International
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Commission

Biology of the Phocoenids

A COLLECTION OF PAPERS

Edited by

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Preface

In recent years, much of the time of the IWC Scientific Committee with respect to small cetaceans has focused on the issue of incidental captures. This culminated in the publication last year of Special Issue 15 on *Gillnets and Cetaceans*. The present volume is a progression from this as it considers the family, the Phocoenidae, which is one of the most vulnerable to fishery-related mortality, whilst at the same time being subject to direct mortality in certain areas. Although a considerable amount of work has been carried out in the North Atlantic and North Pacific on the harbour porpoise and Dall's porpoise, relatively little work has been carried out on the other species. It is gratifying to see the increase in studies in South American waters and it is to be hoped that the publication of this volume will encourage Governments and scientists to begin much-needed and focused research on this family throughout the world. It is particularly important that financial and practical support be given to studies in the developing countries. Only with such an effort can the demise of some Phocoenid populations to the tragic level of the vaquita be avoided.

G.P. Donovan
Series Editor

Cover photograph
Harbour porpoises in the Bay of Fundy, Canada.
Photo courtesy of John Y. Wang, Porpoise Rescue Program

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15 [1994]-Gillnets and Cetaceans.
Eds W.F. Perrin, G.P. Donovan and J. Barlow.
i-ix + 629pp.; ISBN 0 906975 28 X

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Introduction

The Phocoenidae is an evolutionary old family and the six living porpoise species are organised into two subfamilies. The division is based on fossil and recent indications of two evolutionary lineages. The subfamily Phocoeninae comprises the harbour porpoise (*Phocoena phocoena*), the Burmeister's porpoise (*P. spinipinnis*), the vaquita (*P. sinus*) and the finless porpoise (*Neophocaena phocaenoides*). The subfamily Phocoenidinae contains two species, the Dall's porpoise (*Phocoenoides dalli*) and the spectacled porpoise (*Australophocaena dioptrica*).

The four species of the subfamily Phocoeninae are largely coastal in distribution. The harbour porpoise occurs in coastal waters across the Northern Hemisphere, although in the North Atlantic at least, there have been some sightings far offshore. The Burmeister's porpoise is found in South American waters from southern Brazil to the southern border of Ecuador. The finless porpoise occurs in shallow coastal waters and estuaries from the Persian Gulf, across Malaysia and Indonesia to Japan. In China they are also recorded in riverine waters. The distribution of the vaquita, is confined to the upper Gulf of California, Mexico and is the smallest range for any marine cetacean.

In the subfamily Phocoenidinae, the Dall's porpoise is found across the northern Pacific Ocean and the Bering Sea between 40°N and 60°N and in the Sea of Okhotsk. The spectacled porpoise is found from the waters around the coast of southern South America from Uruguay to the Strait of Magellan in Chile. Sightings and stranded animals have been reported across the sub-Antarctic islands (South Georgia, Auckland Islands, Macquarie Island, Heard Island and the Kerguelen Islands) suggesting an offshore circumpolar distribution of this species in sub-Antarctic waters.

The Phocoenids are subject to harvest by coastal communities in many areas and are particularly vulnerable to incidental mortality in coastal fishing operations. In addition, human activities impose indirect threats, particularly to the coastal porpoises through the detrimental impact on their environment. This includes habitat degradation from pollution, disturbance by ship traffic and boats, noise, physical changes to the habitat and depletion of important prey species by overfishing.

Although the offshore porpoises may face less environmental threats, they have suffered large scale incidental mortality in fishing gear. The Dall's porpoise has recently been subject to directed fisheries and harvested at unsustainable levels in some areas.

The IWC Scientific Committee has reviewed the biology and status of the porpoises and monitored the threats to these small cetaceans. Recommendations for management and research are made as appropriate by the Committee and its sub-committee on small cetaceans and these are discussed in the introductory remarks for each of the species sections. Many of the papers published in this book have been prepared in response to these recommendations.

Inevitably, perhaps, the majority of papers concern the best studied of the Phocoenid populations, the harbour porpoises in the North Atlantic and the eastern North Pacific. Much of the impetus for these studies has come from the identification of potentially serious levels of incidental fishery mortality in developed nations in Europe and North America. There are papers covering a wide range of topics ranging from abundance estimation through to pollution and energetics.

One species which has attracted widespread interest and concern within the Scientific Committee in recent years is the vaquita. This species has the smallest range of any marine cetacean and, numbering only a few hundred, is seriously threatened with extinction. The papers in this volume review the limited available biological information and consider the problems of continuing incidental captures despite many attempts at giving complete protection.

The section on Dall's porpoises is relatively short as much of the work on this species has been carried out in connection with the Japanese salmon driftnet fishery. Much of the information on these porpoises has been published in the IWC Annual Reports, Special Issue 15 and in a series of papers published by the International North Pacific Fisheries Commission.

It is particularly edifying to be able to include a number of papers addressing the relatively little studied Burmeister's and spectacled porpoises. This reflects the major increase in studies in South American waters, particularly in response to concerns about their status as a result of both direct and indirect captures.

Sadly, despite evidence of direct and indirect captures around the world, there are no papers on the finless porpoise in this volume, reflecting the absence of research on this species in all but a few areas. A brief summary of the species is included on pp. 375–6.

The final section of the book includes the report of a workshop held on the age determination of harbour porpoises. Although not an IWC workshop, the report has been presented to the IWC Scientific Committee and it is included here as the results are of importance to studies of many aspects of Phocoenid biology. Thanks are due to The Norwegian Institute for Nature Research who hosted the Workshop and contributed to the funding of this volume.

All papers were reviewed anonymously by at least two scientists. It is particularly important to thank the large number of scientists who acted as reviewers of the papers including: A. Aguilar; J. Barlow; E.W. Born; R.L. Brownell Jr.; S.T. Buckland; J.G. Cooke; G. Desportes; D.E. Gaskin; J.R. Geraci; T. Gerrodette; D.I. Gibson; P. Hammond; M.P. Heide-Jørgensen; J.E. Heyning; A.A. Hohn; T. Kasuya; C.C. Kinze; S.D. Kraus; F. Larsen; J.S. Leatherwood; I. Lindstedt; C. Lockyer; T. Lyrholm; A.R. Martin; M.K. Marx; T. Miyashita; A. Myrick; K. Norris; W.F. Perrin; T. Polacheck; J.A. Raga; A.J. Read; P.J.H. Reijnders; S.B. Reilly; T. Schweder; G. Silber; S. Tanabe; J. Teilmann; P. Thompson; O. Vidal; G. Vikingsson. Special thanks must go to: Helen Sharp who keeps track of the manuscripts, prepares manuscripts for publication and types in many of the revised manuscripts; Stella Duff for proof reading; Julie Creek who typesets all the tables; Helen Richardson who prepares the artwork and helps with the proof reading; and the staff of Black Bear Press.

A. Bjørge and G.P. Donovan
Oslo and Cambridge, 16 November 1995

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Harbour Porpoise

Harbour porpoise in the Bay of Funday, Canada.
Photo courtesy of John Y. Wang, Porpoise Rescue Program.

Harbour Porpoises in the North Atlantic: edited extract from the Report of the IWC Scientific Committee, Dublin 1995

G.P. Donovan and A. Bjørge

INTRODUCTION

At the meeting of the IWC Scientific Committee held in Dublin in May 1995, the special topic addressed by the sub-committee on small cetaceans was the North Atlantic harbour porpoise. A considerable body of new information was presented and we believe that it is important to include this in the present volume. What follows is a slightly edited version of the relevant sections of the report of the sub-committee on small cetaceans. The full version will be published in the *Reports of the International Whaling Commission* 46 in June 1996. We have edited the report to ensure that it can stand alone, occasionally shortening sections and including additional references. For ease we have used the same section numbering as in the original report. The papers referred to at the meeting are all cited in their unpublished form here. Many of these have been submitted for publication in *Rep. int. Whal. Commn* 46 and are presently out for revision and anonymous review. The interested reader should consult *Rep. int. Whal. Commn* 46 when it is published.

5. REVIEW OF HARBOUR PORPOISES IN THE NORTH ATLANTIC

The sub-committee limited most of its discussions to a review of harbour porpoises in the North Atlantic and adjacent waters. No new information was received from the Black Sea.

5.1 Assessment of current knowledge and research methodology

5.1.1 Distribution and stock identity

5.1.1.1 METHODOLOGY

The methodology available to discriminate stocks and current knowledge regarding population structure of small cetaceans was briefly reviewed.

The sub-committee recognised the distinction between biological populations and management stocks (e.g. Donovan, 1991) and attempted to maintain this distinction throughout its deliberations. Taylor (1995) presented information on the system of stock delineation currently used in management of US marine mammal populations. A clearly defined management objective is an essential prerequisite to the formulation of any system of stock structure. After considerable discussion, the sub-committee agreed to use the population structure outlined in Gaskin (1984) as a starting point for its work, modifying this scheme where new information was available. It also agreed to follow a precautionary approach, using smaller stock divisions rather than larger units in the absence of data to the contrary.

Four genetic techniques which have been, or are currently being, applied to harbour porpoises are, in order of increasing sensitivity and resolution: allozyme electrophoresis, restriction fragment length polymorphism (RFLP) analysis of mtDNA, direct sequencing of mtDNA and the use of DNA microsatellite markers. The first technique infers differences in DNA through the examination of proteins, the second and third examine DNA sequence variation in the maternally inherited mtDNA, while the last uses the highly variable nuclear DNA microsatellites.

This topic was considered in some detail at the Workshop on Analysis of Genetic Data to Address Problems in Stock Identity as Related to Management (Dizon and Perrin, 1995). Our current understanding of gene flow between stocks is insufficient to make strong inferences about the significance of genetic frequency data when comparing putative stocks. The absence of a genetic difference should not be used to combine putative stocks, but a significant difference in genetic structure is an indication of long separation between population units and thus an indication of the existence of separate biological populations.

Three recent studies have used genetic techniques to examine population structure of harbour porpoises in the North Atlantic. Andersen (1993) examined allozyme frequencies in porpoises from Dutch, Danish, North Sea, West Greenland and Canadian waters. Wang (1993) used mtDNA RFLP analysis to discriminate populations in the Northwest Atlantic, and Walton (1995) used DNA sequencing to examine population structure in the Northeast Atlantic. The latter two studies suggested that female porpoises might be more philopatric than males (and see below).

Contaminant loads may also provide some information on stock structure. Individual variation in contaminant loads is caused by many factors, including diet, body size, body composition, nutritive condition, incidence of disease, age, sex and reproductive condition. In theory, it is possible to account for these with a large and varied sample, but in practice it is very difficult to completely rule out such sources of variation (Aguilar, 1987). This limits the utility of this approach for stock identity studies and it should only be used in conjunction with other techniques.

Monitoring movements by satellite telemetry also offers an opportunity to investigate stock structure, although the approach is limited by the relatively small number of individuals that can be tagged and monitored. The application of such techniques with harbour porpoises is still in its infancy (Read and Westgate, 1995) but may provide useful information on long-term movements and stock structure in the future. Monitoring the movements of individuals may provide important information on the existence or absence of significant sub-population structure and on the seasonal movements of populations.

Several other techniques may be used to examine stock structure (see review in Donovan, 1991) including morphometrics, analyses of reproductive timing and parasite burdens, but these were not reviewed in detail.

5.1.1.2 CURRENT INFORMATION ON DISTRIBUTION AND POPULATION STRUCTURE

Current information on harbour porpoise distribution and population structure was reviewed in the context of Gaskin's (1984) proposed population divisions. In very few cases was it possible to identify exact boundaries even when there was strong evidence for the existence of separate units. A revised map of the distribution of harbour porpoises in the North Atlantic, taking all relevant information into account, is presented in Fig. 1.

NORTHWEST ATLANTIC

Palka and Read (1995) reviewed harbour porpoise distribution and population structure in the northwest Atlantic. The southern limit is delineated by two stranding records in northern Florida, although the typical southern boundary is Cape Hatteras, North Carolina. The northern limit is 70°N. Within this area, porpoises show strong seasonal migration and are present in northern coastal waters only during summer. Systematic sighting surveys in the Gulf of Maine have demonstrated considerable inter-annual

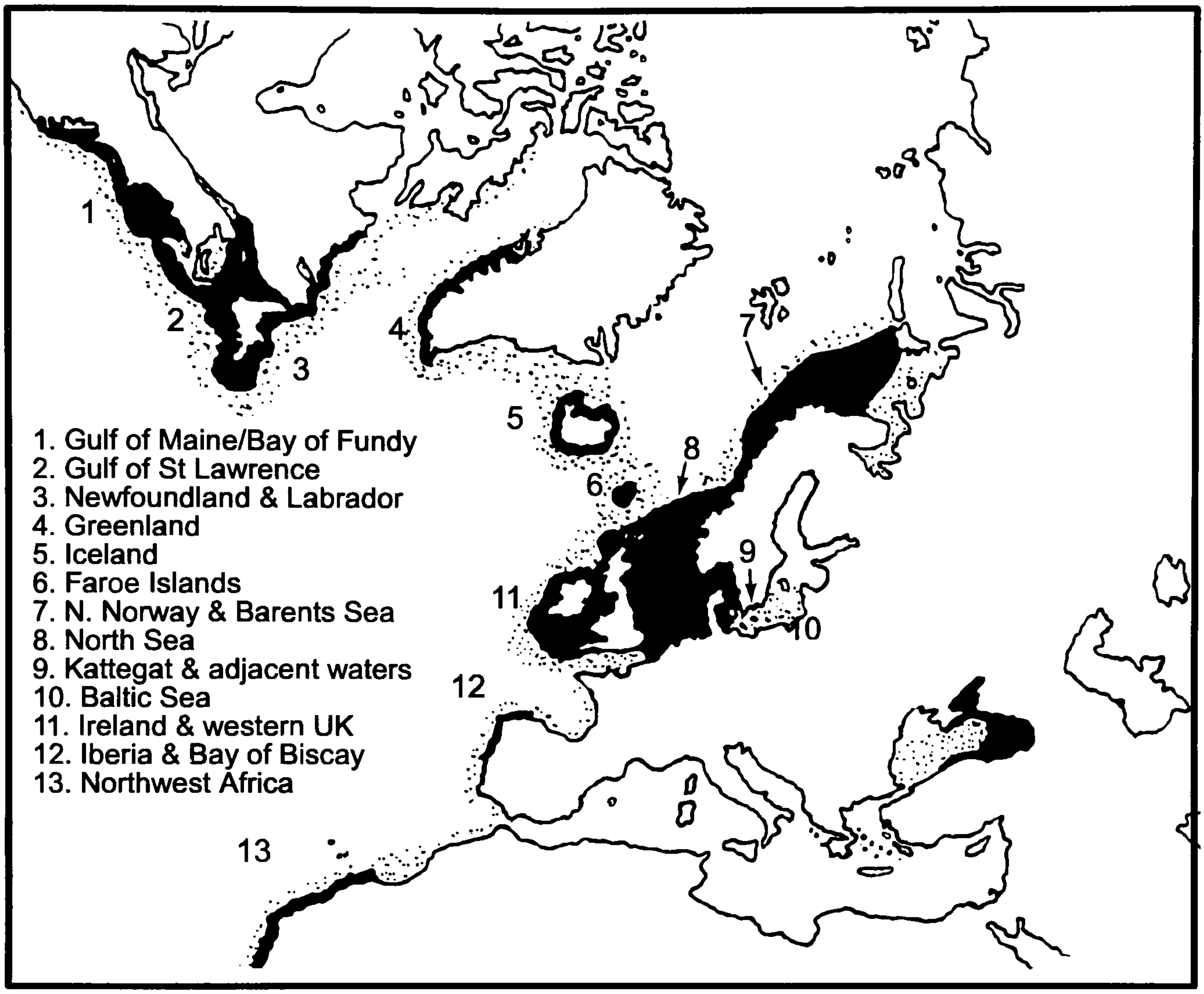

Fig. 1. Distribution of harbour porpoises in the North Atlantic (see text).

variation in summer distribution patterns (Palka, 1995c). Little information exists on winter distribution. Gaskin's (1984) proposed population structure in this region has been supported by evidence from pollutant burdens (Westgate and Johnston, 1995) and mtDNA RFLP analysis (Wang, 1993), which suggest the existence of three more or less separate populations in (i) the Gulf of Maine and Bay of Fundy, (ii) the Gulf of St. Lawrence and (iii) eastern Newfoundland and Labrador. Both the considerable reproductive synchrony (Read and Hohn, 1995) and the extreme mobility of tagged porpoises indicate that it is unlikely that a significant sub-population structure exists within the Gulf of Maine population.

GREENLAND

The distribution of harbour porpoises in Greenlandic waters is described by Teilmann and Dietz (1995). The main distribution lies between Sisimiut and Paamiut in central West Greenland. Sightings and catch records exist only from the spring, summer and autumn months, with a peak from June to October. Few records exists from eastern Greenland and these might represent stragglers from the west coast (Gaskin, 1984). It was agreed to remove Gaskin's sub-population 2.5 (Southeast Greenland) and include these animals with those from West Greenland. An analysis of microsatellite DNA differentiated West

Greenlandic porpoises from those in the North Sea and inner Danish waters (Andersen *et al.*, 1995).

ICELAND AND FAROES

The distribution of harbour porpoises in Icelandic waters was reviewed by Northridge (1995). They have been seen in the deep waters between Iceland and Greenland and between Iceland and the Faroe Islands. There is little information on seasonal distribution, although anecdotal evidence suggests that porpoises may be present year-round. In the absence of data on interchange, it was agreed to consider Icelandic porpoises as a separate population, thereby splitting Gaskin's sub-population 2.6 into two units: Iceland and the Faroe Islands. Larsen (1995) summarised the little information available on the distribution around the Faroes. It should be recognised that there have been no attempts to discriminate between these two putative population units.

NORWEGIAN, BARENTS AND WHITE SEAS

Bjørge and Øien (1995) reviewed the distribution and population structure of harbour porpoises in Norway, based on incidental sighting records, the locations of bycatches, and three systematic sighting surveys (NASS 87, NASS 89 and SCANS). Porpoises are distributed continuously along the Norwegian coast into the Barents Sea. Their northern limit appears to be determined by the boundary between Atlantic and Arctic waters. No new information was presented on the distribution of harbour porpoises in the southeastern Barents Sea or White Sea. Porpoises are distributed over the shelf of the Barents Sea to the north and across the North Sea shelf to the south. It was agreed to use the hiatus in offshore distribution off the mid-coastal region at approximately 66°N (Bjørge and Øien, 1995) to delineate the boundary of the Barents Sea population and the North Sea population to the south. There have been no attempts to discriminate between these two putative stocks or to examine potential differences between porpoises along the coast of Norway and those further south and west in the North Sea.

BALTIC SEA

A provisional definition of the boundary between the Baltic and inner Danish and German waters was adopted, using the Darss underwater ridge (between Darss, Germany and Gedser, Denmark) and Limhamn underwater ridge (at the inner boundary of the Oresund).

Small numbers of strandings and incidental catches are reported year-round in Polish waters near Gdansk, suggesting the existence of a small resident Baltic population (Skora *et al.*, 1988). Benke and Siebert (1995) noted that the number of strandings and incidental sightings indicated that the density of porpoises was much lower in German Baltic waters than in the North Sea. Berggren (1995) reported that very few sightings, strandings, or incidental catches of harbour porpoises had been recorded in recent years in the Swedish Baltic, although anecdotal evidence suggests that they were more abundant in the 1960s. The current northern boundary in the Swedish Baltic appears to lie near Gotland. Porpoises from the Swedish Baltic have been discriminated from those in the Skagerrak by skull morphometrics and from the Norwegian coast by mtDNA RFLP analysis and there are preliminary indications of differences in pollutant burdens between these groups (Berggren, 1995).

KATTEGAT AND ADJACENT WATERS

High densities of porpoises are present in the Kattegat and adjacent waters linking the Baltic and North Seas. The summer distribution of porpoises in this area has been well described from observations made during two aerial surveys (Heide-Jørgensen *et al.*, 1992; 1993), an experimental shipboard survey (Teilmann, 1995a) and the SCANS survey (Hammond *et al.*, 1995). Porpoise densities estimated in this area during SCANS were among the highest recorded during the entire survey. The distribution is continuous from the border with the Baltic Sea (see above) to the border with the North Sea. Due to the unique physiography of the region and the high densities of porpoises, it was agreed to consider this as a separate population, with an arbitrary northern border at the entrance of the Skagerrak. This population division is supported by morphometric and electrophoretic evidence (Kinze, 1985; Andersen, 1993) which separated porpoises from inner Danish waters from those of the Dutch coast.

NORTH SEA

The summer distribution of porpoises in the North Sea has been revealed by the SCANS survey and the analysis of data collected by the Seabirds at Sea Team (Northridge *et al.*, 1995). Information from these systematic surveys has been augmented by smaller scale survey work (Bjørge and Øien, 1995; Camphuysen and Leopold, 1993) and other observations (Addink *et al.*, 1995; Benke and Siebert, 1995; Kock and Benke, 1995; Reijnders *et al.*, 1995; Teilmann, 1995b). In general, harbour porpoises present a continuous distribution across the North Sea, with only a few peripheral areas of low density. There are areas of concentration along the Danish and northern German coasts. Low density areas may demarcate the boundaries of this population in the Channel and the area northwest of the Shetland Islands. The few strandings on the French Channel coast are mostly in winter, and these animals are thought to originate from the North Sea or Celtic Shelf populations (Collet, 1995). Harbour porpoises appear to be virtually absent from the Channel and Dutch coast in summer months; no sightings were recorded in the Channel during SCANS.

The relationship between harbour porpoises in the North Sea and those in adjacent waters is not well understood. Analysis of mtDNA sequences (Walton, 1995) indicates that porpoises from the Netherlands and eastern English coast are distinct from those in the Irish Sea and Celtic Shelf. It also indicates some separation between porpoises in the Shetlands and those in the eastern Irish Sea. Dutch animals apparently have some unusual life history attributes (Addink *et al.*, 1995) and their relationship with other porpoises in adjacent waters of the North Sea is unclear. Interpretation of population structure in this area may be complicated by seasonal movement patterns.

It was agreed to consider porpoises throughout the North Sea, from southern Norway west to the Shetland Islands and south to the Dutch coast, as a single population. This population appears to be distinct from porpoises in northwestern Scottish, Irish and western British waters and the Celtic Shelf, although it is not possible to determine the northern boundary between these units. The southern boundary is the distributional hiatus found in the Channel.

IRELAND AND WESTERN UK

Rogan and Berrow (1995) presented sighting and stranding records for Irish waters. Additional information was obtained during the SCANS surveys (Hammond *et al.*, 1995) and from records of bycatches on the Celtic Shelf (Rogan and Berrow, 1995). These incidental catches were often made at some distance from the coast, adding further credence to the concept that harbour porpoises are not restricted to nearshore waters. Stranding records are available from all areas of the Irish coast, with a concentration in County Cork that probably reflects observer effort. Harbour porpoises are present throughout the year at monitored sites on the east, west and southwest coasts. Additional evidence of the discreteness of harbour porpoises in the Irish Sea comes from an analysis of Caesium-137 levels, which are considerably higher in porpoises from the Irish Sea than those from other areas (Rogan and Berrow, 1995).

IBERIA AND BAY OF BISCAY

Stranding records of harbour porpoises in French Atlantic waters are relatively sparse (Collet, 1995), although the species does occur regularly in the northern portion of the Bay of Biscay throughout the year. The habitat of the Bay of Biscay is considerably different from that in the Channel and harbour porpoises in this area might be part of a more southern Iberian population. There have been no systematic studies of population structure of French porpoises. In Spain, most stranding and incidental catch records are from the Galician coast, with most occurring in late winter and early spring (Lens, 1995). The species appears to be absent from the Mediterranean, with no confirmed records during the last 17 years. Similarly, there have been no recent observations of harbour porpoises in the Canary Islands or Azores. Further support for a concentration of porpoises near the Galician coast is provided by records from Portuguese waters (Sequeira, 1995), where the majority are from the northern and central coast during winter and spring. Porpoises in both Spain and Portugal are unusually large, with several records of specimens greater than 200cm in length. It was agreed that the available information suggested a separate Iberian population.

NORTHWESTERN AFRICA

There is relatively little information on harbour porpoises in northwestern Africa (Smeenk *et al.*, 1992). Recent records indicate a continuous distribution from southern Morocco to Cap Verde, Senegal. Porpoises appear to be fairly common in the coastal waters of Mauritania. Like their Iberian counterparts, northwestern African porpoises are relatively large. It was agreed to follow Gaskin's (1984) original assessment of a separate population of porpoises in northwest Africa, with a northern boundary at the Straits of Gibraltar.

5.1.2 Abundance

5.1.2.1 METHODOLOGY

A number of papers addressed methodological questions in relation to estimating harbour porpoise abundance (e.g. Borchers *et al.*,1995; Buckland and Borchers, 1995; Palka, 1995a and b; Forney, 1995; Garrett and Smith, 1995; Heltsche *et al.*, 1995; Mayo *et al.*, 1995; Teilmann, 1995a). Important factors pertaining to harbour porpoise abundance surveys are: *g*(0), the probability of detecting an animal group on the trackline, classification of duplicates; stratification schemes; types of platforms; spatial clustering; and factors that influence the chances of seeing an animal, such as responsive movements, amount of time spent below the surface and weather conditions (e.g. Beaufort sea state). Details of the methodology are given in IWC (1996).

Two new methods were used during the SCANS surveys. One, developed by Hiby and Lovell, concerned the aerial survey (Hammond *et al.*, 1995). Two aircraft flew in tandem, one behind the other along the same trackline. This allowed the estimation of *g*(0) from duplicates determined on a probabilistic basis. The other new and developing method investigated was a passive acoustic survey (Chappell *et al.*, 1995). An automatic system has been developed which is effective to 200m and possibly to 300–400m. One advantage of acoustic surveys is that in principle they can be conducted in all weather conditions, 24 hours a day, from any vessel. However, it is likely to be some years before they will be sufficiently developed to allow estimation of abundance. One major concern is the variability of vocalisation in target species.

5.1.2.2 ABUNDANCE ESTIMATES

For many reasons, estimates of abundance (and/or of bycatch) often relate to subdivisions of the areas occupied by the putative populations adopted in Fig. 1. For convenience, the sub-committee therefore defined a number of putative management stock areas whose boundaries were often set for administrative, rather than biological reasons (Fig. 2). Accurate and unbiased abundance estimates are required to assess the status of a population or stock. Thus only estimates from systematic surveys have been considered (Table 1).

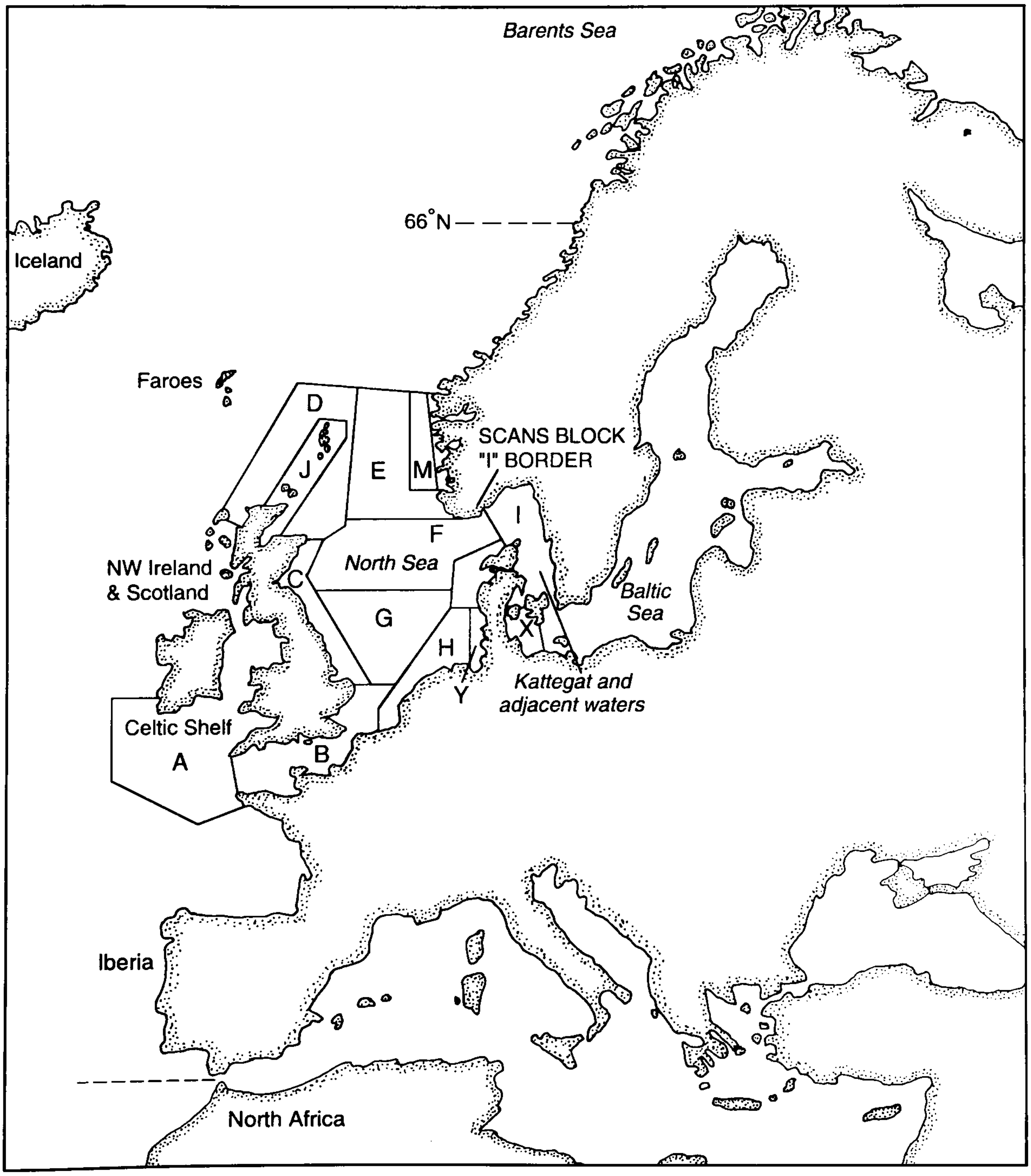

Fig. 2. Harbour porpoise stock divisions. Most (identified by a letter) are derived from SCANS survey blocks. These geographical divisions do not infer biological differences on either side of a line (see text).

Table 1

Abundance estimates of harbour porpoises in the North Atlantic region. There are no estimates for the Gulf of St. Lawrence, Newfoundland, Greenland, the Faroes, the Baltic Sea, Iberia and the Bay of Biscay or Northwest Africa.

Abundance *%CV* 95% CI	Portion of population	Month/year	Methods	Reference
GULF OF MAINE- BAY OF FUNDY				
37,500 *28.8* 26,700-86,400	GOM/BOF	August 1991	Ship LT[1] $g(0)<1$	Palka and Read, 1995
67,500 *23.1* 32,900-104,600	GOM/BOF	August 1992	Ship LT $g(0)<1$	Palka and Read, 1995
47,200 *19.0* 39,500-70,600	GOM/BOF	Weighted average of 1991 & 1992	Ship LT $g(0)<1$	Palka and Read, 1995
ICELAND				
27,000	North of 60° excluding Irminger Sea	June/July 1987	NASS87-ship LT assume $g(0)= 0.7$ ESW=0.41km	Northridge, 1995
N. NORWAY -BARENTS SEA				
11,000 4,790-25,200	Norwegian waters north of 66°N & Barents Sea	July1989	NASS89-ship LT $g(0)=1$	Bjørge & Øien, 1995
KATTEGAT AND ADJACENT WATERS (SKAGERRAK, KATTEGAT, BELT SEAS AND KIEL BIGHT)				
594 *24.9* 368-967	N. Fyn	June 1991	Aerial LT $g(0)=1$	Heide-Jørgensen *et al.*, 1993
502 *14.6* 376-669	N. Fyn	June 1992	Aerial LT $g(0)=1$	Heide-Jørgensen *et al.*, 1993
207 *24.4* 132-331	Kiel Bight	July 1991	Aerial LT $g(0)=1$	Heide-Jørgensen *et al,*. 1993
87 *34.0* 46-166	Kiel Bight	June 1992	Aerial LT $g(0)=1$	Heide-Jørgensen *et al.*, 1993
516 *19.7* 352-757	Great Belt	June 1992	Aerial LT $g(0)=1$	Heide-Jørgensen *et al.*, 1993
91 *38.4* 45-188	Little Belt	June 1992	Aerial LT $g(0)=1$	Heide-Jørgensen *et al.*, 1993
36,046 *30* 20,300-64,100	Skagerrak, Kattegat & Belt Seas (SCANS block I)	July 1994	SCANS Ship LT $g(0)<1$	Hammond *et al.*, 1995
8,060 *25* 4,970-13,100	Belt Seas (SCANS block I')	July 1994	SCANS Aerial LT $g(0)<1$	Hammond *et al.*, 1995
870 *48* 356-2,120	Kiel Bight (SCANS block X)	July 1994	SCANS Aerial LT $g(0)<1$	Hammond *et al.*, 1995

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[1] Line Transect sighting survey

Continued

Table 1 continued

Abundance *%CV* 95% CI	Portion of population	Month/year	Methods	Reference
1,526 *13* 1,241-2,093	Great Belt	April 1994	Ship LT *g*(0)=1	Teilmann, 1995
NORTH SEA				
97-486	Isle of Sylt	June 1991	Aerial LT *g*(0)<1	Heide-Jørgensen *et al.*, 1993
279,367 *18* 197,000-395,000	SCANS blocks: C,D,E,F,G,H,J L,M,Y	July 1994	SCANS Ship LT *g*(0)<1	Hammond *et al.*, 1995
82,600 52,100-131,000	S. Norway & Northern North Sea	July 1989	NASS89 - Ship LT *g*(0)=1	Bjørge & Øien, 1995
750	Dutch waters	1993	Ship LT	Smeenk
0	Channel, SCANS block B	July 1994	SCANS - Ship LT	Hammond *et al.*, 1995
IRELAND AND WESTERN UK				
36,280 *57* 12,800-103,000	Celtic shelf (SCANS block A)	July 1994 ship LT	SCANS *g*(0)<1	Hammond *et al.*, 1995

5.1.3 Mortality

5.1.3.1. INCIDENTAL

(I) METHODOLOGY

Four techniques have been used to estimate bycatch. In order of increasing precision these are: examination of strandings; interviews with fishermen; dock-side monitoring; and observer programmes. The problems associated with the first three are discussed in Perrin, Donovan and Barlow (1994).The most reliable technique is an observer programme, incorporating, where the whole fleet cannot be observed throughout the whole season, a statistical sampling design. Generally, only a sample of the fishing fleet can be observed, so sampling techniques such as ratio estimators have to be used. Three factors to consider when using observer data are: whether the sample is representative of the whole fleet with respect to the season and area; whether all bycaught animals are being recorded; and the magnitude of drop-out, both at and under the water surface. A further advantage of observer programmes is that other types of information can be collected, such as characteristics of the fishery and animals caught in the nets.

In many parts of the world, observer programmes are difficult to implement for logistical, economic or social reasons (see Donovan, 1994). In these cases, alternative techniques to observe the fishery directly need to be explored (e.g. placing observers on patrol vessels, observing from clifftop vantage points).

All sampling techniques require accurate total effort estimates in order to extrapolate the measured bycatch rate of observed trips to the total fleet. The most appropriate measure for effort depends on the type of fishery.

The sub-committee considered what might be the minimum set of fishery statistics necessary to estimate total bycatches of harbour porpoises (or other small cetaceans) in gillnet fisheries; in order to maximise the chances of the necessary data being made available, it is important to keep the data requirements as simple as possible. The following data should be collected on a daily basis by all vessels engaged in gillnetting:

(a) the date;
(b) the location (ideally latitude/longitude, otherwise small statistical area);
(c) the total length of all nets being hauled;

(d) the duration over which the nets were soaked;
(e) the target species.

This, if collected throughout the fishery, will allow estimation of total fishing effort. Provided independent bycatch data are also available, then an estimate of total bycatch can be made. Although data on catch of target species (collected from fish buyers) has sometimes been successfully used to extrapolate bycatch rates in other areas, it was agreed that self-reported catches would not generally be sufficiently accurate for this purpose and might be misleading.

Although these limited data are sufficient to make an appropriate estimate of total effort in a gillnet fishery (i.e. km. hrs of netting), they would be insufficient to investigate broader aspects of harbour porpoise/gillnet interactions which might be of interest. Where a more detailed data collection scheme is feasible, it may be possible to collect more data in order to examine the mechanical or behavioural processes underlying porpoise bycatch. These additional data include:

(a) length of individual nets, number of nets and number of strings deployed;
(b) net height (in metres and meshes to account for tie-downs);
(c) net material;
(d) mesh size;
(e) type of flotation:
(f) hanging ratio;
(g) foot rope type;
(h) depth at which the net was fished;
(i) catch of both target and non-target species.

The sub-committee recognised that this is by no means an exhaustive list (Perrin *et al.*, 1994, p.66). It could certainly be expanded dependent on the objectives of the study.

(II) BYCATCH ESTIMATES

Harbour porpoises can be caught in many types of fisheries. Gillnet fisheries have the greatest catch rates and account for nearly all reported bycatch. However, few other fisheries (e.g. trawl, longline, seine nets) have been monitored. The estimated bycatch and a measure of variability (if available) for each harbour porpoise stock is given in Table 2. Only annual estimates from observer programmes or the number of animals collected by observers or fishermen have been included.

5.1.3.2 DIRECTED

There are few directed takes of harbour porpoises in the North Atlantic.

(I) GREENLAND

The catches in Greenland are seasonal, being highest in summer and autumn (Teilmann and Dietz, 1995, fig. 3); this probably reflects seasonal distribution of the porpoises. Overall catches increased into the 1970s because of increased effort. The minimum long-term overall average was about 700 porpoises annually. Catches have decreased over about the last ten years and have almost ceased at Disko Bay. At present, the largest catches occur in Central West Greenland.

Although most porpoises are taken directly by rifle from powered boats, incidental catches in nets targeted at other species are included in the Greenlandic figures here because they are fully utilised. The recent reduction in catches may be due to cultural changes in Greenland, although data on trends in effort are not available. Fishermen are required to submit reports of their porpoise catches. The total should be considered as

Table 2

Annual bycatch estimates or actual number of harbour porpoises collected in the North Atlantic region. In addition it is known that bycatches occur in the Gulf of St. Lawrence, Newfoundland, and Iceland, but no estimates exist. There is no information for Northwest Africa.

Bycatch *95% CI*	Year	Portion of population	Methods	Reference
Gulf of Maine-Bay of Fundy				
2,900 *1,500-5,500*	1990	Gulf of Maine	Observer programme	Palka & Read, 1995
2,000 *1,000-3,800*	1991	Gulf of Maine	Observer programme	Palka & Read, 1995 Bravington & Bisack, 1995
1,200 *800-1,700*	1992	Gulf of Maine	Observer programme	Palka & Read, 1995 Bravington & Bisack, 1995
1,400 *1,000-2,000*	1993	Gulf of Maine	Observer programme	Palka & Read, 1995 Bravington & Bisack, 1995
200-400	1993	Bay of Fundy	Observer programme	Palka & Read, 1995
80-120	1994	Bay of Fundy	Observer programme	Palka & Read, 1995
Greenland				
1,400	1972		Observer programme[1]	
+700[1]/yr	1900-1993	All	*Directed catch*	Teilmann & Dietz, 1995
Faroe Islands				
"low bycatch"		-	-	T. Martin; Larsen, 1995
North Norway-Barents Sea				
55[1]	1988-1990		Collected by fishermen	Bjørge & Øien, 1995
Kattegat and Adjacent Waters (Skagerrak, Kattegat, Belt Seas and Kiel Bight)				
Unknown but known to exist		Denmark		J. Teilmann
150[1]/yr	1988-1991	Sweden (Skagerrak and Kattegat)	Bycatch and strandings	
17[1]	March-May 1995	Sweden (Skagerrak)	Observer programme	Berggren, 1995
95[1]	1987-1994	Germany (Kiel Bight)	Reported by fisherman	Kock & Benke, 1995
Baltic proper				
4-5[1]/year	1984-1993	Sweden	Collected by fishermen	Berggren, 1995
3[1]	1990-1994	Germany	Collected by fishermen	Kock & Benke, 1995
80[1]/year	1922-1933	Poland	Bounties paid	Skora *et al.* 1988
0-5[1]/year	Currently	Poland	Fishermen's report	Skora *et al.* 1988
North Sea				
75[1]	1988-1990	S. Norway	Collected by fishermen	Bjørge & Øien, 1995
4,629	1993-1994	Denmark[3]	Observer programme	Teilmann, 1995
750/yr	1986-1989	Denmark-one port only		Teilmann, 1995
3,000	1980-1981	Denmark	Fisherman interviews	Teilmann, 1995
21[1]	1990-1994	Germany	Reported by fisherman	Kock & Benke, 1995
Unknown		Scotland	-	-
Unknown		Netherlands	-	-
13[1]	1970-1994	Channel	Collected by fishermen	Collet, 1995
Ireland & western UK				
1,497; *539-2,459*	1993-1994	Ireland	Observer programme	Rogan & Berrow, 1995
552;*198-906*	"	UK	Observer programme	Rogan & Berrow, 1995
Iberia & Bay of Biscay				
6[1]	1970-1994	Atlantic France	Collected by fishermen	Collet, 1995
0[1]	1994	Atlantic Spain	Observer programme	Lens, 1995
14[1]	1978-1994	"	Harbour inspection	Lens, 1995
7[1]	1981-1994	N. Portugal	Reported by fishermen	Sequeira, 1995

[1] Actual number reported, not extrapolated to full fishing effort. [2] Non- Greenlandic salmon driftnet fishery.

[3] most of SCANS blocks L, H, G, F

minimum estimates. There are no data available on struck-and-lost rates for the rifle fishery.

(2) DENMARK
Directed takes in the Little Belt ended at about the end of World War II (Teilmann, 1995b, fig. 5). Catches and effort have been very variable over the last 120 years of the porpoise fishery. Porpoises were also taken in other parts of Denmark until at least the beginning of this century (Kinze, 1995).

(3) POLAND
In the 1920s, from tens to hundreds of bounty payments for porpoise heads were made each year. This also occurred in other Baltic countries. Although some of the bounty payments are likely to have been for porpoises taken incidentally in various local gillnet fisheries, a special fixed net trap for porpoises was set up in Gdansk Bay. The records for this fishery are incomplete, but it certainly did not continue after World War II (Skora *et al.*, 1988; Skora, 1991; Skora, pers. comm.).

(4) FAROES
Larsen (1995) reported that directed catches were historically very low.

(5) NORTHWEST ATLANTIC
Small aboriginal takes occur in Labrador and small catches were formerly made by the Passamaquoddy Indians in Maine. Large directed catches were made in the Gulf of Maine and Bay of Fundy in the 18th and 19th centuries.

5.1.4 Other anthropogenic influences

The Report of the Workshop on Chemical Pollutants and Cetaceans (IWC, 1995b) discusses the question of pollutants and cetaceans and in particular considers the potential of using harbour porpoise populations as a way of addressing the many important and unanswered questions about the effects of pollution on cetaceans. The estimation of pollutant burdens and their effects in cetaceans is very much in its infancy, even though the literature is already extensive, with studies since the early 1960s. In general, most of these studies are descriptive and dominated by information only on the levels of contaminants. Only a few studies have been specifically carried out to try to ascertain the cause/effect relationships between chemical contaminants and pathology.

Hutchinson *et al.* (1995) review information on pollutants in harbour porpoises in the North Atlantic. Other information is given in Addink *et al.* (1995) and Reijnders *et al.* (1995) for Dutch waters; Westgate and Johnston (1995) and Palka and Read (1995) for the western North Atlantic; Sequeira (1995) for Portuguese waters; Rogan and Berrow (1995) for Irish waters; Teilmann and Dietz (1995) for Greenlandic waters; Teilmann (1995b) for Danish waters; Benke and Siebert (1995) for German waters; and Berggren (1995) for Swedish waters.

Relatively few studies on heavy metal contamination in harbour porpoises have been carried out and sample sizes have been very small. Relevant references in addition to those in the review by Aguilar and Borrell (1995) include Kremer (1994), Siebert (1995), Kuiken *et al.* (1993; 1994), Teigen *et al.* (1993). Substantially higher levels of mercury compared to those in other regions were found in harbour porpoises from German waters (Westgate and Johnston, 1995). To date, investigators have not been able to relate any of the described pathological lesions observed in harbour porpoises in European waters directly to toxicity of pollutants. However, current knowledge does not enable us to assess morphological changes of the lymphoid, endocrine and other systems (hormones, enzymes, immunoglobulins, etc.). As a consequence it is important to continue examining the possible long-term effects of contaminants, including heavy metals.

Other potential anthropogenic influences that may affect harbour porpoises (and other cetaceans) include environmental change at (1) the habitat/ecosystem level, or habitat degradation (over-fishing and depletion of food availability, eutrophication and algal blooms, noise pollution, exotic species introduction and marine debris) and (2) the global level (ozone depletion, global warming and changes in sea level).

5.1.5 Population biology parameters

Reliable estimation of biological parameters is extremely difficult in most cases and often not possible, because of the various and usually unknown biases affecting the age, sex and reproductive condition composition of samples coming from incidental kills, directed catches or strandings. Any published estimates must be given careful consideration; uncritical acceptance can lead to serious errors in stock assessment and management.

Caswell *et al.* (1995) estimated a probability density function for maximum population growth rate. The technique combines estimates of fertility parameters for the harbour porpoise with survival rate schedules from other large mammals that give birth to a single offspring at most once annually. A major concern with the paper is that the choice of species used for survival estimates determines the resulting estimate of population growth. Their figure showing the probabilities for different population growth rates overstates our knowledge of the harbour porpoise.

Information on population biology parameters is given in Collet (1995) for Atlantic waters of France; Addink *et al.* (1995) for Dutch waters; Palka and Read (1995) for the western North Atlantic; Lens (1995) for Spanish waters; Sequeira (1995) for Portuguese waters; Rogan and Berrow (1995) for Irish waters; Teilmann and Dietz (1995) for Greenlandic waters; Teilmann (1995b) for Danish waters; Kock and Benke (1995) and Benke and Siebert (1995) for German and North Sea waters; Bjørge and Kaarstad (1995) and Berggren (1995) for Norwegian and Swedish waters; and Smeenk *et al.* (1992) for West African waters.

5.1.6 Ecology

The only new information available to the sub-committee concerned diet: Addink *et al.*, 1995 (Dutch waters); Rogan and Berrow, 1995 (Irish waters); Teilmann and Dietz, 1995, Teilmann, 1995b (Danish waters); Martin, 1995 (British waters); Benke and Siebert, 1995 (German waters); Aarefjord *et al.*, 1995 (Norwegian waters); and Berggren, 1995 (Swedish waters).

The diet of harbour porpoises seems to be more diverse in the eastern Atlantic than in the western Atlantic. Examined stomach contents differed between northern Norwegian and Kattegat waters (Aarefjord *et al.*, 1995). This appears to be related to the bathymetry in the two areas. Pelagic and mesopelagic species were more important in the north, whereas demersal fish were dominant in the south. This reinforces the emerging perception of the harbour porpoise as a species that is not limited to shallow water; it can also forage pelagically on midwater species, allowing it to make a living in deeper, more pelagic habitats than have usually been thought to be typical of the species.

The opinion was expressed that overfishing of some prey species may not constitute a severe problem for harbour porpoises because their ability to feed on a large number of prey species (at least in the northeast Atlantic) would allow them to shift to another prey species if the preferred one(s) were depleted. It was noted that the term 'opportunistic' should probably not be applied to the harbour porpoise, because it is understood to mean that a predator feeds on the most abundant prey available, and it is not known if this is the case. It would be better to classify it as a catholic feeder. It was, however, noted that forcing a predator to switch prey may constitute forcing it into a suboptimal niche or habitat, which may have long-term adverse effects on survivorship and productivity.

In order to better evaluate the direct and indirect impacts of fisheries on populations of harbour porpoises, efforts should be made to find out more about their foraging habits in relation to various types of fishing gear and the species of fish that they catch. For example, stomach contents should also be examined for the target fish species as well as for the porpoises entangled in the gear. Where studied (e.g. Rogan and Berrow, 1995), harbour porpoises have been shown not to be feeding on the target species of the fishery but on its prey. It was also noted that effective study of interactions with fishing gear will probably require the study of the distribution of prey and target species on a very small spatial scale, much smaller than presently documented in fishery literature.

It was suggested that it might be appropriate and useful to include the harbour porpoise in the Barents Sea ecological modelling work presently underway (Walton, 1995; Bogstad *et al.*, 1995).

5.1.7 Status of stocks

The sub-committee considered criteria that might be used to classify the status of harbour porpoise populations. It agreed that the goal should be to identify areas where the effects of bycatch or other human impacts on harbour porpoise populations might not be sustainable in the long term. It is difficult to identify the precise level of fishery mortality that would be sustainable. The USA is adopting new regulations which identify priority stocks of marine mammals using a calculation of what is essentially an upper bound on annual removal levels. In the case of a harbour porpoise stock of unknown status, this value (termed Potential Biological Removal in US law) would be calculated as 1% of a minimum estimate of population size (which is defined as the lower 20th percentile of a statistically-based population estimate).

There was some support for this approach because it explicitly considers the uncertainty of abundance estimates. However, agreement could not be reached on adopting this approach because it could not be thoroughly reviewed by this sub-committee at the meeting in the absence of thorough documentation. It was recognised that a comprehensive evaluation of the available information on this species, with a view to arriving at an agreed formula for offering advice on harbour porpoise status, should be carried out urgently.

As an interim measure, it was agreed that bycatches should not exceed 50% of the maximum growth rate of a population. It was noted that the maximum net production rate of the harbour porpoise could be lower than 4% per year (Palka, 1995a). Given the uncertainty in estimates of both bycatch and abundance, the ratio of these two estimates will be subject to a wide confidence interval. After much discussion, and pending the opportunity to thoroughly evaluate the problem, the sub-committee adopted a figure of 1% of estimated abundance as a reasonable and precautionary level beyond which to be concerned about the sustainability of anthropogenic removals.

In all such cases, further research to refine estimates of abundance and bycatch and to determine whether bycatch is sustainable must be carried out. Documented declines in harbour porpoise populations are a cause for concern and should be brought to the attention of range states. Fishing is not necessarily responsible for declines that may have occurred in harbour porpoise populations and other possible causes of decline should be examined.

BAY OF FUNDY/GULF OF MAINE

The bycatch in this area averaged 1,875 in US waters from 1990–93 and approximately 200 in Canadian waters from 1993–94 (Table 2; Palka and Read, 1995, Bravington and Bisack, 1995). There are additional bycatches in other fisheries. The estimated abundance in this area averaged 47,200 from surveys in 1991–92 (Table 1; Palka and Read, 1995). The minimum bycatch appears to be approximately 4.4% of the population size. This level of bycatch may not be sustainable.

GULF OF ST. LAWRENCE

Gillnet fisheries are known to exist here. Neither the size of the bycatch nor the population size has been estimated for this area.

NEWFOUNDLAND/LABRADOR

Gillnet fisheries are known to exist here. Neither the size of the bycatch nor the population size has been estimated for this area.

