay in shallow water close to the shore. Another problem, as noted by the authors, is that of the 'migrant' whales which are present less often and for a shorter period of time than 'residents'. Use of all the data would introduce more heterogeneity of capture probabilities. Whitehead *et al.* (in press) note that their estimates may be biased downwards for this reason.

(ii) Equal probability of photographing natural marks

For all whales to have an equal probability of having their natural markings photographed, the behaviour which results in the markings being presented in such a way that a satisfactory photographed is obtained must be characteristic of every animal. Even if this is true there may be additional behaviour which affects the length of time which the natural markings are available to be photographed or the ease with which photographs can be taken. If some whales are consistently more difficult to photograph than others or cannot be photographed at all, the resulting heterogeneity of capture probabilities will cause under-estimation of population size. This could occur, for example, if the behaviours presenting the natural marking were dependent upon age or sex, or merely if there were inherent individual variation in the population. The two populations which have been extensively studied by photography of natural markings, North Atlantic humpback whales and southern right whales, are good examples of how individual variation in behaviour could affect the probability of a satisfactory photograph being obtained.

Southern right whales are recognised from the callosity patterns on their heads which can be photographed either from the air or from boats (Payne *et al.*, 1983). Whales must come to the surface to breathe so this is a behaviour that the entire population must exhibit. However, it has been reported that the whales can react adversely to the presence of the survey aeroplane or boats (Payne *et al.*, 1983), as mentioned briefly above. Most whales took no notice of the aeroplane as it circled, continuing the behaviour in which they were involved. Travelling whales were difficult to photograph because they spent so little time on the surface. A few whales seemed deliberately to avoid the aeroplane and a very few whales took fright, swimming or diving rapidly. Response to power-driven boats ranged from allowing very close contact to complete avoidance. On occasion, threat displays were made.

None of this is important unless individual animals consistently display specific behaviours which affect their photographability. In response to aeroplanes, from which the data at Peninsula Valdes are obtained, the only behaviour likely to fall in this category is deliberate avoidance and taking fright, each of which were seen only a few times. Whether or not the same whales were involved repeatedly in this behaviour would be dificult to ascertain because whales exhibiting such behaviour are necessarily more difficult to photograph.

Payne *et al.* (1983) reported that they were able to identify calves only 28% of the time compared to 86% of the time for non-calves, indicating age-dependent differences in the probabilities of obtaining useable photographs. The heads of young calves are often covered with cyamids which obscure the pattern of callosities but this only occurs for the first few months of life. Whitehead *et al.* (in press) did not consider calves in their population estimates. In this case additions to the population are in the form of recruitment to the second year-class.

For humpback whales, the pattern on the ventral surface of the tail flukes (and the shape of the flukes) is only visible when the whale raises its flukes at the beginning of a dive. However, the flukes are not always raised to an angle sufficient for a good photograph. Being able to obtain a suitable photograph therefore depends on a behaviour which is variable. The important point here is whether or not there are specific individuals which consistently fluke-up at lower rates than others. These animals may belong to a recognisable group such as an age-class or a sex-class or, again, there may just be inherent differences among individuals.

Perkins *et al.* (1985) have investigated differences in fluking behaviour among three age-classes, calves, juveniles and adults, which could be recognised in the field at the West Greenland feeding site. The criterion they used to monitor this behaviour was the angle from the horizontal at which the tail flukes entered the water; 0°–35°—useful photograph not possible, 35°–65°—useful photograph possible, 65°–90°—useful photograph probable. The results showed a different pattern for each of the three age classes. Nearly all adults regularly fluked-up at angles between 65°–90°. Calves fluked-up at angles of 65°–90° less regularly and several did not fluke at these angles at all. Juveniles displayed variable fluking behaviour. This demonstrates that there is heterogeneity of capture probabilities in this population which is age-dependent, although it cannot be quantified without additional data or assumptions.

The next step is to see if this information can be used in estimating population size. There are two ways in which this could be done. One is to incorporate the capture-recapture data, stratified by age-class, into a model which allows population size to be estimated from such data. The other is to estimate the bias introduced into estimates of population size from the use of a model which assumes equal probability of capture. Pollock (1981b) and Stokes (1984) describe generalisations of the Jolly–Seber model to allow for age-dependent survival and capture probabilities as noted above. An additional assumption for these models is that each captured animal can be placed in the correct age class without error. Numbers of recaptured animals may also need to be larger to avoid small-sample biases. Pollock (1981b) also describes a test of whether or not survival and capture rates are independent of age. If the available humpback data included age-class and a test revealed capture rates to be age-dependent, Pollock's or Stokes' model could be useful in estimating population size for this species.