GREENLAND

The level of bycatch of harbour porpoises and estimates of directed take suggest that total annual harbour porpoise mortality may exceed 700 (Table 2; Teilmann and Dietz, 1995). No estimates exist of harbour porpoise abundance in this area so it is not possible to evaluate the species' status.

ICELAND

The level of harbour porpoise bycatch in Iceland's large gillnet fishery has not been estimated, but some is known to occur. Harbour porpoise abundance in the waters around Iceland was tentatively estimated at 27,000 in 1987 (Table 1; Northridge, 1995). Insufficient information is available to determine the status of the harbour porpoise in this area.

FAROE ISLANDS

Harbour porpoise bycatch and mortality have not been estimated for the waters around the Faroe Islands. The bottom gillnet fishery is largely in very deep waters and its bycatch is likely to be low. Larsen (1995) indicated that few harbour porpoises are incidentally caught in Faroese fishing gear.

NORTHERN NORWAY AND BARENTS SEA

Bycatch of harbour porpoises has been noted in one fishery and may exist in others, but it has not been possible to estimate total bycatch mortality for this area. The abundance of harbour porpoises is estimated at 11,000 (Table 1; Bjørge and Øien, 1995). Insufficient information is available to determine the status of the harbour porpoise in this area.

NORTH SEA

The bycatch of harbour porpoises has been estimated only for the large Danish gillnet fishery which covers portions of SCANS strata F, G, H and L (Lowry and Teilmann, 1994). The annual bycatch estimate of 4,629 (Table 2; Teilmann, 1995b) is approximately 3.1% of the abundance estimated for those four strata (150,250; Hammond *et al.*, 1995) and is approximately 1.7% of the abundance within all of the SCANS North Sea areas combined. Other gillnet fisheries also exist in the North Sea and are known to take harbour porpoises (Perrin *et al.*, 1994; Bjørge and Øien, 1995). Current levels of bycatch mortality may not be sustainable.

BALTIC SEA

Reports from Germany, Sweden, and Poland indicate that a harbour porpoise bycatch occurs in the Baltic (Berggren, 1995; Kock and Benke, 1995; Teilmann, 1995b), but total levels of bycatch have not been estimated. Although harbour porpoise abundance has not been estimated for this area, historical records clearly indicate that the species was once much more common in the Baltic. Given the decline in abundance, the continued presence of harbour porpoises in the Baltic may be threatened.

KATTEGAT AND ADJACENT WATERS

The abundance in this area has been estimated at 36,000 animals (stratum I, which includes stratum I' of the SCANS survey, Hammond *et al.*, 1995) plus 870 animals (stratum X of the SCANS survey). Bycatches are known to occur in stratum I but there are no estimates of total bycatch. However, bycatches occur year round in Swedish gillnet fisheries in the area (Berggren, 1995) and have also been recorded in Danish fisheries in the Kattegat (Berggren, 1994). In stratum X of the SCANS survey (Hammond *et al.*, 1995), the minimum mortality reported by fishermen (14 per year) is approximately 1.6% of the abundance estimate. Results from an ongoing observer scheme in a subset of the area also indicate a high rate of bycatch (Berggren, 1995). Current levels of bycatch mortality may not be sustainable.

ENGLISH CHANNEL

No harbour porpoises were seen during the SCANS survey in this area. The level of bycatch has not been estimated. Historical records indicate that harbour porpoises were once much more common in the Channel. Because of the decline in abundance, the continued existence of harbour porpoises in the Channel is under threat.

CELTIC SHELF

Harbour porpoise mortality in the Celtic Shelf gillnet fishery has been estimated at approximately 2,000 per year (Table 2; Rogan and Berrow, 1995). The area of this fishery is encompassed by SCANS area A, for which harbour porpoise abundance has been estimated at 36,280 (Hammond *et al.*, 1995). The annual mortality is thus approximately 5.5% of the abundance estimate. This level of removal may not be sustainable.

IRISH SEA, WESTERN IRISH AND WESTERN SCOTTISH WATERS

No estimates of bycatch are available for this area, but gillnet fisheries and harbour porpoises are known to co-occur there. Abundance has been estimated at approximately 19,000 for the seas off southwest Ireland from Galway Bay to West Cork (Rogan and Berrow, 1995), a small subset of the total area. Insufficient information is available to determine the status of the harbour porpoise in this area.

ATLANTIC COAST: FRANCE

No estimates of abundance or total bycatch are available for this area, but some bycatch mortality is known to occur. Insufficient information is available to determine the status of the harbour porpoise in this area.

ATLANTIC COAST: SPAIN

No estimates of abundance or total bycatch are available for this area, but some bycatch mortality is known to occur. Insufficient information is available to determine the status of the harbour porpoise in this area.

PORTUGAL

No estimates of abundance or total bycatch are available for this area, but some bycatch mortality is known to occur. Insufficient information is available to determine the status of the harbour porpoise in this area.

NORTHWEST AFRICA

No estimates of abundance or total bycatch are available for this area. Insufficient information is available to determine the status of the harbour porpoise in this area.

SUMMARY OF ALL AREAS

A clear pattern emerges in those areas with both abundance and bycatch estimates. In all three areas (Bay of Fundy/Gulf of Maine, North Sea, Celtic Shelf) bycatch exceeds 3% of abundance – three times the value that the sub-committee agreed would be sufficient to justify concern about sustainability. Information on abundance and/or bycatch is lacking for many of the areas listed above and the sub-committee recommends the collection of abundance and bycatch data for all areas where this information is lacking.

The sub-committee recognised the difficulty in assessing status by taking a simple ratio of bycatch to abundance in a local area. It was also aware that the areas used do not necessarily correspond to natural boundaries of population structure and that rigid boundaries probably do not exist for any real population. It further recognised that fisheries are dynamic and that levels of effort and fishing methods are constantly changing with changes in fish stocks and technology. Notwithstanding these problems, the sub-committee perceives a broad-scale risk to harbour porpoise populations in the North Atlantic due to problems related to fishery bycatch. In addition, there may be other threats to harbour porpoise populations in this area (e.g. pollution).

5.2 Methods of reducing incidental catches

Neimanis *et al.* (1995) documented information about harbour porpoise entrapments in herring weirs in the Bay of Fundy. In the past, it has been estimated that an average of 70 porpoises are trapped annually and of these about 39% die. An increase in entrapment (Read, 1994) had been reported, but the majority have been released alive. Since 1990, when a cooperative release programme between researchers of the Grand Manan Whale and Seabird Research Station and fishermen was implemented, 194 porpoises have been released alive.

Kraus *et al.* (1995) gave detailed information about a field test of acoustic alarms attached to gillnets in an attempt to reduce harbour porpoise bycatch in the Gulf of Maine. Porpoise bycatch had been regulated by closing the gillnet fishery when the risk of incidental capture was high. In the field trial of the alarms, 13 devices were attached to each string of 12 nets over a two month period. The trials included controls and alarm-activated sink gillnets. The 421 control strings resulted in a bycatch of 25 porpoises, whereas the 423 'active' strings with alarms only resulted in two bycaught porpoises. The difference was highly significant. There was no indication that the target fish catch was reduced in the active strings. In the Gulf of Maine at least, such devices appear to offer an effective means of reducing bycatch. It was emphasised that the results of this experiment should not be extrapolated to other areas or species. Similar studies should be carried out to test the effectiveness of alarms in other circumstances. The overall cost of running the field trial amounted to about US$500,000.

Reijnders *et al.*, (1995) describe a collaborative project comprising investigations on the use of acoustic signals by captive harbour porpoises to detect objects including nets and ropes, entanglement in fishing nets and effects of acoustic alarms on harbour porpoise behaviour (Kastelein *et al.*, 1995; Nachtigall *et al.*, 1995). Cessation of echolocation was among the reactions to one of the Canadian acoustic alarms by captive porpoises. Although this may suggest habituation after short exposures, the field trials of Kraus *et al.*, (1995) did not provide any evidence for immediate habituation. Harmonic variability in the alarms may be an important factor in preventing habituation. Long-term field experiments should be carried out, following the experimental design of Kraus *et al.* (1995), to assess if harbour porpoises habituate to acoustic alarms, reducing their effectiveness in the long term.

Practical matters concerning the relatively high cost of the alarms, the need for maintenance (regular battery checks/changes) and the wear and tear of the devices were discussed in relation to the likelihood of such technology being accepted by fishermen. It was agreed that if acoustic alarms are to be proven effective in the long-term, the practical aspects of their use will need to be assessed. In the Gulf of Maine it was reported that fishermen were eager to use such devices, but this may be linked to a perceived threat of fishery closure should bycatches continue. Work is in progress towards the production of miniature alarms which could be incorporated during net manufacture, fitted with batteries for approximately the working life of the net.

Concern was expressed that use of alarms in areas of high net density may add to the general oceanic noise, but the output of the devices described in Kraus *et al.* (1995) was designed to diminish to ambient levels at about 300m.

The sub-committee greatly welcomed these promising developments, noting that two potential problems with acoustic alarms had not yet been addressed: the risk that harbour porpoises may habituate to the signals and the practicalities (e.g. cost) of the use of alarms in a real-life fishery situation.

5.3 Recommendations

Assessment of harbour porpoise populations in the North Atlantic

For a complete assessment, the following information is required (Donovan, 1994):

(a) magnitude of bycatches;
(b) abundance;
(c) stock identity and seasonal movements;
(d) population biology parameters.

(1) MAGNITUDE OF BYCATCHES

As noted in Perrin, Donovan and Barlow (1994), wherever gillnet fisheries and harbour porpoises co-occur in the North Atlantic, bycatches have been recorded. Robust estimates of the magnitude of bycatches are available for very few fisheries (see Tables 2 and 3).

The sub-committee therefore recommends that range states obtain reliable estimates of bycatch mortality, using statistically sound observer programmes.

Many unreliable approaches have been used to attempt to estimate bycatch mortality. The sub-committee recommends that a full assessment of methods to estimate bycatch be made at next year's meeting. Such an assessment requires input from experts in fisheries practices.

(2) ABUNDANCE

The sub-committee welcomed new estimates of abundance for some large areas of the North Atlantic (see Item 5.1). However, abundance estimates are still lacking for some areas (Table 3).

Table 3

Availability of reliable (see text) and current estimates of abundance and bycatches

Population	Bycatch occurs	Bycatch estimates	Abundance
Bay of Fundy/Gulf of Maine	✓	✓	✓
Gulf of St Lawrence	✓		
Newfoundland and Labrador	✓		
Greenland	✓		
Iceland	✓		
Faroe Islands	✓		
North Norway and Barents Sea	✓		✓
North Sea	✓	✓*	✓
Kattegat and adjacent waters	✓		✓
Baltic Sea	✓		
Ireland and western UK	✓	✓*	✓*
Iberia and Bay of Biscay	✓	✓*	
Northwest Africa	✓		

* Incomplete

The sub-committee recommends that range states, preferably in collaboration (as illustrated by the SCANS survey) urgently obtain estimates of abundance in these areas.

(3) STOCK IDENTITY AND SEASONAL MOVEMENTS

The sub-committee noted that for no area in the North Atlantic was there sufficient information on population structure. In some areas current information is not even sufficient to define adequate management units (see Item 5.1).

The sub-committee recommends that a multinational and multidisciplinary programme, such as that outlined in IWC (1995a, p.185–6) be conducted to improve our understanding of harbour porpoise population structure in the North Atlantic, so that adequate management units can be defined.

(4) POPULATION BIOLOGY PARAMETERS

As noted under Item 5.1.7, the sub-committee had considerable difficulty in interpreting the biological significance of harbour porpoise bycatch in the North Atlantic as expressed as a simple percentage of abundance, even where estimates of both factors were considered robust. It recommends that discussion of this topic be undertaken as a matter of urgency and forms the priority topic for next year's meeting.

(5) REDUCTION OF BYCATCH

The sub-committee recommends that:

(1) additional experimental field trials with acoustic alarms be conducted, using observers and the double blind experimental design in Kraus *et al.*, (1995), both in the same and additional geographical areas, so that the long-term effectiveness in reducing bycatches and the potential for habituation can be assessed;

(2) that further observations of porpoise behaviour in relation to nets both in the field and in captivity be carried out, using platforms of opportunity e.g. cliff-tops, oil rigs, underwater observations, etc. where feasible, and rehabilitation centres;

(3) the effectiveness of acoustic alarms be tested in a practical fishery situation.

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SC/44/SM24

Abundance Estimate of the Gulf of Maine Harbor Porpoise

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ABSTRACT

Shipboard surveys were conducted in the summer of 1991 to estimate the abundance of harbor porpoises, *Phocoena phocoena*, in the northern Gulf of Maine and lower Bay of Fundy. The best estimate is 37,500 (95% CI: 26,600 to 86,400). The estimate is based on the independent team sighting procedure from one ship, which allowed the estimation of $g(0)$: 0.72 (SE=0.06). The abundance estimate presented is substantially higher than previous estimates for the area. This is due to the more extensive areal coverage and the inclusion of $g(0)$ into the estimate. While the statistical precision that was reported here included some sources of uncertainty, others remain to be addressed. The most important of these are the potential downward bias due to animals avoiding the vessel, the highly aggregated spatial distribution of porpoises and the largely unknown effects of heterogeneity of observers, platforms and environmental conditions.

KEYWORDS: HARBOUR PORPOISE; NORTH ATLANTIC; SURVEY-SHIP; ASSESSMENT; $g(0)$.

INTRODUCTION

There are five past surveys that estimated the abundance of harbor porpoise in the Gulf of Maine-Bay of Fundy region (Gaskin, 1977; Prescott *et al.*, 1981; Winn, 1982; Kraus *et al.*, 1983b; Gaskin *et al.*, 1985). Estimates ranged from roughly 3,000 to 15,000 animals. They provided minimum estimates of abundance because of their limited ranges and because of failures of assumptions made in the analyses. In 1991, two surveys were conducted over a much broader area using line transect survey techniques developed to overcome some of the previous methodological problems (Kraus *et al.*, 1983a; Barlow, 1988; Butterworth and Borchers, 1988; Polacheck, 1989; 1994a; b; Polacheck and Smith, 1989; 1990; Øien, 1990; Polacheck and Thorpe, 1990; Polacheck *et al.*, 1990; 1994).

In this paper, I present a new population abundance estimate using data collected during the two 1991 surveys. The reliability of the abundance estimate is assessed and potential sources of uncertainties that were not accounted for are discussed. This paper updates the abundance estimate reported in Smith *et al.* (1991), Anon. (1992) and Read *et al.* (1993).

METHODS

Field procedures

From 22 July – 31 August 1991, a shipboard sighting survey was performed in the offshore waters of the Gulf of Maine-lower Bay of Fundy-southern Scotian shelf area. From 3 – 17 August 1991 a second survey was performed in the shallow inshore bays off Maine (Fig. 1). 'Passing mode' line transect methods (Burnham *et al.*, 1980; Butterworth and Borchers, 1988) were used on both vessels. The independent team sighting procedure was used on one of the ships to allow the estimation of $g(0)$, the probability of detecting a group of animals on the trackline.

The survey area was stratified first by depth, then within the deeper, offshore region by expected harbor porpoise density. This resulted in four strata, referred to as the 'high density', 'intermediate density', 'low density' and the shallower 'inshore' strata (Fig. 1). The abundance estimates for the high, intermediate and low density strata were obtained from data collected aboard the *R/V Abel-J* (106-ft, 15-ft draft). The abundance estimate for the inshore stratum was obtained from data collected aboard both vessels because the *R/V Abel-J* could not enter all of the shallow inshore bays and the smaller vessel, *M/V Sneak Attack* (48-ft, 4-ft draft), could not accommodate the independent team sighting procedure.

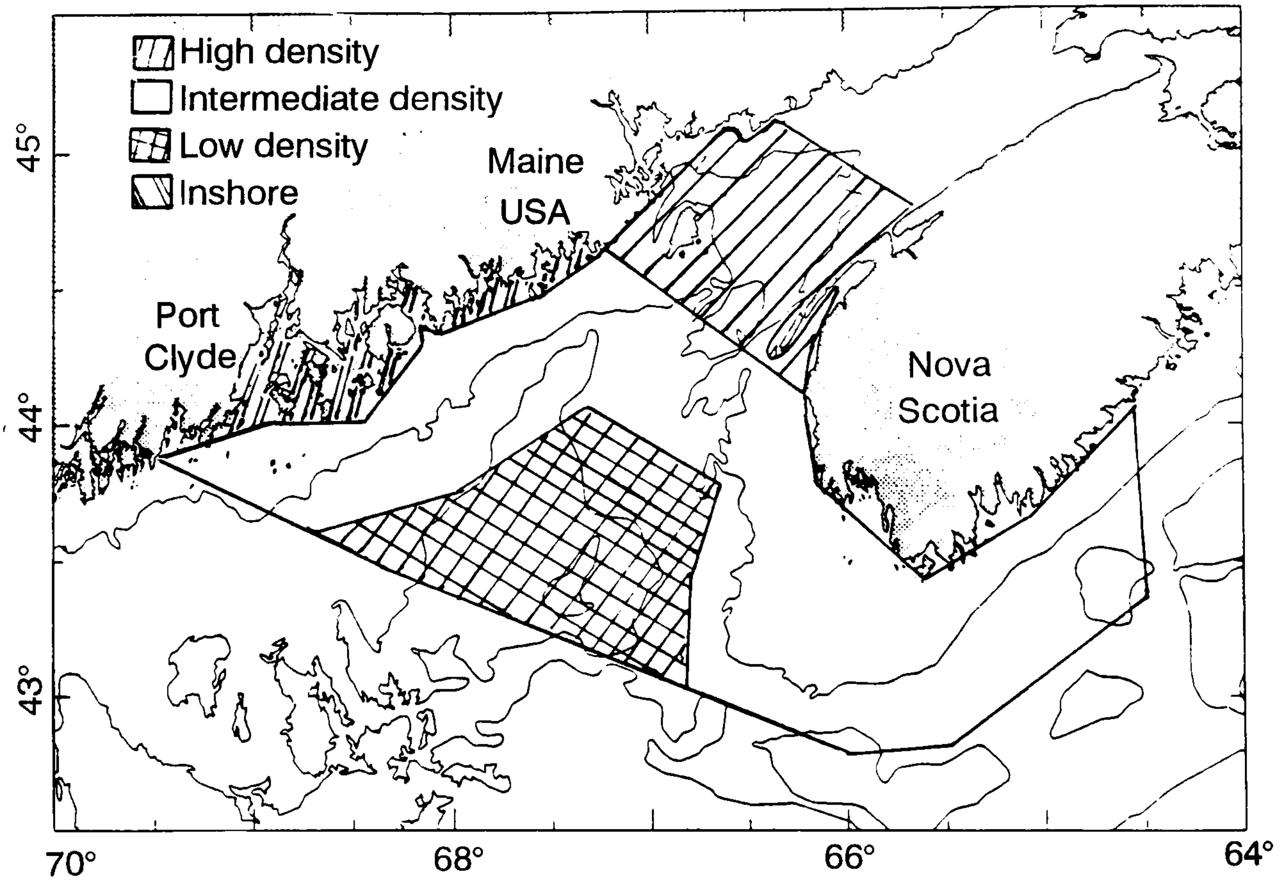

Fig. 1. Study area located in the Gulf of Maine, lower Bay of Fundy and part of the Nova Scotian shelf. Study area divided into four strata: high density; intermediate density; low density; and inshore. Dotted lines represent the 50 and 100 fathom depth contour lines.

Sneak Attack survey

Line transect survey methods were performed in Beaufort sea state two or less along 7 nautical mile (n.mile) transects within four geographical blocks: (A) Penobscot Bay; (B) Jericho and Blue Hill Bays; (C) Frenchman Bay; and (D) Pleasant, Englishman and Machias Bays (Fig. 2). The blocks were assigned on the basis of possible habitat divisions and to facilitate allocation of survey lines. Each block was divided into an inshore and offshore area. The inshore area corresponded to the inshore stratum, defined above, and was delimited as the waters inshore of lines connecting major headlands. The offshore area encompassed waters out to 5 n.miles offshore these lines.

Trackline mileage was allocated in proportion to the surface area of navigable waters. Survey tracklines were divided into 7 n.mile transects (Fig. 3). The sighting team consisted of three observers, a recorder and a helmsman. People rotated among positions every 30 minutes, which was approximately the length of one transect. The ship traveled at 14 knots.

For every detected marine mammal, the data recorded were the position (using LORAN C), species, group size (best, high and low estimate), sighting cue, number of calves, identity of the observer responsible for the sighting, radial distance (estimated visually) and bearing to the initial sighting position (facilitated by the placement of markers of measured radial degrees around the observation area). In addition, at the beginning of each transect and at all marine mammal sightings, vessel speed, water depth, surface water temperature, sea state, swell, weather and glare conditions were recorded (Read and Kraus, 1991).

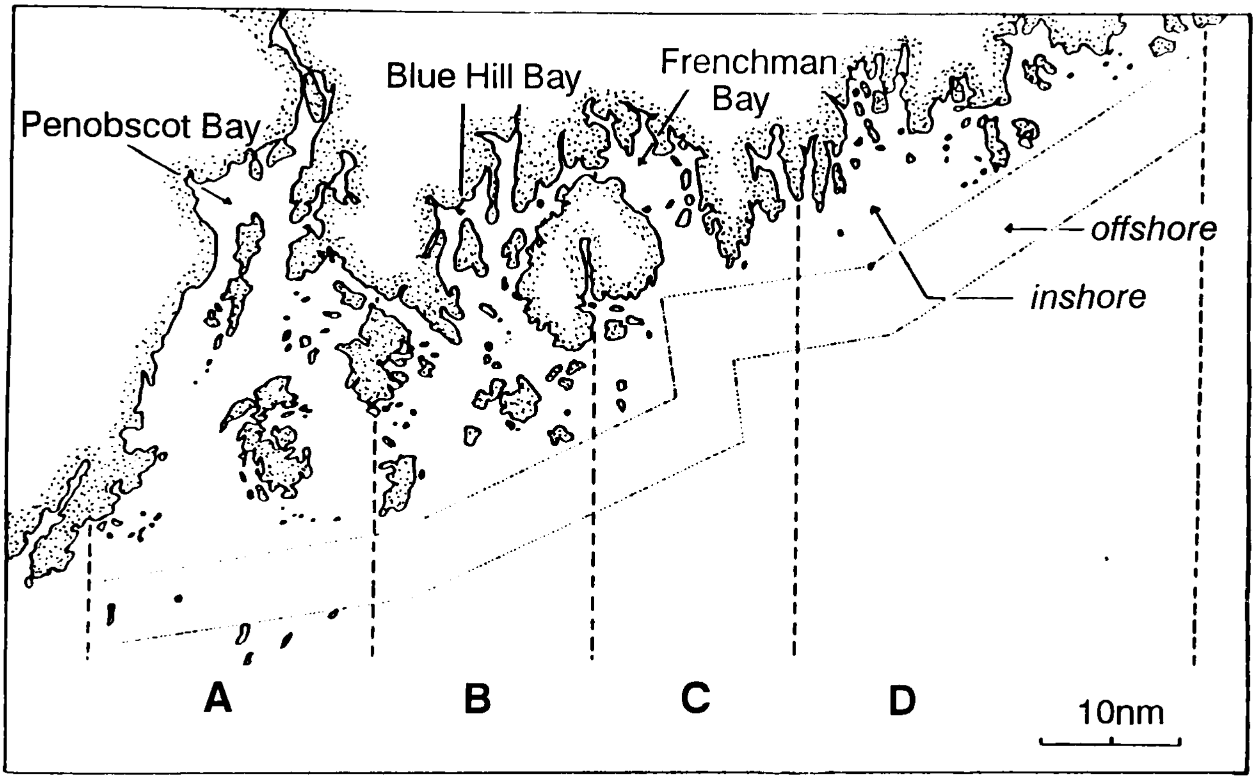

Fig. 2. Area surveyed by the *M/V Sneak Attack* which is divided into four geographical blocks (A, B, C, D). Each block is divided into an inshore area, corresponding to the inshore stratum shown in Fig. 1 and an offshore area 5 n.miles off the inshore area.

Abel-J survey

Trackline mileage in the high density and intermediate density strata was approximately proportional to the stratum area. The trackline length in the low density stratum was less than proportional to the area. The trackline mileage allocation was accomplished by dividing each stratum into 'boxes', each approximately 600 n.miles^2. Within each box, 90–100 n.miles were surveyed, roughly one day's effort. The order in which the boxes were surveyed was chosen randomly with the constraint that the box to be surveyed on the next day could be reached by traveling during the night. The tracklines within a box followed a zig-zag pattern running along hypothesized density gradients (i.e. perpendicular to density contour lines). Because both a northeastern-southwestern (Kraus *et al.*, 1983b) and an

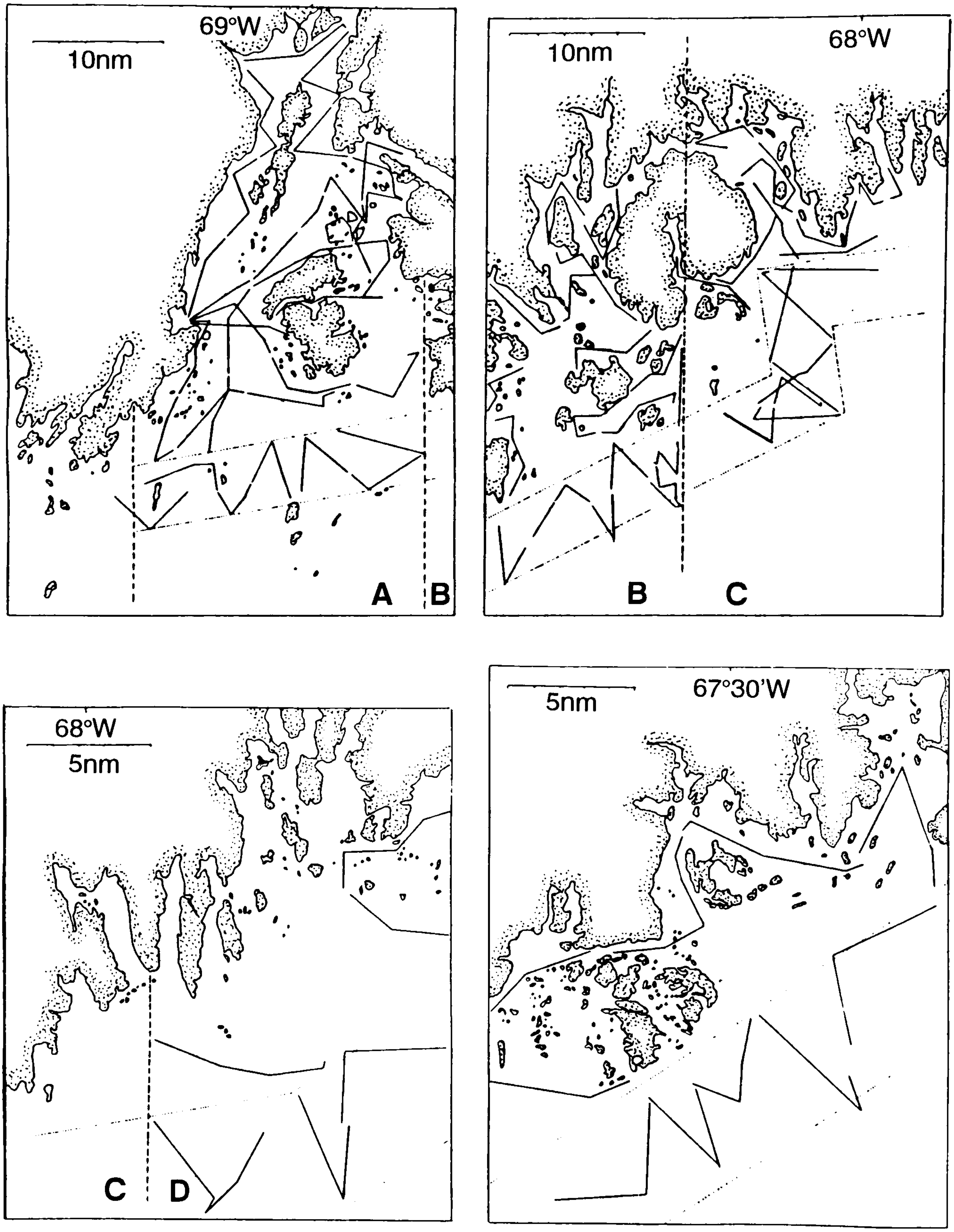

Fig. 3. Tracklines surveyed by the *M/V Sneak Attack* in the four geographical blocks.

inshore-offshore gradient (Gaskin, 1977) had been proposed, some day's tracklines ran north-south (parallel to the shoreline) while other day's ran inshore-offshore (perpendicular to the shoreline) (Fig. 4). The starting point within a box was chosen randomly, again with the constraint that the starting point could be reached by travel during the night.

The tracklines were divided into 'transects' and 'legs' to facilitate estimating a bootstrap confidence interval of the abundance estimate, as has been done in other marine mammal sighting surveys (Øien, 1990; Gerrodette and Wade, 1991). There were 4–8 'transects' per day, where a transect was defined as the time during which the ship's heading and speed was constant. A transect was made up of a consecutive series of 'legs', where a leg was defined as the time during which all conditions were constant. Conditions considered were environmental factors and position of observers, in addition to ship's speed and heading .

The independent observer sighting procedure (Butterworth and Borchers, 1988) was used throughout the survey to allow estimation of abundance corrected for $g(0)$. Two physically separated teams of observers searched simultaneously for marine mammals using the unaided eye. One team was located on the 'upper' crow's nest, 14m above the sea surface, while the other team was located vertically below the upper team on the 'lower' crow's nest, 9m above the sea surface. The two teams could not see or hear each other.

There were four observers per team. Observers did not rotate between teams. Each team surveyed from only one sighting platform. On each observation platform there were three observing positions: port, center and starboard. Observers rotated among positions every 30 minutes, moving from the port to center to starboard observation position and then to a rest position which was not located on the observation platform. Every morning the starting position of the team members was chosen randomly with the constraints that the person in the first rest position rotated systematically and that the time spent in each observation position during the entire survey was approximately the same. Surveys were conducted when the Beaufort sea state was less than or equal to four and the visibility was greater than 500m.

To facilitate determining which groups of animals were detected by both teams, the observers tracked detected harbor porpoise groups, when possible, recording the position of two or three surfacings. The data collected for each marine mammal sighting included: time of sighting (recorded to the nearest second), species, radial distance between the ship and animal group (estimated visually), bearing angle between the ship's line of travel and the line of sight to the animal (measured with a polarus mounted in front of each observation position), group size (best, high and low estimates), direction the group was travelling initially (measured with the polarus), number of mother-calf pairs and sighting cue. The high (low) estimate of group size was defined as the largest (smallest) number of animals that was thought to be in the group. Best group size was defined to be the observer's judgement of most likely estimate of group size.

Data collected by the chief scientist at the beginning of each leg and the end of the day were: position (using LORAN C), ship's speed and bearing, position of each observer and environmental conditions including: wind speed and direction, swell direction and height, Beaufort sea state, presence of rain or fog, percentage of cloud cover, vertical and horizontal position of the sun and glare conditions for each observer as perceived by that observer. The latitude and longitude of each marine mammal sighting was estimated, after the survey, by dead reckoning between the positions recorded for the beginning and end of the leg in which the sightings was made in.

To obtain accurate visual estimates of radial distance between the ship and animal group, the observers were trained and tested. This was accomplished by having observers estimate the distance to a floating wooden replica of a harbor porpoise which was placed at various distances and bearings around the main ship. During the times the replica was being moved using a small boat, the observers, who were standing on their respective observation platform, were instructed not to look at the water. After the replica was placed in the water, the actual distance between the ship and replica was measured from the main ship to the small boat using the ship's radar. Then the small boat moved away from the floating replica and the observers were instructed to find the replica, visually estimate the distance between the ship and replica and then use the polarus to measure the bearing. During training, the actual distance was immediately reported to the observers. During testing, actual distances were withheld until the end of the test. Training and testing occurred for one day before the survey and then during the survey for a few hours each week.

Analytical procedures

Two analytical techniques were used to estimate the abundance within each stratum and within the entire study area. Both techniques allow the estimation of $g(0)$. The first technique estimates $g(0)$ by the product integral method (Butterworth and Borchers, 1988) which assumes the sighting processes of the two teams are independent and consequentially the distribution of sightings detected by both teams (referred to as duplicate sightings) is predicted, not directly estimated. This assumption has often been necessary because of a small sample size of duplicate sightings. However, the sample size of duplicate sightings from this survey was large enough to permit the use of another technique that estimates abundance which is corrected for $g(0)$.

Using the first technique (product integral method), the abundance of animals ($\hat{N}$) was estimated by:

$$\hat{N} = \sum_{i=1}^{4} \hat{N}_i = \sum_{i=1}^{4} \hat{D}_i \cdot A_i = \sum_{i=1}^{4} \frac{n_i \cdot \hat{f}_i(0)}{2.L_i.\hat{g}_i(0)} \cdot \hat{E}(s_i).A_i \qquad (1)$$

where

N_i = estimated abundance of animals, corrected for $g(0)$, within stratum i;
$\hat{D}_i$ = estimated density of animals, corrected for $g(0)$, within stratum i;
n_i = number of unique sightings detected within stratum i;
= $n_{iup} + n_{ilo} - n_{idup}$;
n_{iup} = number of sightings detected by the upper team within stratum i;
n_{ilo} = number of sightings detected by the lower team within stratum i;
n_{idup} = number of sightings detected by both teams within stratum i;
$\hat{f}_i(0)$ = probability density of observed perpendicular distances from stratum i where the distance equals zero
L_i = length of trackline surveyed within stratum i;
$\hat{E}(s_i)$ = average size of porpoise groups detected within stratum i;
A_i = area of stratum i;
i = stratum index, i=1 to 4;
$\hat{g}_i(0)$ = probability of detecting an animal on the trackline within stratum i;
= $\hat{g}_{iup}(0) + \hat{g}_{ilo}(0) - [\hat{g}_{iup}(0) \cdot \hat{g}_{ilo}(0)]$, where

$$\hat{g}_{iup}(0) = \frac{n_{idup}}{n_{ilo}} \cdot \frac{\int_{y=0}^{w} \hat{g}_{ilo}(y)\, dy}{\int_{y=0}^{w} \hat{g}_{iuplo}(y)\, dy} \quad \text{and} \quad \hat{g}_{ilo}(0) = \frac{n_{idup}}{n_{iup}} \cdot \frac{\int_{y=0}^{w} \hat{g}_{iup}(y)\, dy}{\int_{y=0}^{w} \hat{g}_{iuplo}(y)\, dy} \qquad (2)$$

and

$\hat{g}_{iup}(y)$ = probability of the upper team detecting a group at perpendicular distance y within stratum i;
$\hat{g}_{ilo}(y)$ = probability of the lower team detecting a group at perpendicular distance y within stratum i;

$\hat{g}_{iuplo}(y)$ = probability of both teams detecting a group at perpendicular distance y within stratum i;
w = maximum perpendicular distance.

Assuming the sighting processes of the two teams were independent, $\hat{g}_{iuplo}(y)$ was estimated by

$$\int_{y=0}^{w} \hat{g}_{iuplo}(y)\, dy = \int_{y=0}^{w} [\hat{g}_{iup}(y) \cdot \hat{g}_{ilo}(y)]dy \qquad (3)$$

The value of $f_i(0)$ was estimated using the perpendicular distances of the unique sightings (n_i), where the perpendicular distance recorded by the first team that detected a duplicate sighting was used, regardless of which team made the detection.

The second technique used to estimate abundance, referred here to as the direct duplicate method, differs from the product integral method in that the independence assumption (equation 3) was not made. The animal density corrected for $g(0)$, within a stratum, $(\hat{D}_i)$ was estimated directly from the Petersen two-sample mark-recapture equation. Thus, the abundance of animals, $\hat{N}$, was estimated by:

$$\hat{N} = \sum_{i=1}^{4} \hat{N}_i = \sum_{i=1}^{4} \hat{D}_i \,.\, A_i = \sum_{i=1}^{4} \frac{\hat{D}_{iup} \cdot \hat{D}_{ilo}}{\hat{D}_{idup}} \,.\, A_i \qquad (4)$$

where
$\hat{D}_{iup}$ = density of animals as seen by the upper team, not corrected for $g(0)$;
$\hat{D}_{ilo}$ = density of animals as seen by the lower team, not corrected for g(0);
$\hat{D}_{idup}$ = density of animals detected by both teams, not corrected for g(0).

$\hat{D}_{iup}$, was estimated by

$$\hat{D}_{iup} = \frac{n_{iup} \cdot \hat{f}_{iup}(0) \,.\, \hat{E}(s_{iup})}{2L_{iup}} \qquad (5)$$

$\hat{D}_{ilo}$ and $\hat{D}_{idup}$ were estimated similarly. For comparison purposes, the value of $\hat{g}_i(0)$, under the direct duplicate method, was estimated using equation (2) and assuming $\hat{g}_{iuplo}(y)$ (equation 3) was estimated from the observed perpendicular distances of the duplicate sightings.

Both the product integral and direct duplicate technique requires $\hat{E}(s_i)$, the estimated average group size. The observer's best estimates of group size were used. Several methods were used to determine if the probability of detecting a group of animals changed as a function of group size, referred to as size bias (Quinn, 1985; Drummer and McDonald, 1987). For the data collected within each stratum, a plot of group size versus perpendicular distance was inspected. If there was a significant slope, then size bias may exist. In addition, a covariate analysis was performed using the data from each stratum with the software package SIZTRAN (Drummer, 1991). In such an analysis, the probability of detecting a group $(g(y,s))$ is a bivariate function of both observed perpendicular distance, y, and group size, s, (Drummer and McDonald, 1987; Ramsey *et al.*, 1987). A bivariate detection function is described by the usual models (negative exponential, half normal, etc.) with an additional estimable parameter, α, which is defined as the effect of group size on the detection function. When $\alpha=0$ no effect exists and there is no size bias. In a covariate analysis, the null hypothesis $\alpha=0$ is tested using standard likelihood ratio tests. If the test is rejected, then size bias exists.

For both the product integral and direct duplicate technique, the hazard rate model was fit to unsmeared perpendicular distances, unless another model fit the data better, as was determined by the AIC score (Akaike Information Criteria; Akaike, 1974; Burnham *et al.*, 1987) and visual inspection of the fit near the origin, the most critical region

(Burnham *et al.*, 1980). The computer package DISTANCE (Laake *et al.*, 1991) was used to estimate $g(y)$, where the maximum perpendicular distance (w) was 400m. Using 400m, 8 and 9% of the sightings were deleted from the upper and lower team's data, respectively.

Equations (1) and (4) may represent an over-parameterised model. That is, some parameters within the equations may not differ between strata and, therefore, should not be estimated separately (Burnham *et al.*, 1987; Buckland and Turnock, 1992). To create a reduced, more parsimonious model, each parameter was investigated to determine if the values of the parameter from the high density, intermediate density and inshore stratum differ. The low density stratum had only three sightings and was, therefore, excluded from this test. Differences in $E(s_i)$ and n_i/L_i were investigated using Tukey's studentized range (HSD) multiple comparison test within an ANOVA framework (SAS Institute Inc., 1985). The Kolmogorov-Smirnov statistic (Zar, 1984) was used to determine if there were differences in the shape of the $\hat{g}(y)$ curves.

The estimate of $g(0)$, and consequentially the abundance, was dependent on which sightings were determined to be duplicates. Two people (D. Palka and D. Potter) independently categorized each sighting as a duplicate or non-duplicate sighting by examining the time the sighting was made, the location of the group in relationship to the ship, the direction of travel and the best, high and low estimate of group size. Duplicate sightings were rated as 'definite' or 'possible', depending on the confidence of the judgement.

Equations (1)-(5) were used to estimate abundance of porpoises within the high density and intermediate density strata. Because only three harbor porpoise groups were detected in the low density stratum, all by the lower team, the above equations had to be modified. The abundance estimate for the low density stratum was calculated assuming the detection function, $\hat{g}(0)$ and the average group size was the same in the low density as in the intermediate density stratum, while the values of n_i, L_i and A_i were those associated with the low density stratum.

The abundance within the inshore stratum used data collected aboard both the *R/V Abel-J* and *M/V Sneak Attack*. For this stratum, abundance was estimated by the product of three factors: (1) the $\hat{g}(0)$ corrected density of porpoises within the 5 n.mile strip of offshore waters, as determined by the *R/V Abel-J* survey, (2) the area of the shallow inshore stratum and (3) the ratio of the sighting rate of porpoise groups in inshore waters to the sighting rate in the 5 n.mile strip of offshore waters, as determined by the *M/V Sneak Attack* survey.

The variability of an abundance estimate for a stratum or for the whole study area is represented by the coefficient of variation (CV) and 95% confidence interval (CI). The variability is due to two components: (1) the usual sampling variability of parameters found in equations (1)-(5), given the number of duplicate sightings; and (2) the estimated number of duplicates which involves the uncertainties of categorizing a sighting as a duplicate or non-duplicate sighting (referred to as duplicate determination variability).

The sampling variability was estimated by using bootstrap re-sampling techniques (Efron, 1982). A bootstrap sample was generated by randomly selecting data, with replacement, from the original data. The re-sampling unit was a 'transect' of survey effort within a stratum (4–8 transects per day; 13–78 per stratum). Within a bootstrap sample, the number of transects in a stratum was constrained so that the total length of trackline within a stratum equals the trackline length in the actual survey. If after choosing a random transect, the trackline length exceeded the actual track length then only the first portion of the transect needed to reach the desired track length was used in that bootstrap sample. Because there were only three groups of porpoises detected in the low density stratum, the abundance of animals in the low density stratum within a bootstrap sample was estimated as described above, except that n_{low} always equaled three (the actual number of groups observed in the low density stratum). The re-sampling procedure was repeated 1,000 times. Thus for each technique, 1,000 values for each stratum of all estimable parameters in equations (1) – (5) were created.

Assuming the two judges were a random sample from the set of possible competent judges, the duplicate determination variability was expressed by two sets of 1,000 bootstrap samples for each technique. One set was created assuming the duplicate sightings were those that were defined by Judge A and the other set assumed the duplicates were those defined by Judge B.

To obtain an estimate of both the sampling and duplicate determination variability of a parameter, the bootstrap distribution for that parameter using one judge's data was pooled with the respective bootstrap distribution from the other judge, resulting in a 'joint' distribution which contains 2,000 estimates of the parameter (Schweder *et al.*, 1991). This joint distribution estimates the sampling distribution of the parameter. The point estimate of the parameter was defined as the median of the corresponding joint bootstrap distribution. The endpoints of the 95% confidence interval of the parameter was estimated by the 2.5 and 97.5 percentile of the corresponding joint bootstrap distribution. The parameters in which this procedure was applied to was $g_i(0)$, $g_{iup}(0)$, $g_{ilo}(0)$, $g_{idup}(0)$, D_i and N_i. The point estimate of N was defined as the summation of the point estimates of N_i.

The CV of the total abundance [$\mathrm{CV}(\hat{N})$] was calculated using

$$\mathrm{CV}^2\,(\hat{N}) = \hat{\mathrm{var}}(\hat{D}_T)\ /\ \hat{D}_T^2 \tag{6}$$

where

$$\hat{\mathrm{var}}(\hat{D}_T) = \sum_{i=1}^{4} \left(\frac{A_i}{A} \cdot \mathrm{SE}(\hat{D}_i)\right)^2$$

$$\hat{D}_T = \sum_{i=1}^{4} \left(\frac{A_i}{A} \cdot \hat{D}_i\right)$$

and

$\hat{D}_T$ = weighted total density of individuals within all strata;

A = area within all strata.

The $\mathrm{SE}(\hat{D}_i)$ was estimated by the standard deviation (SD) of the 2,000 bootstrap estimates within the joint distribution of density of individuals from stratum *i*.

The percent coefficient of variation of $\hat{N}_i$ ($\%\mathrm{CV}(\hat{N}_i)$) was estimated by:

$$\%\ \mathrm{CV}\ [\hat{N}_i] = \frac{\mathrm{SE}(\hat{N}_i)}{\hat{N}_I} \cdot 100 \tag{7}$$

where the SE of $\hat{N}_i$ equals the SD of the bootstrap $\hat{N}_i$ estimates within the joint distribution and $\hat{N}_i$ is the point estimate of the joint distribution from stratum *i*.

RESULTS

Sneak Attack survey

The *M/V Sneak Attack* travelled 640 n.miles in four geographic areas each of which was divided into the shallow inshore stratum and adjacent offshore five-mile area (Fig. 3). A total of 135 harbor porpoise groups were detected (Table 1). The mean number of sightings per seven mile transect was 1.66 and the mean best estimate of group size was 1.91. There were no significant differences (p=0.28) between the number of porpoise

Table 1

Summary of results from the *M/V Sneak Attack* sighting survey in four geographical areas (A,B,C,D). Each geographical area was divided into an inshore and offshore area. The reported results are track length measured in n.miles, area (n.miles^2), number of detected harbor porpoise groups, number of sightings per number of 7 n.mile transects (sighting rate), number of completed transects and average size of detected groups.

	Area	Track length	Area	No. of groups	Sighting rate (*N*)	Av. group size
A	Inshore	174	350	49	2.09 (23)	1.67
	Offshore	50	100	11	1.38 (8)	1.82
B	Inshore	86	175	25	2.00 (12)	1.64
	Offshore	42	85	9	1.17 (6)	1.56
C	Inshore	64	125	22	2.44 (9)	2.50
	Offshore	51	100	8	1.14 (7)	2.12
D	Inshore	74	150	1	0.17 (6)	2.00
	Offshore	99	200	10	1.25 (8)	2.70
All	Inshore	398	800	97	1.90 (50)	1.85
	Offshore	242	485	38	1.24 (29)	2.05
Total		640	1285	135	1.66 (79)	1.91

sightings per transect in the inshore (1.90, SD=2.23, N=50) and offshore (1.24, SD=1.45, N=29) areas, nor were there significant differences (p=0.89) between the mean group size in the inshore (1.85, SD=1.37, N=97) and offshore (2.05, SD=1.39, N=38) areas (Read and Kraus, 1991). The ratio of the sighting rate of porpoise groups in the inshore stratum to the sighting rate in the offshore five-mile area was 1.53. The value of this ratio was used in the inshore stratum abundance estimate (see below).

Abel-J survey

The *R/V Abel-J* covered approximately 1,961.5 n.miles of trackline in the study area during good weather conditions (Fig. 4; Table 2). In addition, 73.5 n.miles were covered during a bad weather (poor visibility) day; 82.5 n.miles were covered in the inshore bays of Nova Scotia (not in the study area) using both the *R/V Abel-J* and a rigid hulled inflatable 17-foot boat (*Zodiac*[1]); 40.25 n.miles were traveled in Passamaquoddy Bay, Maine (not in the study area) using the *Zodiac*[1]. In total, the trackline length was 2157.8 n.miles.

The data collected during the bad weather day were excluded.

The upper team saw 499 harbor porpoise groups, of which 27 groups were excluded because three had missing data and 24 were made during the bad weather day. This resulted in 472 good sightings detected by the upper team (Fig. 5; Table 2). The lower team saw 391 harbor porpoise groups, of which 16 groups were excluded because they were made on the bad weather day. This resulted in 375 good sightings detected by the lower team (Fig. 5; Table 2). One group of harbor porpoises was detected in the inshore bays of Nova Scotia, another was detected in Passamaquoddy Bay, Maine. These two sightings were not used in the analysis.

The best estimate of $E(s)$ was determined to be the arithmetic mean, $\bar{s}$, because size bias was not significant. This is illustrated by the fact that the slope between group size and

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[1] Mention of trade names does not constitute endorsement by NMFS.

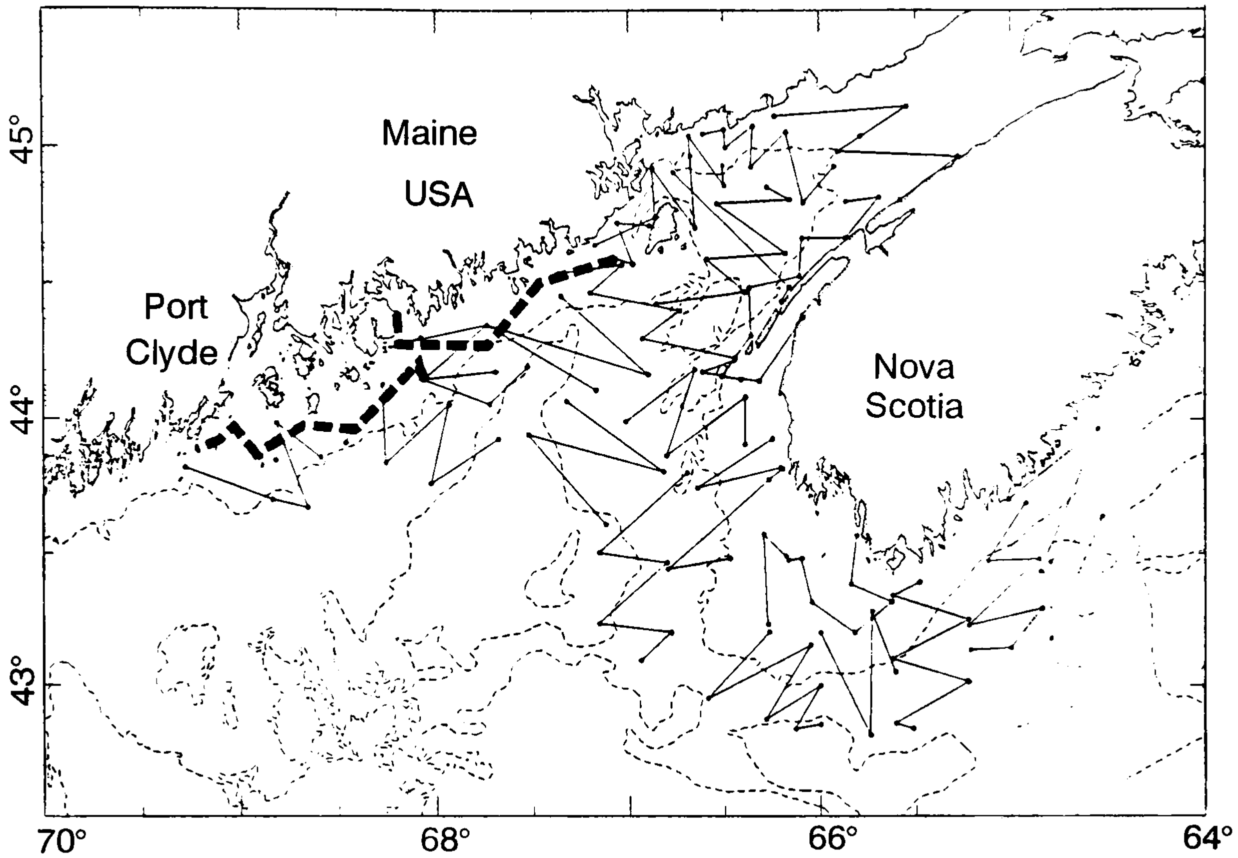

Fig. 4. Tracklines surveyed by the *R/V Abel-J*. Heavy dashed line are tracklines within the 5 n.mile offshore area. Other tracklines are within the high density, intermediate density and low density stratum.

Table 2

Summary of results from the *R/V Abel-J* line transect survey in four strata: high density (High), intermediate density (Interm.), low density (Low) and inshore (Inshore). The reported results are length of trackline in n.miles (% of total length in parentheses), area of stratum in n.miles^2 (% of total area in parentheses), total number of groups detected by the upper and lower teams, (number of groups within a perpendicular distance of 400m from the trackline in parentheses), average size of groups within 400m (%CV in parentheses).

			Number of groups		Av. (%CV) of group size	
Strata	Track length (%)	Area (%)	Upper	Lower	Upper	Lower
High	310 (0.16)	1,552 (0.11)	236 (217)	203 (184)	2.97 (3.9)	2.99 (7.3)
Interm.	1,333 (0.68)	9,038 (0.65)	216 (197)	149 (144)	2.76 (4.2)	2.38 (5.5)
Low	189 (0.10)	2,674 (0.19)	0 (0)	3 (3)	0 -	2.00 (0.5)
Inshore	130 (0.07)	637 (0.05)	20 (19)	20 (17)	4.26 (15.5)	3.29 (14.9)
Total	1,962 (1)	13,901 (1)	472 (433)	375 (345)	2.93 (2.9)	2.75 (4.8)

perpendicular distance, as recorded by the upper team was not significant, (H_0: slope=0 for all strata together, p=0.36). However, the lower team's estimates of group size decreased slightly as perpendicular distance increased (H_0: slope=0 for all strata together, p=0.04). The effect of group size (α in a bivariate model) was not significant for every combination of team and stratum, given the negative exponential, half normal and general exponential model, i.e., there was no obvious group size bias (Table 3).

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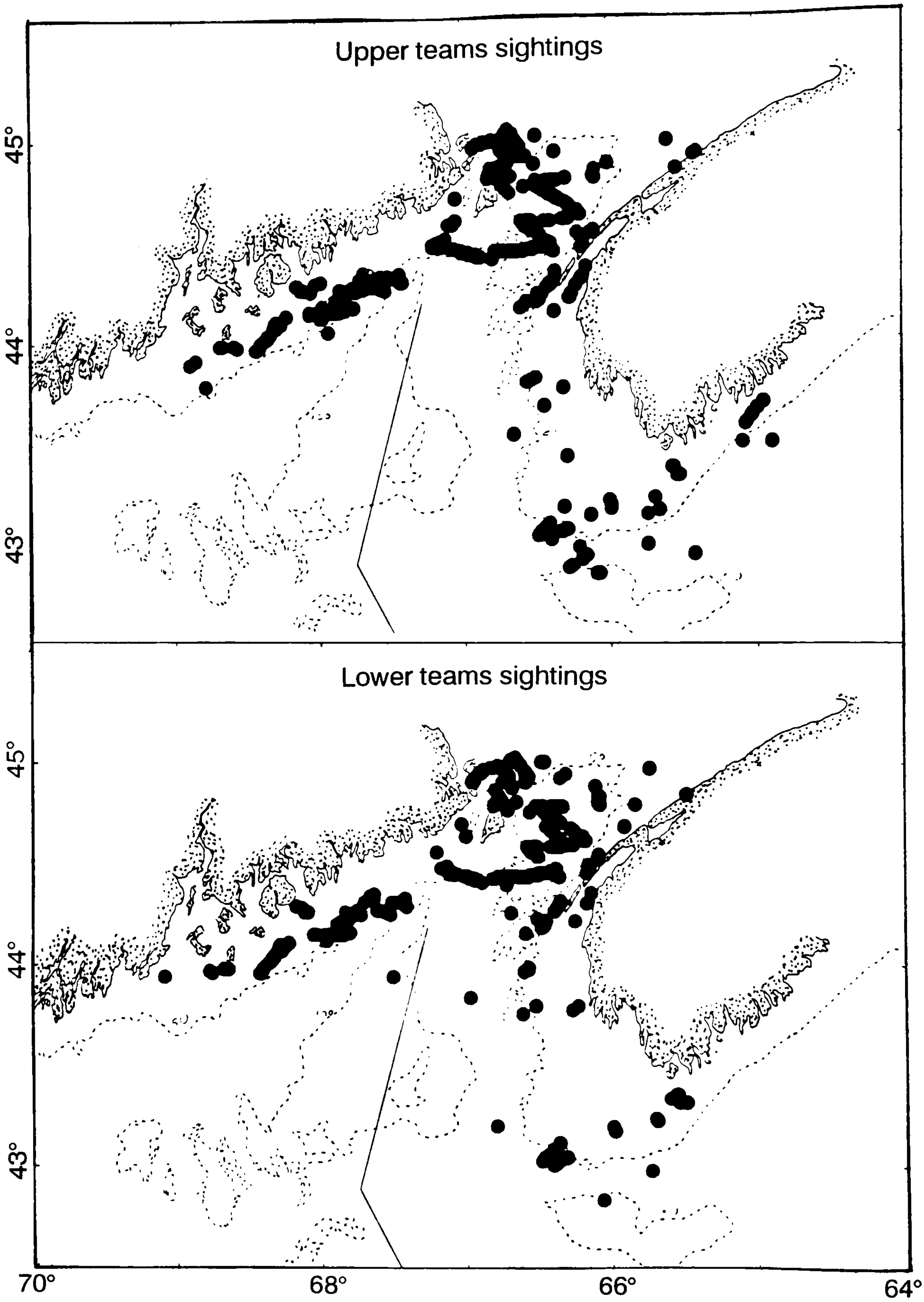

Fig. 5. Location of harbor porpoise groups that were detected by the upper and lower team aboard the *R/V Abel-J*. Solid line through center of area represents the US – Canadian border.

Table 3

The bivariate models that were investigated are negative exponential, half normal and general exponential. Results from each model include the value of α, which reflects the effect of group size ($\alpha=0$ indicates no group size effect), p-value from the test $H_0:\alpha=0$ vs $H_1:\alpha\neq 0$, Akaike information criteria (AIC) and estimated density of schools. * indicates the least AIC value, which represents the best model that fits the data. ◄ indicates the model (bivariate or univariate) that resulted in the greater school density estimate.

Model	Model	α	p-value	AIC	School density
Upper team - high density stratum					
Negative exponential	bivariate	-0.024	0.274	-599.72	3.723◄
	univariate	-	-	-601.70*	3.707
Half normal	bivariate	-0.041	0.310	-617.54	2.345◄
	univariate	-	-	-619.45*	2.344
General exponential	bivariate	-0.008	0.261	-617.20	2.615
	univariate	-	-	-618.75*	2.643◄
Upper team - intermediate density stratum					
Negative exponential	bivariate	-0.369	0.496	-568.17*	0.839◄
	univariate	-	-	-564.22	0.813
Half normal	bivariate	-0.353	0.500	-588.74*	0.533◄
	univariate	-	-	-580.07	0.514
General exponential	bivariate	-0.380	0.500	-587.45*	0.580◄
	univariate	-	-	-578.84	0.579
Upper team - inshore stratum					
Negative exponential	bivariate	-0.189	0.321	-60.18	1.041◄
	univariate	-	-	-62.03*	0.984
Half normal	bivariate	-0.150	0.315	-60.76	0.640◄
	univariate	-	-	-62.65*	0.613
General exponential	bivariate	-0.216	0.333	-59.13	0.760
	univariate	-	-	-61.00*	0.780◄
Lower team - high density stratum					
Negative exponential	bivariate	-0.041	0.207	-515.11	3.201◄
	univariate	-	-	-517.06*	3.185
Half normal	bivariate	-0.048	0.243	-545.47	2.092◄
	univariate	-	-	-547.47*	2.092
General exponential	bivariate	-0.060	0.164	-545.81	2.142◄
	univariate	-	-	-548.43*	2.124
Lower team - intermediate density stratum					
Negative exponential	bivariate	-0.283	0.474	-434.22*	0.667◄
	univariate	-	-	-433.54	0.651
Half normal	bivariate	-0.319	0.497	-447.97*	0.425◄
	univariate	-	-	-443.22	0.411
General exponential	bivariate	-0.318	0.495	-446.62*	0.470
	univariate	-	-	-441.31	0.474◄
Lower team - inshore stratum					
Negative exponential	bivariate	+0.148	0.204	-51.60	0.839◄
	univariate	-	-	-53.50*	0.795
Half normal	bivariate	+0.358	0.109	-52.68	0.527◄
	univariate	-	-	-54.09*	0.495
General exponential	bivariate	+0.301	0.142	-50.74	0.604
	univariate	-	-	-52.34*	0.628◄

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To determine the best reduced, stratified model [equations (1) and (4)], the estimates of group size and encounter rate, along with the shape of the estimated detection functions were compared between strata. The average group size (± 1SD) as estimated by the upper and lower team was 2.93 ±1.75 and 2.75 ±2.46, respectively (Table 2). Mean group sizes did not differ significantly between teams (HSD critical value=2.78; SAS Institute Inc., 1985). Mean group size from the intermediate density stratum (upper: 2.76; lower:2.38)

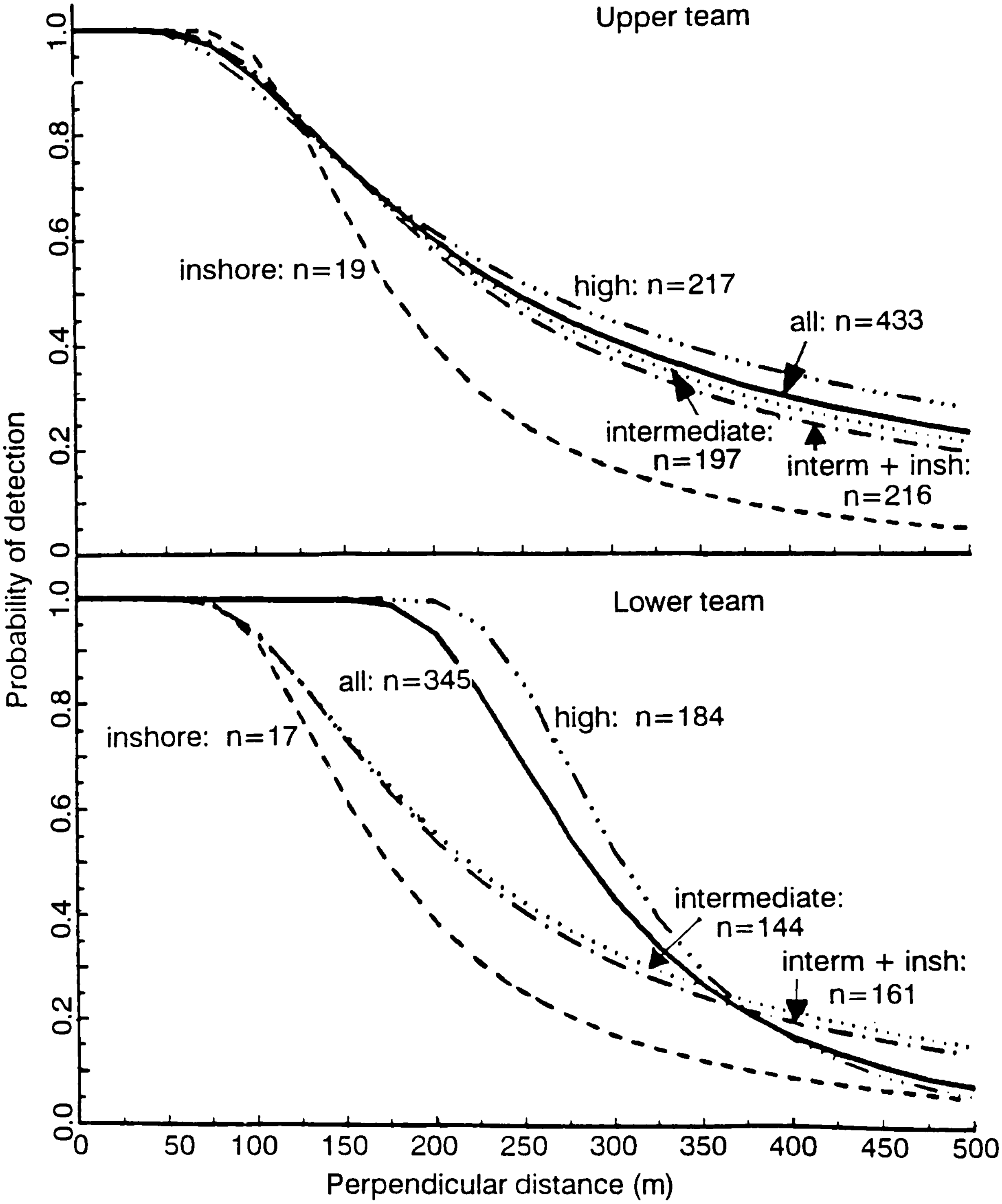

Fig. 6. Detection functions estimated from data collected within the high density, intermediate density and inshore strata by the upper and lower team members (high, intermediate and inshore). In addition, the detection function estimated from data pooled over all strata is displayed (all).

was statistically different than that from either the high density (upper:2.97; lower:2.99) or inshore stratum (upper:4.26; lower:3.29) (HSD critical value 3.32). The encounter rate (n_i/L_i) from the high density stratum (upper:0.76 groups per n.miles; lower:0.66) was statistically different than either the inshore (upper:0.15; lower:0.15) or intermediate density stratum (upper:0.16; lower:0.11) (HSD critical value=3.337). Within a team, there were no significant differences between estimated detection functions for any of the strata (Fig. 6; for all pairwise comparisons within a team the Kolmogorov-Smirnov D value was greater than the critical value for that pair). Thus, the preferred reduced stratified model is where $f(0)$ is estimated from data pooled over strata and the other parameters are estimated by strata.

The number of 'definite' duplicate sightings as determined by Judge A and B was 113 and 138, respectively, while the number of 'possible' duplicates were 54 and 8, respectively (Table 4). The sum of definite and possible duplicate sightings as determined by Judge A and B was 167 and 146, respectively. Using the weighing scheme suggested in Butterworth and Borchers (1988) i.e. sum the number of definite duplicates and 2/3 of the possible duplicates, the resulting numbers of duplicates were 149 (Judge A) and 143 (Judge B). Of the number of harbor porpoise groups detected by the upper team, 35% and 31% of the groups were categorized as either a definite or possible duplicate sighting by Judge A and B, respectively (Table 5).

Table 4

Number of duplicate sightings within three strata (high density, intermediate density and inshore) as determined by two judges (A=Palka, B=Potter). The duplicates were categorized as definitely a duplicate (Definite) or possibly a duplicate (Possible). Definite + Possible is sum of definite and possible duplicates. A weighted number of duplicates is the sum of definite duplicates and 2/3 of the possible duplicates (Definite + 2/3 Possible).

	Definite		Possible		Definite + Possible		Definite + 2/3 Possible	
Stratum	A	B	A	B	A	B	A	B
High	60	71	30	6	90	77	80	75
Intermediate	46	60	22	2	68	62	61	61
Inshore	7	7	2	0	9	7	8	7
Total	113	138	54	8	167	146	149	143

Table 5

Ratio of number of duplicate sightings to number of sightings detected by the upper team. Definition of headings in Table 4.

	Definite		Possible		Definite + Possible		Definite + 2/3 Possible	
Stratum	A	B	A	B	A	B	A	B
High	0.25	0.30	0.13	0.02	0.38	0.33	0.33	0.32
Intermediate	0.21	0.28	0.10	0.01	0.31	0.29	0.28	0.28
Inshore	0.35	0.35	0.10	0.00	0.45	0.35	0.40	0.35
Total	0.24	0.29	0.11	0.02	0.35	0.31	0.32	0.30

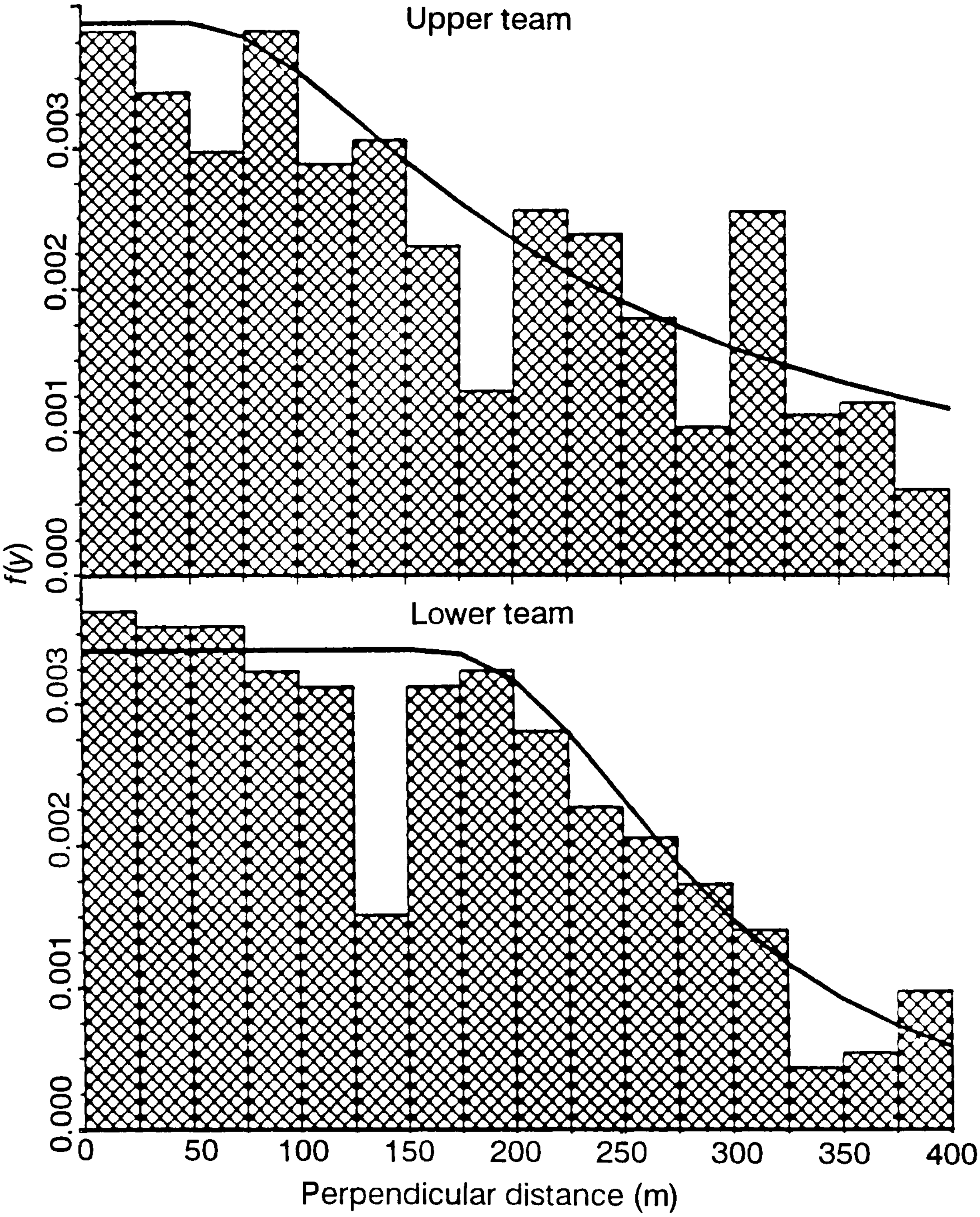

Fig. 7. A histogram of perpendicular distances from all strata that were detected by the upper and lower team is overlaid by the estimated hazard rate detection function.

The strategy of categorizing a duplicate differed between the two judges. Judge A had more stringent criteria for a definite duplicate and looser criteria for a possible duplicate. Of the 138 sightings categorized as a definite duplicate by Judge B, 92 (67%) were categorized as a definite duplicate by Judge A and 122 (88%) were categorized as either a definite or possible duplicate by Judge A (Table 6). However, of the 54 possible duplicates as categorized by Judge A, 20 (37%) were categorized as a non-duplicate sighting by Judge B (Table 6). After both judges reviewed these sightings, it was agreed upon that the criteria used by Judge A to assign a sighting as a possible duplicate was too loose. Therefore, for the rest of this analysis, only the definite duplicate sightings will be used.

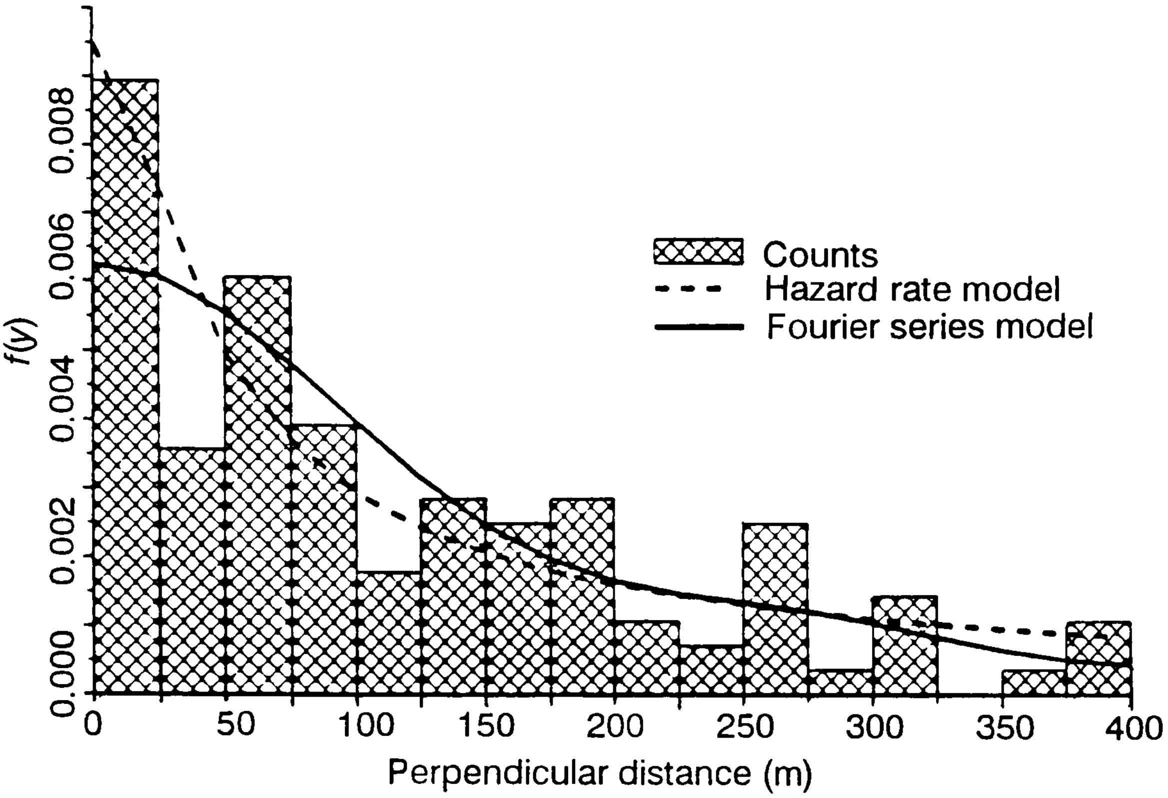

Fig. 8. Comparison of the estimated hazard rate and third order Fourier detection function overlaying a histogram of the observed perpendicular distances of the duplicate sightings as defined by Judge A.

The hazard rate model fitted the perpendicular distance data well (Fig. 7), with the exception of the distance data from the duplicate sightings as assigned by Judge A (Fig. 8). Because of a peak in the perpendicular distances at the origin (near the trackline), a third order Fourier model fit better than did the hazard rate model (Fig. 8), as was noted in Buckland (1985). Therefore, in the bootstrap iterations used to estimate variance, a third order Fourier model was used to fit only the bootstrap duplicate data from Judge A; the hazard rate model was used elsewhere.

The estimated effective half strip width (ESW) for the upper and lower teams was 258m (SE=16.4) and 296m (SE=44.1), respectively (Table 7). This difference is not significant (z=0.81; p=0.42). No significant difference was found between the ESW estimated from

Table 6

Comparison of duplicate classification of each individual sighting that was declared a Definite or Possible duplicate sighting by either of the two judges. If a sighting was declared as a duplicate by a judge but not by the other then that sighting was classified as a non-duplicate according to the latter judge.

		Judge A			
		Definite	Possible	Non-duplicate	Total
Judge B	Definite	92	30	16	138
	Possible	3	4	1	8
	Non-duplicate	18	20	x	39
	Total	113	54	17	185

Table 7

Effective strip half-width (ESW) in meters and its standard error as estimated from data pooled over strata for each team (Upper only and Lower only), for the duplicate sightings as predicted by the product integral method (Upper - Lower) and for duplicate sightings as estimated from the duplicates which were determined by either judge.

Data source	ESW	SE(ESW)	Data source	ESW	SE(ESW)
Upper only	257.7	16.4	Dups only - Judge A	160.3	20.2
Lower only	295.8	44.1	Dups only - Judge B	204.9	24.0
Upper - Lower	260.6	25.8			

the duplicate sightings as determined by Judge A (160m; SE=20.2) and those determined by Judge B (205m; SE=24.0) (z=1.42; p=0.16). The ESW of the duplicate sightings as predicted by the product integral method ($\hat{g}_{up}(y) \cdot \hat{g}_{lo}(y)$) was 261m (SE=25.8) (Table 7).

The point estimates of $g(0)$ for the upper team within the various strata were higher than the corresponding $g(0)$ from the lower team's data (upper: 0.46 to 0.62;lower: 0.33 to 0.52; Table 8), though the differences were not significant (pairwise z-tests). The point estimate of $g_i(0)$ as estimated by the direct duplicate method (range:0.71–0.82) was slightly higher than that estimated by the product integral method (range:0.65–0.75) (Table 9), though the difference between the differences are not significant. An area weighted average of $g(0)$ estimated by the product integral and direct duplicate method was 0.66 (SE=0.07)

Table 8

Estimates of $g_{iup}(0)$ and $g_{ilo}(0)$ as determined by the product integral method and direct duplicate method, where i is the high density, intermediate density, low density and inshore stratum.

		Product integral		Direct duplicate				Product integral		Direct duplicate	
Stratum	Team	$g(0)$	SE(g)	$g(0)$	SE(g)	Stratum	Team	$g(0)$	SE(g)	$g(0)$	SE(g)
High	Upper	0.46	0.06	0.53	0.10	Low	Upper	0.46	0.09	0.53	0.11
	Lower	0.37	0.09	0.43	0.06		Lower	0.33	0.10	0.38	0.07
Interm.	Upper	0.46	0.09	0.53	0.11	Inshore	Upper	0.53	0.13	0.62	0.18
	Lower	0.33	0.10	0.38	0.07		Lower	0.45	0.18	0.52	0.17

Table 9

Estimates of $g_i(0)$ as determined by the product integral method (PI) and direct duplicate method (DD), where i is the high density, intermediate density, low density and inshore stratum. In addition, the area weighted average $g(0)$ is presented.

Stratum	Method	$g(0)$	SE($g(0)$)	Strata	Method	$g(0)$	SE($g(0)$)
High	PI	0.66	0.07	Inshore	PI	0.75	0.14
	DD	0.73	0.07		DD	0.82	0.15
Intermediate	PI	0.65	0.10	Average	PI	0.66	0.07
	DD	0.71	0.09		DD	0.72	0.06
Low	PI	0.65	0.10				
	DD	0.71	0.09				

Table 10

Using either the product integral or direct duplicate method, the following results are presented: estimated density (animals per nmi^2) where $g(0)=1$ (uncorrected density) and its standard error (SE), estimated density including an estimate for $g(0)$ (corrected density) and its standard error and estimated abundance with its standard error and coefficient of variation.

Stratum	Uncorrected density (SE)	Corrected density (SE)	Abundance	SE(N)	CV(N)
Product integral method					
High	10.3 (2.60)	15.6 (3.85)	24,287	5,976	0.25
Intermediate	1.8 (0.50)	2.9 (0.70)	25,820	6,331	0.25
Low	0.15 (0.01)	0.23 (0.04)	616	96	0.16
Inshore	4.2 (1.46)	5.7 (2.36)	3,603	1,506	0.42
Direct duplicate method					
High	3.8 (1.14)	10.9 (5.71)	16,900	8,862	0.52
Intermediate	0.6 (0.22)	1.9 (0.70)	16,944	6,340	0.37
Low	0.15 (0.01)	0.23 (0.04)	616	96	0.16
Inshore	2.0 (1.09)	4.8 (2.29)	3,023	1,459	0.48

and 0.72 (SE=0.06), respectively. This average $\hat{g}(0)$ is the best overall estimate of $g(0)$ for this survey.

The estimated density within the high density stratum was substantially higher than any other stratum (Table 10). The density within the inshore stratum was the next highest, while the density within the low density stratum was the lowest. The product integral technique resulted in higher density estimates than did the direct duplicate method (Table 10), though the differences were not significant (high: $z=0.68$ $p=0.50$; intermediate: $z=1.01$ $p=0.31$; inshore: $z=0.27$ $p=0.28$).

The abundance estimated for the high density and intermediate density strata were similar (Table 10), despite the large difference in strata areas. The product integral abundance point estimates for each stratum was larger than the direct duplicate abundance point estimate for the corresponding stratum, although the differences were insignificant. Total abundance estimates were 37,500 (CV=28.8%) with a 95% CI of (26,600 to 86,400) and 54,300 (CV=16.3%) with a 95% CI of (38,100 to 71,900), as determined from the direct duplicate and product integral techniques, respectively (Table 11). The difference between the total abundance estimates from the two techniques was not significant ($z=1.21$; $p=0.23$).

Table 11

The abundance of each stratum and the entire survey area as estimated by the product integral or direct duplicate method. Also included is the coefficient of variation and upper and lower 95% confidence limits (UCL and LCL) as estimated using bootstrap resampling techniques.

	Abundance (%CV)	LCL	UCL	Abundance (%CV)	LCL	UCL
	Product integral method			**Direct duplicate method**		
High	24,287(0.25)	11,975	34,878	16,900 (0.52)	8,572	45,597
Intermediate	25,820(0.25)	15,082	39,167	16,944 (0.37)	10,702	36,097
Low	616(0.16)	451	804	616 (0.16)	451	804
Inshore	3,603(0.42)	1,308	7,320	3,023 (0.51)	1,239	6,712
Total	54,326(0.16)	38,140	71,930	37,483 (0.29)	26,643	86,369

DISCUSSION

The abundance estimate presented here is larger than previous estimates, largely due to the greater survey area. In addition, most of the previous estimates did not include an estimate of $g(0)$. The estimate of $g(0)$ made from the present dataset (0.72) is similar to that estimated by Barlow (1988) for harbor porpoises (0.78), who also used the two independent team sighting procedure. However, the present estimate of $g(0)$ is larger than the estimate of $g(0)$ for northeastern Atlantic minke whales (0.51; Schweder *et al.*, 1992). Minke whales are also difficult to detect, have no obvious blow and are usually found in small groups. The estimate of $g(0)$ for minke whales was made using the parallel ship sighting procedure and a different analysis procedure.

Of the two techniques to estimate abundance that were presented here, the direct duplicate method is the preferred technique. Both techniques assume the two teams are independent. However, the direct duplicate method uses a weaker version of the assumption. That is, the product integral method predicts the distribution of duplicate sightings to be the product of $g_{up}(y)$ and $g_{lo}(y)$, as estimated separately from data from each platform. The direct duplicate method does not predict the distribution of the duplicate sightings, but directly estimates the distribution from the duplicate sighting's data. As was discussed in Butterworth and Borchers (1988) and Schweder (1990), the independence assumption (equation 3) may not be valid, even on a theoretical basis. Schweder (1990) suggested that this is because some factors may not act independently to the sighting processes of the two teams and therefore, the two teams are conditionally dependent. The two teams in this survey may be conditionally dependent as is evident by the fact that the product integral method predicted more duplicate sightings near the trackline than that observed from the actual duplicate sightings (Fig. 9). This phenomenon was also noted in Butterworth and Borchers (1988). In conclusion, because the direct duplicate method does not explicitly use the independence assumption it is the preferred method. The disadvantage of the direct duplicate method is that a large number of duplicate sightings are required (>40; Burnham *et al.*, 1980) to accurately estimate the $g_{dup}(y)$ distribution.

The estimates presented here have substantial uncertainty, as reflected in the relatively large CV of 28.8%. The largest component of this variation is the encounter rate (n/L; Table 12). By definition, the CV(n/L) should only include sampling variation. However, practically, the CV(n/L) includes both sampling variation and variation in the spatial distribution of the animals. The encounter rate does have spatial structure; i.e. there is evidence of a density gradient related to ocean depth (Fig. 5). Other analysis methods are needed to properly account for this spatial variability, for example, Schweder (1977) and Thompson (1991).

Table 12

Coefficient of variation of various parameters in the density equation. Also, the percentage of the CV of a parameter with respect to the CV of the density when $g(0)$ is assumed to equal one. Estimates are for the high density, intermediate density and inshore stratum, using data from each team.

Parameter	CV	%	CV	%	CV	%	Parameter	CV	%	CV	%	CV	%
Upper team							**Lower team**						
n/L	21.4	75.1	21.3	76.9	31.0	52.8	*n/L*	22.1	86.5	24.0	78.9	26.9	45.8
f(0)	11.7	22.4	10.9	20.1	24.8	33.9	*f*(0)	4.8	4.1	11.1	16.9	25.2	40.2
s	3.9	2.5	4.2	3.0	15.5	13.3	*s*	7.3	9.4	5.5	4.2	14.9	14.0
D	24.7	100	24.3	100	42.6	100	*D*	23.7	100	27.0	100	39.8	100

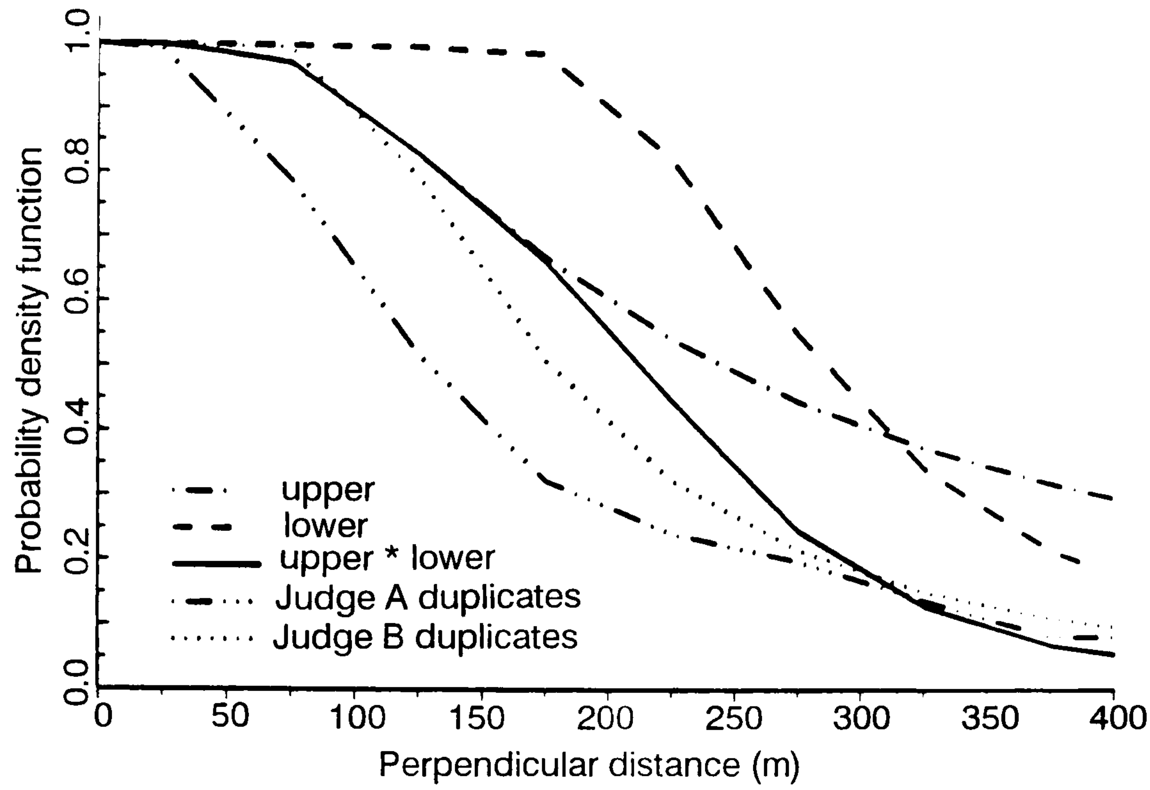

Fig. 9. Comparison of the distribution of duplicate sightings as predicted by the product integral method (upper*lower) and as estimated from the observed perpendicular distances of duplicate sightings which were determined by either Judge A or Judge B. For reference, the distribution of perpendicular distances estimated from the data collected by the upper and lower teams are also displayed.

In addition to the spatial structure in the encounter rate, there are several other possible sources of uncertainty unaccounted for in this study. These sources include incomplete coverage of the animals' range, porpoise avoidance of the ship, observer and/or platform heterogeneity and effects of other environmental conditions on sighting rates and $g(0)$. The boundaries of the study area were selected on the basis of previous sighting data. Sighting surveys were performed from a *Zodiac*[1] and the *R/V Abel-J* in coastal southeastern Nova Scotia and Passamaquoddy Bay, Maine, both regions not included in the survey area. During these surveys two porpoise groups were detected in 131 n.miles of searching. This sighting rate is much lower than that observed during the *M/V Sneak Attack* survey, also in coastal waters. Also, one group of harbor porpoises was reported south of the southern boundary along the Maine coast by the survey team on the *M/V Sneak Attack* (Read and Kraus, 1991). Overall, the spatial distribution of the observed sightings suggest that the *a priori* boundaries nearly reflect the actual boundaries.

It has been suggested that harbor porpoises avoid ships (Gaskin, 1977; Kraus *et al.*, 1983b; Polacheck and Thorpe, 1990). If porpoises alter their behavior before being detected by observers on the ship, then the abundance estimate will be biased (Turnock and Quinn, 1991). In the future, the distance at which the porpoises start altering their behavior should be demonstrated to determine if, and to what extent, the abundance estimate is biased.

Buckland (1992) illustrated that heterogeneities have effects on the abundance estimate. During the present survey it is possible there were heterogeneities between the platforms. This means the relative efficiency of the two platforms may have varied with environmental or other factors (Buckland, 1992). This could be illustrated by the fact that

$g_{up}(0)$ was greater than $g_{lo}(0)$, though the difference was not significant (Table 8). The effect of this heterogeneity on the abundance estimate is unknown. An investigation into whether this and other heterogeneities exist may be feasible because some of the necessary data have already been collected during this survey.

Factors other than perpendicular distance may influence the shape of the detection function and consequentially the abundance estimate. Examples of possible influential factors are group size (Drummer and McDonald, 1987) and Beaufort sea state (Gunnlaugsson and Sigurjónsson, 1990). Not including such factors will result in an incorrect abundance estimate. In this study, group size was determined not to be influential (Table 3). Beaufort sea state information was also collected during this survey. Incorporating Beaufort sea state into the bivariate detection functions in SIZTRAN (Drummer, 1991) resulted in the conclusion that Beaufort sea state was not an influential factor, despite the fact that the sighting rate decreased as Beaufort sea state increased. The same conclusion was reached by Gunnlaugsson and Sigurjónsson (1990). Possible explanations for this contradiction are that the line transect technique is robust to the amount of variability that occurs within the range of Beaufort sea state 0 to 3 or possibly the Beaufort sea state scale is not representative of the overall environmental conditions, which actually does influence the detection function.

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Double Team Field Tests of Line Transect Methods for Shipboard Sighting Surveys for Harbor Porpoises

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ABSTRACT

Results from experiments designed to test the robustness and reliability of shipboard line transect methods for estimating harbor porpoise densities are presented. These experiments were conducted in the western Bay of Fundy using two teams of three observers which searched independently and simultaneously on the same vessel. Two experiments were conducted: one in which observer teams rotated between the top of the wheel house (4.2m above the water) and the crow's nest (7.1m) and the other in which they rotated between the bow (1.8m) and the crow's nest. A total of 434 sightings were made by one team and 490 by the second during 29 half hour transects.

The line transect estimates of density from these experiments tended to be robust to the effects of observer height and team composition. The effect of observer height (within the range of 1.8 to 7.1m) on the detection process for harbor porpoise was small as measured both by estimates of $f(0)$ and comparisons of the frequency distributions of sighting angles, and radial and perpendicular distances. The differences with height that were observed tended to be consistent with what might be expected. However, the proportion of duplicate sightings seen by both teams appears to be small in comparison to the expected proportion given estimates for $g(y)$. These latter results indicate that $g(0)$ was substantially less than one and that direct estimates of $g(0)$ are needed if estimates of absolute abundance are to be obtained from line transect surveys.

KEYWORDS: HARBOUR PORPOISE; NORTH ATLANTIC; SURVEY-SHIP; $g(0)$

INTRODUCTION

Shipboard surveys have been used extensively for estimating the abundances for a variety of marine mammal populations (e.g. Kasuya and Kureha, 1979; IWC, 1986; Barlow, 1988; Øien, 1990b) and the resulting estimates often underlie assessments of the status of these populations. The estimation procedure for the data from these surveys is based on the theory of line transect for perpendicular sighting distances (Burnham *et al.*, 1980; Seber, 1982). The mathematical derivation for the estimators of the density of marine mammals requires several assumptions which are likely to be violated during a shipboard survey. These include:

1. all animals on the trackline are seen;
2. all animals are stationary; and
3. perpendicular sighting distances are measured without bias and error.

In addition, the application of line transect methods requires that the procedures and estimators are 'pooling' robust (i.e. insensitive to variations in the detection process,

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Burnham *et al.*, 1980) since changes in sighting conditions and differences among individual observers are unavoidable.

There have been a number of studies which have attempted to test whether one or more of these assumptions have been violated and to estimate correction factors if a problem existed (e.g. Au and Perryman, 1982; Butterworth *et al.*, 1982; 1984; Leatherwood *et al.*, 1982; Butterworth, 1986; Butterworth and Borchers, 1988; Borchers and Haw, 1990; Øien, 1990a; Palka, 1995). The results of these experiments have been mixed. Often the results provide an indication that a problem may exist, but sample sizes and the statistical power of the tests have been small. When correction factors have been estimated, their effects on density estimates have ranged from only a few percent up to 100% (IWC, 1986; Butterworth and Borchers, 1988; Øien, 1990a). Direct tests of pooling robustness have not been made.

Given the role of shipboard line transect estimates in cetacean assessments, a wide range of field tests are important for validating and evaluating the appropriate degree of confidence to place in the estimates of abundance. The purpose of the present paper is to present results from a three day experiment designed to test the robustness and reliability of shipboard line transect methods for estimating harbor porpoise densities. These experiments were conducted using the double team procedure described in Polacheck and Smith (1989). This experiment was designed not only to test specific assumptions of line transect theory, but also the robustness of the results to different observer teams and searching heights by having two complete sets of observers search independently and simultaneously on the same vessel.

METHODS

Shipboard line transects for harbor porpoise were conducted in the western Bay of Fundy from 22–24 August 1988 near Grand Manan Island (Fig. 1). This area was chosen because harbor porpoise are known to congregate there during this season (Neave and Wright, 1968; Gaskin, 1977; 1984). The cruise was conducted aboard the NOAA/NMFS RV *Gloria Michelle*, a 20m converted shrimp trawler. All transects were carried out at a speed of 9 knots.

A total of 29 half hour transects were conducted during which two teams of observers searched independently from different positions on the vessel and recorded all sightings of harbor porpoises. Observer teams rotated between searching positions, and an awning over the lower observer team ensured the independence of the two data sets. Apart from transects 9–14 on 24 August, observer teams rotated between sighting positions on top of the wheel house (4.2m above the water) and the crow's nest (7.1m above the water). These transects comprised experiment 1. The final six transects on 24 August comprised experiment 2, when teams rotated between the crow's nest and the bow of the vessel (1.8m above the water). Except in one case when time did not permit, transects were replicated in the sense that after the completion of a half hour transect the observer teams would change positions, the vessel would turn 180° and a second transect would be conducted. However, strong currents led to only moderate success in duplicating the same course (Fig. 1).

All transects were conducted under good visibility conditions and when sea state was less than or equal to Beaufort 2 (except for one transect when the sea state was 3). An attempt was made to orient transects to minimise glare conditions directly on the trackline during the experiments (i.e. replicate pairs of transects that were conducted early or late in the day were generally run in a northerly or southerly direction).

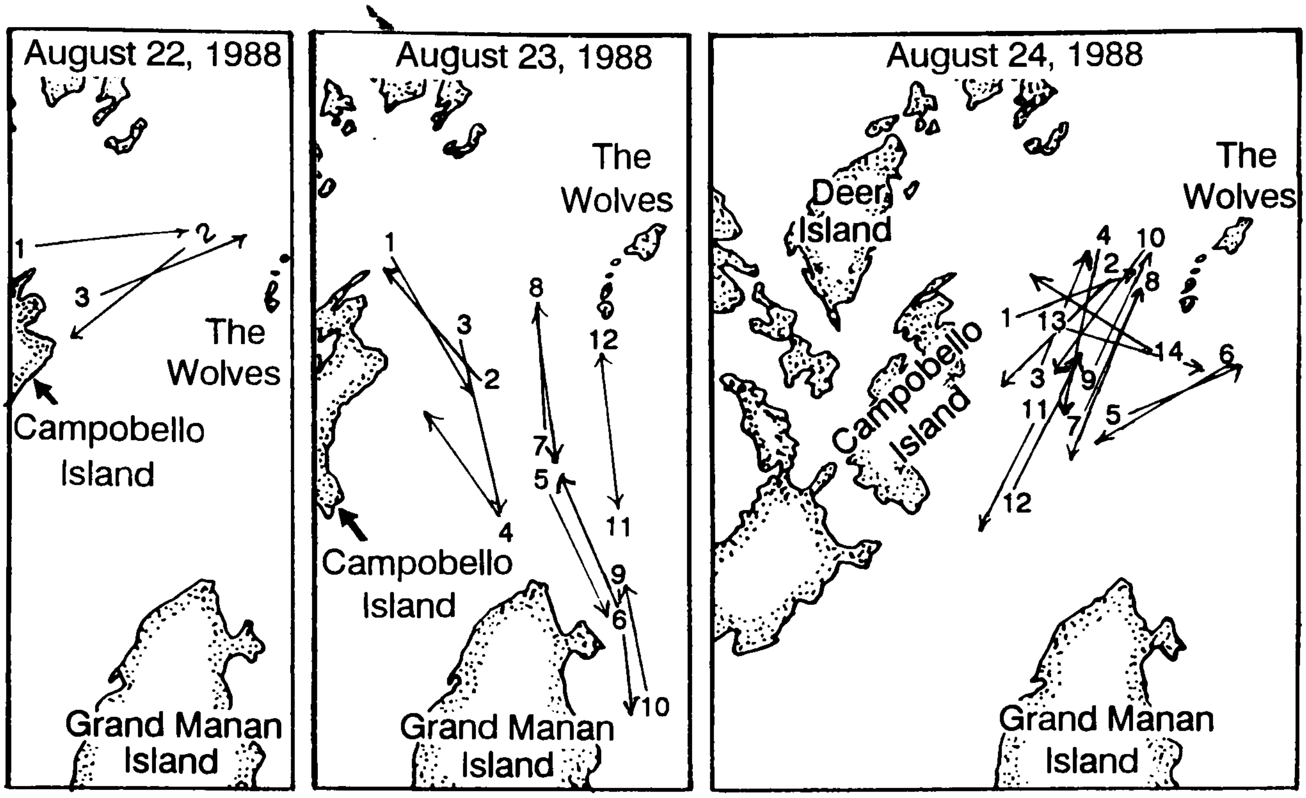


Fig. 1. Location of all transects completed during the harbor porpoise line transect experiments aboard the NOAA/NMFS R/V *Gloria Michelle*.

Searching strategy

Each team was composed of three observers and a data recorder. Each observer had previous experience in cetacean shipboard surveys. The six observers were divided into the two teams, by first pairing individuals based on their previous experience, and then randomly assigning members of a pair to a team. Within a team, observers rotated between the port, center and starboard viewing positions after every pair of replicate transects. The center observer searched directly ahead to cover the trackline and the two side observers searched their respective sides of the trackline. A break of at least 15 minutes was taken between each pair of transects to avoid observer fatigue. Binoculars were not used for searching but only to confirm sighting cues, estimate school size and determine swimming direction.

Data collection

Standard line transect data were collected including: (1) the estimated radial sighting distance at which an animal was sighted, (2) estimated sighting angle, (3) estimated group size, (4) time of sighting, (5) observer position, (6) the observer making the sighting, (7) environmental conditions (e.g. sea state and glare) and (8) the swimming direction of the animals. Radial sighting distances were based on visual estimates. Prior to conducting any of the transects, observers were first trained and then tested for their ability to estimate radial sighting distances. In the tests conducted after training, all observers' estimates were within 20% and showed no obvious bias. Individual peloruses were located at each viewing position and were used to measure sighting angles.

Analytical techniques

Analyses presented in this paper include standard chi-square comparisons of the frequency distributions of sighting angles, radial distances and perpendicular distances both between teams and among sighting positions. Line transect estimates of density and *f*(0) were calculated using the hazard rate model (Hayes and Buckland, 1983; Buckland, 1985). The effect of smearing the sighting angles and radial distances to account for the fact that observations are frequently lumped or rounded (Butterworth, 1982; Hammond, 1984; Buckland and Anganuzzi, 1988) was examined. Smearing had little effect on the line transect estimates or on the comparisons between teams and sighting positions and tended to provide a slightly better fit to the hazard rate model. These results are used in the paper.

Identification of duplicate sightings

The position of each sighting with respect to the transect line was plotted to investigate the fraction seen by both teams (duplicate sightings) compared to those only seen by one team. Several factors make identification of duplicates difficult. These include:

(1) sighting times being recorded to the nearest minute (the vessel moved around 300m per minute);
(2) measurement error in sighting angles and radial distances; and
(3) movement of animals between the sighting of a school by one team and the sighting by the other.

A variety of different criteria were used to estimate the proportion of duplicate sightings. These were based on the recorded position and time of each sighting and included various combinations of limits on the distance and time between two sightings, implied swimming speed and the position of the sightings relative to the vessel.

RESULTS

Comparison of sighting rates

Team 2 had a slightly higher overall sighting rate than team 1 (16.9 per half hour transect versus 15.0). However, neither team tended to see consistently more sightings on individual transects (Table 1). Surprisingly, observer height had no apparent effect on determining which team made more sightings. The proportion of transects in which team 2 made more sightings than team 1 was similar no matter whether it was in the higher or lower sighting position (Table 1). In addition, the number of sightings for the two teams on the same transect were highly correlated (Fig. 2, $r = 0.92$).

Comparison of the number of sightings between the first and second transect in the 14 pairs revealed generally similar sighting rates (Fig. 3); the correlation for team 2 ($r = 0.77$) was higher than for team 1 ($r = 0.58$). There was a tendency for the number of sightings to be less during the second transect of a pair when the sighting rates were high.

Table 1

Comparison of the number of transects in which a team had the greater number of sightings by observer height.