If age-class has not been recorded consistently, however, it may be more appropriate to attempt to estimate bias due to heterogeneity of capture probabilities. Perkins *et al.* (1985) have used their data on fluking behaviour in West Greenland to approximate this bias by making some additional assumptions concerning the proportion of animals in each age-class unavailable to be sampled and the age-structure of the population. They estimate a maximum negative bias of about 10% of population size from their data. Work conducted on Silver Bank has provided data for a similar calculation for the whales on a breeding ground (P. Reid, pers. comm.).

An alternative method of estimating bias due to heterogeneity of capture probabilities would be to use the proportion of whales encountered which were photographed in each age-class as input to simulation models of the type used by Carothers (1973a) or Gilbert (1973). Data suitable for such an exercise may already exist but several assumptions would have to be made in the simulation. Nevertheless, this approach could have merit in providing an independent estimate of bias.

(iii) Treatment of photographs

The way in which the photographs of natural markings are handled is an important aspect of this application of capture-recapture methods. There are two major considerations. The first concerns the quality of the photograph and whether or not it should be considered as part of the sample. This decision should be based strictly upon photographic quality and be unaffected by the ease in which the animal can be identified, thereby ensuring that more easily identified whales are not included in the samples more often than those less easily identified. This would result in heterogeneity of capture probabilities and the associated negative bias in population estimates.

Perkins *et al.* (1984; 1985) graded their photographs of humpback tail flukes based on four criteria; image sharpness, contrast, resolution and the relative size of the tail in the frame. All photographs of poor quality were deleted from the data used in the capture-recapture analyses in order to 'minimise error and avoid duplication'. This should also have the desirable effect of ensuring that each photograph is accepted into the sample independently of how easy the whale is to identify.

Baker *et al.* (1985) graded their photographs of North Pacific humpbacks according to the proportion of the flukes visible and the visibility of the trailing edge of the flukes. This classification goes some way towards ensuring equal probability of identifying animals but no mention is made by the authors of the quality of the photographs.

Payne *et al.* (1983) graded the reliability of their identification of southern right whales from callosity patterns using a system which coded photographs from 'identified with confidence' down to those whose usefulness was considered doubtful. This system of grading identifiability should not be confused with the Perkins *et al.* (1984; 1985) system of grading photograph quality and definitely should not be used as a criterion for including photographs in the sample. Darling and Morowitz (1983) used a system similar to Payne's for grading photographs of North Pacific humpback tail flukes. Kraus and Prescott (in press) used composites constructed from photographs of the same animal taken from several angles to identify North Atlantic right whales. These composites are graded according to their completeness. This system may present problems in the application of capture-recapture models because ability to identify may be a function of how complete the composite is and there may be different levels of completeness for composites of the same animal constructed at different times.

The second consideration concerns the process of 'marking'. A whale in a photograph should not be designated as 'marked' unless it is certain that it will definitely be recognised again in a future photograph of acceptable quality. It is not necessary to consider all whales photographed as 'marked'. Whales whose natural markings are indistinct or contain little information should not be included as 'marked' animals because this will serve to introduce possible errors and duplication of the type envisioned by Perkins *et al.* (1984; 1985). For capture-recapture purposes, such animals can simply be ignored as though they were never photographed.

Whether or not a whale should be accepted as 'marked' is, of course, a subjective decision but it should be possible to base decisions upon some predetermined guidelines. Such guidelines could be as strict or as lenient as desired. The object in determining at what level to accept or reject a photograph as 'marking' a whale should be to maximise the number of 'marked' animals whilst minimizing the chances of accepting a photograph and then failing to recognise a subsequent photograph of the same animal or, indeed, of making an incorrect re-identification. Experience is probably the most useful guide here. Clearly, bias should be avoided if at all possible but if sample sizes are very small there may be a case for preferring a small increase in bias over a large decrease in precision, as propounded by Cormack (1979), among others.

The technique of digitising the information in a photograph to store in a computer and facilitate analysis could be useful here. An objective function such as the percentage black (or white) pixells present in a photograph or the percentage of pixells the same in two photographs, or both, could be used to eliminate existing photographs which could not possibly match the new one being processed. Whether or not such a process were considered to be cost-effective would depend upon such things as number of incoming photographs, personnel available to process the photographs, etc.

A final note here is that photographs which are insufficiently well-marked to be considered as part of the m_i or s_i are nevertheless still part of the sample, n_i. In typical capture-recapture studies, only those animals of the n_i which die are not considered as marked, and as a result are not returned to the population. In capture-recapture studies of whales using photographs of natural markings, no animals are killed during a sampling period. Those chosen not to be counted as 'marked' are, therefore, still part of the population alive just after the sample. This difference does not affect estimates of population size.