	Number of transects		
Team in crow's nest	Team 1 > Team 2	Team 1 < Team 2	Equal
Team 1	4	8	2
Team 2	5	8	2
Total	9	16	4

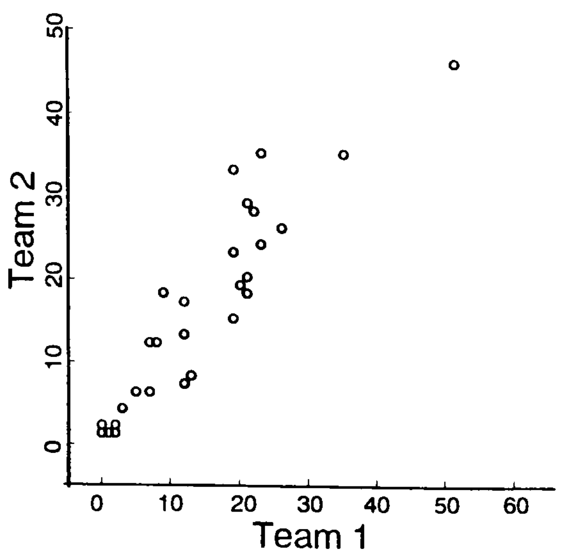


Fig. 2. Comparison of the number of sightings seen by each team during the same transect.

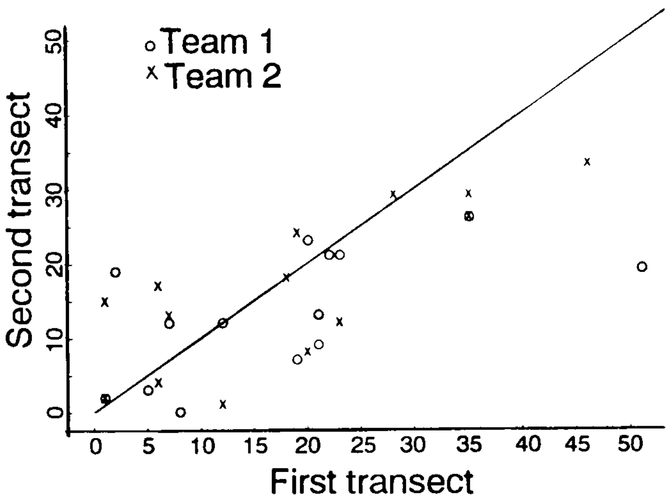


Fig. 3. Comparison of the number of sightings seen by each team during the first and second pair of the replicated transect lines.

Comparison of sighting distributions

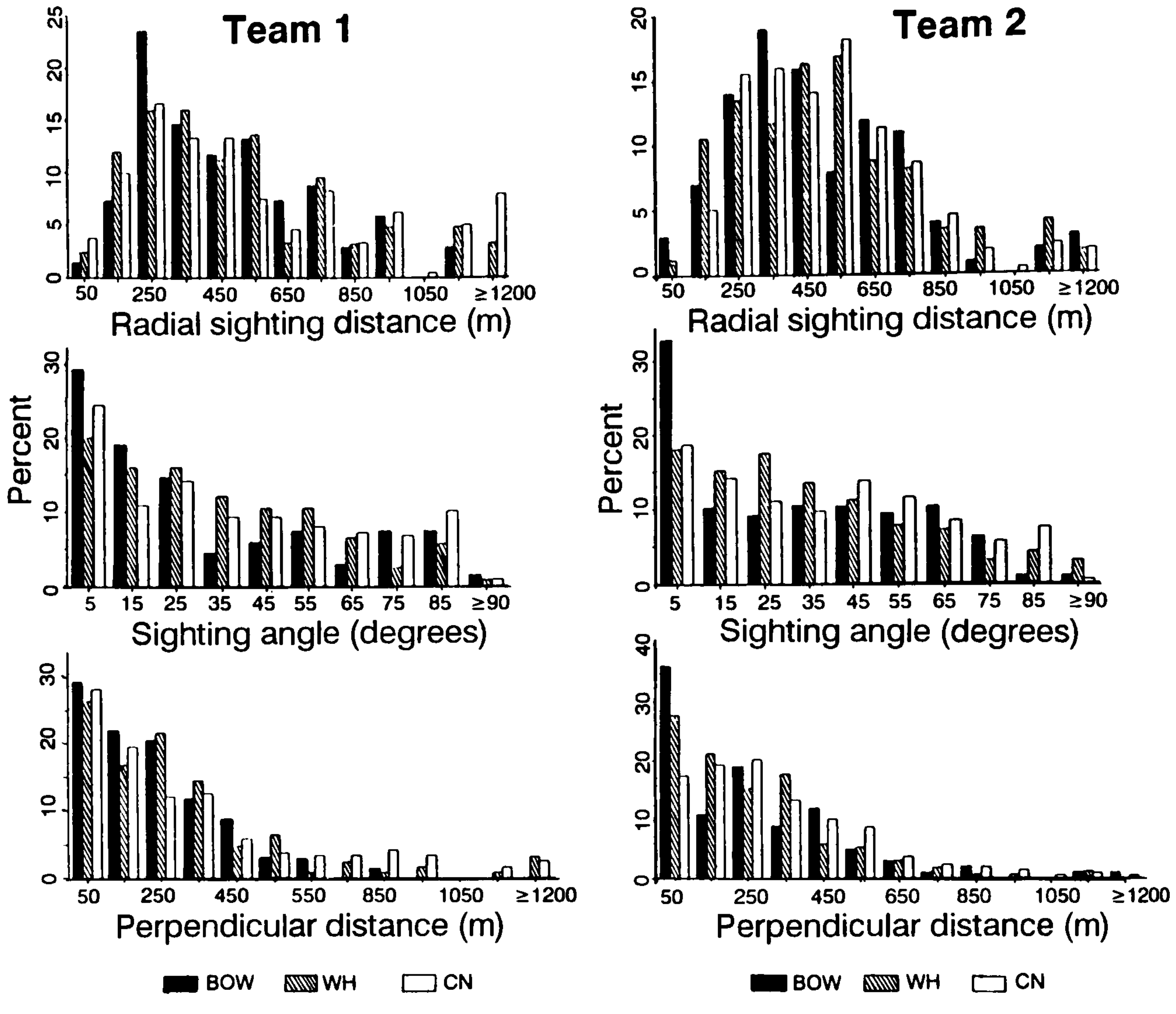
The frequency distributions of sighting angles, radial sighting distances and perpendicular distances were similar both between teams and among the different sighting positions (Figs 4 to 6). Chi-square comparison tests indicate no significant differences within a team among the different sighting positions (Table 2). Tests comparing the distributions between the two teams at the same position suggest no differences for the bow and wheel house positions, although the distribution of radial sighting distances and (possibly) sighting angles in the crow's nest were significantly different (Table 3).

Despite the general lack of significant differences based on the chi-square test, there was a tendency for these distributions to be shifted towards larger values with increased observer height (Figs 4 and 5). Thus, the mean radial sighting distance, sighting angle and perpendicular sighting distance for each team increased between the two extreme differences in height (i.e. the bow and the crow's nest) (Table 4). The differences were significant at the 0.05 level based on a t-test for radial and perpendicular sighting distances for team 1 and for radial sighting angle and perpendicular distance for team 2 (Table 4).

Table 2

Results of Chi-square comparison tests for differences in the frequency distributions for radial sighting distances, sighting angles, and perpendicular sighting distances for the same teams at different height sighting positions.

		Radial sighting distance (df=10)		Sighting angle (df=9)		Perpendicular sighting distance (df=10)	
		Wheel house	Crow's nest	Wheel house	Crow's nest	Wheel house	Crow's nest
Team 1	Bow	6.08	10.82	5.78	8.53	11.1	12.3
	Wheel house	-	7.56	-	8.51	-	13.3
Team 2	Bow	10.93	13.28	14.28	16.30	14.1	17.1
	Wheel house	-	10.70	-	15.70	-	13.1



Figs 4 and 5. Comparison of the frequency distribution of radial sighting distances, sighting angles and perpendicular sighting distances for different sighting positions for team 1 (Fig. 4) and team 2 (Fig. 5).

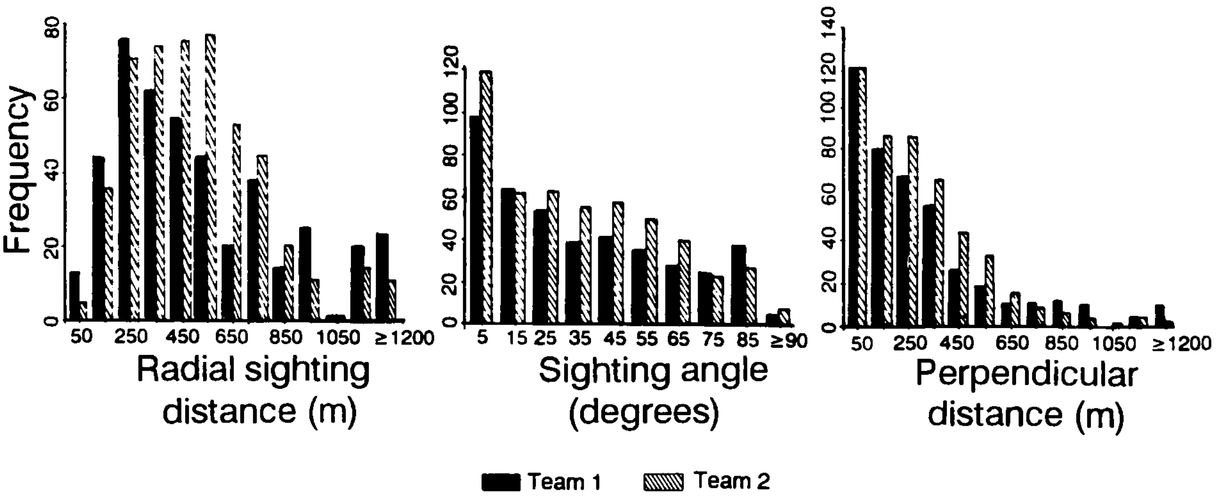


Fig. 6. Comparison of the frequency distribution of radial sighting distances, sighting angles and perpendicular sighting distances between teams pooled across the same sighting positions.

Table 3

Results of chi-square comparison tests for differences in the frequency distributions for radial sighting distances, sighting angles, and perpendicular sighting distances between the two observer teams at the same sighting position.

Position	Radial sighting distance (df=9)	Sighting angle (df=9)	Perpendicular sighting distance(df=10)
Bow	9.33	16.68	6.90
Wheel house	8.45	6.20	8.08
Crow's nest			
Experiment 1	21.76[1]	16.61	20.69[1]
Experiment 2	37.00[2]	8.59	16.12
Combined	45.40[2]	24.23[2]	9.51

[1] $P< 0.05$. [2] $P< 0.01$.

Table 4

Comparison of mean radial sighting distances, sighting angles, and perpendicular sighting sistances for each observer team and different sighting position. Numbers in parenthesis are estimates of the standard error.

	Team 1			Team 2		
	Bow	Wheel house	Crow's nest	Bow	Wheel house	Crow's nest
Radial sighting distance	508.0 (31.9) n=68	550.8 (34.4) n=125	650.8 (28.0) n=241	534.1 (31.2) n=100	532.5 (21.5) n=171	548.6 (18>6) n=219
Radial sighting angle	33.0 (3.3) n=68	36.7 (2.3) n=125	38.8 (1.86) n=241	31.8 (2.6) n=100	34.9 (2.0) n=170	39.8 (1.8) n=218
Perpend. sighting distance	227.3 (22.3) n=68	312.0 (32.5) n=125	336.6 (22.4) n=241	255.0 (24.9) n=100	259.0 (16.6) n=170	317.9 (17.5) n=218

Comparison of the detection function

The estimated detection functions [$g(x)$] when the distributions of perpendicular sighting distances are fitted with the hazard rate model tended to be similar for both teams and for the different sighting positions (Figs 7 and 8; Table 5). In all cases the estimated function indicated a shoulder (i.e. a region around the trackline where the probability of detection is nearly constant) up to a distance of 100 to 400m. With the exception of the results from the crow's nest for team 1 during the second experiment, the estimates of $f(0)$ increased with height. The detection functions suggest an increased relative probability of detection (i.e. $g(0)$ assumed constant) with increased height for animals located at greater distances from the trackline. Most of the differences with height occur in the tails of the sighting functions and the differences in the width of the shoulder for the different heights were small.

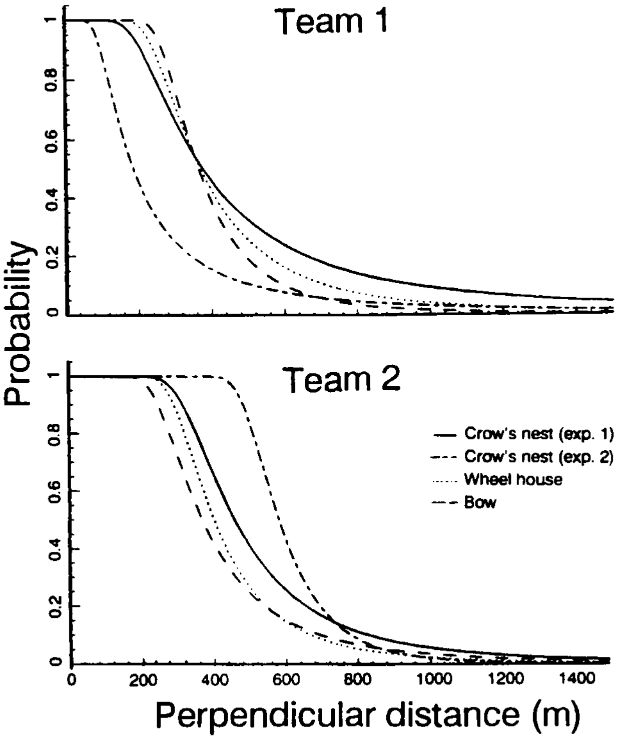


Fig. 7. Comparison of the estimated hazard rate detection function at different sighting positions for each team.

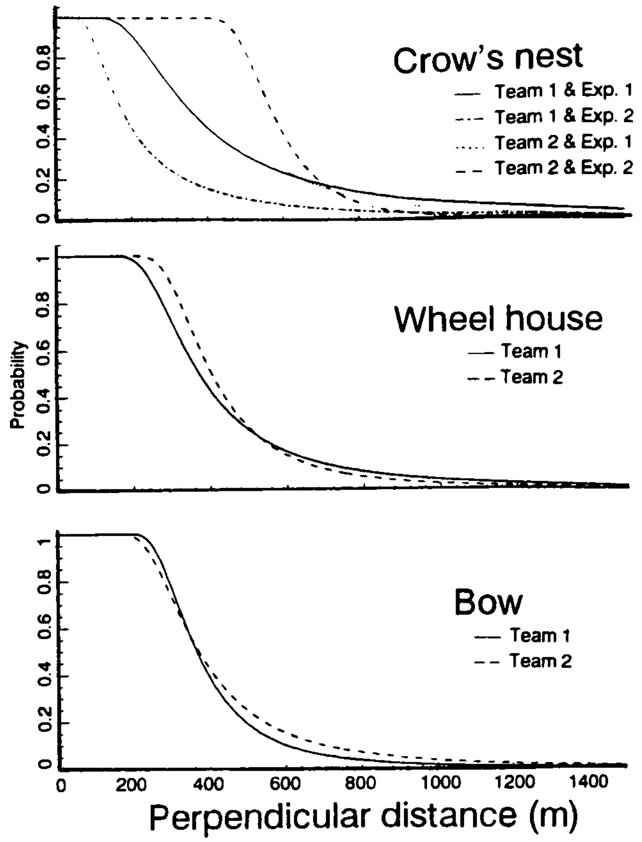


Fig. 8. Comparison of the estimated hazard rate detection function between the two observer teams at the same sighting position.

The estimated detection functions were remarkably similar for the two teams for the bow and wheel house sighting positions (Fig. 8). However, the hazard rate model did not provide a good fit to the data for team 2 in the bow position based on a chi-square goodness of fit test (Table 5). The estimated detection functions for the crow's nest suggest that the two teams may have searched differently in this position and that there may have been some interaction between the sighting process and the density of sightings. Thus, the detection function for team 1 tended to have a narrower shoulder than for team 2 and this tendency was accentuated during the second experiment when the density of sightings was high.

Comparison of school size estimates

The mean school size over the period of the experiment was 5.25 based on data pooled from both teams and all positions. The estimated mean school size by team 1 of 5.70 (SE=0.33, n=434) was only slightly but still significantly different than the estimate of 4.85 (SE=0.22, n=476) by team 2 based on a t-test (p=0.032). The difference in the mean estimated school size between the two teams was largely due to the magnitude and frequency of estimates for large schools. Only thirty of the 908 school size estimates were greater than or equal to 20 with 18 by team 1 and 12 by team 2 (there were no school size estimates between 15 and 20). If these 30 schools are excluded, then the difference in the mean school size is reduced to 0.39 from 0.85 and the difference is not significant if a t-test is used. The size of a large school is clearly more difficult to estimate accurately and a closer examination of the data suggested that at least a large part of the difference between

Table 5

Comparison of the estimates of $f(0)$ and the parameters for the hazard rate detection model for each observer team, sighting position and experiment.

Position	$f(0)$	SE of $f(0)$	a	b	Chi-square[1]	N
Team 1						
Crow's nest						
Exp 1	1.98	0.23	-2.34	3.02	6.43	135
Exp 2	3.65	0.53	-3.49	2.86	9.22	106
Pooled	2.57	0.25	-2.77	2.86	13.97	241
Wheel house	2.25	0.21	-3.20	3.85	2.75	125
Bow	2.43	0.25	-4.21	4.81	2.66	68
Team 2						
Crow's nest						
Exp. 1	1.87	0.15	-2.86	4.21	2.42	135
Exp. 2	1.62	0.11	-3.87	7.49	10.03	83
Pooled	1.83	0.11	-2.97	4.54	2.77	218
Wheel house	2.20	0.14	-3.77	4.74	4.14	170
Bow	2.28	0.22	-3.35	4.00	19.33	100
Pooled						
Crow's nest						
Exp. 1	1.90	0.13	-2.53	3.53	4.89	270
Exp. 2	2.56	0.23	-3.15	3.33	20.59	189
Pooled	2.06	0.11	-2.73	3.52	15.54	459
Wheel house	2.22	0.12	-3.45	4.36	5.17	295
Bow	2.37	0.17	-3.75	4.35	15.86	168

[1] Degrees of freedom = 7 .

Table 6

Comparison of mean school size estimates of harbour porpoises by sighting position and observer team. Numbers in parentheses are estimates of the standard error.

Position	Team 1		Team 2	
Bow	4.01 (0.38)	n= 68	4.59 (0.42)	n= 99
Wheel house	6.41 (0.74)	n=125	5.12 (0.38)	n=167
Crow's nest pooled	5.80 (0.44)	n=241	4.77 (0.34)	n=210
Experiment 1	6.21 (0.68)	n=135	5.22 (0.50)	n=127
Experiment 2	5.28 (0.48)	n=106	4.07 (0.41)	n= 83

the two teams with respect to large schools was due to (1) distant sightings (>1,500m) made by one team not seen by the other and (2) one team calling a large 'group' or 'aggregation' a single sighting while the other team split it in two or more sightings.

Comparison of estimates made during the same set of transects suggests that the main differences in the estimates were between the two teams and that searching position had little effect (Table 6). Thus, the magnitude of the difference in the mean school size estimates for sightings made from the crow's nest and the wheel house during the first experiment for either team was small (0.20 and 0.10) compared to the difference between the two teams either from the same platform (0.99 and 1.29) or on the same set of transects (1.09 and 1.19). During the second experiment, the differences in the estimates of mean school size are smaller and more similar when comparisons are made between teams during the same set of transects but in different positions than either for the same team or the same position on different transects. In this experiment, there appears to be little indication of either a position or a team effect.

Comparison of line transect density estimators

Estimates of harbor porpoise densities (number of sightings per square kilometer) were similar between the two teams on the same set of transects (Table 7). The design of the experiment provided four such comparisons (e.g. team 1 in the crow's nest and team 2 on top of the wheel house or at the bow and *vice versa*). In all four cases, the relative ranking of the density estimates were the same for both teams.

Table 7

Comparison and density (number of sightings per square kilometer) estimates between the two observer teams from the same set of transects. Numbers in parenthesis are estimates of the standard error.

Team in Crow's nest	Experiment 1		Experiment 2	
	Team 1	Team 2	Team 1	Team 2
Team 1	1.44 (0.30)	2.04 (0.36)	7.37 (2.16)	4.34 (1.11)
Team 2	1.37 (0.37)	1.24 (0.38)	3.32 (0.47)	2.71 (0.27)

The differences between the density estimates for the two teams on the same set of transects were not significantly different based on a t-test. However, such comparisons do not take into account the paired nature of the data collection (i.e. both teams were searching the same water). As an alternative, a jackknife estimate and its standard error were calculated for the differences between the density estimates between the two teams on the same set of transects. This was done by successively deleting the data for one transect, recalculating the density estimate for both teams (including $f(0)$), and then using the difference in density for each of the 'pseudo' replicates as the test statistic. For the first experiment, the jackknife differences in the density estimates were significant when team 1 was in the crow's nest (mean difference=-1.02, SE=0.17) and not significant when team 2 was in the crow's nest (mean difference=0.06, SE=0.20). The significant difference resulted from the fact that team 2 saw nearly 26% more sightings than team 1 while the estimates of $f(0)$ for the two teams were similar. Jackknife results for the second experiment are not presented because there were only three replicates and the hazard rate model had problems converging and fitting some of the replicates with reduced sample sizes.

If the number of harbor porpoises per square kilometer as opposed to the number of schools are compared, the differences in all four cases were not significant based on a simple t-test (Table 8) and a similar jackknife procedure resulted in no significant differences for experiment 1 (mean differences=-0.62 and 1.69 with respective SE=1.49 and 1.04). The lack of a difference in this case during the first experiment when team 1 was in the crow's nest appears to be the result of an interaction between number of sightings and estimates of school size.

Table 8

Comparison of estimates of the number of individual harbour porpoise per square kilometer (number of sightings times mean school size) between the two observer teams from the same set of transects. Numbers in parenthesis are estimates of the standard error which were estimated based on the standard errors for the mean school size and the density of sightings and the variance estimate for a product of two random variables (Seber, 1982).

Team in	Experiment 1		Experiment 2	
Crow's nest	Team 1	Team 2	Team 1	Team 2
Team 1	8.94 (2.11)	10.94 (2.01)	38.94 (12.00)	19.90 (5.44)
Team 2	8.78 (2.59)	6.47 (2.09)	13.33 (2.27)	11.04 (1.56)

Duplicate sightings

Fig. 9 provides example maps for four of the 29 transects comparing the estimated position of sightings made by each team on the same transect. These maps suggest that sightings seen by one team are frequently not seen by the other. The maps for the other transects not shown were similar in this regard.

Estimates of the proportion of sightings that were seen by both teams based on various criteria for judging whether two sightings were similar, ranged from 0.04 to 0.54 (Table 9). The requirement that the estimated position of a sighting by both teams was within 200m and that the implied swimming speed of the harbor porpoise was less than 100m per minute yielded the lowest estimates of the proportion of duplicate sightings. The criterion based only on sightings being within 300m gave the highest estimates. Restricting the elapsed time to 3 minutes, the implied swimming speed to less than 200m per minute, or sightings to the same side of the vessel in combination with a maximum distance requirement, resulted in lower estimates of the proportion of duplicate sightings than a distance requirement of 200m by itself.

Table 9

Estimates of the total number of sightings and the proportion of sightings which were seen by both teams based on different criteria for judging whether a sighting was a duplicate. Low density transects were defined as ones in the total number of sightings by both teams which did not exceed 20; medium density transects were ones in which the number was greater than 20 but did not exceed 40, and high density transects were ones in which the number exceeded 40. P = the estimate proportion. N = the estimated combined total number of unique sightings (i.e. sightings seen only by team 1 plus sightings seen only by team 2 plus sightings seen by both teams). D = distance. S = swimming. Si = sighting.

	Sighting density							
	Low		Medium		High		All transects	
Criterion	P	N	P	N	P	N	P	N
D <100m	0.04	96	0.08	198	0.15	530	0.12	824
D <200m	0.09	92	0.20	178	0.35	450	0.28	720
D <300m	0.18	85	0.33	161	0.54	396	0.44	642
D <200m and time < 3 min	0.06	94	0.20	179	0.35	452	0.27	725
D <200m and S speed < 100m/min	0.03	97	0.06	201	0.14	534	0.11	832
D <200m and S speed < 200m/min	0.05	95	0.10	195	0.27	480	0.20	770
D <200m and Si on same side	0.08	93	0.13	190	0.24	489	0.19	772

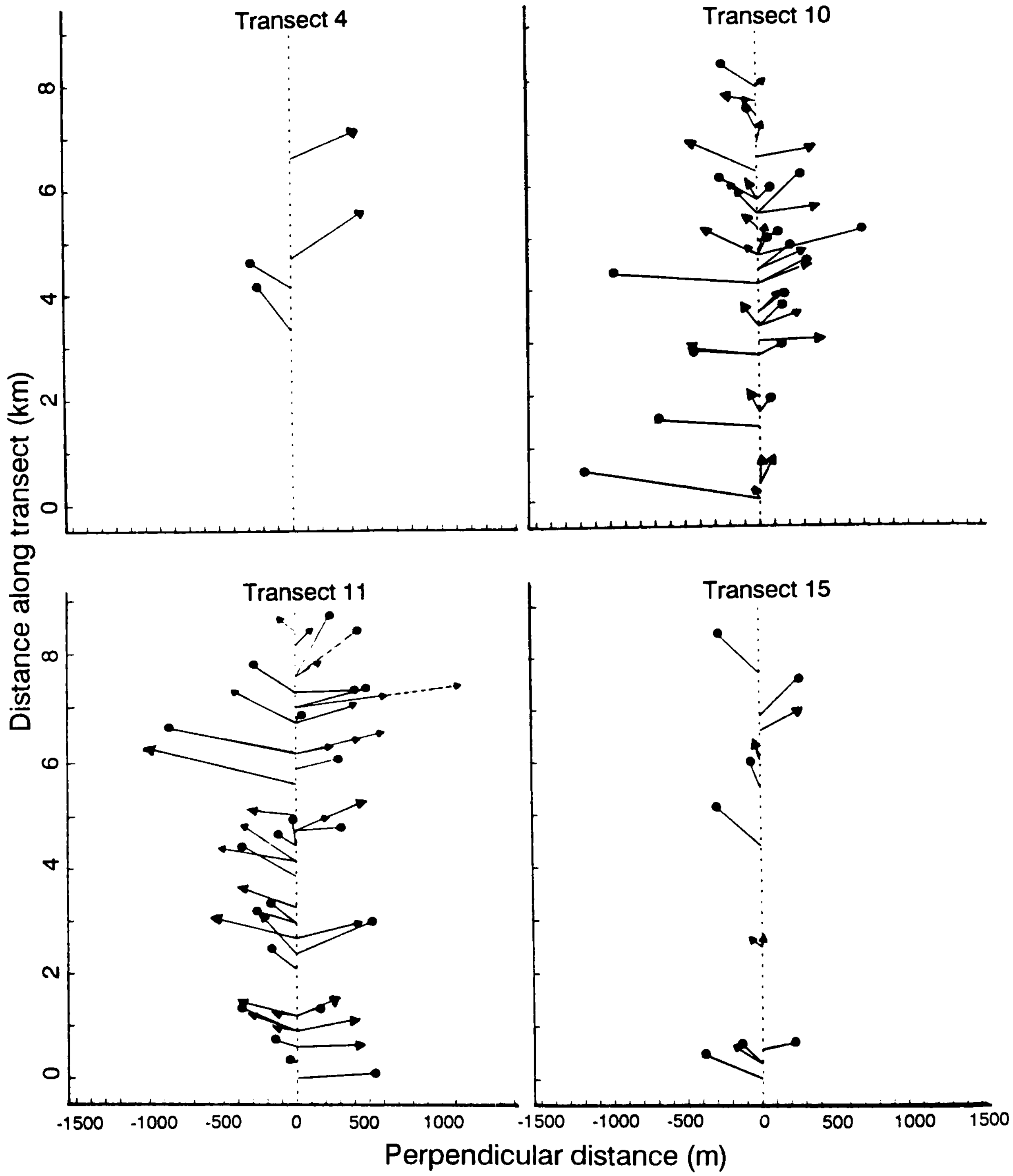


Fig. 9. Example maps showing the estimated position relative to the transect line of harbor porpoise sightings by each observer team on individual transects. The circle or triangular symbol represents the location of the school at the time of sighting, while the line connecting the symbol to the trackline shows the position of the vessel. (Note that the scale of the perpendicular distance axes in these maps is greatly expanded relative to transect axis.)

Estimates of the number of sightings seen by both teams increased with the density of sightings. Thus, on transects in which the total number of sightings by both teams did not exceed 20, the estimates of the proportion of sightings seen by both teams ranged from 0.04 to 0.18 compared to 0.15 to 0.54 for transects in which the number of sightings exceeded 40 (Table 9). It should be noted that as the density of sightings increases the likelihood of falsely identifying two unique sightings as a duplicate increases. As such, the estimated proportions during the low density transects are likely to be the most accurate.

Table 10

Comparison of the effect of height on the proportion which were seen by both sets of observers on different criteria for judging whether a sighting was a duplicate. Data within a sighting position have been pooled across the two teams of observers. N=the estimated total number of unique sightings (i.e. sightings seen only by team 1 plus sightings seen only by team 2 plus sightings seen by both teams). P=the estimated proportion. S=swimming. Si=sighting. Sp=speed.

	Experiment 1 Wheel house/Crow's nest		Experiment 2 Wheel house/Bow	
Criterion	P	N	P	N
Distance <100m	0.10	515	0.16	309
Distance <200m	0.24	455	0.35	265
Distance <300m	0.36	416	0.58	226
Distance <200m & time <3 min	0.23	458	0.34	267
Distance <200m & S Sp <100m/min	0.09	517	0.13	315
Distance <200m & S Sp <200m/min	0.16	486	0.26	289
Distance <200m & Si on same side	0.16	486	0.25	286

Comparison of estimates of the proportion of duplicate sightings when one of the two observer teams was at the bow versus on top of the wheel house (i.e. experiment 1 versus experiment 2) suggests that the probability of a sighting being detected by both teams increased with an increased differential in height (Table 10). However, the density of sightings encountered during experiment 2 was greater than during experiment 1. As such, the difficulty of accurately determining if sightings are duplicates at high densities is more likely the cause of the differences in Table 10 than the differential in height.

DISCUSSION

Results from these double team experiments suggest that comparable data from shipboard line transect surveys for harbor porpoises and perhaps other species can be collected by different teams of experienced observers and that estimates of density tend to be robust with respect to the effects of observer height and team composition. While none of the overall density estimates in terms of numbers of individuals were significantly different, the fact that the density estimates for the number of schools for one comparison based on the jackknife procedure were significantly different and that the estimates of school size between the two teams also tended to be different does raise concerns. However, at least part of the difference between the two teams appears to be related to whether they treated the relatively few large aggregations as a single large school or several smaller ones. Thus, team 1 tended to have a lower sighting rate and higher school size estimates, which on several transects appeared to be related to a single large 'aggregation'. The problem of what constitutes a distinct sighting or school is hard to define in areas of locally high density. A more standardized approach should be developed so that results are more easily compared in future double team experiments and so that line transect results can be pooled across different observer teams.

Table 11

The expected proportion of duplicate sightings based on the product integral for the hazard rate model for all combinations of the parameter estimates for the hazard rate model in Table 5.

Hazard rate parameter		Hazard rate parameter A and B														
A	B	-2.34	-3.49	-2.78	-3.20	-4.21	-2.86	-3.87	-2.97	-3.77	-3.35	-2.53	-3.15	-2.73	-3.45	-3.75
		3.02	2.86	2.86	3.85	4.81	4.21	7.49	4.54	4.74	4.00	3.53	3.33	3.52	4.26	4.35
-2.34	3.02	0.50	0.39	0.46	0.53	0.56	0.55	0.56	0.55	0.56	0.54	0.53	0.49	0.52	0.55	0.55
-3.49	2.86	0.39	0.43	0.41	0.43	0.46	0.39	0.37	0.39	0.43	0.43	0.39	0.44	0.41	0.43	0.45
-2.78	2.86	0.46	0.41	0.45	0.50	0.52	0.48	0.47	0.48	0.51	0.50	0.47	0.48	0.48	0.51	0.51
-3.20	3.85	0.53	0.43	0.50	0.59	0.62	0.59	0.60	0.60	0.62	0.60	0.57	0.54	0.57	0.61	0.61
-4.21	4.81	0.56	0.46	0.52	0.62	0.67	0.62	0.61	0.62	0.66	0.63	0.59	0.58	0.60	0.65	0.65
-2.86	4.21	0.55	0.39	0.48	0.59	0.62	0.63	0.67	0.64	0.64	0.60	0.59	0.53	0.58	0.62	0.61
-3.87	7.49	0.56	0.37	0.47	0.60	0.61	0.67	0.80	0.70	0.65	0.60	0.62	0.52	0.60	0.62	0.60
-2.97	4.54	0.55	0.39	0.48	0.60	0.62	0.64	0.70	0.66	0.65	0.60	0.60	0.53	0.59	0.62	0.61
-3.77	4.74	0.56	0.43	0.51	0.62	0.66	0.64	0.65	0.65	0.67	0.63	0.60	0.57	0.60	0.65	0.65
-3.35	4.00	0.54	0.43	0.50	0.60	0.63	0.60	0.60	0.60	0.63	0.60	0.57	0.55	0.58	0.62	0.62
-2.53	3.53	0.53	0.39	0.47	0.57	0.59	0.59	0.62	0.60	0.60	0.57	0.56	0.51	0.56	0.59	0.58
-3.15	3.33	0.49	0.44	0.48	0.54	0.58	0.53	0.52	0.53	0.57	0.55	0.51	0.52	0.52	0.56	0.56
-2.73	3.52	0.52	0.41	0.48	0.57	0.60	0.58	0.60	0.59	0.60	0.58	0.56	0.52	0.56	0.59	0.59
-3.45	4.26	0.55	0.43	0.51	0.61	0.65	0.62	0.62	0.62	0.65	0.62	0.59	0.56	0.59	0.63	0.63
-3.75	4.35	0.55	0.45	0.51	0.61	0.65	0.61	0.60	0.61	0.65	0.62	0.58	0.56	0.59	0.63	0.64

The results from these experiments also indicate that the effect of observer height (within the range of 1.8 to 7.1m) on the detection process for harbor porpoise is small as measured both by estimates of $f(0)$ and comparisons of the frequency distributions of sighting angles, and radial and perpendicular distances. However, the differences with height that were observed in these distributions tend to be consistent with what might be expected.

Differences in environmental sighting conditions during the different transects do not appear to be a significant factor in the results. It should be emphasised that, for all of the comparative results between the two teams, all data were collected on the same transects. As such, the results were collected when both teams were searching under the same set of enviornmental conditions. As such, differences in environmental conditions during the various transects would not effect the comparisons between teams.

For the comparisons within teams (e.g. the effect of height on the detection function), sea state and glare conditions appear not to be a significant factor. Thus, sea state conditions, as measured by the Beaufort scale, were equal during 10 out of the 14 replicate pairs and overall sea state conditions were very similar within each experiment irrespective of the position in which a team was searching (Table 12). With respect to glare, each observer team was asked to classify glare conditions for the port, center and starboard searching positions during each half hour transects as being none, slight, moderate and severe. There was some discrepancy in the ranking between the two teams with team 1 generally ranking glare conditions as being somewhat worst on the same transect (Table 13). Table 13 also suggests that perception/effect of glare may be somewhat greater at lower sighting positions (i.e. the apparent discrepancy between the two teams ranking is greater when team 2 was in the crow's nest). However, overall, the difference in glare conditions when a team was in the crow's nest or not within an experiment was not great and does not appear to a large factor in the comparative results within a team.

The results from these experiments, raise serious concerns about the assumption that $g(0)$ equals one and, consequently, the use of the density estimates for estimating absolute abundances without separately estimating this value. The low estimated proportion of duplicate sightings, particularly during low density transects (Tables 9 and 10), suggests that $g(0)$ may be substantially less than one. To evaluate these estimated proportions, the expected proportion of duplicate sightings was calculated from the joint integral of $g(y)$ assuming that the probability of detection was independent for the two observer teams. Calculations were performed for all combinations of parameter estimates for the hazard rate model in Table 5. The results of these calculations suggest that the expected proportion of duplicate sightings should have been in the range of 0.37 to 0.80 (Table 11).

Table 12

Number of half hour transects conducted at different Beaufort states.

		Beaufort state			
Experiment	Team in Crow's nest	0	1	2	3
1	Team 1	1	5	5	0
	Team 2	1	6	4	1
2	Team 1	1	2	0	0
	Team 2	1	2	0	0

Table 13

Number of transects in which glare conditions for each sighting was ranked as 0=none; 1=slight; 2=moderate; 3=severe. Each team made independent ranking of glare conditions.

			Glare conditions											
			Port				Center				Starboard			
Experiment	Team in Crow's nest	Team doing the ranking	0	1	2	3	0	1	2	3	0	1	2	3
1	Team 1	Team 1	5	3	1	2	5	6	0	0	6	2	1	2
		Team 2	6	2	2	1	7	2	2	0	6	2	1	2
	Team 2	Team 1	4	5	1	0	5	4	1	0	5	4	1	0
		Team 2	9	1	1	0	9	2	0	0	9	4	0	0
2	Team 1	Team 1	1	1	0	1	1	2	0	0	0	3	0	0
		Team 2	0	2	0	1	0	3	0	0	2	1	0	0
	Team 2	Team 1	1	2	0	0	0	2	1	0	1	1	1	0
		Team 2	2	1	0	0	2	1	0	0	2	1	0	0

The estimated observed proportions of duplicate sightings (Table 9) were almost always below this range and were substantially lower than this during low density transects.

As pointed out by Schweder (1990), the probabilities of detection for the two teams in an independent observer experiment are only conditionally, not completely, independent. This factor would mean that the expected proportion of duplicate sightings may actually be higher than those calculated in Table 11. Observer heterogeneity could result in an opposite bias in the expected proportion (IWC, 1990). However, since members of the observer teams were kept constant throughout the experiments, observer heterogeneity is not likely to be a significant factor in the results which did not pool data across teams. Moreover, since the detection functions for the two teams appear similar, the actual heterogeneity between the two teams appears to be small.

In order to get an indication of the magnitude of $g(0)$, the method of Butterworth and Borchers (1988) for independent observer data was applied to data pooled across observer teams to estimate $g(0)$ for the three different observer positions. The number of duplicate and unique sightings used in these calculations were based on the criteria that two sightings within either 100m or 200m were considered duplicate. The estimated values for $g(0)$ ranged from 0.22–0.41 for the 100m criterion and 0.47–0.79 for the 200m criterion (Table 14) and indicate that $g(0)$ was less than 1.00. These values should be interpreted with caution because of the difficulty in identifying duplicate sightings. However, the percentage of duplicates based on the 100m criterion is closer to the range of estimates for the proportion of duplicates found in low density transects in which the problem of correctly identifying duplicates is less. As such, the low estimates of $g(0)$ based on the 100m criterion suggest that $g(0)$ was small (i.e. <0.45) during these experiments. In addition, the values for $g(0)$ are probably overestimated because of the problem of conditional independence (Schweder, 1990). No method exists to estimate the magnitude of the bias from this source without additional data or assumptions.

Small values for $g(0)$ for harbor porpoise are not unexpected when the combination of a difficult to see sighting cue (small dark dorsal fin), short sighting distances and animal movement are considered. The nature of the cue makes probability of detection during any given surfacing small (particularly as the distance from the vessel increases).

Table 14

Estimates of $g(0)$ for the three observer positions based on the method of Butterworth and Borchers (1988) for independent observer data. The estimates were calculated using the hazard rate parameter estimates for the data pooled across observer team for each sighting position. The number of duplicate sightings and the total number of sightings were estimated based on the criterion that two sightings within either 100m or 200m were considered to have been the same group of animals.

	Experiment 1		Experiment 2	
Position	100m	200m	100m	200m
Bow	-	-	0.34	0.65
Wheel house	0.28	0.59	-	-
Crow's nest	0.22	0.47	0.41	0.79

Moreover, the total time period during which animals can potentially be sighted is small not only because sighting distances tend to be short, but because animals frequently spend only a fraction of their time at the surface. This combination of features is not unique to the harbor porpoise and would be expected to some degree for other cetaceans that occur singly or in small groups. As such, it is not surprising that independent observer experiments for minke whales have resulted in estimates of $g(0)$ less than one (Butterworth and Borchers, 1988; Øien, 1990b). The problem of deriving accurate and precise estimates for $g(0)$ is critical given the importance of ship based line transect abundance estimates in marine mammal assessments. The assumption that $g(0)$ equals one should not be considered valid without supporting field tests.

The apparent ship avoidance behavior of harbor porpoise that was also observed during the experiments described here (Polacheck and Thorpe, 1990) suggests a further confounding problem in deriving density estimates. Avoidance behavior results in negative bias in density estimates even if $g(0)$ equals one (Smith, 1979; Burnham *et al.*, 1980). Avoidance behavior may also be a contributing factor to the low proportion of duplicate sightings. This would be a large factor only if animals moved substantially farther from the trackline during the time available for detection after the initial sighting by one team. In general, the actual time at risk appears to be small and avoidance behavior, thus, would appear to be a small factor.

In conclusion, the results from the double team experiments described here suggest that shipboard line transect methods for harbor porpoises can be reasonably robust to both observer height and team effects. However, the results also suggest that, in general, $g(0)$ should not be assumed to equal one and that direct estimates of $g(0)$ are needed to obtain absolute abundance estimates.

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The Effect of Increasing Observer Trackline Effort in Shipboard Line Transect Surveys for Harbor Porpoise

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ABSTRACT

Previous double team experiments testing line transect methodology for harbor porpoise indicated that a relatively small proportion of the sightings were actually seen by both teams. Results of an additional field experiment designed to test the effect of concentrating additional observer effort along the transect line are presented. Observer effort was varied by rotating two extra observers between two independently searching teams of three members each and instructing the two additional observers to concentrate their searching effort on the trackline. This additional effort had a differential effect on the two teams. For one team, the distribution of perpendicular sighting distances became highly concentrated on the trackline when the additional observers were present while for the other team the additional observers had little effect. Difficulties were encountered in determining which sightings were seen by both teams, particularly on transects in which the density of sightings was high. However, the actual proportion of duplicates, at least for the lower density transects, appears to be low and the additional observers did not have a consistent effect on the duplication rate between the two teams. A large amount of heterogeneity also existed among the individual observers based on comparisons of the distribution of perpendicular sighting distances when each individual observer occupied the center viewing position and based on the actual number of sightings detected by each observer.

KEYWORDS: HARBOUR PORPOISE; SURVEY-SHIP; NORTH ATLANTIC; *g*(0)

INTRODUCTION

Line transect sighting surveys have been conducted to estimate abundances for a variety of marine mammal populations and the resulting estimates are increasingly being used as the basis for assessing the status of these populations and for management decisions. A basic assumption of standard line transect theory is that all animals directly on the trackline are seen. If this assumption is not met, the resulting abundance estimates are underestimated by a factor inversely proportional to the fraction actually detected (Burnham *et al.*, 1980; Seber, 1982). Recent research indicates that in many survey situations (particularly for smaller cetaceans that occur in small groups – e.g. harbor porpoise, minke whales), a substantial fraction of the animals on the trackline are not detected and thus that the probability of detecting an animal on the trackline is less than one (Barlow, 1988; Øien, 1990; Schweder *et al.*, 1991; Polacheck, 1995). However, the estimation of this probability, which is generally referred to as $g(0)$, has proved difficult and currently no satisfactory and generally agreed upon method exists (IWC, 1990). The fraction of animals that are missed on the trackline will be a function of both the surfacing/diving times of the target animal and the detection process of the observers.

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Recent concerns about the effects of incidental takes by bottom tending gillnets has highlighted the critical need for estimates of abundance for a number of different small cetacean stocks including many harbor porpoise populations (IWC, 1994). The estimation of $g(0)$ is likely to be a major source of uncertainty in any future line transect surveys of these populations. Lower bound estimates of population size due to $g(0)$ being unknown can be obtained by assuming that $g(0)$ equals one. In order to minimise the potential range between such a lower bound estimate and the actual population size, it is important when planning and designing abundance surveys, to understand the extent to which the detection process can be altered to increase $g(0)$. However, even if $g(0)$ is substantially less than one, lower bound estimates can be useful for monitoring trends in relative abundance provided the variation in $g(0)$ between surveys is small. For this reason, it is also important to understand the extent to which $g(0)$ may vary due to observer heterogeneity.

Results from double team experiments testing line transect methods for harbor porpoise in the Bay of Fundy indicated that the proportion of sightings which were actually seen by both teams may be very small (e.g. between 4–50%) and suggested that $g(0)$ in these experiments was substantially less than one (Polacheck, 1995). The purpose of the present paper is to report the results from an additional double team experiment in which the number of observers was varied. The experiment also provided an opportunity to collect information on differences in the performance of individual observers. The results provide an indication of the importance of the number of observers and observer heterogeneity on the detection probability for animals on the trackline.

METHODS

The experiment was conducted from 19–21 August 1990 near Grand Manan Island (Fig. 1). This area had been used in previous experiments and was chosen because harbor porpoises congregate there during summer and early fall (Neave and Wright, 1968; Gaskin, 1977; 1984). The cruise was conducted aboard the R/V *Abel-J*, a 106ft oceanographic research vessel and the general experimental procedures were similar to those used in previous experiments (Polacheck and Smith, 1989; Polacheck, 1995). These experiments were part of a longer, multi-purpose cruise which investigated both line transect methodology and the summer distributional range of harbor porpoise in the Gulf of Maine/Scotian Shelf region.

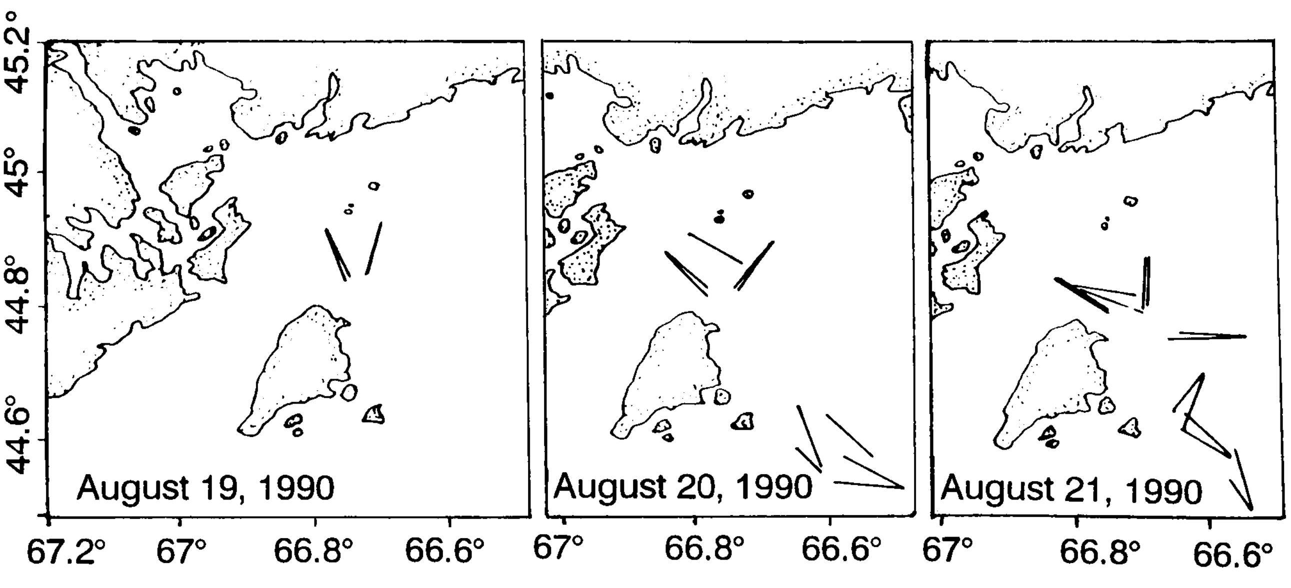

Fig. 1. Location of all transects during the extra observer experiment.

The R/V *Abel-J* has a tall mast located in the bow section with two crow's nest platforms, one 15m above sea level and one 6m. The base of both platforms is made of sheet steel and during normal searching operations it is not possible to see individuals on one platform from the other. Sets of three observers formed two core observer teams that remained at one location for the entire experiment (team 1 in the upper crow's nest and team 2 in the lower). Previous experiments had suggested that the difference in observer height should not be a major factor in the results (Polacheck, 1995). In addition to the core teams, two additional observers ('rovers') rotated between the two teams so that each team alternated between having three and five members on successive transects.

Cruise tracks and position of teams

A total of 30 half hour transects were conducted. During all transects each team (including rovers) searched as an independent unit and recorded all marine mammal sightings. Transects were replicated in the sense that after the completion of a transect, the rovers would change platforms, the vessel would turn 180° and a second transect would be conducted. However, strong tidal currents led to only moderate success in duplicating the same course (Fig. 1). A break of at least 15 minutes was taken between each pair of transects to avoid observer fatigue. During this time, observers in the core teams would rotate between the port, center and starboard viewing positions.

Transects were laid out so that minimal or no glare existed directly on the trackline during the experiments (i.e. replicate pairs of transects that were conducted early or late in the day were run in northerly or southerly directions). This also meant that any adverse glare tended to be similar for each member of a replicate pair (i.e. any glare that existed on the port side of the vessel in one direction would affect the starboard side in the reverse direction).

Sighting strategy

As in previous cruises, within the core team, the center observer was instructed to search directly along the trackline and the two other observers searched their respective sides of the trackline. Binoculars were not used for searching but only to confirm sighting cues, estimate school size and determine swimming direction. The core teams were instructed to maintain the same searching strategy and behavior irrespective of the presence of the 'rovers'. The rovers were located next to (and usually slightly above and behind) the center observer and instructed to concentrate all of their effort on the trackline.

Observer experience

There was a wide range of previous experience among the observers. Two of the observers had no experience of cetacean sighting surveys prior to this cruise. However, as the experiment was conducted seven days into the cruise after over 300 harbor porpoise schools had been seen during 40 half hour transects, the two novices who had acted as recorders and assistants had gained some understanding of the search image, species identification and general line transect procedures. The observers were ranked with respect to experience. Two of intermediate rank were selected as rovers and the remainder were paired based on experience and randomly assigned to teams.

Data collection

Standard line transect data were collected, including, (1) the estimated radial sighting distance at which an animal was first sighted, (2) estimated sighting angle, (3) estimated group size, (4) time of sighting, (5) observer position, (6) the observer making the sighting, (7) environmental conditions (e.g. sea state and glare) and (8) the swimming direction of the animals. Radial sighting distances were estimated visually[2]. Individual peloruses were located at each viewing position for the core observers and were used to measure sighting angles. Synchronised stop watches were used to determine the time of each sighting (to the nearest second).

For logistical reasons there was only one additional person available to act as a recorder. The recorder rotated with the rovers so as to maximise the potential difference in the coverage of the trackline between the core teams with and without rovers. Observers did not feel the lack of a recorder to be a great detriment and in some instances when the density of sightings was great, it even appeared to be more efficient.

Detecting duplicate sightings

Mapping of the position of each sighting with respect to the transect line was done to investigate which sightings were seen by both teams. In the analyses presented, a duplicate sighting means any school (as opposed to single surfacing event) which was detected by both teams during the period in which the school was potentially visible. Although times of sightings were recorded to the nearest second compared to the nearest minute in the experiment reported in Polacheck (1995), similar difficulties were encountered in attempting to determine duplicates. There are three main sources for this uncertainty:

(1) measurement error in sighting angles and radial distances;
(2) timing errors and delays in recording the actual moment when a school was detected; and
(3) potential movement of animals between the sighting of a school by one team and its possible sighting by the other.