CONCLUDING REMARKS

The intent of this paper is to assess the applicability of capture-recapture methods to estimate population size using photographs of naturally marked whales. The preceding discussions demonstrate that these methods can be useful if certain key issues are addressed. Three concerns arise as being important.

The first is that the population being sampled must be defined. This is particularly important for capture-recapture studies because the population must be sampled at least twice and preferably many times. Therefore, it is not possible to avoid the issue by claiming to have estimated the size of the population in a given area at a given time as can sometimes be done, for example, with line transect sampling. Unless the population is 'geographically closed' estimates of its size will be meaningless because it is not known to which 'population' the estimates refer.

The second concern is that samples must be representative of the population being studied. For most multiple sampling studies all samples must be random because animals are marked as well as recaptured each time. For the two-sample Petersen model, however, only one sample need be random providing that there is uniform mixing between samples, any mortality acts equally on marked and unmarked animals and at any given location each whale has the same probability of being sampled. The problem of unequal probabilities of capture within a sampling occasion for naturally marked whale populations is limited to the case where there are inherent differences in the catchability of individuals. This is probably a feature of all capture-recapture studies and it results in a downward bias in population estimates. In some circumstances estimators of population size are available for models which allow heterogeneity of capture probabilities, but populations of whales do not lend themselves easily to the necessary experimental design. As a result it may be more appropriate to try to estimate the effect upon population estimates of any heterogeneity.

The third concern is that of obtaining sample sizes which are sufficiently large to provide precise estimates of population size. Whether or not adequate samples can be obtained is dependent largely upon the sampling scheme, the size of the population being studied and the resources which can be committed. Large populations require larger samples for precise estimates and sampling whales usually requires the use of a boat or an aircraft, both of which are expensive to operate and maintain. For a two-sample experiment, Robson and Regier (1964; summarised by Seber, 1982, pp. 64–70) provide formulae and graphs which enable sample sizes to be determined for given expected population size and level of precision of population estimate.

The concept of the precision of a population estimate, the necessary sample size and the importance of satisfying model assumptions is an important one. For a population new to scientific study of this kind we may be interested initially only in the order of magnitude of population size in which case sample sizes could be relatively small and violation of model assumptions unimportant. For a better idea of population size, say with a confidence interval of about ±50 to 100%, sample sizes would need to be much larger and major violations of model assumptions would be important. This is approximately the level at which capture-recapture studies of naturally marked whale populations currently are. For management purposes, population estimates need to be much more precise so that sample sizes must be large and model assumptions need to be carefully considered.

In an ideal world these concerns should be taken into account at the stage of planning the experiment. However, long-term studies of whale populations tend to evolve rather than be planned down to the last detail, and capture-recapture may not have been high on the list of initial priorities. In addition, at the time when photo-identification of the two most studied populations began, many of the important studies of capture-recapture experiments had not yet been undertaken. For these data sets, therefore, it is a case of being aware of the problems and doing the best that can be done. For studies which have yet to be carried out, many of the problems can be avoided or minimised by thoughtful design.

As a practical guide to a successful capture-recapture study using photographs of naturally marked whales, there are several points that can be emphasised. In the field, sampling should be planned so that the population can be defined and so that representative samples of sufficient size can be taken. The larger the sample, the more precise the estimate of population size and the less important is heterogeneity of capture probabilities. If necessary, experiments should be undertaken to investigate and quantify heterogeneity of capture probabilities. In the laboratory, all photographs should be selected for inclusion in a sample based on objective measures of their quality. The use of computers can result in substantial savings in time when processing photographs.

For analysis, it is more difficult to make definitive statements because it is likely that no model is an adequate description of the experiment. For example, there is no estimator of population size for an open population model in which heterogeneity of capture probabilities is allowed. However, some models are more appropriate than others. A multi-sample closed population model is clearly inappropriate for data collected over many years because population size would be substantially over-estimated as a result of the failure of the assumption of population closure. These models could realistically be used on sub-samples collected within a major sample, but there would be serious doubts about whether representative samples of sufficient size could be obtained. The application of closed population models may be limited in practice, therefore, to the use of the Petersen estimator on pairs of samples. This choice has the disadvantage of being open to biases caused by an open population as well as heterogeneity of capture probabilities.

There are a number of possibilities for open population models. The basic Jolly–Seber model does not allow heterogeneity of capture probabilities and the resulting estimates of population size can be negatively biased by a substantial amount if this exists. There are modifications which allow probabilities of both survival and capture to be age-dependent (Pollock, 1981b; Stokes, 1984) and these could be useful if animals can be assigned to age-classes when sampled. Another variation of the Jolly–Seber model is to assume survival to be constant as proposed by Jolly (1982). This may also be a useful model for whale populations but heterogeneity of capture probabilities could still be a serious problem. Cormack's (1981, in press a,b) log-linear models allow variations on the standard Jolly–Seber model which can give useful insights into the suitability of particular models for analysing particular data sets. Recent research on this problem includes R. A. Myers' (pers. comm.) method of estimating population size by incorporating the fitting of a model with a parameter describing heterogeneity.