Two approaches were used to estimate the number of duplicate sightings. The first used a combination of limits on the swimming speed, distance, time and difference in sighting angle to classify sightings as duplicates or not.

The second approach involved individually comparing each sighting by one team with all other sightings by the other during a given transect, using a computer program which calculated the distance, time and implied swimming speed and direction of travel assuming two sightings were the same. These calculations plus the time of sighting, radial sighting distance, sighting angle, school size and swimming direction for all potential duplicates (i.e. any sighting by the other team during the same transect) were displayed sorted by the calculated distance between sightings. From this information, a judgement was made whether a particular sighting had been seen by the other team. All identified duplicates were scored as being either almost definite, probable or questionable. While this approach has a subjective element, it allowed a more integrated assessment of all the available information. However, as the density of sightings on a transect increased, it became increasingly difficult to make a determination (e.g. more than one school would appear to have some possibility of being a duplicate, yet no school would appear to be highly likely). For this reason and because of time constraints, this approach was used only on the 19 transects in which the total number of sightings by both teams was less than 15.

Analyses

Analyses used include standard chi-square comparisons of the frequency distributions of sighting angles, radial distances and perpendicular distances. In addition, line transect estimates of $f(0)$, (i.e. the probability density of perpendicular distances evaluated at zero)

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[2] Prior to this experiment, extensive training and testing of observers abilities to estimate radial distances were conducted as part of a feasibility study testing the potential of an electronic inclinometer to function as a range finder.

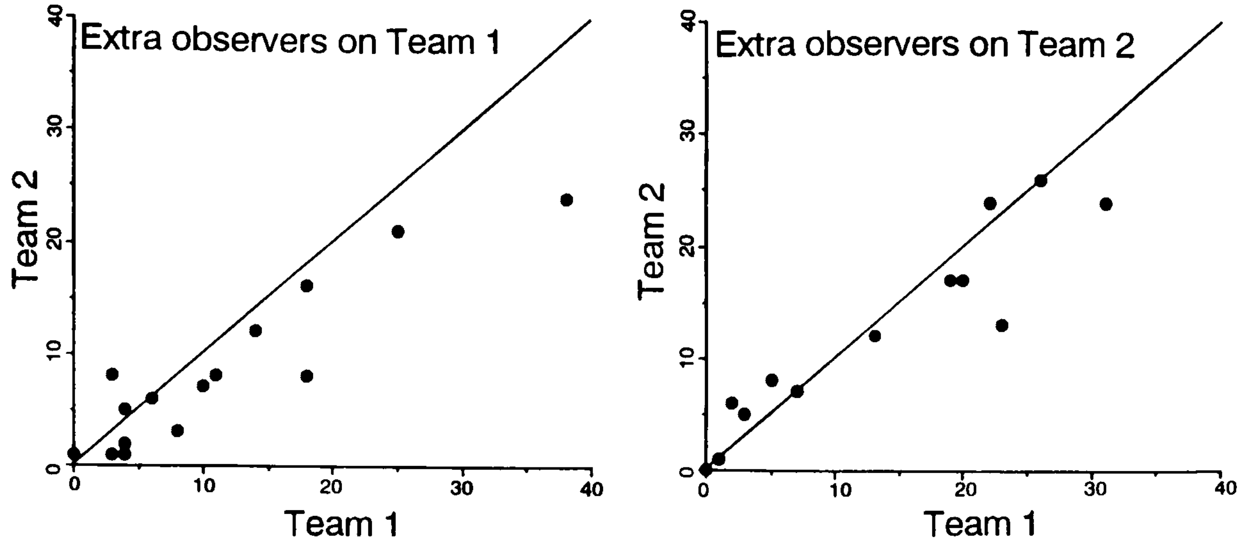

Fig. 2. Comparison of the number of sightings seen by each observer team during the same transects.

and density were calculated using both the hazard rate model (Hayes and Buckland, 1983; Buckland, 1985) and the Fourier series method (Burnham *et al.*, 1980).

Duplicate sighting rates are expressed as the proportion of sightings seen by one team that were also seen by the other team (i.e. n_{dup} / n_1 or n_{dup} / n_3)[3].

RESULTS

Comparison of sighting rates

The apparent effect of rovers on the overall sighting rate was not consistent for the two teams (Fig. 2). In 11 out of 14 transects (excluding one tie) when the rovers were associated with team 1, that team made the most sightings; whereas for team 2 this only occurred in 4 of 9 transects (excluding 3 zero and 3 tie transects).

Sighting rates for the two teams also appeared to be differentially affected by the presence of the rovers (Table 1). For transects when the rovers were associated with team 1, the average sighting rate per transect for team 1 (11.0) was significantly greater than for team 2 (8.2) based on a paired *t*-test (mean difference = 2.8, SE=1.1) while when the rovers were associated with team 2, there was no significant difference (i.e. 11.5 versus 10.7, mean difference =0.8, SE=1.0). However, as pointed out by one reviewer, these

Table 1

Comparison of the mean sighting rate (number of sightings per 30 minute transect) for each core observer team with and without the two additional roving observers. The numbers in parentheses are estimates of the standard error.

	Team 1	Team 2		Team 1	Team 2
Rovers present	11.0 (2.6)	10.7 (2.4)	Rovers absent	11.5 (2.8)	8.2 (1.9)

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[3] This is not directly comparable to that used in Polacheck (1995) where proportion of duplicates was calculated as the proportion of all sightings that were seen by either team which were also seen by both teams (i.e. $n_{\mathrm{dups}}/n_1+n_2-n_{\mathrm{dups}}$).

differences do not necessarily mean that the effect of the rovers on the two teams was significantly different.

This reviewer suggested that a linear model be used which includes terms for team, rover, local density and team*rover interaction. Since the object of these experiments was not to test sighting rates directly in a linear modelling framework but to have paired and comparable line transect estimates of density for different size observer teams, the data are somewhat confounded when analysed in a linear modelling framework (e.g. there are no direct team comparisons without the rovers and the team*rover interaction term is confounded by differences in local density and possibly sighting conditions on replicate pairs of the same transect line).

If a simple linear model is used with terms for team, rover, team*rover interaction and a blocking term for pairs of transects (i.e. local density), none of the non-blocking terms are significant. The reason for the difference in significance in this case compared to the paired t-tests is that for this linear model the blocking factor fails to take into account the more powerful blocking of simultaneous observations during any given transect.

A second blocking factor can be introduced into the linear model which is for simultaneous observations on the same transect. With this second blocking factor, the team effect is significant ($p<0.021$) while the rover effect is not significant ($p>0.186$). The team*rover interaction effect is completely confounded with the second blocking factor (i.e. the rovers could only be on one team during any set of simultaneous observations) and thus there is no satisfactory way to test this interaction effect which also takes into account the more powerful blocking factor. If one were to assume that the mean square error for the team*rover interaction was the same as for the main effects of team and rover on simultaneous transects than the team*rover interaction would be almost significant ($p=0.056$). This provides some support for the interaction effect. However, this is not a fully valid test because it fails to take into account the heterogeneity between each of the individual paired transects (i.e. the reduction in the sum of squares due to the team*rover effect would not be unlikely given the variance among the four observed sighting rates within a pair of transects).

Thus, even though the results of the paired t-test strongly suggest a team*rover interaction and the ANOVA results indicate a team effect, the possibility cannot be excluded based on the ANOVA results that the lack of a significant difference in the pair t-test results when the rovers were associated with team 2 is due only to sampling variability and not an interaction effect. As such, the data combined with the experimental design are insufficient to statistically conclude that there is a team*rover interaction. However, the power to detect such an interaction is relatively small.

Comparison of sighting distributions

The presence of additional observers also appeared to have very different effects on the distribution of perpendicular sighting distances at which animals were detected between the two teams (Fig. 3). For team 1, the distributions with and without the rovers were remarkably similar (and not significantly different) with a relatively broad shoulder out to around 300m ($\text{chi}^2=1.36$, df=5). By contrast, the presence of the rovers in team 2 resulted in a distribution that was concentrated near the origin (i.e. 45% of the sightings were detected within 100m); with no rovers, only 22% of the sightings were concentrated within 100m and 32% occurred between 100–200m. The perpendicular sighting distributions for team 2 with and without the rovers were significantly different ($\text{chi}^2=23.1$, df=6).

An examination of the angle and radial distance components (Figs 4 and 5) shows that the presence or absence of rovers made little difference for team 1. For team 2 however, a marked increase in the percentage of sightings detected at small angles, and a small

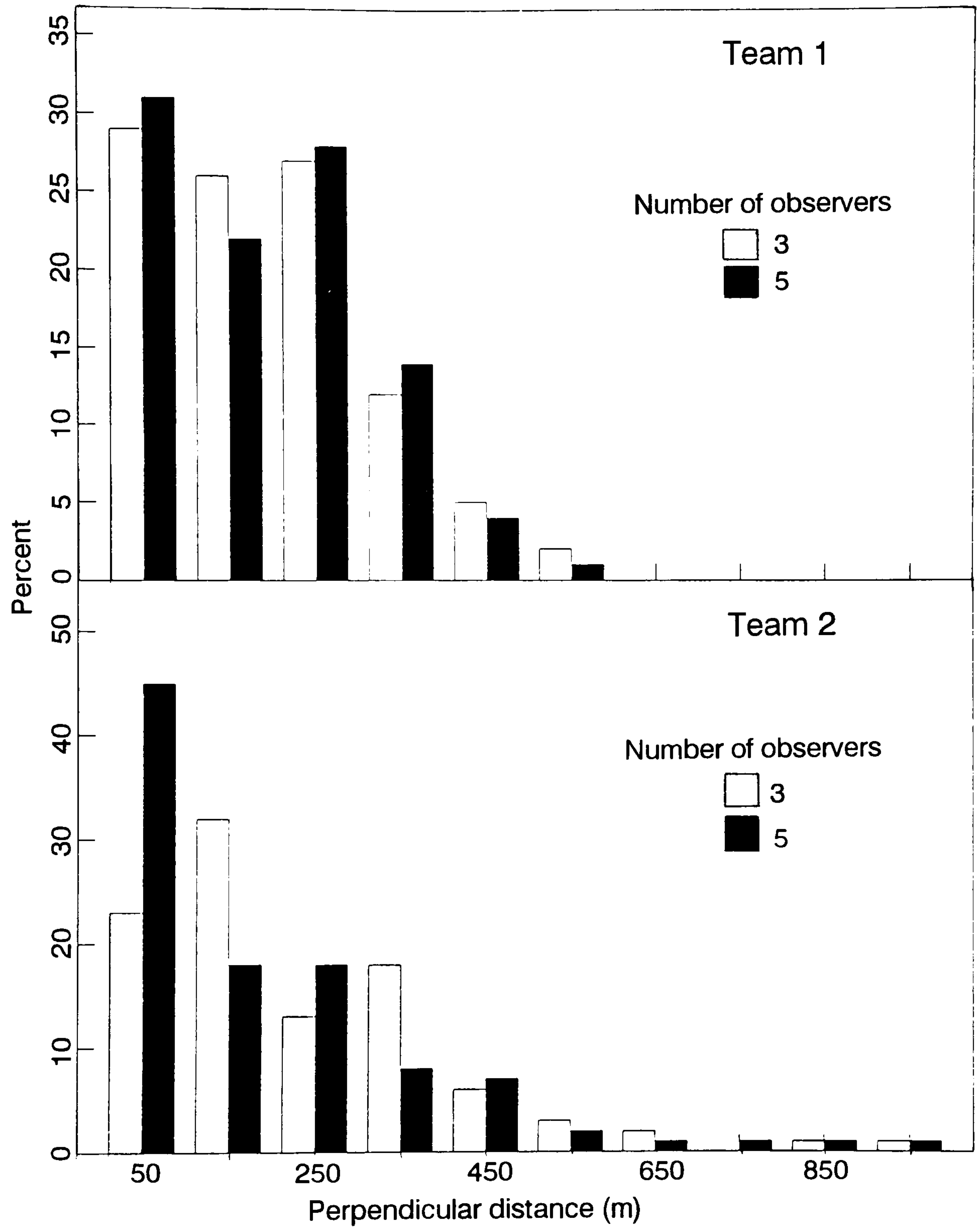

Fig. 3. Comparison of the frequency distributions of perpendicular sighting distances for each core observer team with and without the additional two roving observers.

increase in radial sighting distances occurred when rovers were present. As for perpendicular distances, the distributions of radial sighting distances and angles were not significantly different with and without the rovers for team 1 (respective chi^2 of 6.35 and 2.22 with 7 df). For team 2 the differences in the angle distributions were significant but the radial distances were not (chi^2=20.34 and 4.8 with 7 df).

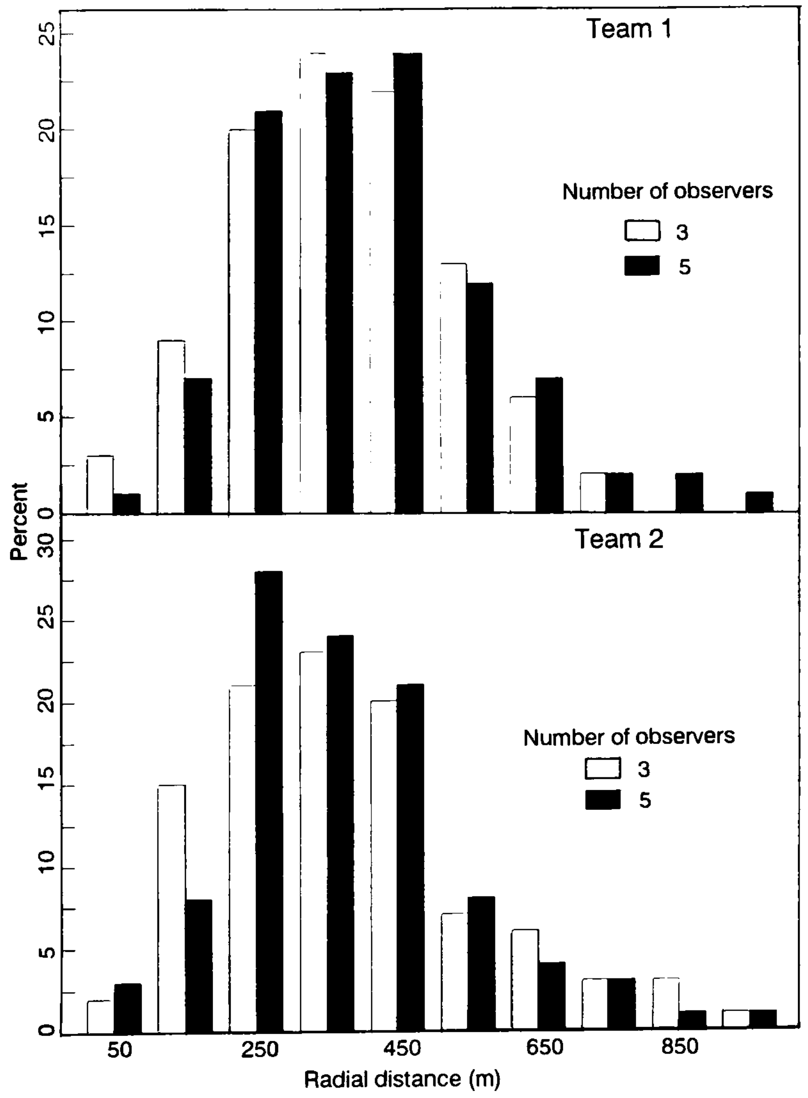

Fig. 4. Comparison of the frequency distributions of radial sighting distances for each core observer team with and without the additional two roving observers.

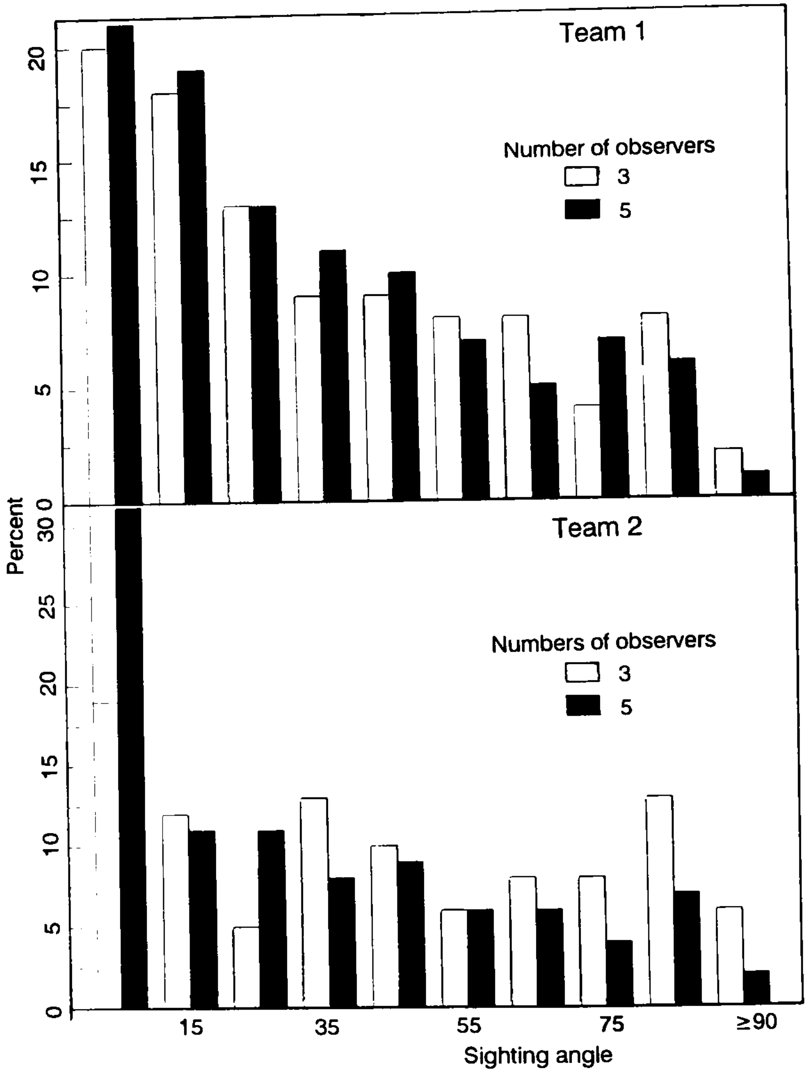

Fig. 5. Comparison of the frequency distributions of radial sighting angles for each core observer team with and without the additional two roving observers.

Individual observer effects

A more detailed examination of the distribution of perpendicular sighting distances indicates that these varied depending upon which observer was in the central position (Fig. 6). Thus, for observer B of team 1 and observers A and B of team 2, the modes of their team's distributions were only centred around the trackline when the rovers were present. With no rovers, more sightings were seen between 100–200m than 0–100m from the trackline. In contrast, for observer C of team 2, the mode was centred around the trackline with and without rovers, although the distribution was substantially more concentrated near the origin when the rovers were present. For observer C in team 1, the distribution was relatively flat out to 300m with and without rovers. The number of sightings for observer A of team 1 when the rovers were present was too small (i.e. 14) to make any meaningful comparison.

The differences within a team shown in Fig. 6 do not appear to be directly related to the previous experience of the observer who was occupying in the center viewing position. On both teams, the A observers were those with no previous experience. Lack of experience might explain the large difference with and without rovers when the A observer of team 2 was in the center (i.e. this observer may not have detected sightings that more experienced ones would have). The two B observers had the most experience and made the most sightings (Table 2). However, an examination of the perpendicular sighting distance distributions for each individual when they were in the center viewing position (Fig. 7), shows that when rovers were not present, the most experienced observers had distributions which were the least concentrated near the trackline. All observers except the B observer on team 1 had concentrated distributions when the rovers were present. The distributions for the rovers were also highly concentrated around the trackline (Fig. 8).

The total number of sightings detected by each individual provides a crude measure of heterogeneity among the observers (Table 2). Overall the number per observer ranged from 36 to 125, although among core observers with previous experience the range was considerably smaller (82 to 125). The number of sightings by one of the novice observers nearly equalled the number for the two intermediate core observers (79 compared to 82 and 83) while the numbers for the two roving observers ranged from 45 to 73. (Note that the two roving observers always had the competition of four other observers so that their expected number of detections would be less than those of the other observers if all observers were equal.) Both of these results suggest, not surprisingly, that factors other than experience are important in determining the heterogeneity among observers.

Line transect estimators

The estimates of $f(0)$ based on the hazard rate model with and without the two additional observers were not significantly different (assuming normality) for both observer teams (Table 3). This lack of a difference is somewhat surprising for team 2 given the large and significant difference in the distribution of perpendicular sighting distances. The reason appears to be due to the significant lack of fit of the model to the underlying data for team 2 (see the chi-square values in Table 3). The poor fit stems from two different sources (i.e. the dip near the origin for distributions without rovers and the high peak at the origin with rovers). The hazard rate model smooths over these to provide similar estimates. For comparative purposes, Fourier series estimates of $f(0)$ and density were also calculated (Table 3). The two estimates of $f(0)$ for team 2 are statistically different. Without rovers, $f(0)$ equalled 5.32 (SE=0.37) and with rovers $f(0)$ equalled 10.8 (SE=1.12).

The estimates of density (assuming $g(0)=1.0$) show a similar pattern to the estimates for $f(0)$ (Table 3). Jackknife estimates of the difference in density for the two teams were

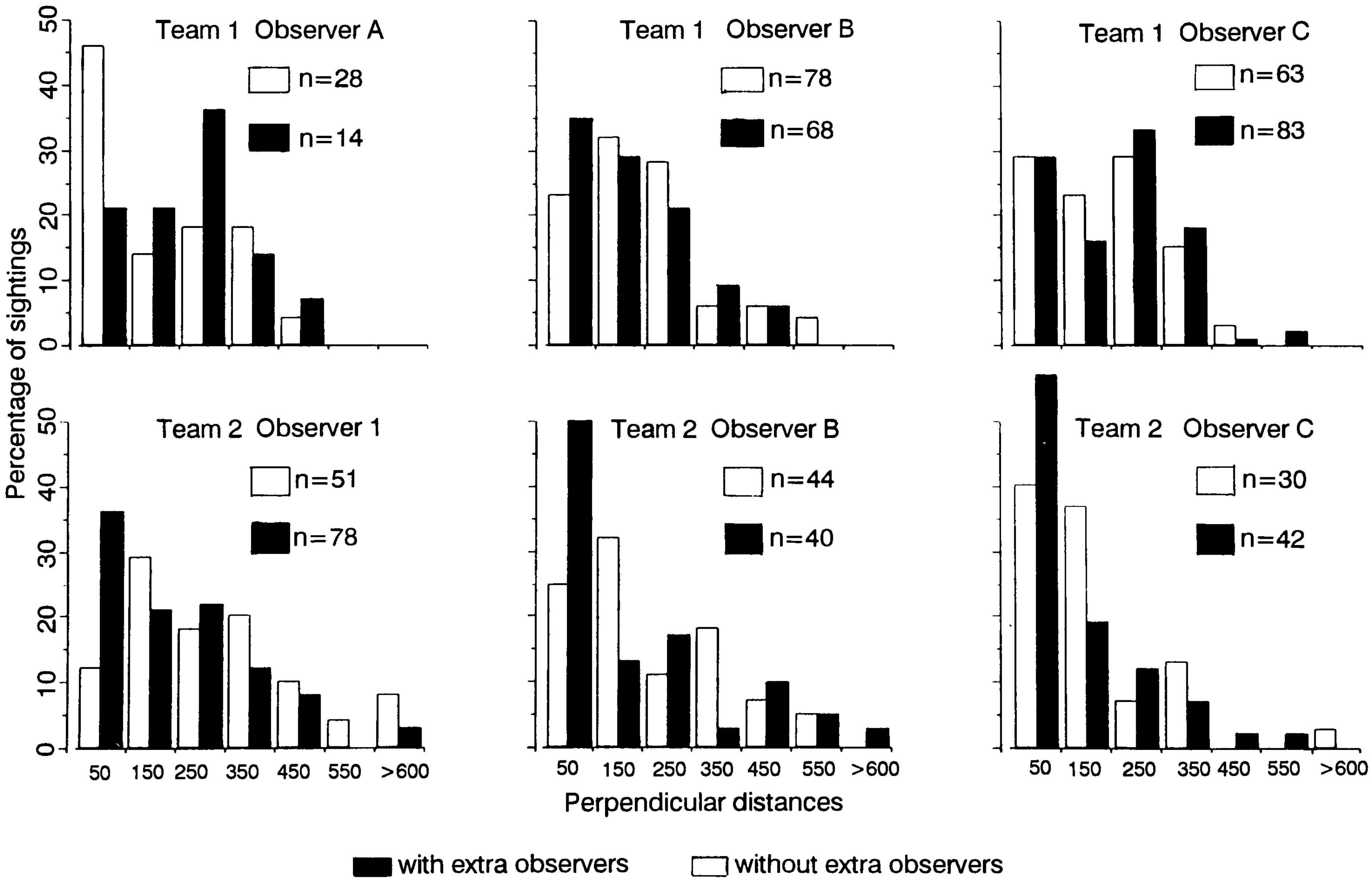

Fig. 6. Comparison of the frequency distributions of perpendicular sighting distances seen by a team for all combinations of individual observers in the center viewing position with and without the additional two roving observers.

Table 2

The number of sightings made by each individual observer.

		Rover present		No rover		
Team	Obs.	Center position	Side position	Center position	Side position	Total
1	A	4	31	6	38	79
	B	21	26	37	41	125
	C	19	14	17	32	82
2	A	6	9	5	16	36
	B	12	27	15	39	93
	C	9	26	9	39	83
		With team 1		With team 2		
Rovers	A	29	-	16	-	45
	B	42	-	32	-	74

calculated in order to take into account the covariance in the number of sightings due to both teams simultaneously searching the same area. A direct paired comparison could not be made because the sample sizes for each individual transect were insufficient to provide independent estimates of $f(0)$ (also see Burnham *et al.*, 1980, for a discussion of using the jackknife approach for estimating variances for line transect density estimates). The jackknife estimates were calculated by successively deleting the data from one transect, recalculating the density estimate for each team (including $f(0)$), and then using the difference in density for each of the 'pseudo' replicates as the test statistic. For the hazard rate model, the jackknife estimates of the mean difference were statistically significant when the rovers were with team 1 (mean difference = 2.24, SE=0.63) but not with team 2 (mean difference = –0.57, SE=1.93). Neither of the differences in density were statistically significant for the Fourier series model, although the jackknife estimate of the mean difference when team 2 had the rovers (mean difference = 3.66, SE=1.88) was close to the 0.05 level.

Duplicate sightings

Fig. 9 provides example maps for 4 of the 30 transects comparing the estimated position of sightings made by each team on the same transects. These maps are similar to those presented in Polacheck (1995). In both instances they suggest that sightings seen by one team are frequently not seen by the other.

Table 4 provides estimates of the proportion of sightings by one team which were estimated to have been seen by the other team based on method 1. A wide variety of different limits for the four criteria for determining a duplicate were explored, only some of which are presented here. Placing limits on the maximum swimming speed at which a school would have had to travel for it to have been a single school, and to have been at the two locations recorded by both observer teams appeared to be the most important factor, and is also the criterion most closely related to potential biological limits. (It should be noted that sightings within 100m and 15 secs of each other were considered as duplicates to account for potential errors in distance and angle measurements that would lead to unrealistically high speeds.)

The results for maximum swimming speeds of 200–300 m/minute (6.5–9.7 knots) with a restriction that two sightings should occur within 2–3 minutes of each other probably

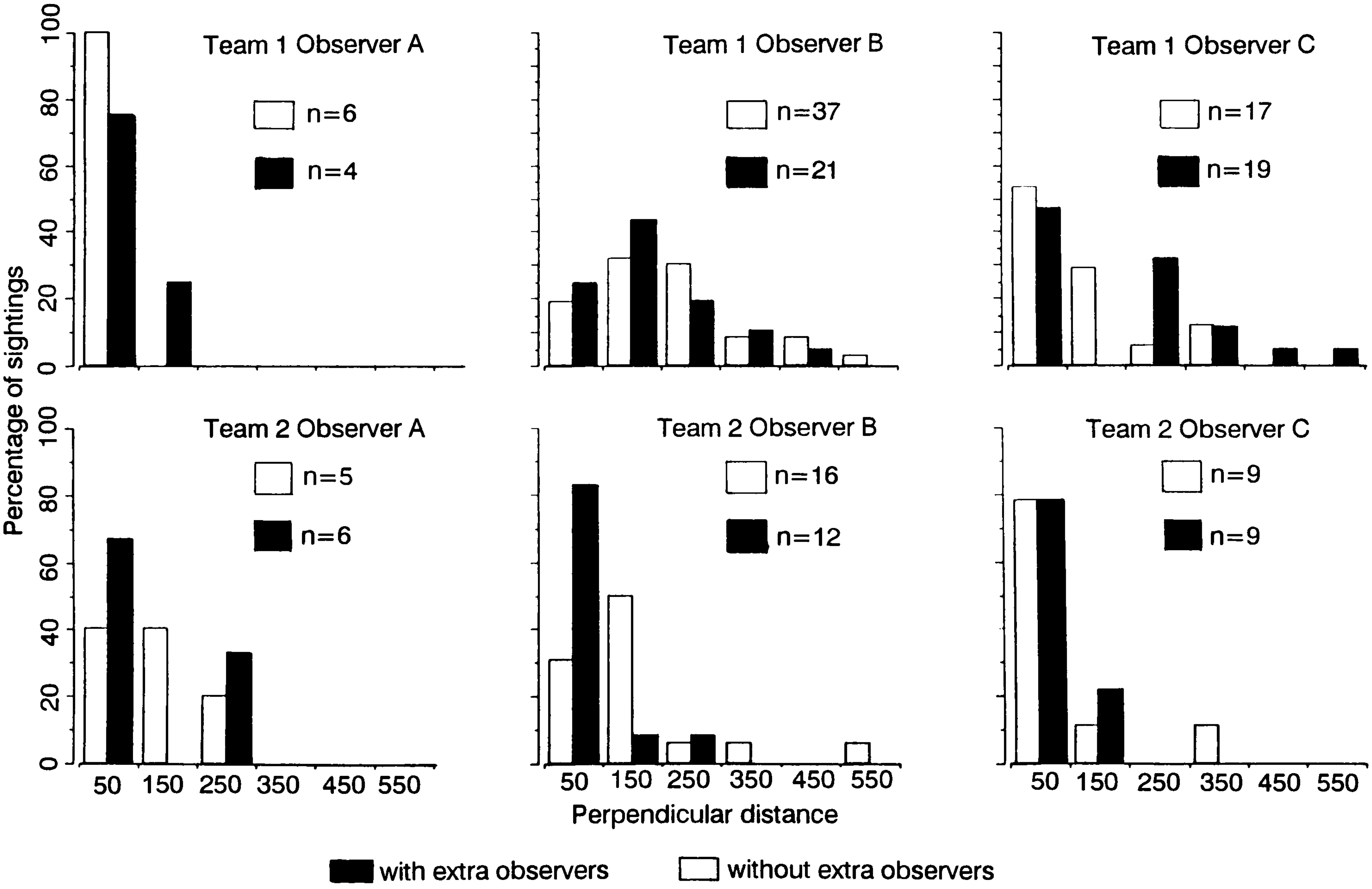

Fig. 7. Comparison of the frequency distribution by individual observer for perpendicular sighting distances for those sightings that were actually seen by that observer when he was in the center viewing position.

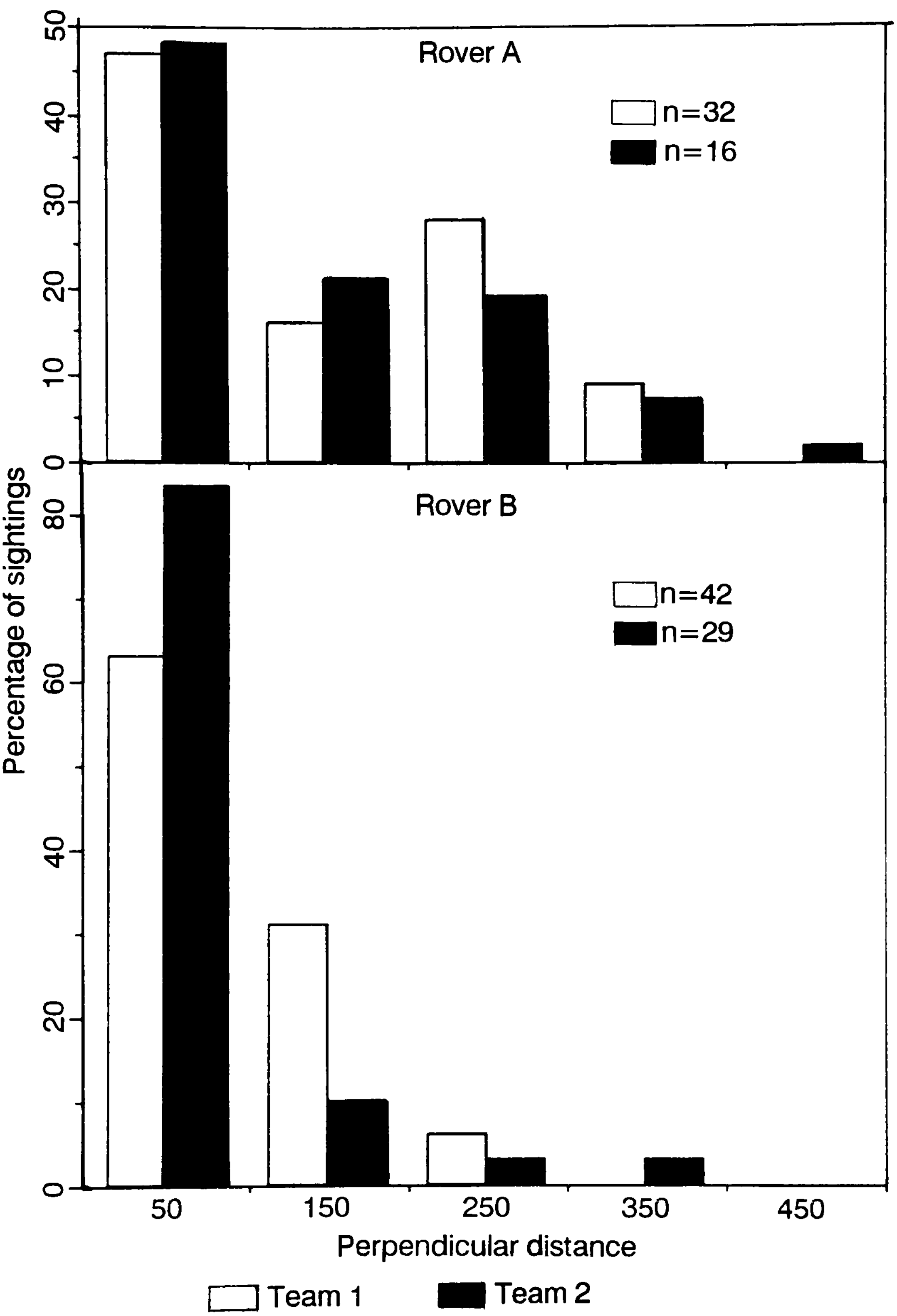

Fig. 8. The frequency distributions of perpendicular sighting distances for those sightings that were actually detected by the roving observers.

provide the best estimates of the possible maximum proportion of duplicate sightings. It is important to place a limit on the maximum time between two sightings as well as the maximum swimming speed because as the time between two sightings becomes large the required speeds for an animal to travel between two locations approaches the speed of the vessel through the water (i.e. approximately 300 m/minute). For this to have occurred

Table 3

Comparison of estimates of $f(0)$ and density (number of sightings per mile) for teams 1 and 2 with and without extra observers. The numbers in parenthesis are estimates of the standard errors.

	Team 1		Team 2	
	Rovers	No Rovers	Rovers	No Rovers
Hazard rate				
$f(0)$	5.02 (0.22)	5.24 (0.27)	6.71 (0.55)	4.26 (0.27)
Chi-square (4 df)	4.16	2.03	19.19	9.75
Density	5.81 (1.41)	6.32 (1.60)	7.54 (1.79)	3.68 (0.86)
Fourier series				
$f(0)$	5.29 (0.61)	6.05 (0.28)	11.66 (1.12)	5.26 (0.38)
Number of coef.	2	1	2	7
Density	6.47 (1.70)	7.30 (1.84)	13.09 (3.24)	4.54 (1.08)

would require that animals followed the vessel undetected for relatively long time periods when in fact animals appear to be avoiding survey vessels (Polacheck and Thorpe, 1990)[4]. Within these speed/time limits, the estimated proportion of duplicates ranged from 15–92%[3]. The duplicate sighting rate estimates do not suggest a consistent effect for the presence of extra observers, particularly at different densities (see discussion). As was found in Polacheck (1995), estimates of the proportion of duplicates based on limits tend to be greatest for transects in which the density of sightings was high. Since the potential for mistakes increases with the density of sightings, the estimates for the lower density transects should be considered as the most reliable and realistic.

The second approach for identifying duplicates, which was only carried out for the low density transects, found that it was difficult to distinguish duplicates unambiguously. Of those which were identified as possible duplicates, 40% were considered to be questionable, while only 14% were judged to be almost definite. The difficulty is due to the fact that sightings tend to be clustered spatially and temporally even on low density transects. The apparent effect of the rovers based on this second approach depends upon whether the questionable sightings are considered as duplicates (Table 5). If they are not, the results both with respect to the estimated proportion of duplicates and the effects of the extra observers are similar to those obtained using the first approach with a limit on the maximum speed of 200 m/minute and a 2 minute time limit (Tables 4 and 5).

Sighting conditions

The comparative results and differences in the response of the two teams to additional observer effort does not appear to be related to differences in weather/sighting conditions during the replicate pairs of transects. For comparisons between teams with and without extra observers, all data were collected on the same transects and as such both teams experienced the same environmental conditions.

For comparisons within a team, transects (as noted above) were laid out so that no or minimal glare existed directly on the trackline. Each observer team was asked to classify glare conditions for the three sighting positions during each half hour transect as being

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[4] Avoidance behaviour does not appear to be a major factor in the results for the effect of the rovers on the two observer teams. The distribution of radial distance was similar for the two teams; most sightings occurred within 500m of the vessel and the mode in the perpendicular sighting distance distributions was within the distance interval (100m) nearest the trackline in all cases but one.

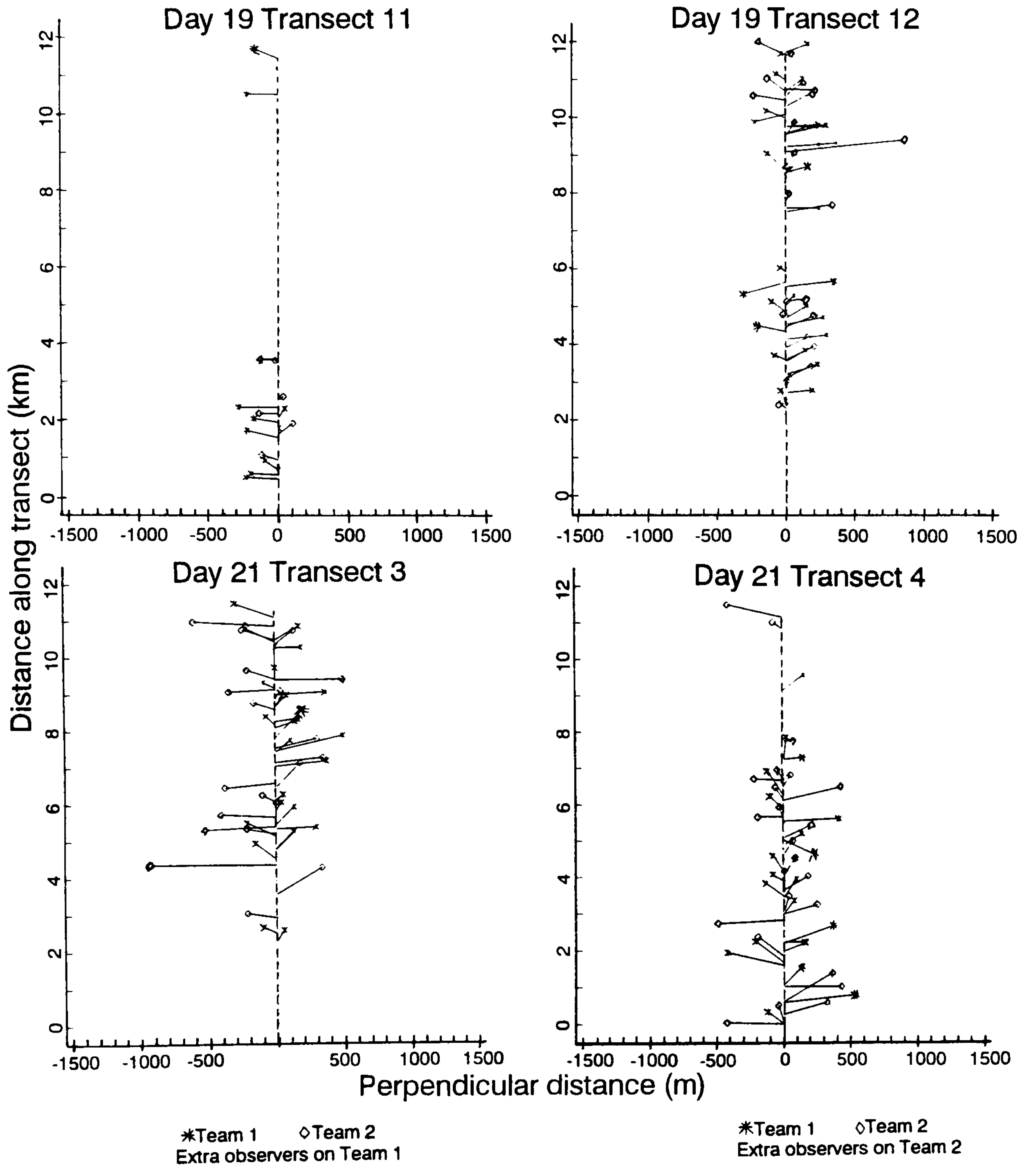

Fig. 9. Example maps showing the estimate position relative to the transect line of harbor porpoise sightings by each observer team on individual transects. Transects 11 and 12 on the 19th and transects 3 and 4 on the 21st constitute replicate pairs. The diamonds and asterisks indicate the estimated location of a school at the time of sighting, while the line connecting the symbol to the dashed trackline shows the position of the vessel at the time of sighting. (Note that the scale of the perpendicular distance axis in these maps is greatly expanded relative to the trackline axis. The reader should also note that these maps may tend to give an exaggerated impression of the frequency of sightings at large angles and radial distances and should refer to Figs 3–5.)

none, slight, moderate or severe. For the centre position, both teams classified glare as none for all transects. There was some discrepancy in the ranking between the two teams for the side positions with team 2 generally ranking the glare conditions as somewhat worse than team 1 on the same transects (Table 6). In addition and in spite of the fact glare

Table 4

Estimates of the proportion of one team's sightings that were also seen by the other team based on different criteria for estimating which sightings were duplicates. Transects were classified as low density if the total number of sightings by both teams was less than 15, medium density if the number was between 15 and 30 and high density if the number was greater or equal to 30.

Criteria	Density of sightings	Proportion of team 1's sightings seen by team 2		Proportion of team 2's sightings seen by team 1	
		Rover	No rovers	Rovers	No rovers
Max. swimming speed=200/min Max. time diff. = 2 min.	low	0.22	0.22	0.15	0.26
	medium	0.35	0.69	0.75	0.51
	high	0.37	0.31	0.36	0.49
	pooled	0.33	0.33	0.36	0.45
Max. swimming speed=300m/min Max. time diff. = 3 min.	low	0.37	0.28	0.19	0.44
	medium	0.52	0.85	0.92	0.77
	high	0.62	0.69	0.80	0.82
	pooled	0.54	0.66	0.71	0.72
Max. swimming speed=200m/min	low	0.31	0.39	0.26	0.37
	medium	0.52	0.92	1.00	0.77
	high	0.54	0.57	0.67	0.72
	pooled	0.49	0.58	0.63	0.66
Sample size	low	32	18	27	27
	medium	52	13	12	35
	high	81	141	121	61
	pooled	165	172	160	123

should have been similar for each member of a replicate pair (since transects were laid out so that glare was restricted to one side of the vessel), the resulting glare conditions on one side of the trackline tended to be somewhat better for those transects in which team 1 did not (i.e. team 2 did) have extra observers (Table 6). However, these differences would not appear to be the cause of the differential response between the two teams with extra observers. Thus for team 1 the differences in glare conditions apparently did not effect the distribution of perpendicular sighting distances while for team 2 the distribution of perpendicular distance was concentrated near the trackline when the extra observers were present (i.e. when glare was less). This is the opposite effect that would be expected if the difference in glare conditions was the significant factor underlying the difference in response between the two teams.

Table 5

Estimates of the proportion of a team's sightings that were also seen by the other team based on the second approach for determining duplicates (see text for details of this approach). Note that this method was only applied to low density transects (i.e. transects in which the total number of sightings by both teams was less than 15).

Team	Rovers	All possible duplicates	Questionable duplicates eliminated	n	Team	Rovers	All possible duplicates	Questionable duplicates eliminated	n
1	Present	0.38	0.19	32	2	Present	0.30	0.07	27
	Absent	0.50	0.11	18		Absent	0.44	0.22	27

Table 6

Number of half hour transected in which the most severe glare conditions for either the port or starboard viewing sector were ranked as none, slight, moderate or severe. Each team made independent ranking of glare conditions. Note that the glare conditions for the center or forward sector was always judged to be none during all transects.

Team without extra observers	Team doing the ranking	Glare condition ranking			
		None	Slight	Moderate	Severe
Team 1	Team 1	8	2	3	2
	Team 2	6	3	6	0
Team 2	Team 1	10	3	2	0
	Team 2	7	5	3	0

The difference in the results within the teams when extra observers were or were not present also does not appear to be related to sea state. Thus, sea state, as judged by the Beaufort scale, ranged from zero to four during the experiment with all but one pair of transects being conducted with sea states less than or equal to two. The sea state for each pair of a replicate was always within one unit and sea state was equal for each of the individual transects for 11 out of the 15 replicates. For the four other replicates, sea state conditions were slightly worse during those transects in which team 1 did not (i.e. team 2 did) have extra observers (Table 7). However, the difference in sea state within these four replicates appears to have little effect on the overall results. For team 2, the same number of total sightings was made during these four replicates with and without the extra observers (i.e. 10 with and 10 without). For team 1, a total of only five extra sightings were detected under the slightly better sea state conditions with no extra observers. This small differnece in the number of sightings cannot account for the difference in the results between or within the two teams with and without the extra observers.

DISCUSSION

The experiments suggest that concentrating additional observer effort on the trackline will have variable effects on the detection process depending upon the individual observers. The results clearly indicate that for team 2 additional observers markedly changed its distribution of perpendicular sighting distances and its overall sighting rate relative to team 1. These two results strongly suggest that the additional observers resulted in a higher proportion of potential sightings near the trackline being detected. The results for team 1 (i.e. the lack of change in the sighting rates, density estimates and distributions of sightings angles and distances) suggest that the additional observers had little effect on the

Table 7

Number of half hour transects conducted at different Beaufort states.

Team without extra observers	Beaufort state					Team without Extra observers	Beaufort state				
	0	1	2	3	4		0	1	2	3	4
Team 1	3	5	6	0	1	Team 2	3	8	3	1	0

overall detection process. However, it is possible that the lack of a difference could be due to the underlying true density having been higher during the transects when the rovers were associated with this team (i.e. the detection curve remained constant and only $g(0)$ changed). Moreover, the difference in the distribution of perpendicular distance, with and without rovers, when the most experienced observer was in the center viewing position suggests that rovers may also have had an effect on this team.

The estimates of duplicate sighting rates do not provide consistent results for the effects of the extra observers particularly at different density levels. If the estimated rates for the low density transects are considered as the 'best', then the results suggest that the proportion of team 2's sightings that were seen by team 1 increased when the rovers were associated with team 1 while the presence of the rover on team 2 either had little effect or may possibly have decreased the proportion of team 1's sightings seen by team 2. Such results further suggest that the additional observers had differential effects on the sighting efficiency and detection process for the two teams. However, caution should be used in interpreting these proportions as the sample sizes for these low density transects are relatively small and the differences are generally not significant.

The problem of determining whether a sighting was seen by both teams means that an unresolvable and perhaps unacceptably large degree of uncertainty must be expected if duplicate sighting rates from experiments such as these are used to estimate $g(0)$. The problem stems from two factors: (1) that animals can move a significant distance during the time that they are available to be seen; and (2) that sightings tend to be clustered spatially, even on low density transects. Over 45% of the sightings within a team had another sighting within an estimated 300m and even on low density transects this percentage was around 20%. Since harbor porpoise can swim such a distance in the 1 to 3 minutes that they are potentially in view, it becomes difficult, if not impossible, to decide whether a sighting that occurred within two to three minutes and several hundred meters of a sighting seen by the other team is actually the same or a different group of animals. This problem becomes increasingly difficult to resolve at higher densities. Tracking and recording the position of a school once it was detected might be a possible solution but such an approach would be logistically difficult and numerous other schools would undoubtedly go undetected while trying to perform this tracking.

However, even if this ambiguity did not exist, the movement of the animals could have a substantial effect on the expected duplication rate. A third of the animals that were judged as possible duplicates, using the second approach, moved more than an estimated 100m in their perpendicular distance relative to the trackline between the time they were sighted by one team and the time they were sighted by the other; the average change was 79m. If animals are moving a substantial distance relative to the trackline, then $g(y)$ will vary significantly during the time available for detection and this variability would need to be accounted for when calculating the expected proportion of duplicates.

Comparing differences in $g(y)$ and density estimates at two or more levels of searching effort is one approach that has been developed for attempting to estimate $g(0)$ (Butterworth and Best, 1982; IWC, 1982; Cooke, 1985; Zahl, 1989; Borchers, 1991). It requires that a simple functional relationship exists for $g(y)$ at different effort levels. Experiments in which different transecting speeds were used to obtain a range of relative searching effort have been conducted but have not produced useful estimates of $g(0)$ (Butterworth and Best, 1982; Cooke, 1985; Butterworth, 1986; IWC, 1986; Joyce *et al.*, 1988). Changing the number of observers has been suggested as an alternative and perhaps more efficient method to achieve variation in trackline effort (Zahl, 1989). However, the results presented here suggest that no simple relationship exists between $g(y)$ at the two different effort levels and that the nature of the relationship will depend upon the actual observers (e.g. Figs 3–7). Different observer teams are likely to yield substantially different relationships. To the extent that these results can be generalised, varying the number of observers does not appear to provide a workable approach for estimating $g(0)$.

The fact that the distribution of perpendicular distances for both teams had a dip near the trackline when the most experienced observers were in the center position without the rovers, that was eliminated when the rovers were present, suggests that ensuring that observers are adequately covering the trackline is difficult. All observers were instructed to concentrate their searching effort on the trackline when in the center viewing position and they were also well aware of the importance of not missing animals directly on the trackline, both in terms of the experiment and the resulting line transect density estimates. As such, the distribution of perpendicular sighting distances with the most experienced observers in the center position should have had the highest frequency of sightings concentrated near the trackline if a relationship exists between experience and sighting efficiency. The total number of sightings by the two most experienced observers exceeded the number of sightings by other members of the core teams (Table 3). This result combined with the dip in the frequency near the trackline for the actual sightings made by these two observers when they were in the center position without rovers (Fig. 7) indicates that the translation of observers' instructions into actual behaviour can be problematical, perhaps as the result of unconscious competition to make the greatest number of sightings. However, the distributions for the two roving observers (Fig. 8) were highly concentrated near the trackline and indicate that it is possible to obtain concentrated searching effort on the trackline.