The computer programs CAPTURE (Otis *et al.*, 1978) for closed populations, POPAN (Arnason and Baniuk, 1980) for open populations and Cormack's (1980, in press a,b) programs for use with the GLIM statistical package for both open and closed populations allow analysis of the data and testing of the assumptions without the user having to construct his/her own models. The use of such programs helps to save time and reduce analytical errors.

In conclusion, capture-recapture methods can be useful for estimating the population size of naturally marked whales as long as the experimenter is aware of the problems which he or she is likely to encounter. Careful experimenter planning is crucial but thoughtful use of the available analytical methods can rescue data collected in violation of some of the model assumptions. However, it is pertinent, as a final comment, to cite Begon's (1983) study of the use and abuse of the Jolly–Seber model. Of those studies he investigated, the majority either drew conclusions from estimates with no reference to their precision or neither checked nor justified the assumptions of their models. Users of capture-recapture methods should try to ensure that their publications do not end up on the wrong side of one of Begon's tables should he decide to follow up his study at a future date.

SUMMARY

1. The use of natural markings to identify an animal has several advantages over altering its physical appearance in capture-recapture studies. Animals do not have to be handled, appropriate markings are not lost, there is no physical effect on the animal so that catchability and survivorship are not affected. Disadvantages are the greater amount of time required for identification, the greater chance of error in identification and the possibility that markings may change with time.

2. An analysis should be undertaken to determine the effects, if any, on estimates of population size of humpback whales of any changes with time in the pattern on the ventral surface of the flukes using another identifying feature such as the dorsal fin.

3. The Petersen two-sample estimator gives a valid estimate of population size at the time of the first sample if mortality only occurs, but if both mortality and births occur population size will be overestimated at the time of both samples by an amount which can be estimated if birth and death rates can be approximated.

4. Multiple-sample closed population models allow heterogeneity of capture probabilities to be modelled but are clearly inappropriate for long series of data collected at yearly intervals.

5. Open population models (multiple sample) such as the Jolly–Seber model accommodate births and deaths but heterogeneity cannot be accounted for and estimates of population size are less precise because of the complexity of the model.

6. Tests of the departure of data from model assumptions should be undertaken but it should be recognised that their power is weak and that they may not be independent, e.g. tests for closure and equal catchability. Because of this, possible bias in population estimates and the level of such bias should also be investigated experimentally, e.g. stratification of data to investigate heterogeneity of capture probabilities.

7. The use of existing capture-recapture computer programs can be a great help in allowing straightforward testing of model assumptions and analysis of data.

8. The most appropriate method of analysis for data consisting of annual or six-monthly samples is either the calculation of a series of independent Petersen estimates, or the use of the Jolly–Seber model or a variation on it. Where data can be divided into sub-samples within a major sample the ability of closed multiple-sample models to account for heterogeneity of capture probabilities could be made use of.

9. The age-dependence in rates of mortality to be expected in whale populations is not sufficiently strong to cause a significant bias in estimated population size as a result of violation of the assumption of equal probability of survival for all animals.

10. Bias in estimates of population size resulting from heterogeneity of capture probabilities is negative, is less for intermediate sampling occasions in a Jolly–Seber analysis, decreases as the proportion of animals captured increases, but increases as the range of capture probabilities increases.

11. Experimenters should, therefore, try to minimise the variation in capture probabilities and aim for as large a sample size as possible in order to minimise the

bias in estimates of population size resulting from heterogeneity of capture probabilities.

12. Heterogeneity of capture probabilities can be introduced, with resulting negative bias in population estimates, if some individual animals are consistently less available to be seen in the sample area. No heterogeneity or bias results if animals missing from the sample area are a random sample of the population. If some individuals are never available to be seen they are excluded from the experiment.

13. Heterogeneity of capture probabilities can also be introduced if individual animals consistently display specific behaviour which results in there being inherent differences in their availability to be photographed.

14. Selection of photographs to be included in a sample should be based strictly upon criteria of photographic quality to avoid more easily identified animals being included in the samples more often than those less easily identified, another way that heterogeneity could be introduced into the data.

15. An animal should only be considered as 'marked' if it is certain that it will be recognised in a future photograph of acceptable quality. For capture-recapture purposes, photographs of whales whose natural markings are indistinct or contain little information should simply be ignored.

16. In the use of capture-recapture methods on populations of naturally marked whales, it is important to consider the desired level of precision of a population estimate and the associated sample sizes and importance of satisfying model assumptions.

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