The most common approaches for estimating $g(0)$ rely on the estimation of the proportion of duplicate sightings (Hiby and Hammond, 1989). Conceptually, this approach is similar to a mark/recapture experiment where the sightings by one team are considered to constitute the markings, and the sightings by the other team constitute the recaptures. Similar to a mark/recapture experiment, this approach is subject to bias due to both heterogeneity and lack of unconditional independence in the detection probabilities between the two teams (Butterworth and Best, 1982; Schweder, 1990; Buckland, 1992). The problem of unconditional independence and many of the sources of heterogeneity will lead to $g(0)$ being positively biased. However, observer heterogeneity can lead to either negative or positive bias. The large differences in the perpendicular sighting distance distributions when different observers occupied the center viewing position plus the large range in the actual number of sightings seen by different observers suggests that the amount of observer heterogeneity can be large (see also Gunnlaugsson and Sigurjónsson, 1990). If the proportion of duplicate sightings is to be used as a basis for estimating $g(0)$, then the results presented here suggest that the effects of observer heterogeneity must be accounted for if the direction of the likely bias is to be known.

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Distribution and Abundance of Harbour Porpoise, *Phocoena phocoena*, in Norwegian waters

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ABSTRACT

This paper presents information on the distribution of harbour porpoise in Norwegian coastal and adjacent waters based on incidental sightings during the period 1964–1968, bycatches in the driftnet salmon fishery in 1988 and two dedicated cetacean sightings surveys in 1988 and 1989. Estimates of pod size and abundance of harbour porpoise in the Norwegian and Barents Sea are given. The information available indicates a divided offshore distribution during summer for harbour porpoises in Norwegian waters, with a southern component in the North Sea area and a northern component from Lofoten and into the Barents Sea. The abundance estimates were about 82,600 porpoises (CV 0.24) for the southern component and about 11,000 porpoises (CV 0.44) for the northern component.

KEYWORDS: HARBOUR PORPOISE; ASSESSMENT; SURVEY-SHIP; SIGHTINGS-INCIDENTAL; INCIDENTAL CAPTURE; NORTH ATLANTIC

INTRODUCTION

When the International Whaling Commission (IWC) Scientific Committee reviewed the status of stocks of harbour porpoise (*Phocoena phocoena*) in 1983, both Andersen and Clausen (1983) and Gaskin (1984) reported that a significant population decline had occurred in the Baltic and North Sea region. This decline was assumed to be a consequence of pollution, disease or incidental catches (or a combination of these). The Committee noted (IWC, 1984) the paucity of information available and recognised that the population(s) in that region may have been seriously reduced. It further noted that the coast of Norway may be of great importance as the eastern North Sea habitat of this species. The Committee advised an augmentation in harbour porpoise research by member countries, including increased effort with respect to stock identification, abundance estimation and the reporting of bycatches. Despite this, in most countries relatively little additional research occurred and the Committee has repeated its concerns over harbour porpoises in the eastern North Atlantic since then (e.g. IWC, 1994).

A research project on the harbour porpoise was initiated in Norway in 1988. The aims of this project were to assess the incidental catches of harbour porpoises and to collect samples from incidentally caught porpoises for further analysis of *inter alia* growth and reproduction, feeding and genetic stock identification. This paper summarises the results of the bycatch studies and presents the first abundance estimates of harbour porpoises in Norwegian waters.

MATERIAL AND METHODS

This study is based on information from three sources: (1) incidental sightings in the period 1964–1988; (2) systematic records of sightings and effort made during a Norwegian

Sighting Survey in 1988 and as part of the North Atlantic Sighting Survey in 1989 (NASS-89); and (3) incidental bycatches in driftnets set for salmon in 1988.

Incidental sightings

Incidental sightings have been recorded at the Institute of Marine Research (IMR) since 1964 (reported by letter or telephone from the public, IMR research vessels, coastguard, whaling and fishing vessels). The lack of quantitative information on effort makes it impossible to infer trends in abundance but the information can be used to support the other findings on the distribution of porpoises in Norwegian waters.

Systematic sightings

In July 1988, a sighting survey covering the Norwegian and Barents Seas was conducted by Norway (Øien, 1990). In July of the following year, Norway, as part of NASS-89 (a multinational survey of the North Atlantic), covered the northern North Sea, the eastern parts of the Norwegian Sea, the Barents Sea and the waters west of Spitsbergen as shown in Fig. 4. As the main objective of these surveys was to assess the abundance of minke whales and other large whales in the Northeast Atlantic, they did not have optimum stratification with regard to harbour porpoises. An earlier survey (part of NASS-87) only covered waters north of *ca* 67°N and made few (9) harbour porpoise sightings (Øritsland *et al.*, 1989); it is not discussed further in this paper.

Abundances have been calculated by block using standard line transect methods (Burnham *et al.*, 1980) with abundance N

$$N = \left(\frac{n}{L}\right) \cdot \left(\frac{1}{2w}\right) . s . A$$

where (n/L) is the sighting rate, $2w$ the effective search width, s the mean school size and A the area of the block. Effective search half-widths w have been estimated by fitting a hazard-rate model with a detection function of the form

$$g(y) = (1 - \exp [- \left(\frac{y}{a}\right)^{(1-b)}])$$

(Hayes and Buckland, 1983) to perpendicular distance data calculated from estimated radial distances and angles read from an angle board. The variance of N has been calculated by combining the variances of its components, where the variance of the sighting rate has been calculated from the daily variation. Abundances have been calculated assuming that $g(0)=1$. Only primary sightings, i.e. sightings made while running on transect in search mode and with estimated radial distances and angles to sightings recorded, have been used for abundance calculations. Confidence intervals have been estimated as suggested by Buckland (1992).

Incidental catches

The salmon fishery in Norway is organised into 34 salmon districts. Until 1988, driftnetting was allowed in 18 of these districts on the west and north coast. The salmon districts are shown and compared with marine fisheries statistics areas in Fig. 2. A total of 580 fishermen were licensed for the salmon driftnet fishery and all licensed fishermen were requested to report on incidental catches of harbour porpoises during a six-week period from late May to early July 1988. The incidental catches were recorded by licence-holder, day and salmon district. Good information on effort was available for this fishery, and effort, given as driftnet-meter-hours per week and salmon district, is used in this paper to compare the incidental catch per unit fishing effort (CPUE) in different areas.

RESULTS

Incidental sightings

A total of 90 incidental sightings of harbour porpoises were recorded between 1964 and 1988. The sightings are given by Marine Fisheries Statistical Area in Table 1 and their geographical distribution is shown in Fig. 1a.

Information on pod size was recorded for 58 of the 90 incidental sightings of harbour porpoises (Table 2). The estimated mean pod size from these is 5.02 (CV 0.3493). The recorded number for one of these sightings were 100 porpoises. Excluding this gives a mean pod size of 3.35 (CV 0.1648).

Table 1

Incidental sightings (1964-88) and bycatches of porpoises in driftnets set for salmon. Incidental sightings are recorded by Norwegian Marine Fisheries Statistics Areas. No effort data are available for these sightings. Incidental catches are recorded by Salmon Fisheries Districts* and then grouped to approximate marine fisheries statistics areas. Salmon districts are grouped to approximate the marine fisheries areas. **Effort in the salmon fishery is given as 1,000 net-meter-hours. ICNMH is Incidental Catch per Net Meter Hour.

	Incidental sightings		Bycatches in salmon driftnets (May-July 1988)			
Marine fisheries statistics area	May-July	All months	Salmon districts*	No.	Effort**	ICNMH
08 Egersundbanken	11	13	11-12-14	5	6,927	0.72
28 Vikingbanken	11	22	15-16-17	18	14,958	1.20
07 Møre	0	2	18-19-20-22	19	23,916	0.79
06 Helgeland	0	0	24-25	16	33,550	0.48
00+05 Vestfjorden-Malangsgr.	4	10	26-27-28	20	13,620	1.47
04 Vest-Finnmark	5	8	29-30-31	18	27,710	0.65
01-02-03-10-11-12-13-14	25	32	-	-	-	-
20-21 Bear island and West	0	3	-	-	-	-
Totals	56	90	-	96	120,681	0.80

Table 2

Pod sizes from the Norwegian Sighting Survey July 1988, the North Atlantic Sighting Survey 1989 (NASS-89) and from incidental sightings. *Numbers in brackets are the overall mean pod sizes.

	Incidental sightings		Sighting survey 88		NASS-89	
Pod size	Frequency	%	Frequency	%	Frequency	%
1	25	43.1	18	47.4	67	45.0
2	9	15.5	13	34.2	33	22.1
3	8	13.8	4	10.5	20	13.4
4	2	3.4	1	2.6	12	8.1
5	5	8.6	1	2.6	5	3.4
6	1	1.7	0	-	1	0.7
7-10	3	5.2	0	-	5	3.4
11-15	3	5.2	1	2.6	4	2.7
16-20	0	-	0	-	0	-
21-50	1	1.7	0	-	2	1.3
51-100	1	1.7	0	-	0	-
Total sightings*	58 (5.02)		38 (2.15)		149 (2.92)	

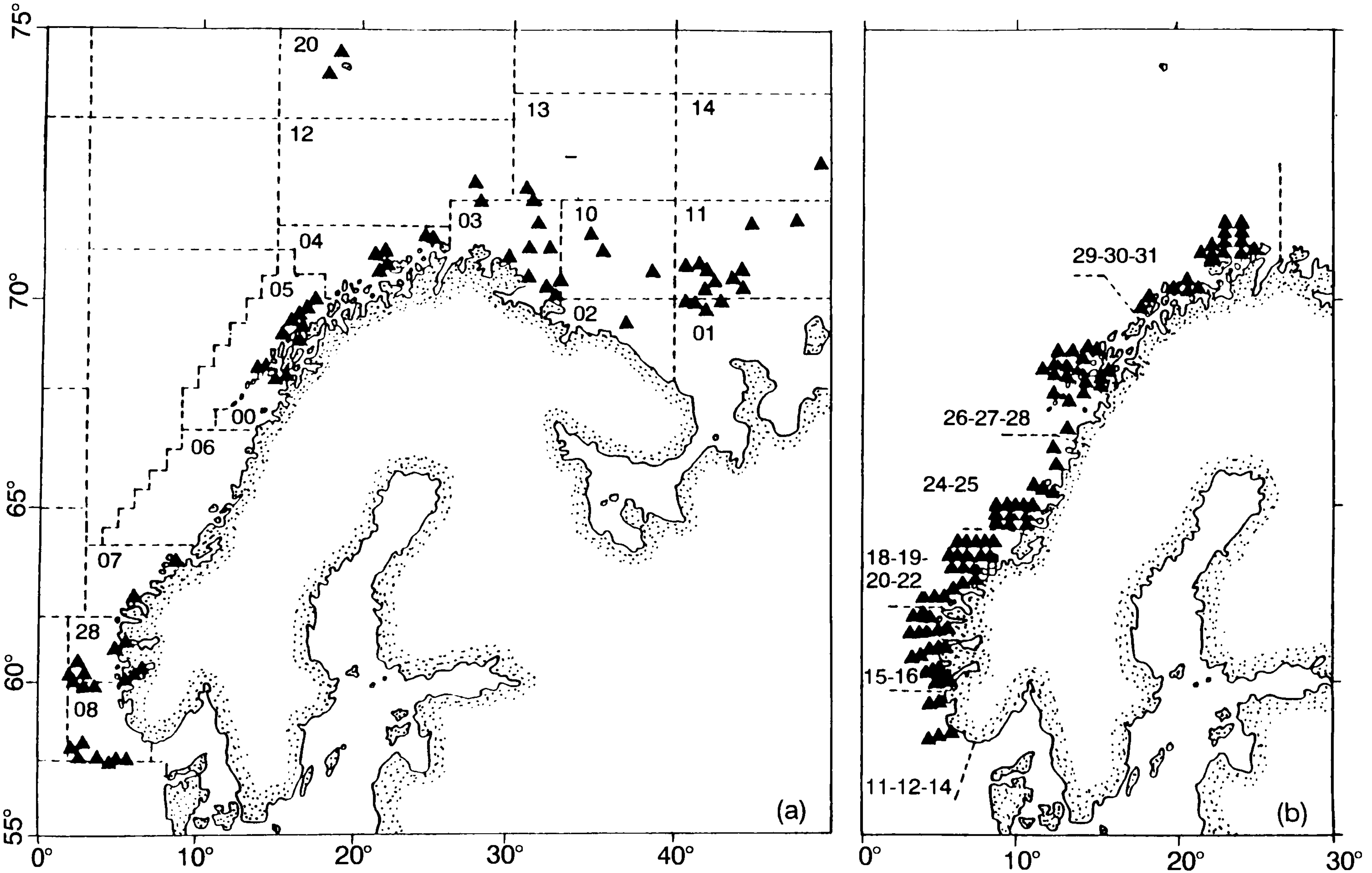

Fig. 1. (a) Shows the geographical distribution of incidental sightings of harbour porpoises recorded in Norwegian coastal and adjacent waters in the period 1964–1988, and the Marine Fisheries Statistics Areas. There is an additional incidental sighting at 77°N off the southwest coast of Spitsbergen, Svalbard. Each plot may represent more than one sighting recorded at the same position. (b) Shows the incidental bycatches of harbour porpoises in driftnets set for salmon in June and July 1988, and the Salmon Districts grouped to approximate the Marine Fishery Statistics Areas.

Sighting surveys

The Norwegian Sighting Survey 1988

A total of 38 observations (79 individuals) of harbour porpoises were made during the Norwegian Sightings Survey 1988 (Fig. 2). Of these, 33 groups were observed during primary search effort of which 22 groups were recorded with radial distance and angle.

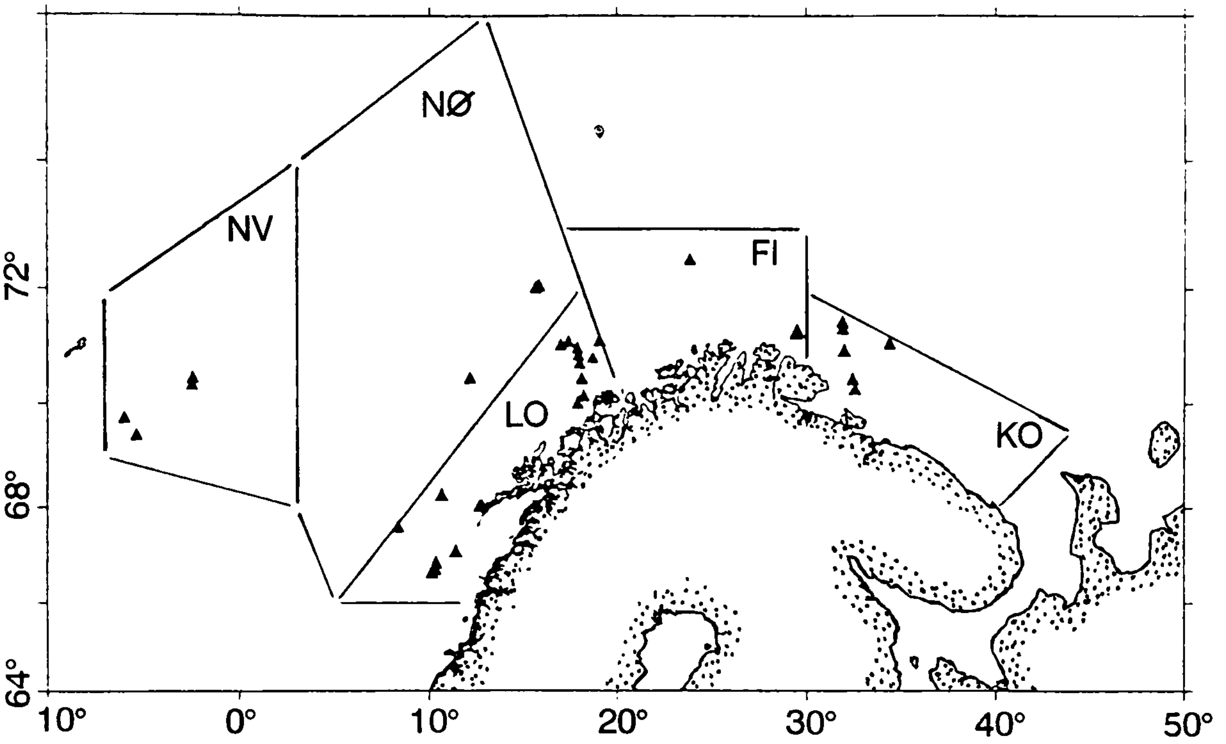

Fig. 2. Sightings of harbour porpoise and surveyed blocks at the Norwegian Sighting Survey 1988.

The perpendicular distance distribution of these sightings is extremely spiked with 15 observations seen less than 0.05 n.miles from the trackline and as many as 7 of these 15 seen on the trackline, which also raises the question of rounding errors in the data. All perpendicular distances were less than 0.27 n.miles. Fitting a hazard-rate function to these data is problematic and the resulting search widths varied non-systematically with degree of data grouping. In terms of goodness of fit, the fits were generally better as the number of groups decreased and the decision was taken to base tentative estimates on a grouping into 0.1 n.miles bins. This gives a detection function of the form $g(y)$ = 1-EXP [(-y/0.081)(1–3.69)] and an effective search half-width of 0.1105 n.miles (CV 0.447). Although this does not leave any degrees of freedom for testing the goodness of fit, it was still chosen as a conservative approach given the data and the following considerations: (i) fitting a negative exponential model to the data results in an effective search half-width of 0.0574 n.miles (CV 0.2840); (ii) the median in the data is less than 0.05 n.miles; (iii) the effective search half-widths based on the hazard-rate are less than 0.10 n.miles, and in most cases considerably so, when finer groupings than the one based on 0.1 n.miles are used; (iv) the resulting search-width is in accordance with the one estimated from the 1989 survey which was conducted in the same way as the 1988 survey operationally. It should be noted that narrow strip widths for harbour porpoises have also been reported from other surveys (e.g. Palka, 1995).

The estimated mean pod size from the 1988 data was 2.15 individuals (CV 0.19), although almost half (47.4%) of the porpoises were solitary. Excluding the single large observation (14 individuals, Table 2) gives a mean school size of 1.76 (CV 0.09). For the abundance estimates, the mean school size per block was used (a school of 14 animals was excluded for that block).

Estimates of density and abundance of harbour porpoises in each survey block are given in Table 3. The estimated total abundance in the surveyed area was 10,100 individuals (CV 0.45; 95% CI 4,370–23,200).

North Atlantic Sighting Survey 1989, NASS-89

A total of 149 pods of harbour porpoises comprising 429 individuals were recorded on Norwegian vessels during NASS-89. The observations are grouped into two geographical components (Fig. 3); a southern component mainly in the North Sea area and a northern component from Lofoten and northwards.

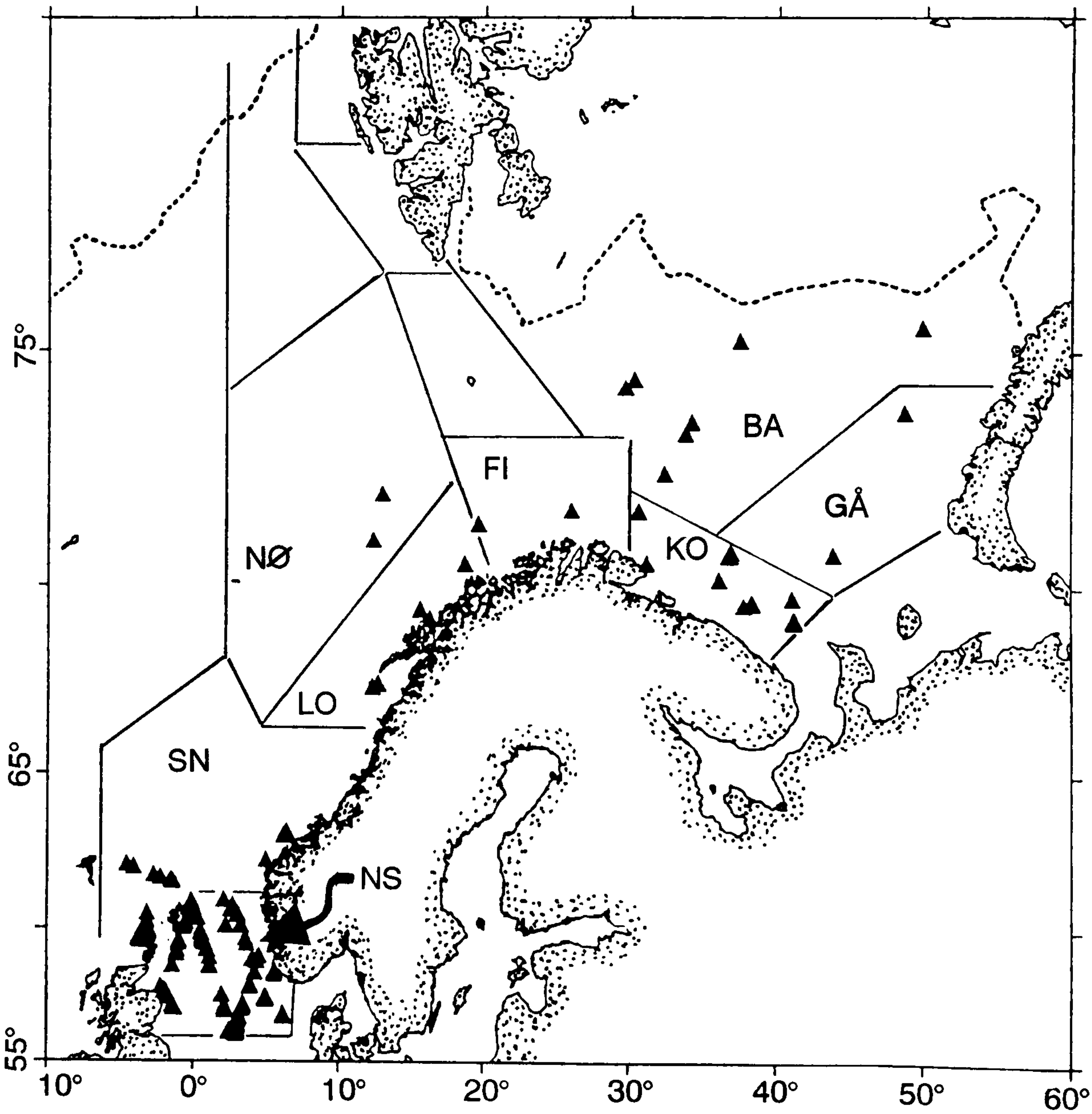

Fig. 3. Sightings of harbour porpoise and surveyed blocks by Norwegian vessels in NASS-89. The dotted line is the approximate ice-edge.

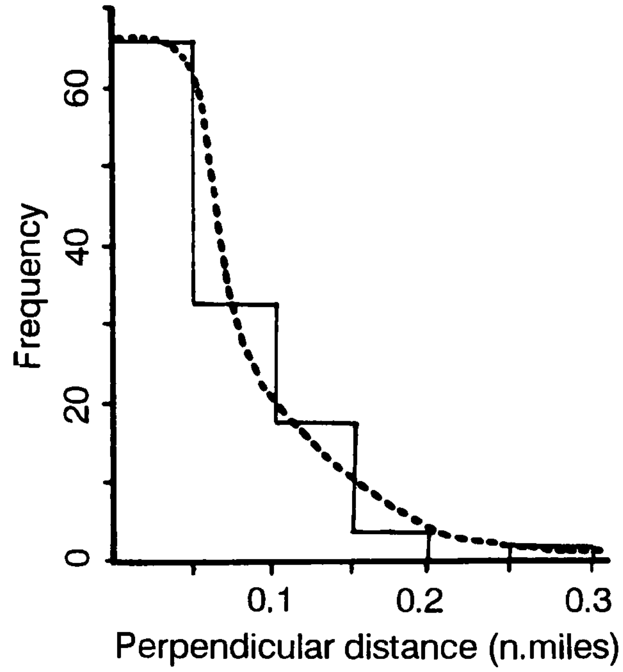

Fig. 4. Perpendicular distance distribution for harbour porpoise sightings recorded at NASS-89. The fitted detection function is shown as a dotted line.

Of the recorded pods, 123 were primary sightings and thus used for abundance calculations. For this purpose a hazard-rate detection function was fitted to the perpendicular distance data grouped by 0.05 n.miles (Fig. 4) to estimate the effective search width (Goodness of fit test: $\chi^2=6.3$, df = 3, $p>0.05$). The fitted detection function then has the form:

$$g(y)\ 1\text{-EXP}\ [\,-\,(y\,/\,0.070)^{(1-3818)}]$$

The effective search half-width is 0.095 n.miles (CV 0.095). Total abundance in the surveyed area (Table 4) is 93,600 (CV 0.22; 95% CI 61,500–142,000); 82,600 (CV 0.24; 95% CI 52,100–131,000) in the southern component and 11,000 (CV 0.44; 95% CI 4,790–25,200) in the northern component (see Fig. 4). A comparison between blocks surveyed both years is given in Tables 3 and 4.

The effective search widths varied little between blocks and thus the pooled data have been used in these estimations. Information on pod size is given in Table 2. The maximum pod size recorded was 30 individuals. The large pod observations have not been included in the analysis although they have been recorded as primary sightings. This is because of the difficulties involved in recording distance and angle to a large pod.

Incidental catches

The salmon driftnet fishermen reported a total of 96 incidentally caught porpoises during the six-week period. The incidental catches and the fishing effort are given in Table 1 and the geographical distribution of the incidental catches is shown in Fig. 1b.

DISCUSSION

Distribution

Harbour porpoises have been recorded in all Norwegian waters from the fjords to deep oceanic waters at approximately 5°W and 70°N. The northernmost sighting was made at almost 77°N off the west coast of Spitsbergen, Svalbard. The incidental sightings are

Table 3

Abundance estimates of harbour porpoises based on records from the Norwegian Sighting Survey in July 1988, by blocks as defined in Øien, 1989. Effective search half width is estimated by fitting a hazard-rate detection function to perpendicular distances pooled over blocks. Numbers in brackets are coefficients of variation.

Block	NV	NO	LO	FI	KO
Search effort, *L*, aut.m.	487.7	2,010.9	1,089.3	548.5	904.0
Area: *A*, sq.nm	52,719	101,339	37,944	28,129	28,315
No. of pods, *n*	5	2	10	2	3
Sighting rate, *n/L*	0.0103	0.0010	0.0092	0.0036	0.0033
	(0.5715)	(0.4400)	(0.3780)	(0.6996)	(0.8784)
Effective search, half width, *w*, nm		0.1105	(0.4470)		
Mean pod size, *s*	2.00	1.67	1.92	1.40	1.71
	(0.3536)	(0.2000)	(0.1713)	(0.1750)	(0.1667)
Porpoise density, ind/sq.nm	0.0932	0.0076	0.0799	0.0228	0.0255
	(0.8071)	(0.6583)	(0.6099)	(0.8485)	(0.9996)
Abundance	4,914	766	3,033	641	723
	(0.8071)	(0.6583)	(0.6099)	(0.8485)	(0.9996)
Abundance all blocks		10,077	(0.4463)		

Table 4

Abundance estimates of harbour porpoises based on records from Norwegian vessels in the North Atlantic Sighting Survey July 1989 (NASS-89), by blocks as defined in Øien, 1990. Effective search half width is estimated by fitting a hazard-rate detection function to perpendicular distances pooled over blocks. Numbers in brackets are coefficients of variation.

Block:	BA	CA	KO	FI	LO	NO	SN	NS
Search effort, *L*, nm	1955.8	923.8	1299.5	582.6	1231.7	1858.4	1508.6	1751.1
Area: *A*, sq.nm	146,909	46,380	26,840	26,221	35,784	101,823	135,953	73,484
No. of pods, *n*	7	2	7	1	2	1	25	78
Sighting rate, *n/L*	0.0036	0.0022	0.0054	0.0017	0.0016	0.0005	0.0166	0.0445
	(0.3579)	(0.7164)	(1.0547)	(1.0162)	(1.2597)	(1.2296)	(0.3497)	(0.2356)
Effective search, half width, *w*, nm				0.095	(0.095)			
Mean pod size, *s*	2.86	1.0	1.5	2.0	2.0	1.0	1.79	3.56
	(0.4416)	(0)	(0.1782)	(0)	(0.5)	(0)	(0.1249)	(0.1433)
Porpoise density, ind/sq.nm	0.0542	0.0116	0.0427	0.0179	0.0169	0.0026	0.1566	0.8347
	(0.5764)	(0.7227)	(1.0739)	(1.0207)	(1.3586)	(1.2333)	(0.3834)	(0.2918)
Abundance	7,969	583	1,145	470	603	268	21,284	61,335
	(0.5764)	(0.7227)	(1.0739)	(1.0207)	(1.3586)	(1.2333)	(0.3834)	(0.2918)
Abundance all blocks					93,612	(0.2165)		
Abundance southern component (North Sea area)					82,619	(0.2381)		
Abundance northern component (Lofoten - Barent Sea area)					10,994	(0.4435)		

mostly from the southeastern Barents Sea (Fig. 1a), off the coast of northern Norway southwards to the Lofoten-Vestfjorden area, off the west coast of southern Norway and in the North Sea area. The distribution probably also reflects the general interests of IMR research vessels where certain areas receive more emphasis than other areas. However, a comparison of the incidental sightings with the incidental catches of porpoises per unit effort in the salmon fishery provides some indication of distribution and relative abundances. The porpoises seem to be relatively more abundant in the northern North Sea area and in the Vestfjorden-Vesteralen area, while being relatively less abundant in the intermediate Helgeland area.

The sightings made by NASS-89 further support the suggestion of a divided offshore summer distribution of harbour porpoises in Norwegian waters. Samples collected for genetic stock identification may provide further information on possible sub-population structures in Norwegian waters.

Abundance estimates

The systematic surveys were designed and conducted primarily to obtain information on the abundance of minke whales and other large whales and amongst other problems, the stratification chosen may therefore not be suitable for harbour porpoises. An additional problem is related to the rather small (albeit typical) perpendicular distances observed, resulting in a very narrow effective strip width. An alternative fitting of the perpendicular distances to a negative exponential model gives an effective search half-width of 0.0574 (CV 0.28), which illustrates the problems involved. The large coefficients of variation, further emphasise the associated uncertainty. However, except for the Lofoten area, where the estimate from 1988 was 3,033 and the estimate from NASS-89 was 603, the estimates for blocks surveyed both years were similar.

A major factor to be considered is that 'the assumption that all animals on the trackline are seen ($g(0)=1$), is probably violated. Preliminary estimates of $g(0)$ for harbour porpoises from an experimental survey in the North Sea in 1990 (Øien, 1992) indicate a $g(0)$ of around 0.7 for *two* observer teams combined. Evidence from other areas (e.g. Polacheck, 1995) also indicates that the assumption $g(0)=1$ for harbour porpoises probably introduces a negative bias in the abundance estimates'.

Incidental catches and mortality of porpoises in Norwegian fisheries

In the 1988 postal survey, 96 porpoises were reported caught during the six week period (about half the season) from late May to early July 1988. After the 1988 fishing season the government imposed a ban on the use of driftnets for salmon fisheries in Norwegian waters.

In 1989 and 1990 we have looked into other Norwegian gillnet fisheries to assess the incidental catches of porpoises. Reported bycatches indicate that the incidental catch of porpoises per unit fishing effort (net-meter-hour) in other net fisheries (bottom set nets) are far less than in the former salmon driftnet fishery. We therefore believe that in Norwegian waters porpoises are particularly vulnerable to surface driftnets as compared to bottom set nets due to the topography of these waters.

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SC/42/SM30

Sightings of Harbour Porpoises (*Phocoena phocoena*) in Swedish Waters Before 1990

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ABSTRACT

This paper examines trends in abundance and distribution of harbour porpoises in Swedish waters. Returns from questionnaires suggested a decline in number of sightings per year in all areas around the Swedish coast between the 1950s and 1980s. A network of observers was organised in 1988. A comparison of observations made by the network between 1988 and 1989 showed a decline in mean number of sightings per observation day. The results presented indicate that harbour porpoises have declined in Swedish waters during the 1960s and 1970s and continue to decline in the late 1980s. Few sightings have been reported from the Baltic Sea since the 1960s. Dedicated surveys were made during both 1988 and 1989 by sailboat and aeroplane. Few harbour porpoises were sighted during these surveys. Results show that aerial surveys are a preferable survey method.

KEYWORDS: NORTH ATLANTIC; HARBOUR PORPOISE; INCIDENTAL CAPTURE; SIGHTINGS; FISHERIES; STRANDINGS; DISTRIBUTION; TRENDS

INTRODUCTION

The harbour porpoise (*Phocoena phocoena*) is the only cetacean species that regularly inhabits Swedish waters. Bycatch and stranding statistics have been used to suggest that harbour porpoises in Swedish waters decreased in abundance during the 1960s and 1970s and then increased during the 1980s (Lindstedt and Lindstedt, 1988). However, there have been no direct estimates of harbour porpoise abundance made in Swedish waters. Bycatch and/or stranding statistics cannot be used to infer population trends unless they take into account a number of factors including: (1) variation in fishing effort; (2) changing fishing techniques; and (3) variation in effort to recover strandings. In a first attempt to more reliably examine trends in population abundance and distribution, this paper reports on the results of (a) a sighting questionnaire; (b) a sighting network established in 1988; and (c) the first dedicated sighting surveys undertaken.

METHODS

Questionnaire

A questionnaire was designed in 1987 after consultations with researchers at Stockholm University experienced in questionnaire surveys. The questionnaire consisted of two parts: the first general and the second more specialised, with equal sets of questions for the four decades 1950–1980. A draft questionnaire was tested on a randomly picked group of 15 representatives from coastguards, ferry operators and fishermen. They were asked to answer the draft questionnaire and to give comments on understandability, feasibility and design. The eight respondents who returned the completed questionnaire were also interviewed on the telephone for further comments.

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After modifications, the questionnaire was circulated to all coastguards and ferry operators along the Swedish coast and to 625 fishermen randomly selected from Västervik in the Baltic Sea to Strömstad on the west coast of Sweden (Fig. 1). In total, 700 questionnaires were distributed. Only data from the second part of the questionnaire are discussed in this paper. Respondents gave information (by decade) on: which years they had been out to sea; which areas; which seasons of the year; in what type of boat; whether they saw porpoises and, if so, how many times and in which areas. Effort was calculated as number of observer-years spent at sea for each decade. Qualitative comparisons of the summarised data were made between decades to examine potential trends in harbour porpoise abundance. The data are not suitable for statistical analysis.

Observer network

Questionnaire participants were also asked if they would report future observations. A network of 150–160 observers was established. Sightings and effort have been reported since May 1988 on standardised forms. Observers were asked to send in a form and report each sighting as they occur; if no sightings were made, observers reported their effort at least every third month. Effort is reported as how many days were spent at sea during the period and in which areas. The observers are spread around the southern Swedish coast, which has been divided into the five areas shown in Fig. 1.

This paper examines the records for the initial two year period of the network, from May to November for 1988 and 1989. The number of sightings was chosen as a more reliable index of abundance than the estimated number of harbour porpoises observed in comparisons between years. Later data are discussed by Berggren and Arrhenius (1995).

Statistical procedures were performed using SAS-STAT (SAS Institute Inc, 1988). The data set included a large number of zero observations and thus a nonparametric test (the Wilcoxon Two-Sample Test) was used because the data violate the assumption of normality required for parametric tests.

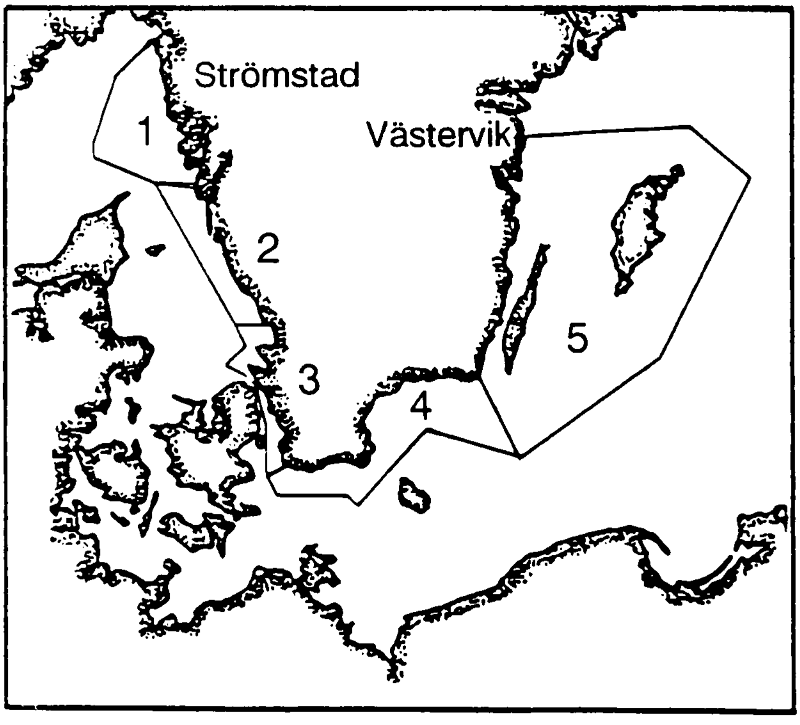

Fig. 1. The map shows the five study areas in Swedish waters used in the questionnaire and covered by the observer network.

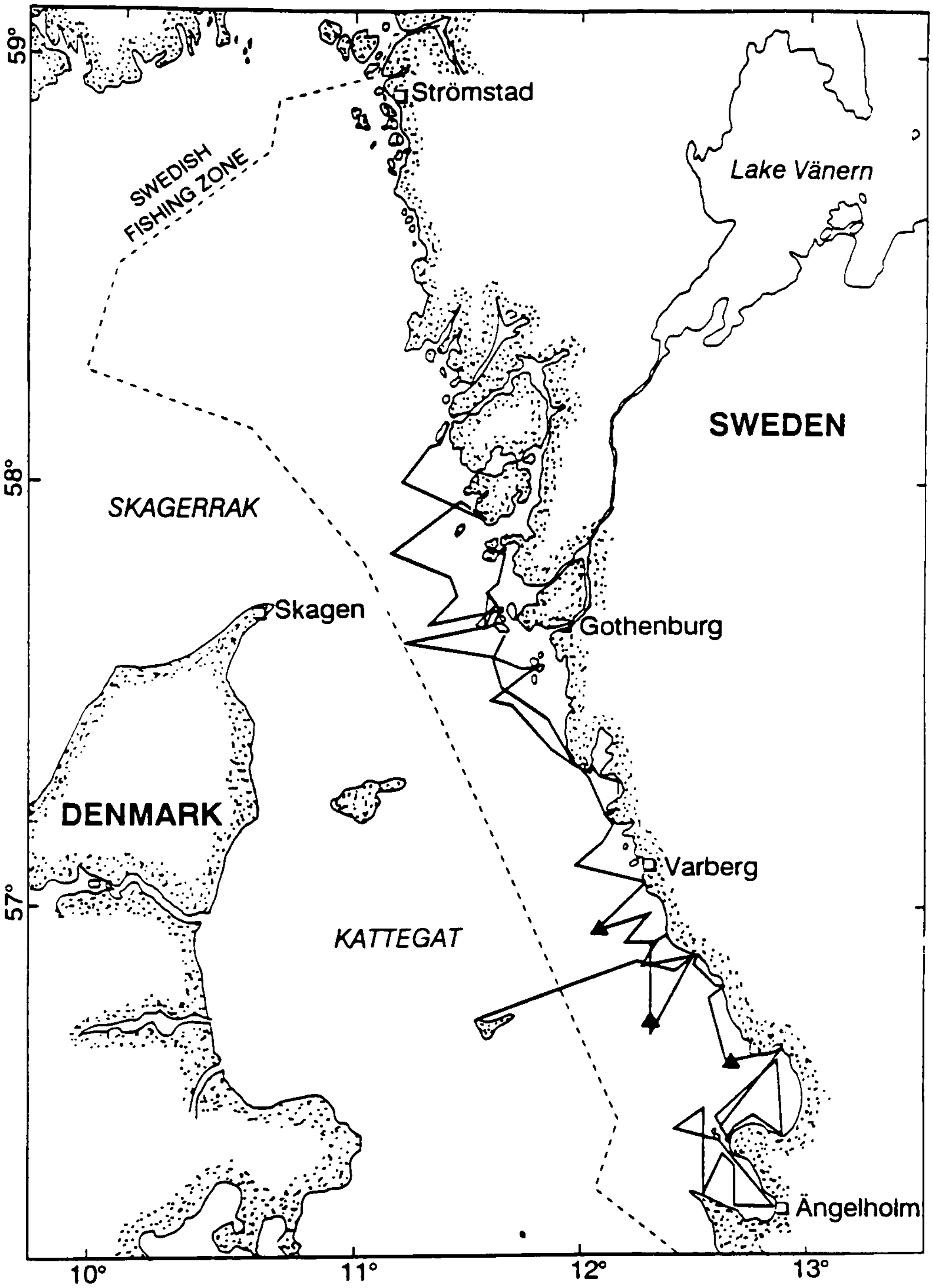

Fig. 2. Boat survey tracks in Swedish waters in July-August 1988. Legend: (▲) shows positions for harbour porpoise sightings.

Surveys

From June-August 1988, a six-week cruise was conducted with a 9m sailboat on the west coast of Sweden (Fig. 1, Area 1 and 2). Surveys were performed under sail. Following the trackline one observer, sometimes two, stood by the mast (1.5m above sea level) and scanned either port or starboard side, 180°-360° or 0°-180°. Survey tracks with continuous effort are shown in Fig. 2. In May 1989, a three-week cruise was conducted with a 9m sailboat in Area 1 (Fig. 1). The same survey methods were used as in the 1988 survey, although different tracklines were used in order to cover areas not surveyed the previous

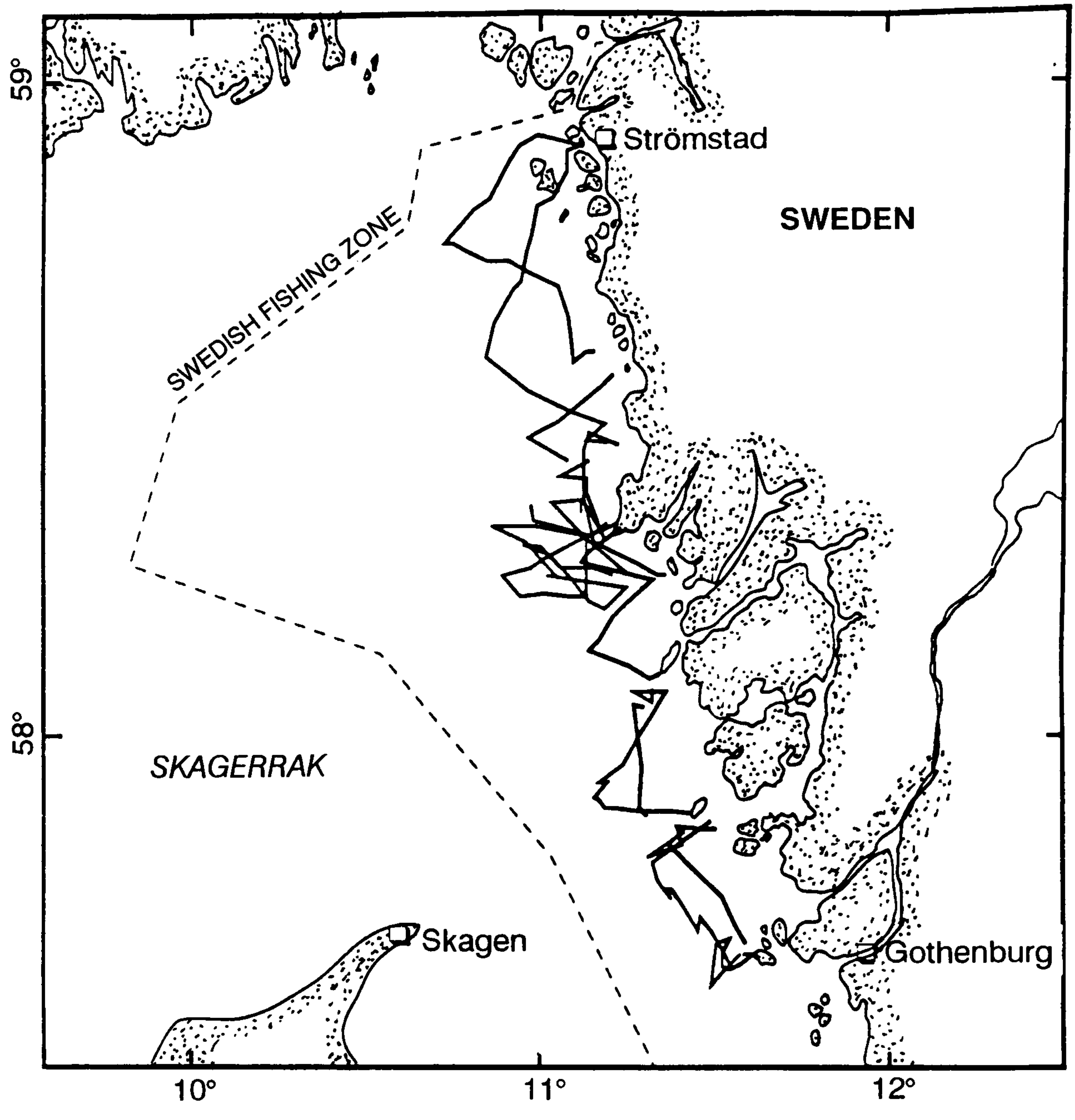

Fig. 3. Boat survey tracks in Swedish waters in May 1989. All surveys were in Area 1.

year. Survey tracks with continuous effort are shown in Fig. 3. Insufficient sightings were made to attempt to obtain a population estimate.

In 1989, an aerial survey was carried out so that a greater area could be covered. The survey was conducted with a highwing *Cessna* (model 172) in the same area as the boat survey. Strip transect methodology was used during the survey (e.g. see Barlow *et al.*, 1988). A 400m transect strip was surveyed on one or two sides of the plane depending on how many observers were available. Transect lines were flown perpendicular to the coast at an altitude of 165m and a speed of 165–175 km/h. Survey tracks are shown in Fig. 4.

All field studies were performed in Beaufort sea state 0–2, as many authors have reported the major effect of sea state on sightability of harbour porpoises (e.g. Gunnlaugsson *et al.*, 1988; Palka, 1992).

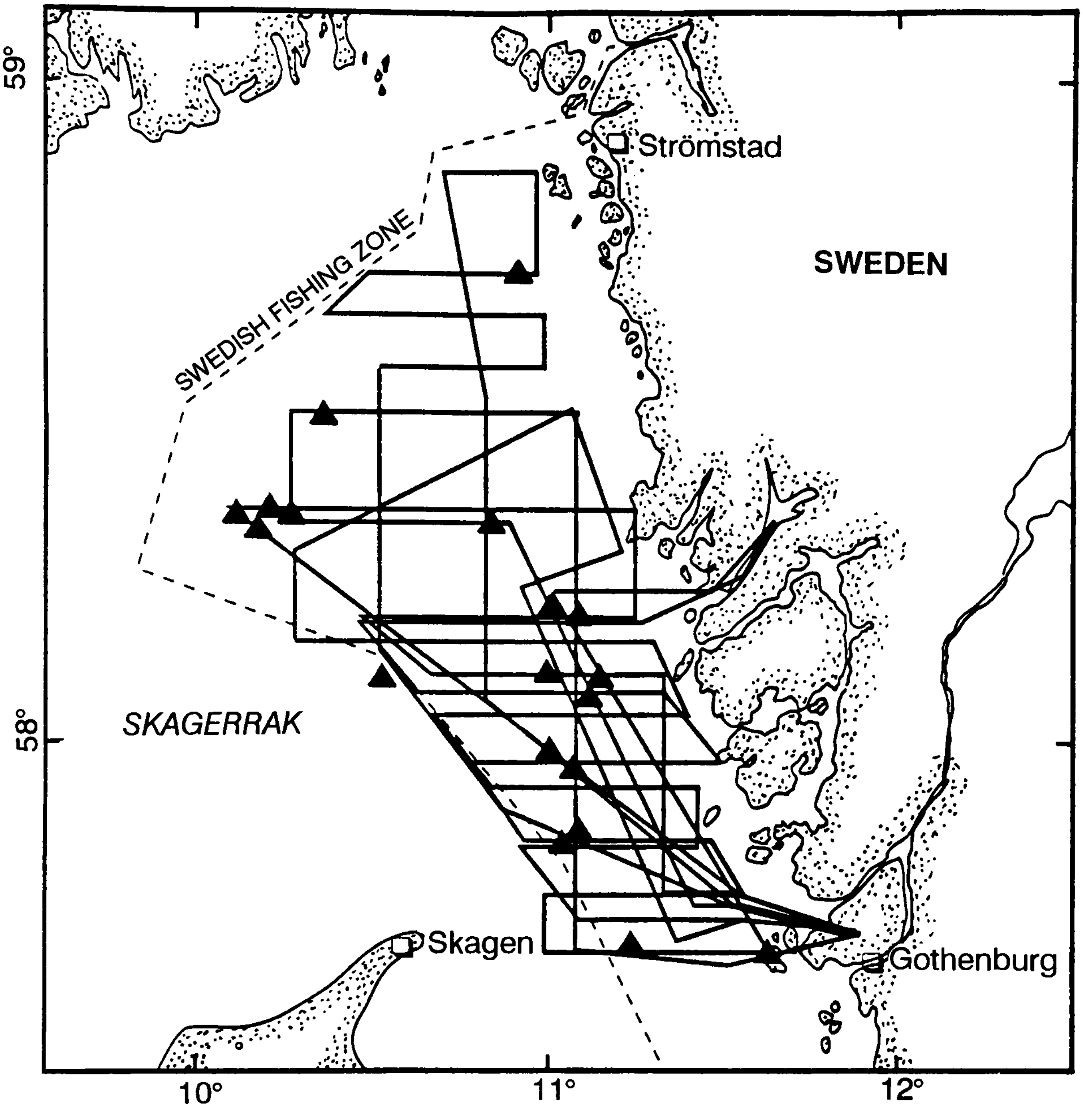

Fig. 4. Aerial survey tracks in Swedish waters in May 1989. Legend: (▲) shows positions for harbour porpoise sightings.

RESULTS

Questionnaire

Data from the respondents (n=175, 35% of those asked) indicated a 4.0 fold decline in Area 1, an 8.4 fold decline in Area 2 and a 9.2 fold decline in Area 3 in the number of harbour porpoise sightings per observer year since the 1950s (Fig. 5 and Table 1). In Areas 4 and 5 virtually no sightings made during the 1970s and 1980s (Fig. 5), indicating a dramatic deline in abundance in these areas.

Observer network

Sightings reported by the network of observers are shown for each area during May through November 1988 and 1989 (Table 2). Almost equal numbers of sightings and numbers of harbour porpoises were reported in 1988 and 1989. However, more days were

Table 1

Harbour porpoise sightings in Swedish waters during the decades 1950-1980 as reported by respondents to a questionnaire.

Area 1				Area 2				Area 3				Area 4				Area 5			
1950s	1960s	1970s	1980s	1950s	1960s	1970s	1980s	1950s	1960s	1970s	1980s	1950s	1960s	1970s	1980s	1950s	1960s	1970s	1980s
No. sightings																			
1093	977	421	340	640	692	296	118	458	410	156	126	346	96	5	6	154	89	5	1
No. observation years																			
329	431	509	411	169	249	339	261	104	198	328	264	139	186	317	338	94	116	198	242
Sightings/obs. years																			
3.322	2.267	0.827	0.827	3.787	2.779	0.873	0.452	4.404	2.071	0.476	0.477	2.489	0.516	0.016	0.018	1.638	0.767	0.025	0.004
No. of observers																			
42	48	58	63	24	28	37	39	18	24	35	40	22	24	38	52	11	12	22	36

Table 2

Harbour porpoise sightings in Swedish waters reported by observer network during May through November 1988-1989.

	Area 1		Area 2		Area 3		Area 4		Area 5		ΣArea 1-5	
	1988	1989	1988	1989	1988	1989	1988	1989	1988	1989	1988	1989
No. porpoises sighted	68	126	90	86	67	18	2	0	0	0	227	230
No. sightings	30	45	36	26	7	8	1	0	0	0	74	79
No. observation days	1,980	3,507	1,598	3,539	1,165	1,228	684	758	528	560	5,955	9,592
Sightings/obs. days	0.015	0.013	0.023	0.007	0.006	0.007	0.001	0	0	0	0.012	0.008
No. of observers	32	39	31	35	20	12	11	7	5	5	99	98

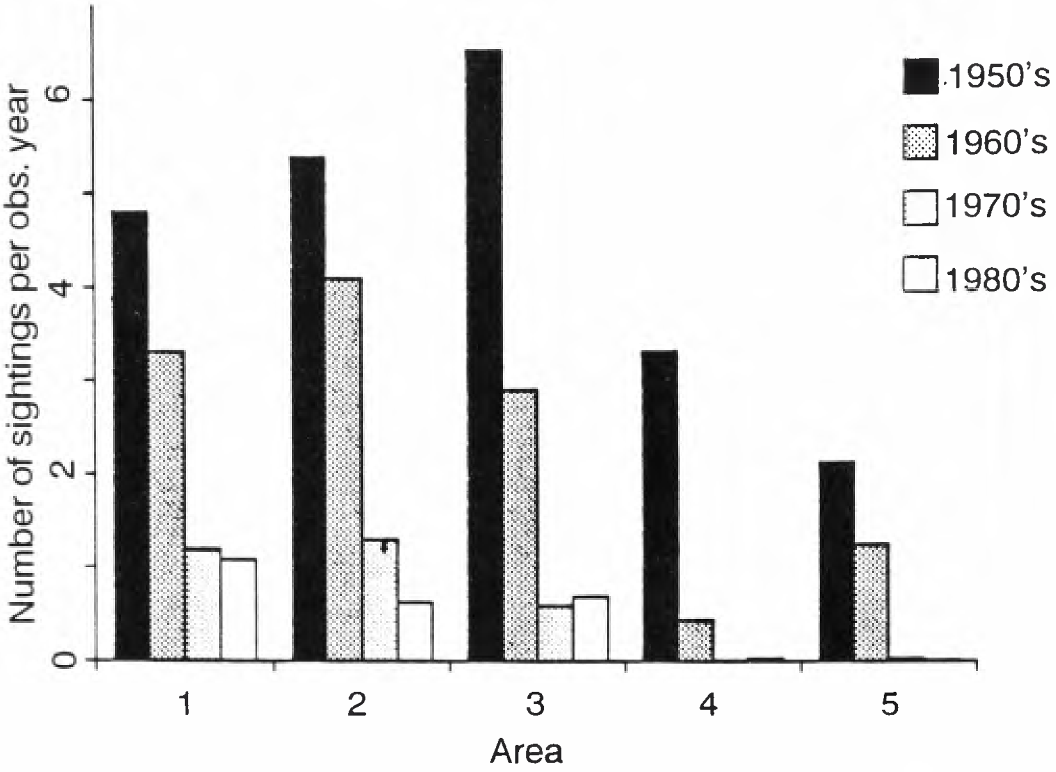

Fig. 5. Mean number of sightings of harbour porpoises in Swedish waters per observer-year for each decade as determined from questionnaire returns.

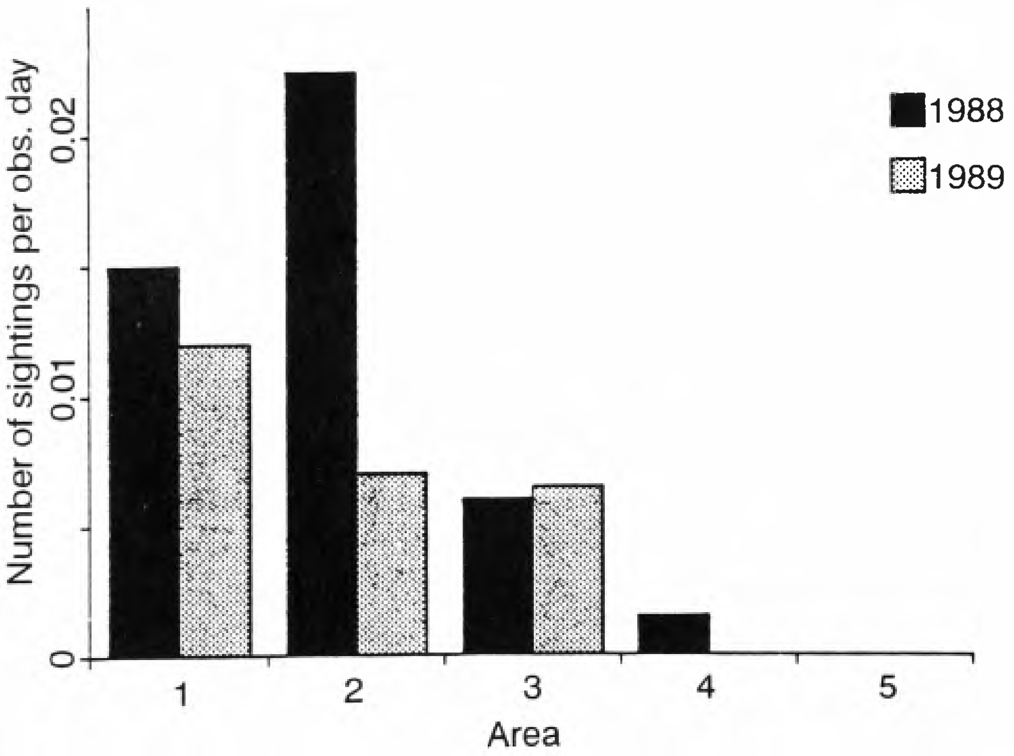

Fig. 6. The graph shows mean number of sightings of harbour porpoises per observer-day made by the network during May through November 1988 and 1989 in Swedish waters. The different areas correspond to the map (Fig. 1).

spent at sea in 1989 and a comparison of number of sightings per day for 1988 and 1989 shows a 34% decrease (*P*=0.0394, Wilcoxon Two-Sample Test). In Fig. 6, a comparison between years and different areas is made which shows that the decrease has occurred in Area 2 (*P*=0.0103, Wilcoxon Two-Sample Test). No significant differences can be detected in Areas 1, 3, 4 and 5. Only one sighting, in Area 4 in 1988, was reported from the Baltic Sea (Area 4 and 5). During spring and autumn most sightings were made in coastal waters, whereas in the summer months (June through August) observations were made further offshore.

Surveys

During the dedicated cruise in 1988, 20 days and 732km were sailed along transects and a total of eight porpoises were sighted on three occasions (Fig. 2). All three sightings were made in Area 2. In 1989, 13 days and 773km of transects were sailed (Fig. 3), but no porpoises were sighted. During the 1989 aerial survey, 15.5 hours and 2,296km of transects were surveyed during seven days and 26 porpoises were sighted on 19 occasions (Fig. 4).

DISCUSSION

Notwithstanding the well-known difficulties associated with questionnaire surveys (e.g. see Lien *et al.*, 1994) the relatively large number of questionnaire respondents did not contradict the previous inferences from bycatch and stranding data that harbour porpoise abundance declined in Swedish waters during the 1960s and 1970s. The questionnaire results also suggest that the decline continued during the 1980s and may still be occurring.

It is of course not possible to reach firm conclusions from data based on memory from the 1950s. However, these are the only data available or likely to become available for that period, the sample size was large and the data were standardised by examination of relative trends over the time period; whilst non-conclusive, the inference is strong.

The results from the two first years of the observer network support the indication from the questionnaire results that harbour porpoises may still be declining in Swedish waters. Although interpretation of the observer network data is problematic for a number of reasons, including: the use of non-experts; the probable differences in effective effort between observer days; and the fact that an analysis of data from only two years is not satisfactory when looking at trends.

A further potential bias in all the data could be the movement of animals within and between areas. For example, Kinze (1990) reported an increase in the number of animals sighted in his survey Area 1 (comparable to our Area 2) during the second quarter of 1989.

Virtually no recent sightings have been made in the Baltic Sea, supporting earlier reports (e.g. Andersen, 1982) that the harbour porpoise had almost disappeared from the Baltic. No porpoises were seen in Area 1 during either boat survey (although there was very little effort in 1988). The area had been chosen for the 1989 survey because of the large number of reports of observations made there in May 1988. That animals were also present in the same area in May 1989, was revealed by both the aerial survey data and reports from the observer network. This suggests that aerial surveys are more appropriate than boat surveys in large low density areas.

To the extent possible, data have been standardised by looking at relative trends and by correcting for effort as observer day in the different areas. In the shipboard censuses the tracklines used differed in 1988 and 1989, precluding comparison even if sufficient data were available. Despite the obvious shortcomings in the available data, the inferences are all the same direction, a long-term decline in harbour porpoises in Swedish waters. This is a cause for concern and warrants further investigation.

Three factors could be responsible, either singly or in combination, for any decline in harbour porpoise abundance in Swedish waters: depletion of prey; incidental catches; and disturbance by human activities. With respect to prey, the Atlantic herring stocks (*Clupea harengus*), the most important food species for the harbour porpoise (Recchia and Read, 1989; Aarefjord *et al.*, 1995), were depleted in the northeastern Atlantic in the late 1960s (Murphy, 1977). The question of bycatches has been discussed extensively elsewhere (Berggren, 1994; IWC, 1994). The apparent change in distribution between the summer and winter months coincides with increased boat activity in coastal waters and the harbour porpoises may be moving offshore in response to this increased human activity. All three factors require further investigation particularly in areas with high densities of harbour porpoises. Further studies are needed to confirm any trends in abundance and distribution (see Berggren and Arrhenius, 1995).

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Densities and Seasonal Distribution of Harbour Porpoises (*Phocoena phocoena*) in the Swedish Skagerrak, Kattegat and Baltic Seas

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ABSTRACT

Strip transect aerial surveys were conducted in the Skagerrak and Kattegat Seas for 8 days in June-August, and 2 days in October 1991. Nine sightings of harbour porpoises were recorded in the Skagerrak during 2,161km of transects and 16 sightings in the Kattegat during 1,995km surveyed. The summer densities were 0.021 porpoises/km^2 in the Kattegat Sea and 0.013 porpoises/km^2 in the Skagerrak Sea. The densities in October were a magnitude lower suggesting a seasonal change in distribution. Uncorrected minimum abundance estimates were calculated for the Skagerrak and Kattegat survey areas during June-August and compared to minimum bycatch levels of harbour porpoises in Swedish fisheries during the same months and areas, as reflected by carcasses submitted by fishermen. The results indicate that bycatch levels are not likely to be sustainable. A voluntary programme for fishermen, coastguards and ferry operators reported sightings of harbour porpoises year round during a five year period; 1988–1992, in the Skagerrak, Kattegat and Baltic Seas. A total of 332 sightings (949 porpoises) were reported but only one sighting was from the Baltic. The sighting rate per effort (SPUE) for the Skagerrak was about twice that for the Kattegat. The only trend in SPUE over the five year study period was a decline in the Skagerrak Sea in 1992, compared to 1988–91. Harbour porpoises were sighted throughout the year in the Skagerrak and Kattegat Seas, with a peak occurrence during the spring and summer months. The low densities recorded in the Skagerrak and Kattegat Seas during the aerial surveys, compared with documented bycatch in these areas and the lack of trends in the sighting rates reported, indicate that the status of harbour porpoises in these areas is uncertain. The virtual lack of sightings in the Baltic Sea and the threat posed by bycatches in the area indicate that harbour porpoises in the Baltic Sea are endangered.

KEYWORDS: NORTH ATLANTIC; HARBOUR PORPOISE; SIGHTINGS-INCIDENTAL; SURVEY-AERIAL; INCIDENTAL CAPTURE; FISHERIES; DISTRIBUTION; TREND; MANAGEMENT

INTRODUCTION

The status of harbour porpoises (*Phocoena phocoena*) is uncertain throughout its range (IWC, 1994). Large documented bycatches in fisheries may be a serious threat to the survival of the harbour porpoise in several areas in the North Atlantic (Smith *et al.*, 1993; Berrow *et al.*, 1994; Vinther, 1994 and see Perrin *et al.*, 1994). Several international bodies including the International Whaling Commission (IWC), the Agreement on the Conservation of Small Cetaceans of the Baltic and North Seas (ASCOBANS) and the International Council for the Exploration of the Seas (ICES) have expressed concern about the lack of information on abundance, distribution, movements and population structure of harbour porpoises throughout the world. Unfortunately, only during the last decade has this need for data been recognised for small cetaceans. Long time series of data, or large changes, are necessary to detect trends in abundance (Anganuzzi, 1993).

In the absence of long time series of data, although the limitations of such surveys are well known (Lien *et al.*, 1994), some studies have used questionnaire surveys to attempt to discern trends in distribution and abundance of harbour porpoises (e.g. Tregenza, 1992; Berggren and Arrhenius, 1995). The results from the questionnaire by Berggren and Arrhenius (1995), indicated a serious decline in the number of sightings in the Skagerrak, Kattegat and Baltic Seas over the period of the 1950s-1980s. The dramatic decline in the Baltic Sea suggested that harbour porpoises are probably endangered in this area. Results from morphometric skull comparisons have shown that harbour porpoises from the Baltic Sea are morphologically distinct from animals in the Kattegat and Skagerrak Seas indicating that animals from these areas do not interbreed (Börjesson and Berggren, 1993).

The harbour porpoise was apparently common in the Baltic Sea in the 19th and early 20th century (Aguayo, 1978), but unfortunately there are no abundance or density estimates available for these time periods. The catch records from the porpoise drive fishery in the Danish Belt Seas represent the only existing historical data on animals in these areas. The hunt for porpoises averaged more than 1,000 animals per year during periods in the 19th century (Andersen, 1982; Kinze, 1995). This hunt and similar Polish hunts date back to the 14th century (Andersen, 1982; Skora *et al.*, 1988). No hunt for porpoises has been recorded in these areas since World War II. Andersen (1982) proposed that the animals caught in the drive fishery in the inner Danish Belt Seas were animals migrating from the Baltic Sea to the North Sea. However, this migration route has never been confirmed and it is possible that animals moving from the adjacent Kattegat Sea into the Belt Seas were also hunted in the Belt area. The introduction of monofilament nets in the fisheries around 1960 probably increased bycatches and thereby reduced the possibilities of a recovery of the harbour porpoise in the Baltic Sea.

The harbour porpoise is the only cetacean regularly occurring in the Swedish Skagerrak, Kattegat and Baltic Seas and no densities or distribution patterns have previously been generated for these areas. During preliminary boat and aerial surveys in the Skagerrak and Kattegat Seas in 1988–1989, Berggren and Arrhenius (1995) reported very few sightings, indicating low numbers present in the areas during the time of the surveys. In two adjacent areas, Heide-Jørgensen *et al.* (1992) estimated the abundance of harbour porpoises; in the Great Belt area (457 animals, 95% CI 288–726) and in the Bay of Kiel (160 animals, 95% CI 96–267) using pod size estimates from the same surveys.

Berggren (1994) reported minimum bycatch levels between 1973–1993 in Swedish waters identifying bycatches as the major threat to harbour porpoises in the Skagerrak, Kattegat and Baltic Seas. The harbour porpoise is listed as threatened in all Swedish waters but few conservation measures have been initiated.

The general concern that harbour porpoises were sighted less frequently and had even disappeared from certain areas around Sweden, led us to attempt to document trends in densities and seasonal distribution of harbour porpoises in the Swedish Skagerrak, Kattegat and Baltic Seas. This paper is based on data from two sources; strip transect aerial surveys conducted in the Skagerrak and Kattegat in 1991; and a voluntary programme in which fishermen, coastguard and ferry operators opportunistically recorded sightings of harbour porpoises and effort during the five year period, 1988–1992 from the Skagerrak, Kattegat and Baltic Seas. Preliminary results from the two first years of the programme are given in Berggren and Arrhenius (1995).

MATERIAL AND METHODS

Aerial survey

Strip transect aerial surveys were conducted in the Skagerrak and Kattegat Seas (Fig. 1) during 10 days in 1991 (9 and 10 June; 2, 4 and 30 July; 4, 8 and 13 August; 26 and 27 October).

A high-wing aircraft (*Cessna* 206 Amphibian) was used. Unfortunately, the aircraft was equipped with floats which prevented searching on the trackline and the first 115m on either side of it (Fig. 2). The two observers therefore surveyed two strips, 115–315m,

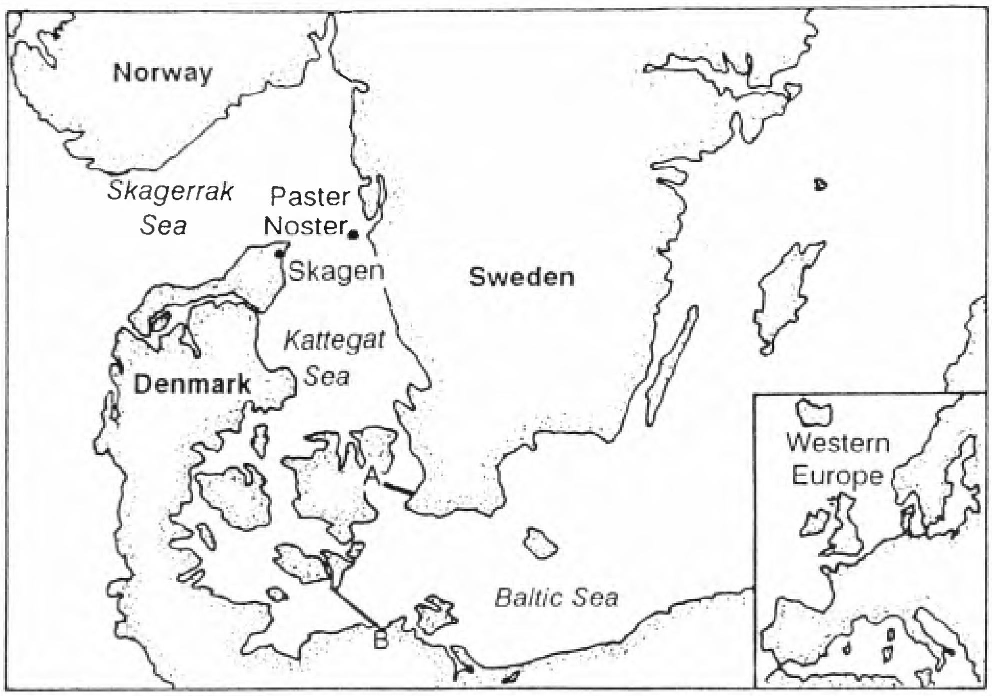

Fig. 1. The map shows the geographical location of the study areas. The position of the Limhamn and Darss underwater ridges, the western borders of the Baltic Sea, are indicated by the letters A and B respectively.

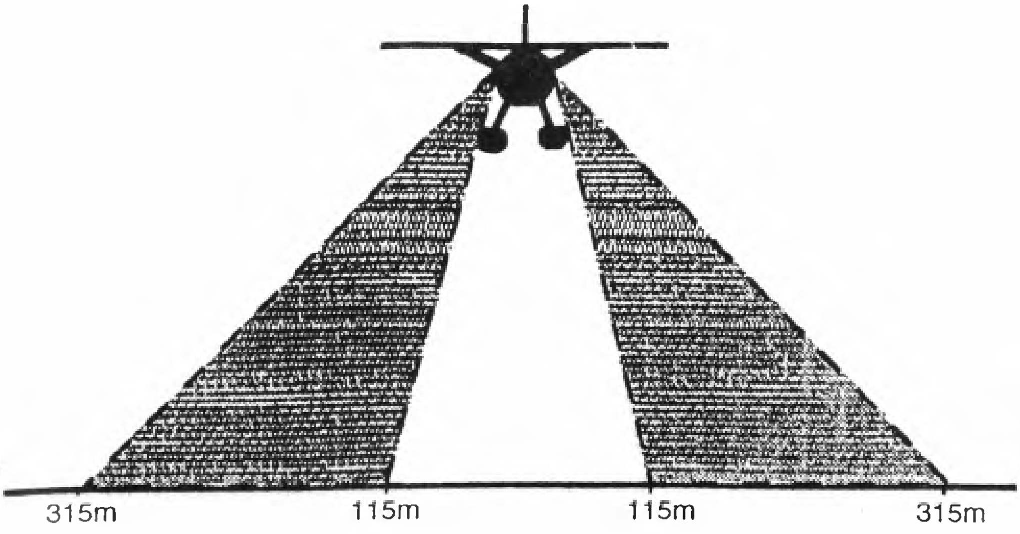

Fig. 2. The configuration of the 200m transect strips used in the aerial survey.

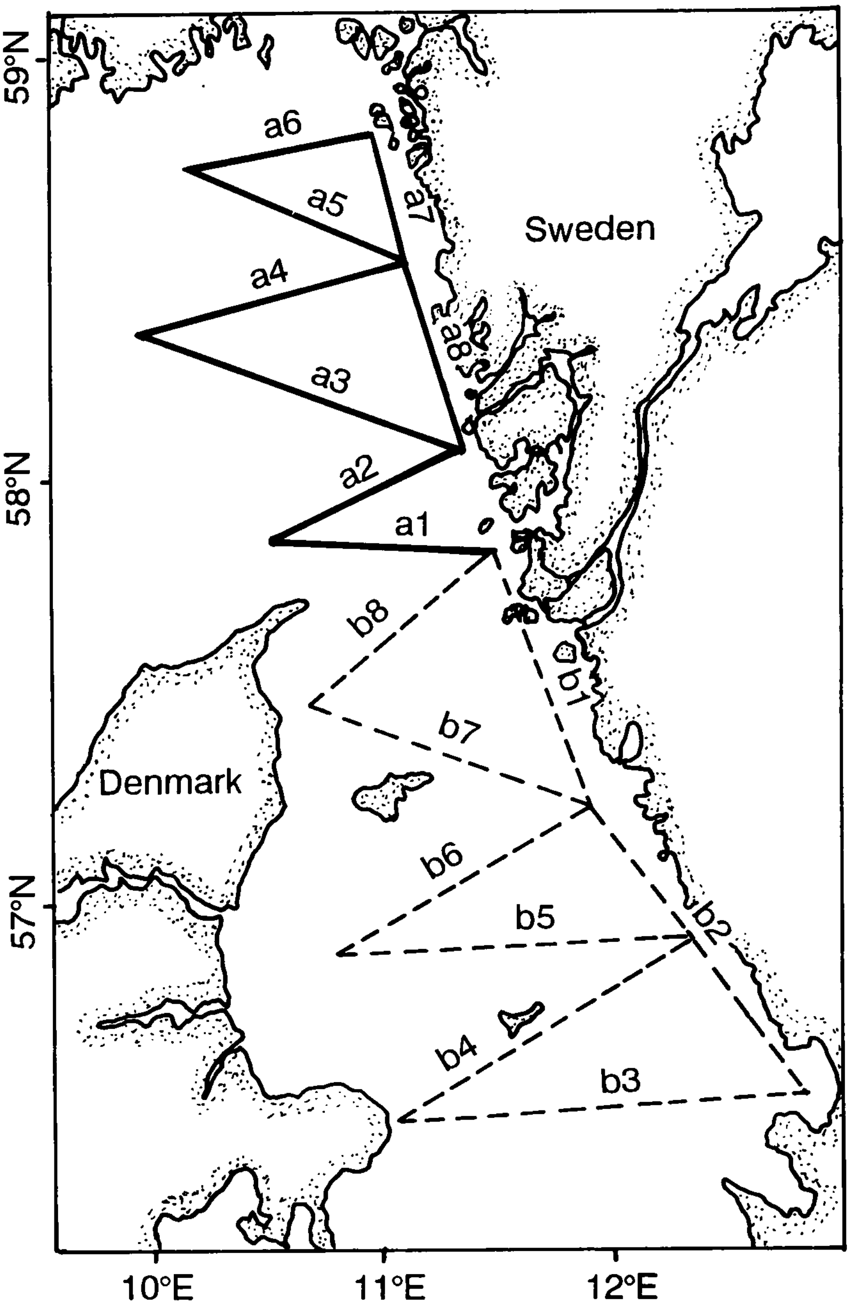

Fig. 3. The locations of the individual aerial survey transects in the Skagerrak Sea (solid tracks) and Kattegat Sea (dotted tracks).

parallel to the trackline. Surveys were run along 16 predetermined fixed zig-zag tracklines: a1-a8 in the Skagerrak Sea and b1-b8 in the Kattegat Sea (Fig. 3) at an altitude of 165m and an air speed of 170–180km/hr. The survey date, transect number, length of transect and the number of sightings recorded on each trackline are shown in Table 1. Information on sighting rates from voluntary observers (see below) suggested that densities might be different in the Skagerrak and Kattegat Seas and that stratification between areas might be necessary. Transect lines were placed in the two areas to give as representative coverage as possible. The chosen zig-zag pattern minimised the risk of an animal being detected on two neighbouring transect lines and also avoided long transit times between transect lines. The surveys were conducted from south to north to minimise effects from glare and waves on sighting conditions. The prevailing southerly winds generate wind induced waves from the south. The start and end points of all tracklines were logged into an onboard Global

Table 1

Statistics from the aerial surveys in the Skagerrak (a1-a8) and Kattegat Seas (b1-b8) in 1991.

Date	Transect	Km	Sightings	Date	Transect	Km	Sightings
10 June	a1	57.4	0	10 June	a8	52.8	0
02 July	a1	57.4	0	02 July	a8	52.8	0
30 July	a1	57.4	1	30 July	a8	52.8	0
08 August	a1	57.4	0	08 August	a8	52.8	0
27 October	a1	57.4	0	27 October	a8	52.8	0
10 June	a2	51.8	0	09 June	b1	74.1	2
02 July	a2	51.8	0	04 July	b1	74.1	0
30 July	a2	51.8	0	04 August	b1	74.1	0
08 August	a2	51.8	0				
				09 June	b2	93.5	0
10 June	a3	79.6	1	04 July	b2	93.5	2
02 July	a3	79.6	0	04 August	b2	93.5	1
30 July	a3	79.6	1	26 October	b2	93.5	1
08 August	a3	79.6	0				
27 October	a3	79.6	0	09 June	b3	113.0	4
				04 July	b3	113.0	1
10 June	a4	66.7	1	04 August	b3	113.0	0
02 July	a4	66.7	0	26 October	b3	113.0	0
30 July	a4	66.7	0				
08 August	a4	66.7	0	04 July	b4	100.0	0
27 October	a4	66.7	0	04 August	b4	100.0	3
				26 October	b4	100.0	0
10 June	a5	55.6	1				
02 July	a5	55.6	0	04 July	b5	101.9	0
30 July	a5	55.6	1	26 October	b5	101.9	0
08 August	a5	55.6	0				
27 October	a5	55.6	0	04 July	b6	80.6	1
				26 October	b6	80.6	0
10 June	a6	43.5	1				
02 July	a6	43.5	1	04 July	b7	75.9	1
30 July	a6	43.5	0	26 October	b7	75.9	0
08 August	a6	43.5	1				
27 October	a6	43.5	0	04 July	b8	64.8	0
				26 October	b8	64.8	0
10 June	a7	35.2	0				
02 July	a7	35.2	0				
30 July	a7	35.2	0				
08 August	a7	35.2	0				
27 October	a7	35.2	0				

Positioning System (GPS)-unit (*Garmin* 100 Aviation) prior to the surveys. The GPS was used to check that the aircraft stayed on course and kept correct speed and altitude. The latter was also checked with the aircraft's altimeter.

Hand held tape recorders were used to record all information and time was taken from digital time pieces synchronised before take-off. Sighting conditions were recorded at the start and end of each trackline and whenever they changed. Conditions were defined as good (Beaufort 0–1), moderate (Beaufort 2) or poor (Beaufort ≥3) on each side of the aircraft by the observers. Only data for good and moderate conditions are included here given the sensitivity of harbour porpoise sighting rates to sea state (e.g. Gunnlaugsson *et al.*, 1988; Heide-Jørgensen *et al.*, 1992). Wind speed, wind direction, wave height, wave direction and percentage glare was also recorded for each side of the aircraft. The strip width was determined by horizontal indicator lines marked on the aircraft window and wing struts prior to the surveys using handheld declinometers. For each porpoise sighting, the following was recorded: time, position (latitude/longitude from the GPS), declinometer angle, group size and heading of the animal(s). Perpendicular sighting distances from the trackline were later calculated from the declinometer angle. On some occasions, the aircraft departed from the trackline and circled to determine the pod size. The surveys were resumed at the point where the aircraft left the track.

Glare sometimes covered 50% of the survey area on one side of the aircraft. However, a pair-wise comparison of the mean number of sightings on the side with glare (0.333) and without glare (1.082), showed no significant difference (t-test for paired samples, p=0.108, df=11) thus the data were not corrected for glare.

The survey altitude was chosen to minimise the effect of the aircraft on porpoise surfacing behaviour and to maximise the possibility that animals were detected by the observers (for discussion, see Barlow *et al.*, 1988 and Heide-Jørgensen *et al.*, 1992). The only obvious reaction by harbour porpoises to the aircraft was noted when the aircraft circled to determine pod size and animals sometimes responded by rapid diving. No reliable information on diving behaviour of harbour porpoises is available for these or adjacent waters.

Density calculations

Densities were calculated using only the surveys when all transects (a1-a8 or b1-b8) were completed. The following equation was used to generate the density of animals in the strata surveyed (Buckland *et al.*, 1993):

$$D=N/2WL \qquad (1)$$

where D is the density (number porpoises/km^2), N is the number of porpoises sighted, W is the width of the transect and L is the length of the transect surveyed. The coefficient of variation (CV) was calculated as (Sokal and Rohlf, 1981):

$$\text{CV}=\text{Standard deviation/mean} \qquad (2)$$

Minimum uncorrected abundance estimates were generated by multiplying the density from (1) with the size of the area covered; 6,000km^2 in the Skagerrak Sea and 13,000km^2 in the Kattegat Sea.

Sighting rates from the surveys were also calculated as either the number of sightings or the number of animals seen per 1,000km surveyed using the total survey effort in the Skagerrak and Kattegat Seas for comparison with other studies that used these measures (Silber, 1990; Forney *et al.*, 1991; Barlow *et al.*, 1993; Silber *et al.*, 1994).

Insufficient sightings were made to allow line transect calculations within the strips searched to estimate abundance. The abundance estimates generated from these aerial surveys should be regarded as absolute minimum estimates due to the difficulties in fulfilling the stringent strip transect assumption that all animals within the strip should be detected (Buckland *et al.*, 1993).

Bycatch estimate

Minimum bycatch estimates of harbour porpoises in the Skagerrak and Kattegat Seas, in Swedish fisheries only, were taken from Berggren (1994). Berggren reported that 270 harbour porpoises were collected from bycatches between 1989 and 1991. Of these, 4%

Table 2

The frequency distributions of the number of years observers were active in the observer programme.

Area	Participants years (%)					Total number of observers active
	5	4	3	2	1	
Skagerrak	18.9	20.8	13.2	13.2	34.0	53
Kattegat	15.4	21.2	9.6	19.2	34.6	52
Baltic Sea	31.6	26.3	5.3	10.5	26.3	19

were taken in the Skagerrak and 9% in the Kattegat during the months June and August (see fig. 2 in Berggren, 1994). This resulted in a minimum of 4 and 8 (4% and 9% of 270/3) bycaught harbour porpoises per year during the three summer months in the Skagerrak and Kattegat Seas, respectively.

Observer programme

As a follow-up to a questionnaire study in 1987 (Berggren and Arrhenius, 1995), a group of volunteer observers was organised and asked to report sightings of harbour porpoises and effort in three areas; the Swedish Skagerrak, Kattegat and Baltic Seas (Fig. 1). The boundaries between these areas were taken from Fonselius (1994). The brackish waters of the Baltic Sea are maintained by the boundaries of the Darss underwater ridge (between Darss, Germany and Gedser, Denmark) and the Limhamn underwater ridge (at the inner border of the Öresund). There is no similar boundary between the Kattegat and Skagerrak Seas. However, we adopted the arbitrary divide by Fonselius (1994) between Skagen, Denmark and Pater Noster, Sweden.

The observers (fishermen, coastguard and ferry personnel) were asked to report opportunistically recorded sightings while working at sea. In addition, they were asked to report effort as the number of days spent at sea per month and the area. For this purpose, a sighting form was designed and distributed, return postage paid. Date, time, number of animals observed, position, heading of animals and weather conditions were reported for each sighting. Observers submitted forms regularly between 1988 and 1992. If no sightings were made, a form was still submitted every three months reporting effort and area surveyed during the time period. When an observer covered more than one area during the reporting period, effort was divided between the areas covered. In total, 124 observers were active during the five year study period (Table 2). Only data from observers active for at least twelve months with at least five days at sea per month are included. Table 2 shows the frequency distribution of the number of years observers were active in the three different areas.

The nature of these data preclude statistical analysis for trends. However, a visual evaluation of the summarised and plotted data has been used to imply trends in seasonal distribution and sighting rates.

RESULTS

Aerial survey

In total, 9 sightings (9 animals) were recorded in the Skagerrak Sea covering 2,161km transects and 16 sightings (18 animals) in the Kattegat Sea on 1,995km transects surveyed.

Table 3

Summary of data and statistics from strip transect surveys in the Skagerrak and Kattegat Seas during June-August 1991. All surveys were performed in Beaufort sea state 0-2.

Area	Skagerrak	Kattegat
Area (km^2)	≈6,000	≈13,000
Transect numbers	a1-a8	b1-b8
Total transect length (km)	442.5	703.8
Strip width (km)	2 x 0.2	2 x 0.2
No. of surveys	4	1
No. of porpoises sighted	9	6
No. of sightings	9	5
Mean animals/km^2	0.013	0.021
Coefficient of variation	0.67	0.75*
Total survey effort (km)	1,770	1,365
No. of porpoises sighted	9	17
No. of sightings	9	15
Mean group size	1	1.13
Sightings per 1,000km	5	11
Animals per 1,000km	5	12.5

* Calculated from n=3 surveys of b1-b3.

The densities for the complete surveys in the Skagerrak and Kattegat Seas in June-August were 0.013 porpoises/km^2 (CV=0.67) and 0.021 porpoises/km^2 (CV=0.75) respectively (Table 3). The October survey (1,020km) covering the same areas recorded no sightings in the Skagerrak Sea and a density of 0.002 porpoises/km^2 in the Kattegat Sea. The minimum uncorrected abundance estimates for the Skagerrak and Kattegat Seas were 78 animals (0.013 porpoises/km^2 × 6,000km^2) and 273 (0.021 porpoises/km^2 × 13,000km^2) respectively.

The sighting rate in June-August was 5 sightings (of 5 animals) per 1,000km surveyed in the Skagerrak Sea and 11 sightings (of 12.5 animals) per 1,000km in the Kattegat Sea (Table 3).

The mean pod size for the pooled sample was 1.08 (CV=0.26). A single female/calf pair was recorded on 4 July in the Kattegat Sea.

Bycatch versus abundance estimate

The Swedish bycatch during June-August in the Skagerrak Sea was approximately 5% of the abundance estimate (4 bycaught/78×100%) and 3% (8 bycaught/273×100%) in the Kattegat Sea.

Observer programme

A total of 332 sightings (949 harbour porpoises) were reported from 60,841 days spent at sea by 124 observers in the Skagerrak, Kattegat and Baltic Seas between 1988–1992 (Table 4). The effort and the number of observers active in the three different areas were relatively constant over the five year study period. The only apparent change in the number of sightings per observation day was in the Skagerrak Sea in 1992 where less than half the number of sightings per day was recorded compared to 1988–1991 (Table 4). Except in 1992, the sighting rates reported from the Skagerrak were almost twice those in the Kattegat.

Table 4

Summary of data from the observer programme in the Swedish Skagerrak, Kattegat and Baltic Seas between 1988-1992. The number of harbour porpoises, sightings, average group size with the coefficient of variance (CV), the total number of observation days, sighting rates and number of observers active are shown.

Date	No. porpoises sighted	No. sightings	Group size	CV group size	No. observation days	Sightings/ obs. day	No. of observers
Skagerrak							
1988	99	33	3.1	0.69	3,043	0.011	32
1989	123	47	2.7	0.78	5,423	0.009	36
1990	119	40	3.0	0.81	4,115	0.010	34
1991	126	51	2.6	0.76	4,347	0.012	28
1992	56	17	3.5	0.93	3,915	0.004	27
Kattegat							
1988	94	31	3.1	0.88	4,958	0.006	36
1989	114	37	3.2	0.62	8,015	0.005	44
1990	91	23	4.0	0.55*	5,908	0.004	29
1991	49	22	2.4	0.74	5,111	0.004	24
1992	77	30	2.8	0.78	5,446	0.006	28
Baltic Sea							
1988	0	0	0	0	1,957	0	17
1989	1	1	1	-	2,181	0.001	13
1990	0	0	0	0	1,864	0	14
1991	0	0	0	0	2,527	0	16
1992	0	0	0	0	2,031	0	14

* One sighting of 20 harbour porpoises was excluded.

Only one sighting of one harbour porpoise was recorded in the Baltic Sea during the five year duration of the programme.

The mean pooled estimate for pod size for all areas was 2.8 animals (CV=0.82, using equation 2).

The seasonal occurrence of the reported number of sightings per observation day shows a peak during spring and summer months (March-August) in the Skagerrak and Kattegat Seas (Fig. 4). The data also show that animals were present in both areas year round.

DISCUSSION

Aerial survey densities and sighting rates

This study presents the first densities and seasonal distribution patterns for harbour porpoises in the Skagerrak and Kattegat Seas.

Densities from the aerial surveys were lower than the strip-census density estimation reported by Heide-Jørgensen *et al.* (1992) in their 1991 surveys in the area north of Fyn (0.074 porpoises/km^2) and similar to their calculated estimate for the Bay of Kiel (0.013 porpoises/km^2). However, they used a different survey methodology and a different aircraft with better downward visibility. The inability to see porpoises within 115m of the trackline during our surveys is a major problem when comparing our results to those in other areas.

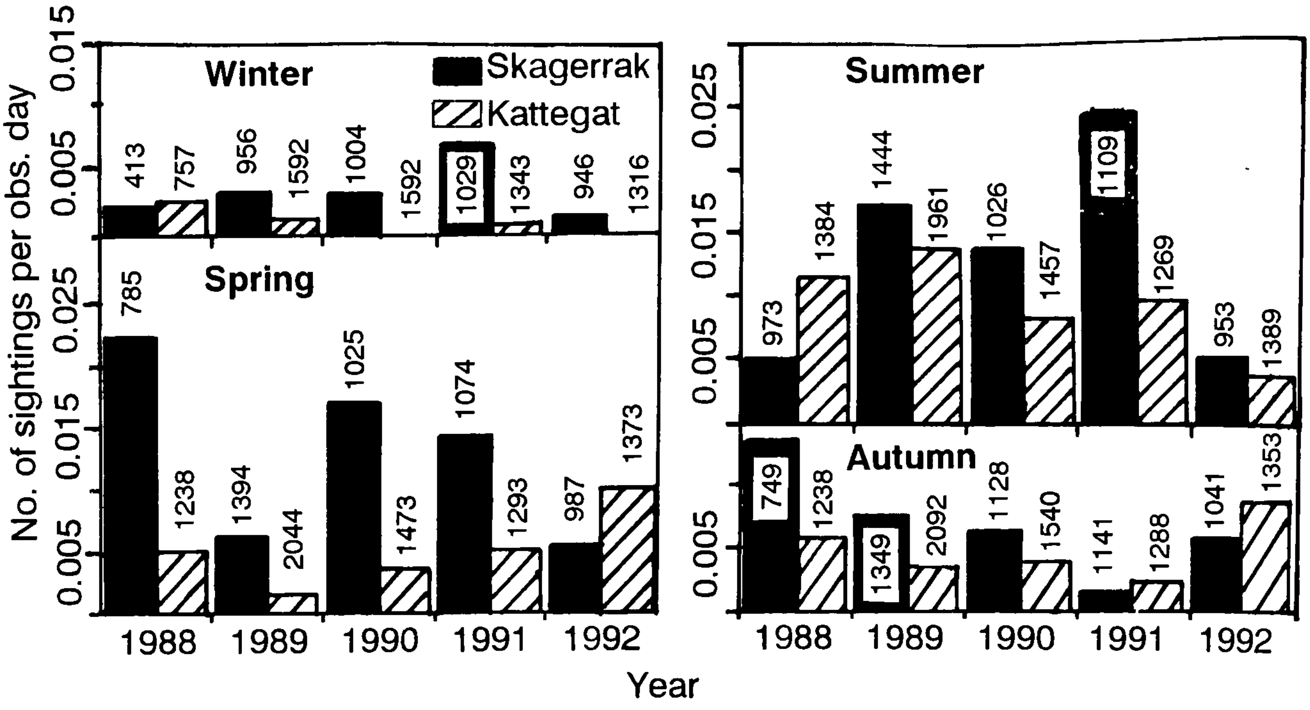

Fig. 4. The number of recorded sightings per observation day in the observer programme is shown for winter (December-February), spring (March-May), summer (June-August), and autumn (September-November) 1988–1992 for the Skagerrak and Kattegat Seas. The number on top of each bar indicates the total number of observation days.

Our density estimates were much lower than those recorded for aerial surveys off the coast of central California (0.56 porpoises/km^2; Barlow *et al.*, 1988). Other studies have reported sighting rates per 1,000km surveyed rather than densities. Our sighting rates were clearly lower than the 25 sightings (of 47 harbour porpoises) per 1,000km reported by Forney *et al.* (1991) off Central California, and in fact more in the range recorded for the endangered vaquita (*Phocoena sinus*) in the upper Gulf of California, Mexico, 1–8 sightings (of 1.8–16 animals) per 1,000km (Silber, 1990; Barlow *et al.*, 1993; Silber *et al.*, 1994).

Bycatch versus abundance

The question of the likely productivity of harbour porpoise populations is one that has taxed biologists for some years (e.g. Woodley and Read, 1991; Caswell *et al.*, 1995). As an interim measure, before a major review of the issue in 1996, the IWC Scientific Committee agreed that annual catches of 1% or more of the estimated abundance for a population would give rise to concern about sustainability (Donovan and Bjørge, 1995). The comparisons between the minimum calculated estimate of abundance and the minimum known bycatch (Berggren, 1994) during the same time period and areas (June-August in the Skagerrak and Kattegat Seas), suggest that harbour porpoises suffer high mortality from bycatches in the areas (3–5%); levels not likely to be sustainable. It should be stressed that both abundance and bycatch estimates used in the comparison presented here are minimum uncorrected estimates subjects to large degrees of variation and uncertainty and warrant further investigation to determine the status of harbour porpoises in these areas. Future and more accurate evaluation of the status of harbour porpoises in the North Sea and adjacent areas will be possible using data from the large scale abundance survey (SCANS) performed in 1994 (Hammond *et al.*, 1995). However, the results from this survey were not available during the preparation of this paper.

There was no apparent trend in the number of sightings reported per day at sea by the observer programme over the five year period, except in the Skagerrak Sea in 1992 where less than half the number of sightings per day was recorded compared to 1988–1991.

Seasonal distribution

The seasonal distribution patterns presented here from reported sightings concur with information from retrieved bycatches and strandings of harbour porpoises and indicate that animals are present throughout the year in the Skagerrak, Kattegat and Baltic Seas (Berggren, 1994). Although also reflecting poorer weather, the lower sighting rates during autumn and winter suggest that some animals leave the study areas at this time, probably wintering in the adjacent North Sea. A similar change in distribution has been noted in the northwestern Atlantic (Gaskin, 1984). Preliminary stomach content analyses of harbour porpoises from the Skagerrak and Kattegat Seas showed that herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) were the dominant prey species by weight (Berggren, 1995). Herring was also found to be the most important prey in the northwest Atlantic (Recchia and Read, 1989). There are both spring and fall spawning stocks of herring in the Skagerrak and Kattegat Seas (Ackefors, 1977). The spring stock migrates from the North Sea to spawn in the Skagerrak and Kattegat Seas in early spring and return in the fall to the wintering grounds of the North Sea (Rosenberg and Palmén, 1982). It is possible that harbour porpoises in the Skagerrak and Kattegat Seas follow the migration route of their primary prey and move out into the North Sea during autumn or early winter.

Group size

Estimated group sizes from the aerial surveys (means from 1–1.13) and incidental sightings (means 2.6–4.0) were different. The aerial survey group size may have been underestimated due to the short time animals were visible and possible changes in behaviour when the aircraft circled overhead, as has been noted during other aerial surveys (e.g. Barlow *et al.*, 1988; Heide-Jørgensen *et al.*, 1992). However, 'incidental' group sizes may be overestimated due to the fact that larger groups are easier to detect and/or the overestimation of group sizes by untrained observers. This suggests that the numbers of sightings rather than animals should be used to compare sighting rates between areas and over time.

Baltic Sea

The single observation in the Baltic Sea shows that animals are still present in the area, but at extremely low sighting rates that indicate no signs of recovery of the species in the area.

Harbour porpoises are no longer hunted in the Baltic Sea. However, it may be that the hunt reduced the animals in the area to very low numbers and that the present level of bycatches (Skora *et al.*, 1988; Berggren, 1994) are too high for the population to sustain given the species low reproductive rate (Sørensen and Kinze, 1994) and limited capacity for population increase (Woodley and Read, 1991). In addition to bycatches, contaminants and habitat degradation as a result of increased human activities may also have limited the recovery potential of harbour porpoises in the Baltic Sea.

CONCLUSIONS

The original aim of the aerial surveys discussed was to monitor trends in densities and distribution of harbour porpoises in the Skagerrak and Kattegat Seas over time. Unfortunately, funding difficulties made such long term goals impossible.

However, the low densities recorded in the Skagerrak and Kattegat Seas during the aerial surveys, compared to the documented bycatch in these areas and the lack of trends in the sighting rates in the observer programme, indicate that the status of harbour porpoises in these areas is uncertain.

The virtual lack of sightings in the Baltic Sea and the threat posed by bycatches still recorded in the area, indicate that harbour porpoises in the Baltic Sea are endangered.

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An Assessment of the Status of the Harbour Porpoise in Central California

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ABSTRACT

Harbour porpoise (*Phocoena phocoena*) in California are subject to incidental mortality in gillnet fisheries. The status of this population is uncertain. We review information on population structure and conclude that porpoises in central California should be managed as a separate stock. We review information from several surveys and estimate that the porpoise abundance in this area is approximately 3,300. The impact of several fisheries is considered and the fishery mortality from 1969–89 is estimated for the halibut gillnet fishery. In the mid-1980s, this fishery took 200–300 harbour porpoise per year. Estimates for the 1970s and early 1980s are extrapolated from current mortality rates and historic catch records. Based on the maximum plausible life history parameters, the maximum population growth rate for harbour porpoise is estimated to be 9.4% per year. Using this estimate and a model of density dependence, the abundance in the year 1969 is back-calculated by adding estimated harvests and subtracting estimated population growth. Using ranges in parameters to express some of the uncertainty in their estimation, the population in 1989 is estimated to be at 30–97% of its 1969 abundance. Given the broad range of this estimate and the fact that it does not incorporate all sources of variation, we conclude that it is impractical to manage this population based on its status relative to carrying capacity.

KEYWORDS: HARBOUR PORPOISE; NORTH PACIFIC; ASSESSMENT; BIOLOGICAL PARAMETERS; DENSITY-DEPENDENCE; INCIDENTAL CAPTURE; SURVEYS; STOCK IDENTITY; MANAGEMENT

INTRODUCTION

The harbour porpoise (*Phocoena phocoena*) commonly occurs along north-temperate coastlines of the Pacific and Atlantic Oceans (Gaskin, 1984; Barnes, 1985). In California, it is found only in the northern and central parts of the state, north of Point Conception. In central California, harbour porpoises are killed incidentally in a halibut gillnet fishery which expanded rapidly circa 1979 (Diamond and Hanan, 1986; Barlow *et al.*, 1994). This paper reviews information on harbour porpoise abundance and dynamics in the area and assesses the potential impact of incidental fishing mortality.

Several previous reports have considered the status of harbour porpoise populations in California. In the first general assessment of marine mammals by the US National Marine Fisheries Service (NMFS, 1980), porpoise mortality was mentioned as occurring in several fisheries, including some in California but insufficient information was available to assess the impact on porpoise stocks. As evidence of gillnet mortality in California became more apparent, Szczepaniak and Webber (1985) considered the status of harbour porpoise in the eastern Pacific, with an emphasis on California. They reviewed the available information and discussed potential factors that could affect the species, but they could not determine the impact of incidental catches in fisheries on the porpoise stocks. Barlow

(1987) combined information on abundance and estimates of historical fishing mortality to assess the impact of the halibut fishery on harbour porpoises in California. He concluded that, based on the estimated abundance of 1,854 porpoise in 1985, a closed population in central California would have been reduced to between 29–81% of its 1970 abundance due to this fishery. This report updates Barlow (1987) using extensive new information.

The paper addresses the following topics: (1) the stock identity of harbour porpoises in central California; (2) their abundance based on existing estimates for central California; (3) trends in their abundance; (4) incidental catch data for California gillnet fisheries since 1969/70; (5) estimated maximum population growth rate; (6) the current abundance relative to pre-fishery abundance.

POPULATION STOCK STRUCTURE

The concept of a stock is commonly used in management of populations of wild animals. It is used to describe a collection of animals that can be sensibly managed as a single unit (Larkin, 1972; MacCall, 1984; IWC, 1990). Historically, the criteria for identifying discrete stocks have been: (1) physical discontinuities in distribution of individuals; (2) habitat discontinuities; (3) evidence of restricted movement from tagging studies; or (4) demonstration of genetic or morphological differences between two groups (Donovan, 1991). Although these may be sufficient conditions for defining sensible management units, they are not necessary conditions.

Gaskin (1984) proposed a subdivision of harbour porpoise populations in the Pacific Ocean based on discontinuities in habitat type. He grouped the animals along the coasts of California, Oregon and Washington together in a unit which is separate from the porpoises found in the inland waters of Puget Sound and those found in British Columbia and southeastern Alaska. No evidence exists for discontinuities in harbour porpoise distribution along the coasts of California, Oregon and Washington. Studies incorporating genetic and telemetric techniques are in progress but at present provide no information on stock identity.

Aguilar (1987) discussed the use of chemical pollutant studies in considering marine mammal stock identity questions. The accumulation of environmental contaminants is believed to occur slowly over the life of an individual and thus tissue concentrations cannot change rapidly when environmental concentrations change. If concentrations differ between two areas and if movement of animals between those areas is restricted, contaminant concentrations in marine mammal tissues might be expected to differ. If animals move freely between two areas, no difference would be expected.

Calambokidis and Barlow (1991) found significant differences in concentrations of pollutants in tissue samples of harbour porpoises collected along the coasts of California, Oregon and Washington. They examined the ratio of PCB to DDE and the ratio of HCB to DDE, and for both they found significant differences between regions ($p<0.001$) and with latitude ($p<0.001$). Neither ratio varied significantly with animal sex or length. Within California, samples came from the three southern Regions (Fig. 1). Region 1 was represented by two samples whose ratios of PCB to DDE did not overlap with the ratio for the other two regions. Region 2 (Monterey Bay samples) overlapped with Region 3, but the range in values was much less than for Region 3. These results suggest both a strong gradient in environmental contaminants and a restricted movement of porpoises within local regions.

If harbour porpoise movement is restricted within central California but harbour porpoises from California to Washington are managed as a single stock, harbour porpoise abundance in California could be severely depleted. Because of limitations inherent in

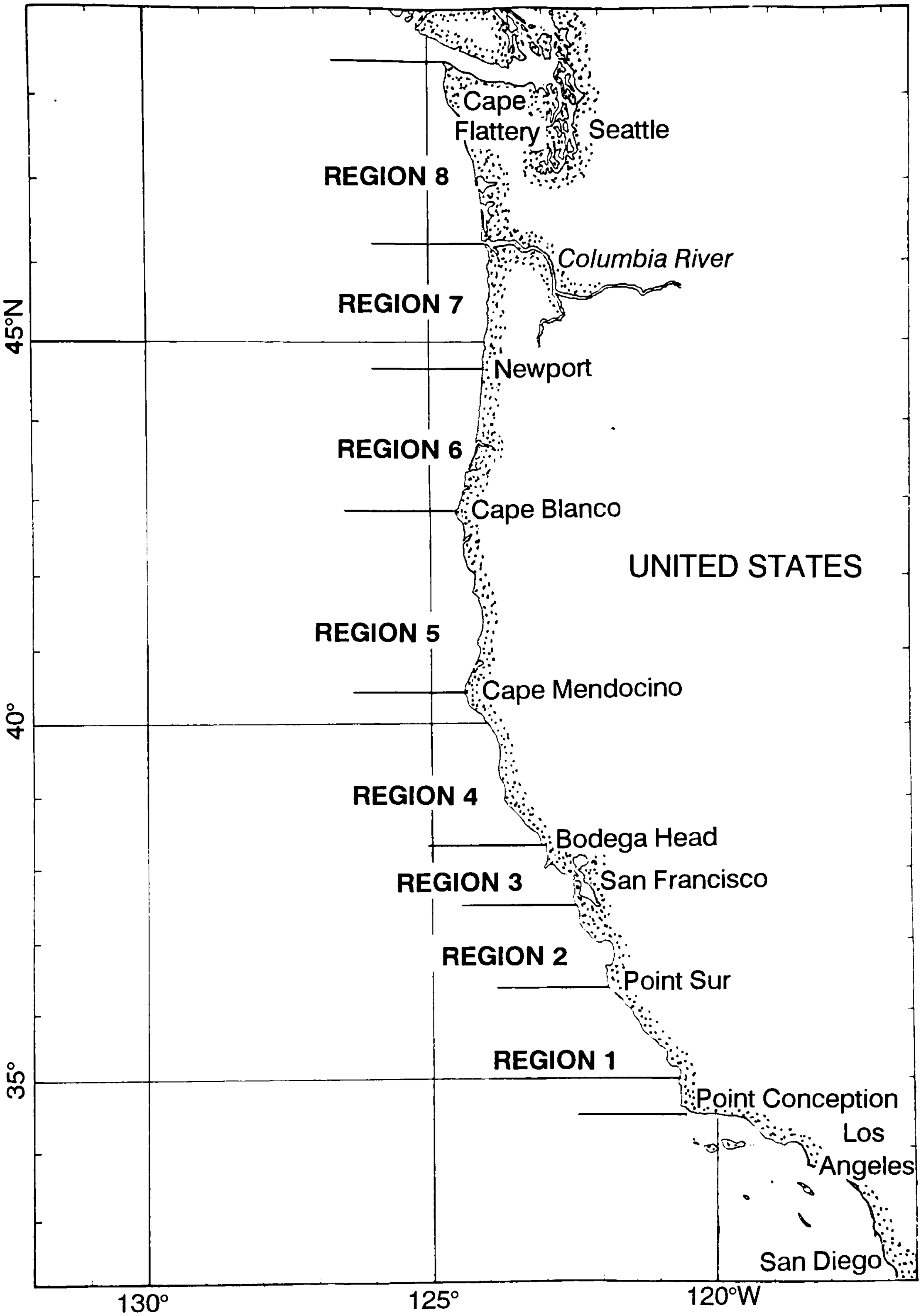

Fig. 1. The Pacific coastline and statistical regions used for abundance estimation and fishing mortality estimation. Central California includes Regions 1, 2 and 3.

using pollutants as stock indicators (Aguilar, 1987), it is not possible to say definitively that porpoises do not move to or from central California. Current evidence does, however, support the hypothesis that harbour porpoise movement is restricted in California. We make the 'conservative' assumption that the overall porpoise mortality in the central California gillnet fishery includes only those animals resident in central California (Regions 1–3, Fig. 1).

ABUNDANCE

Information on harbour porpoise abundance in California is available from five sources. These are considered in detail below and a combined estimate of harbour porpoise abundance is derived.

(A) US Mineral Management Service (MMS) aerial line transects

Modified aerial line transects were used to census all cetaceans in central and northern California (Dohl *et al.*, 1983). Estimates of harbour porpoise abundance ranged from 1,600 (summer) to 3,000 (autumn) in central and northern California combined. These estimates are, however, almost certainly too low because no correction was made for approximately 70% of animals that would be diving (and hence invisible to aerial observers) at any given instant (Barlow *et al.*, 1988). Adjusting for diving animals (multiplying by a factor of 3.2, see Survey B below), yields a rough estimate of 5,100 to 9,600 harbour porpoise in California. Because variance estimates are not available and because separate estimates were not made for central California, these estimates are not used in making a combined estimate of abundance.

(B) NMFS and California Department of Fish and Game (CDFG) aerial strip transects

Two aerial surveys were conducted in September of 1984 and 1985 using strip transect methods (Barlow *et al.*, 1988). Because sampling requirements for strip transects of harbour porpoise are stringent, many of the data that were collected were not useful for estimating abundance and the geographic coverage of the remaining data was insufficient to estimate abundance reliably. Based on a model of diving behaviour, a correction factor of *ca* 3.2 was developed (Barlow *et al.*, 1988) to account for submerged individuals that were missed. Uncertainty in this factor introduces considerable uncertainty in estimating porpoise density from aerial surveys. The aerial survey results were useful, however, in corroborating density estimates from ship surveys. Based on the limited areas surveyed under good sighting conditions, the corrected mean density was estimated as 1.79km^{-2}. This corresponds to an estimate of 1.73km^{-2} (adjusted for 22% missed trackline animals) from Survey C described below (table 8 in Barlow *et al.*, 1988). Data from these aerial surveys are not used to derive a combined estimate of abundance.

(C) NMFS ship line transects

Harbour porpoise abundance was also estimated from four ship surveys carried out between 1984 and 1986 which covered the entire coast between Point Conception, California and Cape Flattery, Washington (Barlow, 1988). Line transect methods were used on all surveys, with slight improvements being made between surveys. Density along the 18m isobath was estimated from two surveys (September 1984 and September 1985). The remaining two surveys were used to investigate seasonal changes in distribution, changes in distribution with water depth and applicability of line transect assumptions. Density was extrapolated to other depth strata using three alternative models of porpoise depth distribution. Subsequent data on the depth distribution of harbour porpoise

(Barlow and Forney, unpubl. data) corroborate Barlow's (1988) primary model. Corrections were made for an estimated 22% of animals missed by the observers, and variance was estimated using a combination of bootstrap and jackknife approaches. Using the primary depth distribution model, harbour porpoise abundance (corrected for missed animals) was estimated as 1,667 (SE=895) for central California and 45,713 (SE=7,865) for the states of California, Oregon and Washington.

(D) Farallon Research Associates, ship line transects

Vessel surveys were conducted in autumn 1986 for harbour porpoises in the Gulf of the Farallones (Szczepaniak, 1987), approximately half the area of Region 3 (Fig. 1). Line transect methods were used from 10–11m boats. Variance was calculated as in Survey C above. Approximately 764 linear km of transects were conducted under all sighting conditions. Estimates of porpoise density ranged from 0 to 1.95km^{-2} in the four strata that were used. The estimate of porpoise abundance was 1,033 (SE=523) or, adjusting for 23% missed trackline animals, approximately 1,268 porpoises.

(E) Cascadia Research Collective ship line transects

Vessel surveys for harbour porpoises were conducted in 1987–9 from the mouth of Tomales Bay to just south of San Francisco (Calambokidis *et al.*, 1990), i.e. most of Region 3 (Fig. 1). Line transect methods were used from 10–13m vessels. All depths were sampled uniformly out to approximately 100m depth. Variance in estimated density was based on a combination of empirical and analytical variance estimators. Approximately 1,800 linear km were surveyed. Using data collected on the 452km of transects conducted under very good sighting conditions, the mean density was 1.06km^{-2} (adjusted for 50% missed trackline animals). Fall surveys showed slightly higher abundance than the other seasons, but this difference was not significant. The adjusted estimate of porpoise abundance for all seasons was 1,719 (SE=523).

Combined estimate

Here we determine a combined estimate of harbour porpoise abundance in Central California using the results of Surveys C and E. For Survey C, the total distances surveyed in Regions 1, 2 and 3 were 377, 198 and 174km (respectively). For Survey E, the total distance surveyed in Region 3 was 1,800km. Survey C is the best source of estimates for Regions 1 and 2, but Survey E clearly provides the largest sample size and best estimate for Region 3. The greater abundance in Region 3 from Survey E (1,719) versus Survey C (112) is corroborated by the independent estimate from Survey D (1,268 for a portion of Region 3). The combined estimate for Regions 1–3 is thus 3,274 (SE 1.029). The standard error was calculated as the square root of the sums of variances for each Region. Surveys C and E occurred between September 1984 and September 1989. The combined estimate is assumed to represent the abundance near the midpoint of these surveys, April 1987.

TRENDS IN PORPOISE ABUNDANCE

In 1986–93, aerial surveys were flown in central California to estimate trends in harbour porpoise abundance. An analysis of covariance model was used to test for annual trends in sighting rates (year being the covariate) while controlling for other significant factors which affect sighting rate (area, sea state and cloud cover). Preliminary analyses of the 1986–89 data showed no statistically significant trends in abundance (Forney *et al.*, 1991); however, addition of subsequent data indicated a significant decline in abundance ($p<0.1$) from 1986–93 (Forney, 1995).

INCIDENTAL FISHERY MORTALITY

In California, harbour porpoise are extremely rare south of Point Conception (Norris and McFarland, 1958; Gaskin, 1984) and fishing regulations prohibit gillnets north of the Russian River; therefore, we only consider gillnet fisheries in central California (Regions 1, 2 and 3 in Fig. 1). Diamond and Hanan (1986) report that incidental porpoise mortality is largely limited to large-mesh, bottom-set entangling nets (gillnets, suspendered gillnets and trammel nets; henceforth termed 'gillnets'). Their use in California is reviewed by Herrick and Hanan (1988). Currently, they are used in the halibut fishery (which also takes flounder and shark species) and historically they were also used for white seabass. One porpoise death has also been observed in a small-mesh gillnet in the white croaker fishery near San Francisco.

White seabass fishery

The white seabass (*Cynoscion nobilis*) is a large (up to 38kg) member of the croaker family (Thomas, 1968). A valuable fishery for this species has existed in California since the early 1900s, with total landings reaching a maximum of approximately 1,400 metric tonnes in 1922 (Fitch, 1949). This has since declined and current commercial catches are very small; the stock is considered badly depleted (Methot, 1983). Fish were taken primarily by purse seines in the early 1900s, but this was prohibited in 1939 and since then large-mesh (6.0 to 7.5 inch) gillnets have been the primary fishing method (Thomas, 1968; Methot, 1983).

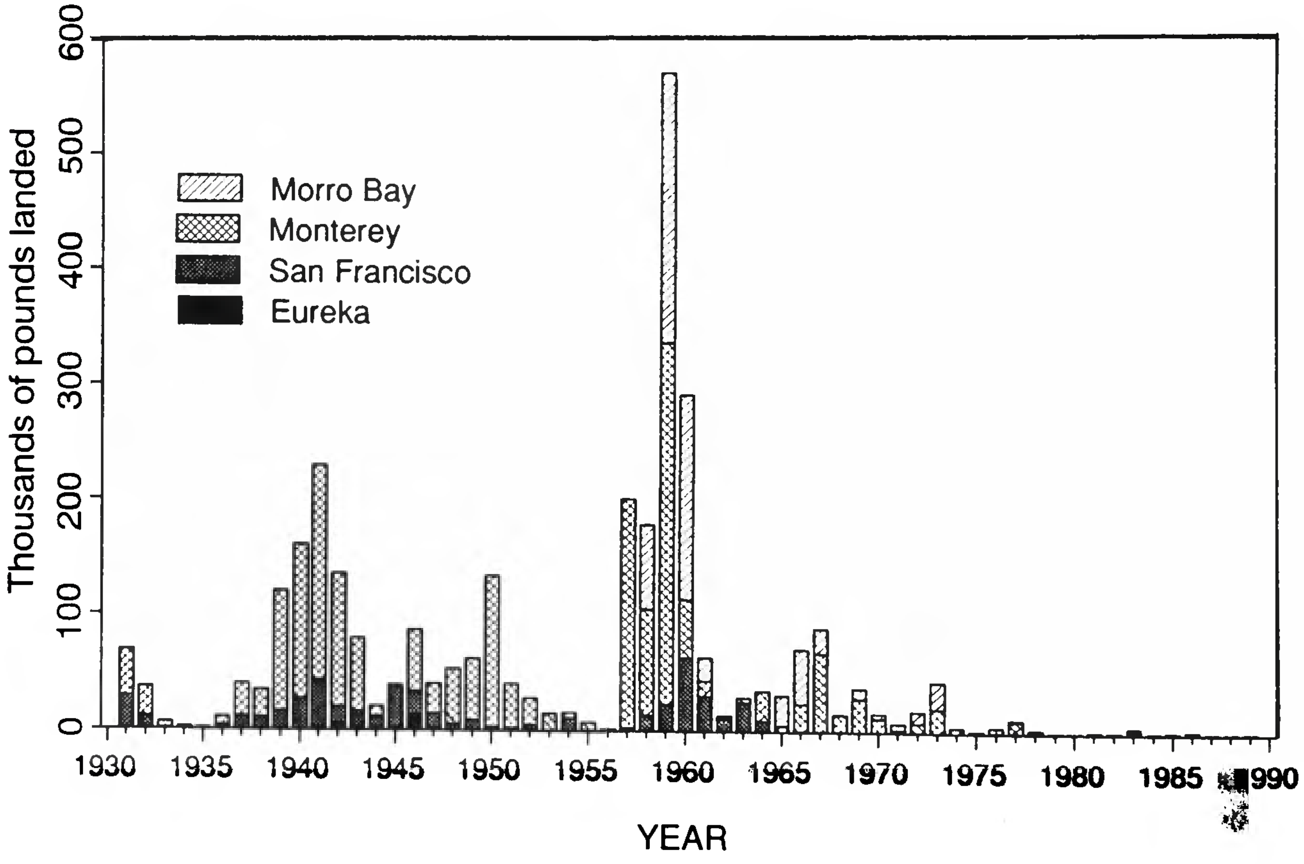

Fig. 2. Total pounds of white sea bass landed from Morro Bay to Crescent City in 1931–89 (CDFG, 1931). Statistical areas include Eureka, San Francisco, Monterey and the port of Morro Bay. CDFG landing records for Morro Bay are not reported for all years. Values for 1977 to 1989 are based on preliminary estimates.

Since 1930, landings north of Point Conception have been variable but typically small (Fig. 2), whereas northern landings were very high *ca* 1959, when the seabass distribution shifted to the north (Methot, 1983), possibly associated with a strong El Niño event.

Norris and Prescott (1961) reported that six harbour porpoises were caught in a seabass gillnet in Morro Bay, California on 6 December 1958 in water depth of approximately 15 fathoms. A few days earlier, the same vessel reportedly caught four porpoises off Pismo Beach, California (Norris and Prescott, 1961). Insufficient data exist from which to estimate rates of porpoise mortality in white seabass nets.

California halibut fishery

The California halibut (*Paralichthys californicus*) is also caught in large-mesh gillnets. California halibut have been fished many years in central California (Fig. 3). Coastal gillnetting has not been allowed north of Region 3 for any species. Total halibut landings are highly variable (Fig. 3) and perhaps, cyclic (Methot, 1983). Fishing methods have changed from being predominantly bottom trawling to predominantly entangling set nets (Methot, 1983). Nets are set on the bottom at 3–30 fathoms (5–55m) and are retrieved after 12–48hrs (typically 24hrs). Monofilament nylon and multi-strand nets are used with stretched-mesh sizes of 8 inches or greater. Nets are from 100–400 fathoms (185–740m) in length with an average of 200 fathoms (370m). Peak fishing activity occurs in July-August and we define a fishing year as between 1 April and 31 March.

The greater use of gillnets coincided with (and perhaps caused) an increase in the number of dead harbour porpoises found on beaches in central California in the early 1980s (Szczepaniak and Webber, 1985).

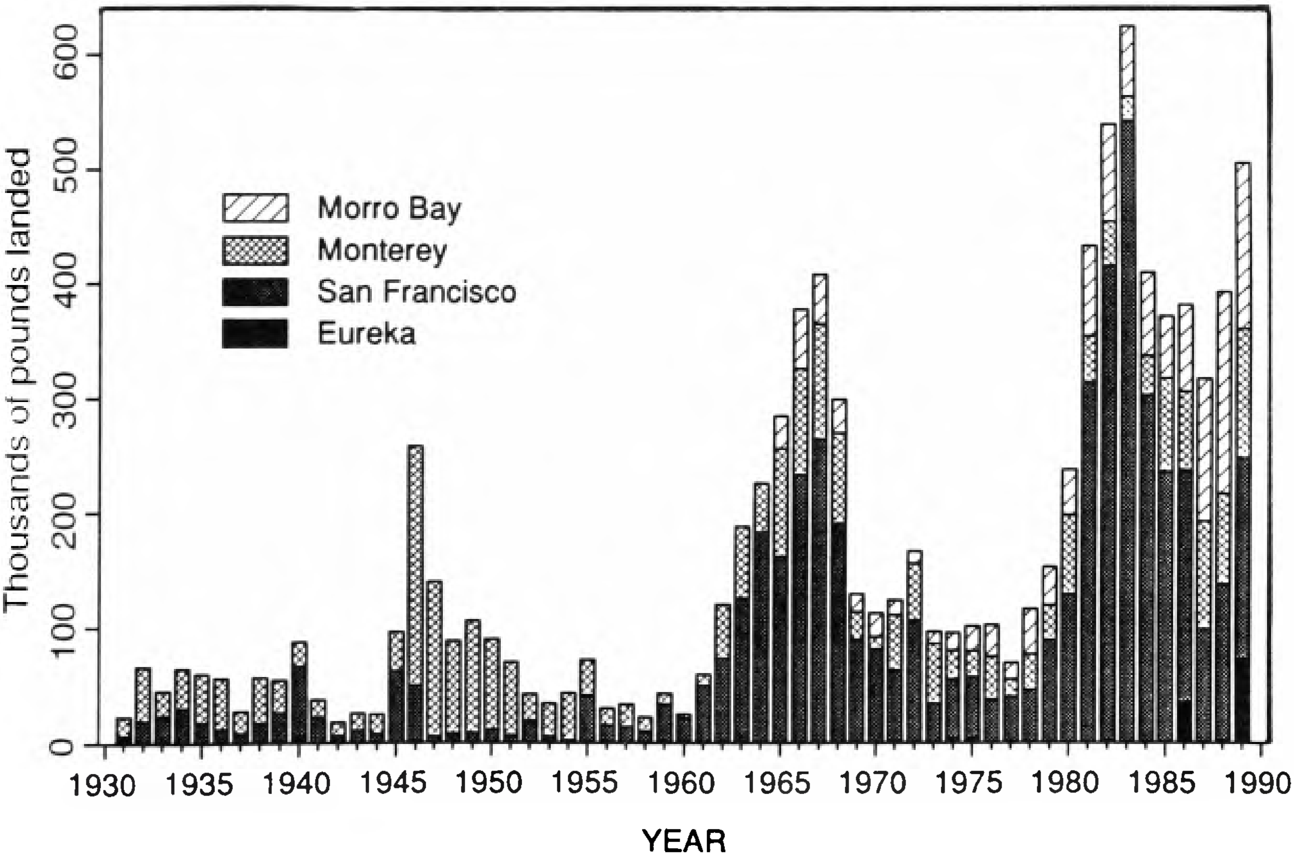

Fig. 3. Total pounds of halibut landed from Morro Bay to Crescent City in 1931–89 (CDFG, 1931). Statistical areas include Eureka, San Francisco, Monterey and the port of Morro Bay. CDFG landing records for Morro Bay are not reported for all years. Values for 1977 to 1989 are based on preliminary data reports.

There have been several changes in halibut fishing that were probably due to the incidental catch of harbour porpoises, sea otters and marine birds in gillnets in California (Herrick and Hanan, 1988). Based on the results of several studies of incidental catches in this and other gillnet fisheries, California State limited the deployment of gillnets and required net modifications, restricted areas open to fishing and halted the expansion of the fishery with a limited entry program. This has resulted in a large reduction in gillnet use since 1987.

The CDFG has estimated the number of harbour porpoise killed in halibut set nets for the fishing years 1983/84 through 1986/87. Kill estimates were made by calculating the average number of porpoise that die per net-haul and extrapolating to the total number of halibut net-hauls. The average kill rate per net-haul is estimated by observing a sample of net-hauls using CDFG observers either aboard cooperating fishing vessels, from a CDFG vessel or from shore with high powered telescopes. Estimates of the total number of halibut net-hauls is made from mandatory captains' logbooks and landing records (Diamond and Hanan, 1986).

Three methods were used to estimate annual porpoise mortality in recent years (a straight ratio estimate, a negative binomial model and a bootstrap bias-corrected estimate), and all gave very similar results (Diamond and Hanan, 1986; Hanan *et al.*, 1986; 1987; Hanan and Diamond, 1989). Although the bias correction is small, we use bootstrap estimates which have been stratified by geographic areas (Table 1). Bootstrap confidence limits are also give in Table 1 for 1983/84 to 1985/86, but are not available for 1986/87. Very few gillnets were observed during the 1987/88 fishing year, but an estimate of the total number of net hauls is available (E. Konno, pers. comm.). Porpoise mortality in 1987/88 was estimated by multiplying the average kill per net-haul from 1983/84 through 1986/87 (0.0275) by the estimated number of net hauls in 1987/88 (2,145).

Preliminary estimates of porpoise mortality for 1969/70 to 1982/83 and for 1988/89 were made using a different measure of fishing effort and using the recent estimates of the number of porpoise killed per unit of this fishing effort. For these years, the only available measure of fishing effort is the number of halibut landings (i.e. the number of CDFG landing receipts for California halibut) that could be attributed to gillnets. This measure of fishing effort is less accurate than the measure used to estimate kill in 1983/84 to 1987/88; however, it is the only measure of effort available for the period prior to 1983/84. We stratified halibut landings into three categories of gear type: set nets (entangling gear, gillnets and trammel nets), unidentified gear (including unspecified 'nets') and other gear (primarily trawl nets). The proportions of central California halibut landings attributed to these gear types are shown in Fig. 4.

A gradual increase can be seen in the proportion of landings attributed to entangling nets from a low in 1974/75 to a high in 1985/86. A general improvement in reporting can also be seen in the decreasing fraction of unidentified gear during the same time period (with the exception of 1983/84 and 1984/85). The large increase in unidentified gear in these two fishing years was accompanied by a large decrease in the reported catch attributed to gillnets. The timing of this change in reporting corresponds with a time period when gillnets were coming under increasing criticism by conservationists. Therefore, in 1983/84 and 1984/85, the majority of landings with unspecified gear type may have been from gillnets.

The total number of halibut landings attributed to gillnets was estimated as the sum of known gillnet landings plus a fraction of the landings for which gear type was not specified. Landings attributed to unidentified gear types were prorated based on the fraction of gillnet and other-gear landings. For the years 1983/84 and 1984/85, when unidentified gear may have been predominantly gillnets, the unidentified landings were prorated based on

Table 1

CDFG estimates of harbor porpoise mortality in halibut set nets for fishing years 1983/84, 1984/85, 1985/86 and 1986/87. Estimates are based on the bootstrap method with area stratification (Diamond and Hanan, 1986; Hanan *et al.*, 1986; Hanan *et al.*, 1987 and Hanan and Diamond, 1989). Regions are those shown in Fig. 1. Confidence limits (95%) are based on a bootstrap method for 1983/84 to 1985/86 and are estimated as +/- 2SE for 1986/87.

Year	Region	Porpoise mortality	Upper CL	Lower CL
1983/84	1	78	11	145
	2	47	0	108
	3	173	20	326
	Total	303	124	482
1984/85	1	27	3	57
	2	26	0	64
	3	192	86	298
	Total	226	108	334
1985/86	1	37	1	73
	2	55	0	129
	3	134	68	200
	Total	226	120	332
1986/87	1	101	n.a.	n.a.
	2	26	n.a.	n.a.
	3	70	n.a.	n.a.
	Total	197	61	333

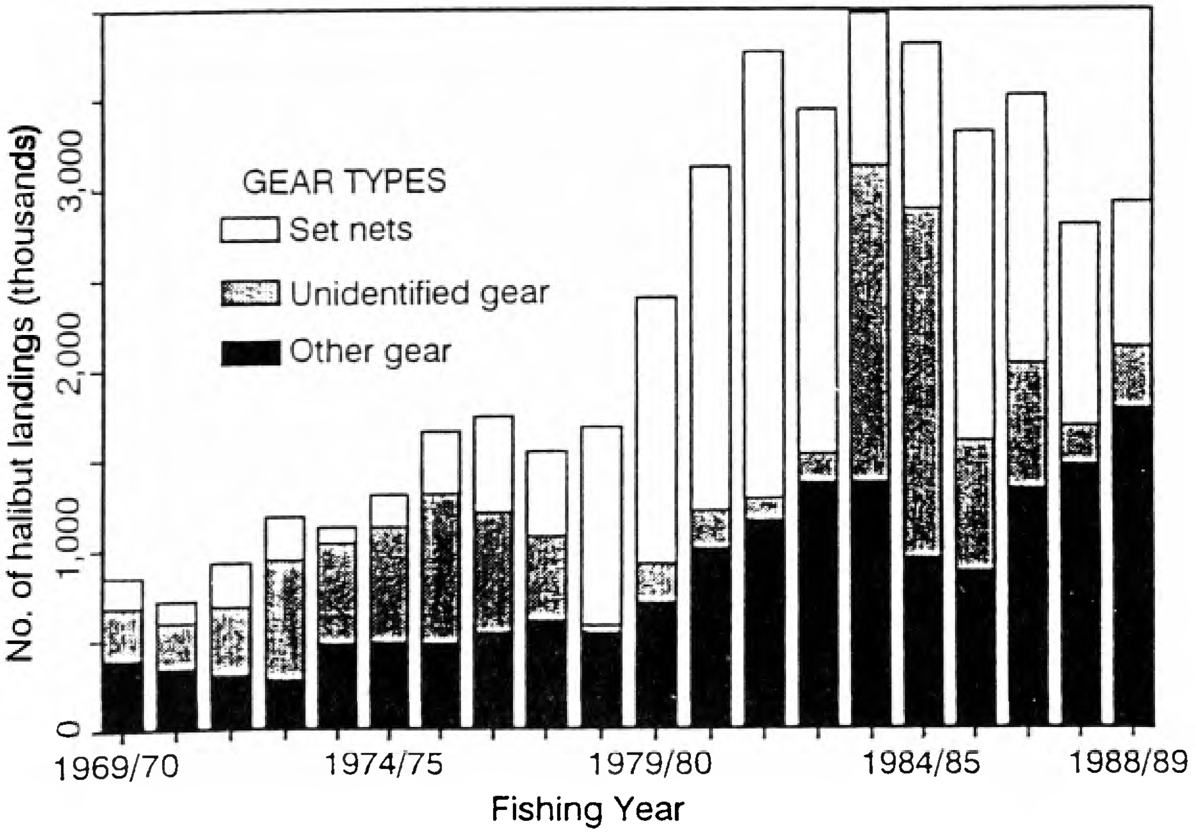

Fig. 4. Proportion of total number of halibut landings attributed to the indicated gear types during the fishing seasons from 1969/70 to 1988/89. Data include ports from Point Conception to Crescent City (to correspond with the halibut landings in Fig. 3). Gillnets were not used between the mouth of the Russian River and Crescent City.

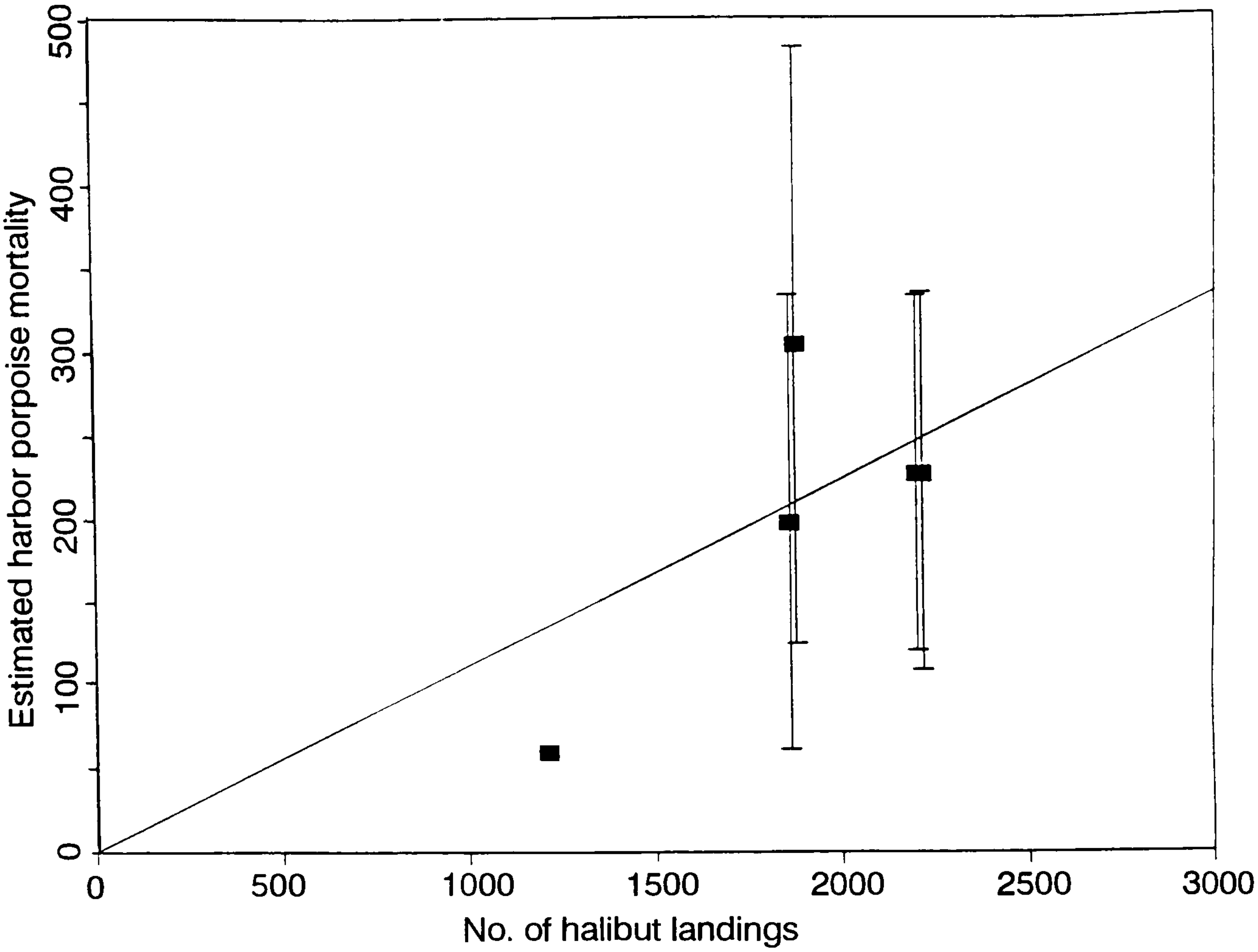

Fig. 5. Relationship between porpoise mortality in set nets and number of halibut gillnet landings for 1983/84 to 1987/88 fishing years. Landings are limited to north of Point Conception. Error bars indicate 95% confidence limits for estimates of porpoise mortality (Table 1) and are not available for 1987/88. Line indicates least-squares regression which was constrained to pass through the origin.

the fraction of gillnet and other-gear landings in the adjacent years (1982/83 and 1985/86, respectively). Total landings attributed to gillnets are given in Table 2.

The rate of porpoise mortality per halibut landing was estimated by regression (Fig. 5) using the CDFG mortality estimates for 1983/84 through 1986/87 and the estimated gillnet landings for the same time periods (forcing the regression through the origin). The resulting rate (0.110 porpoise killed per landing) was multiplied by the gillnet landings to estimate porpoise mortality from 1969/70 to 1982/83 and for 1988/89 (Table 2).

White croaker fishery

White croaker (*Genyonemus lineatus*) is caught in small-mesh gillnets in central California. This fishery is centered around San Francisco and Monterey Bay. The fishery developed rapidly since 1979, and in 1985 the landings of white croaker in central California (860,000 pounds) exceeded the maximum historical landings of white seabass and California halibut in this area (CDFG, 1931).

Since 1980, the retrieval of approximately 200 white croaker nets have been observed by CDFG employees working in central California (Hanan *et al.*, 1987). Of these, only one

Table 2

Estimated number of California halibut landings attributed to set nets, estimated harbor porpoise mortality due to gillnets and estimated harbor porpoise population sizes for the fishing years 1969/70 to 1987/88. Samples of CDFG landing records are limited to ports from Point Conception to Crescent City. California halibut landings attributed to set nets are based on known gillnet landings plus a prorated fraction of landings attributed to unspecified gear. Porpoise mortality for 1983/84 through 1986/87 are from Table 1. The preliminary estimates of porpoise mortality are based on regression of porpoise mortality to halibut landings using data from 1983/84 to 1985/87. The back projection estimates of porpoise mortality are based on the preliminary estimates and on the ratio of abundance in the given year to that of 1987/88. Porpoise population sizes are for the start of each fishing year and were calculated from the back projection model using an initial population size of 3,274 porpoise and parameters $z = 3.5$ and $R_m = 0.094$.

Fishing year	Number of gillnet halibut landings	Preliminary	Gillnet porpoise mortality	Back-projected	Back-projected porpoise population size
1969/70	256	28		64	4,461
1970/71	190	21		47	4,459
1971/72	419	46		100	4,455
1972/73	565	62		133	4,404
1973/74	178	19		41	4,337
1974/75	353	39		82	4,350
1975/76	696	77		158	4,328
1976/77	869	96		191	4,256
1977/78	676	74		146	4,177
1978/79	1,131	124		232	4,149
1979/80	1,629	179		232	4,060
1980/81	2,053	226		360	3,919
1981/82	2,573	283		402	3,754
1982/83	2,015	222		292	3,557
1983/84	1,884		(303)		3,466
1984/85	2,219		(226)		3,339
1985/86	2,206		(226)		3,305
1986/87	1,866		(197)		3,274
1987/88	1,214		(59)		(3,274)
1988/89	916	101		101	3,417
April 1989					3,508

resulted in the death of a harbour porpoise. This rate (0.005 porpoise per net) is considerably less than the average rate observed for halibut nets (0.027). Insufficient information exists to estimate the total porpoise mortality attributable to white croaker nets.

POPULATION GROWTH RATES

Maximum growth rates

Limits can be placed on the maximum rate of population growth based on constraints imposed by the biology of the animal. Reilly and Barlow (1986) used this approach to estimate maximum growth rates for delphinid cetaceans, but their model, based on constant survival rates for all adult ages, did not consider ranges of parameters that would represent the harbour porpoise. Barlow and Boveng (1991) attempted to estimate the maximum growth rate specifically for harbour porpoise using an age-varying survival model.

In order to estimate a maximum growth rate for harbour porpoise, Barlow and Boveng (1991) chose the maximum birth rate parameters that would appear to be feasible for harbour porpoise. Harbour porpoise are believed to mature at approximately 3 to 5 years (Gaskin, 1984), and in the western Atlantic a mean age of sexual maturation was estimated as 3.1 to 3.4 years (Read, 1990a). Gestation lasts about 10.6 months (Read, 1990b). They therefore estimated the maximum growth based on females maturing at age 3.1 and giving birth first at age 4. Lactation continues after birth for a period up to 8 months (Gaskin *et al.*, 1984). Simultaneously pregnant and lactating females have been found in samples from several populations (Gaskin *et al.*, 1984), indicating that mature females can give birth every year. This is verified by cases where individually recognisable females were accompanied by different calves in consecutive years (Watson, 1976; Taylor and Dawson, 1981). The percentage of mature females that give birth each year has been estimated at 74–86% (Read, 1990a) and is typically believed to be less than 100% (Gaskin *et al.*, 1984). For their maximum growth rate, Barlow and Boveng assumed that mature females give birth to one calf each year.

To estimate age-specific mortality rates, Barlow and Boveng (1991) use an approach based on selecting a model life table from a species with similar life-history traits and re-scaling its survivorship curve by an estimate of harbour porpoise longevity. Three alternative life tables were used: (1) northern fur seals; (2) Old World monkeys; and (3) human females *ca* 1900. To re-scale these life tables for harbour porpoise, the time scale of each was divided by an estimate of the longevity of the respective species and multiplied by an estimate of the longevity of harbour porpoise. Longevity was defined as the age of the 99th percentile of a stable age distribution. This 99%-longevity was estimated as 10 years for harbour porpoise and 18, 34 and 81 years (respectively) for the other three species. Resulting survivorship curves are illustrated in Fig. 6.

To summarise, the assumed biological constraints on population growth in harbour porpoise are: the minimum calving interval is 1 year; the youngest age at first birth is 4 years; and the 99%-longevity is 10 years. Using these values, population growth rates are 0.917, 0.989 and 1.094, respectively for survivorship models 1, 2 and 3. These range from a decrease of 8.3% per year to an increase of 9.4% per year. Because the first two models do not allow population growth, they are not given further consideration. Maximum population growth rate is assumed to be 9.4% per year. It should be emphasised that this is a theoretical maximum and that no cetacean population has been known to grow at such a high rate.

Current growth rates

The maximum growth rates calculated above indicate how rapidly a population might grow given the best conditions that could occur. [In California, current estimates of age at attainment of sexual maturity are greater and pregnancy rates are less than the values used above (A. Hohn and R. Brownell, pers. comm.)]. These maximum rates are likely to occur only when population size is relatively small and individuals are not competing or having other detrimental influences on each other. As populations increase, growth rates decrease, until at some point growth stops entirely and the population reaches an equilibrium. This equilibrium population size is called carrying capacity, *K*. Due to fishing mortality, current populations are likely to be less than *K*; hence, current growth rates are likely to be positive, but less than the maximum rate calculated above.

The expected relationship between growth rate and population size has been termed density dependence. Recruitment rates are often substituted for population growth rates

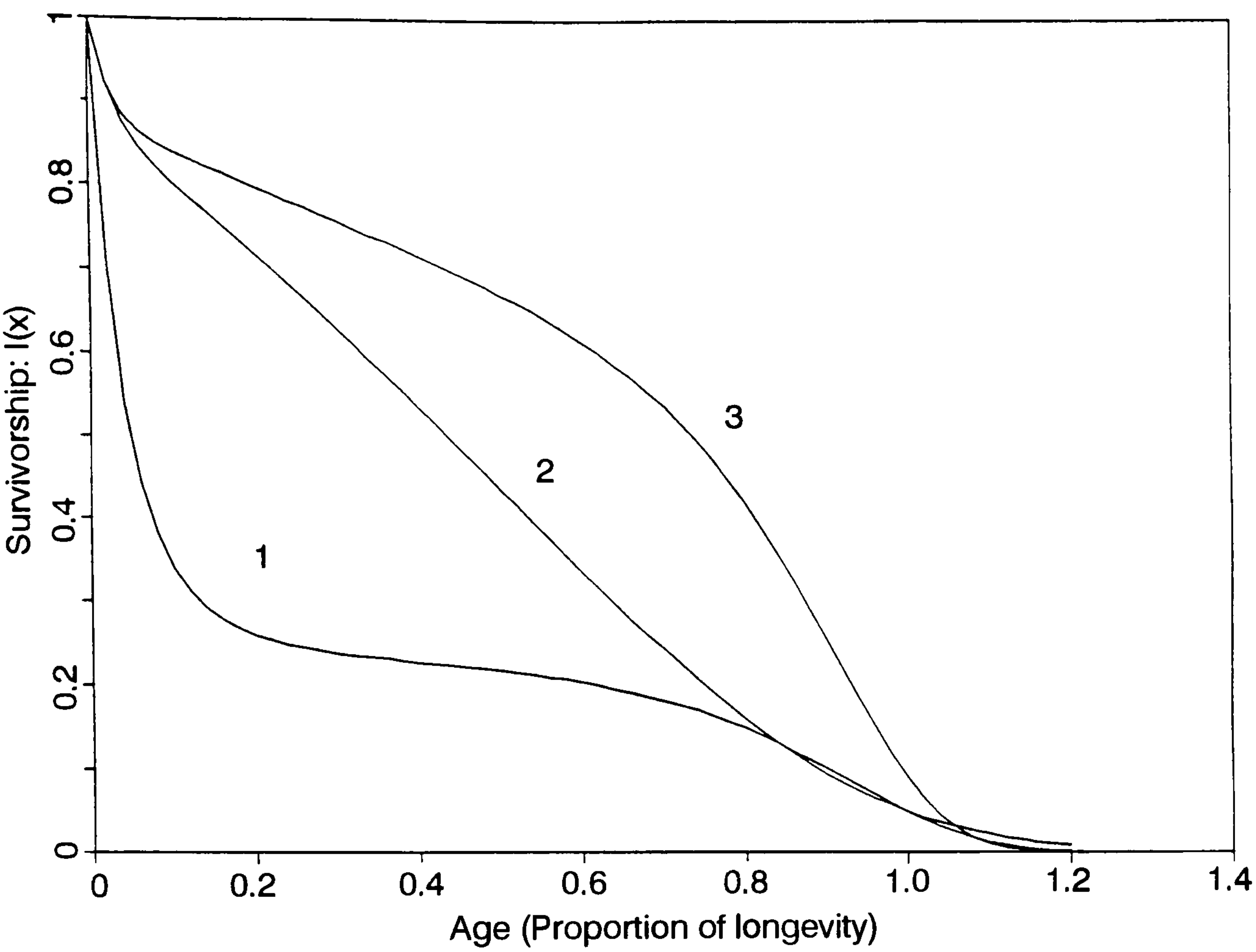

Fig. 6. Survivorship curves used to estimate maximum rates of population growth. Model survivorship curves (Barlow and Boveng, 1991) are based on (1) northern fur seals, (2) Old World monkeys and (3) human females circa 1900. For harbour porpoise, longevity (as defined for the above curves) is assumed to be 10 years.

in expressing density dependent relationships. The net recruitment rate, R, is directly related to the finite rate of population growth, λ, by the following relationship: $R = \lambda - 1$. The maximum net recruitment rate, R_m, was thus estimated above as 0.094. In this paper density dependence is modelled as (Allen, 1981):

$$R(N) = R_m(1 - (N/K)^z) \quad (1)$$

where N = population size, and
z = shape parameter.

The shape parameter, z, adds considerable flexibility in determining the shape of the density dependent response. This model of recruitment rate has been used previously in studies of small cetaceans (Smith, 1983) and whales (Allen, 1981).

The parameter z is extremely difficult to estimate. Empirical evidence indicates that z is typically greater than 1.0 for long lived mammals, including all marine mammals (Eberhardt and Siniff, 1977; Fowler, 1981). Based on theoretical arguments Gilpin *et al.* (1976) also show that selection favours higher values of their parameter, Θ, (hence $z >$ 1.0) for animals which (like mammals) are less sensitive to environmental fluctuations. In previous estimates of current growth rate for dolphins, values of 1.0, 3.5 and 11.5 have been used for z (Smith, 1983). These correspond to maximum net productivity (MNP) occurring at 50, 65 or 80% of K (respectively). Lacking any new information, the same range is used here.

PRE-FISHERY ABUNDANCE

The ratio of recent abundance (taken as April 1, 1989) to carrying capacity, N/K, is estimated by assuming populations were at carrying capacity at the time when use of set nets for halibut became common (1969). Population size at April 1, 1969 is estimated using the Smith and Polacheck (1979) back-projection model:

$$N_T = \frac{N_{T+1} + \frac{H_T}{2}}{1 + R(N_T)} + \frac{H_T}{2} \tag{2}$$

where N_T = abundance at time T
N_{T+1} = abundance at time $T + 1$
H_T = number killed during time period T
$R(N_T)$ = population growth rate as a function of abundance

The back-projection model was applied to the abundance estimate for April 1987 to estimate abundance in April 1986. This process was repeated for each year, back to 1969. The population in 1969 was assumed to be at carrying capacity for the purpose of estimating population growth rate, $R(N)$, in subsequent years. In order to account for the greater number of animals at risk in earlier years, the preliminary estimates of the number of porpoise killed from 1969/70 to 1982/83 (Table 2) were multiplied by the ratio of porpoise abundance in 1987/88 to the abundance in the given year. Because of the dependence of the model on its resulting estimate of population size in 1969 and on estimates of abundance in intervening years, the model must be applied recursively. The back-projection was repeated until estimates of population size in 1969 converged. Population size in April 1989 was estimated from abundance in April 1987 by reversing the back-projection model (Smith and Polacheck, 1979, Eq. 1).

Input parameters for the back-projection model include estimates of current population size, fishing mortality from 1969 to present (Table 2), the maximum rate of population growth (R_m) (Table 3) and the shape parameter for population growth (z). Because of uncertainty in estimates, ranges of values were used for the above parameters. The choice of these ranges are described below.

Three alternative values were used for population size in 1987 to represent a range of uncertainty. These include the mean abundance for central California (Regions 1–3), the mean plus one standard error and the mean minus one standard error.

Two alternative values were used to represent the maximum population growth rate of harbour porpoise in California. The first value, $R_m = 0.094$, was based on a survivorship curve patterned after human females (Fig. 6). The second value, $R_m = 0.0$, was based on the possibility that growth in harbour porpoise populations may be affected by pollutants, vessel traffic, other fisheries, or other human encroachments aside from direct mortality in the halibut fishery. Indirect human affects were also considered in a previous assessment of dolphin stocks affected by the yellowfin tuna fishery and a maximum growth rate of zero was considered possible (Smith, 1983). Given the history of harbour porpoise disappearance in other areas, it is important to explore the possibility of a zero growth rate.

Three alternative values were used for the shape parameter, z, in the population growth equation. The values used (1.0, 3.5 and 11.5) correspond to maximum net productivity levels at 50, 65 and 80% of carrying capacity (respectively) (Smith, 1983). Based on information presented above, the value of 50% ($z = 1.0$) is a reasonable lower limit. The values of 50, 65 and 80% were chosen on the basis of their previous use in dolphin population assessments (Smith, 1983) and no basis exists for choosing a best estimate among these three. An example of back projected population sizes are given in Table 2 for an estimated 1987 population size of 3,274 and parameters z of 3.5 and R_m of 0.094.

Table 3

Estimates of the ratio of forward-projected abundance (April 1989) to back-projected abundance (April 1969) based on estimates of R_m, z, historical gillnet mortality (Table 2) and population size in April 1987. Population size estimates are for central California. Upper and lower population estimates are based on +/-1SE.

		Maximum net recruitment rate, R_m				Maximum net recruitment rate, R_m	
Population size	MNPL	0.00	0.094	Population size	MNPL	0.00	0.094
2,245	50% *K*	0.30	0.47	4,303	50% *K*	0.53	0.69
	65% *K*	0.30	0.65		65% *K*	0.53	0.85
	80% *K*	0.30	0.81		80% *K*	0.53	0.97
3,274	50% *K*	0.44	0.60				
	65% *K*	0.44	0.77				
	80% *K*	0.44	0.95				

Estimates of the ratio of current abundance to abundance in 1969 are given in Table 3 for the above range of input parameters. It is difficult to assess the status of harbour porpoise in 1969 with certainty, but in the following discussion it is assumed that populations were at *K*. Assuming that the population in central California is a separate stock and is capable of growing at 9.4% per year, and using the central estimate of porpoise abundance (3,274 animals), the current population is estimated to be slightly above its maximum net productivity level. Using the same combination of parameters with a zero growth rate results in the conclusion that the population is below its maximum net productivity level.

DISCUSSION

The harbour porpoise population affected by California gillnet fisheries may range from 30–97% of their historical (1969) abundance. This range is too broad to be of much practical use in management. Confidence limits (if calculable) would be even broader. The values given in Table 3 were based on what we considered to be almost equally plausible values for three parameters (population size, z, and R_m). The confidence limits for each would be broader than the range we chose. In addition there is uncertainty in the estimates of annual mortality. It is unlikely that we will be able to precisely estimate the status of harbour porpoise in California relative to historical carrying capacity using this approach.

Violations of several assumptions could cause the above estimates to be high and thus the relative status of harbour porpoise could be worse than predicted. First, and most important, is the assumption that porpoises were at carrying capacity in 1969. Harbour porpoise are known to have been taken in white seabass gillnets in the late 1950s. Gillnets for halibut were being used in 1969 (Fig. 4) and presumably were used prior to that time. Evidence is cited above for the disappearance of harbour porpoise from San Francisco Bay long before 1969. Pollution, vessel traffic and fishing mortality may have reduced the abundance in all of central California prior to 1969. Second, gillnet mortality since 1983 was based on estimates of the number of sets made. Because some sets are not reported, mortality may have been underestimated (Diamond and Hanan, 1986). Finally, being at the fringe of the species' range, harbour porpoises in California may never attain the high demographic rates measured elsewhere and a maximum growth rate of 9.4% may be unattainable.

Violation of several other assumptions could, however, cause the above estimates to be low, and thus the relative status of harbour porpoise could be better than predicted. First, submerged animals missed during ship surveys cause an underestimate of the population size. Secondly, if emigration has occurred from the north, porpoise in central California would be at a higher fraction of carrying capacity. If the emigration rate is high enough, the designation of a separate management stock in central California is invalid. Currently the only information on movement rates are those based on pollutant residues which indicate restricted movement patterns within central California. Sample sizes in that study are small and may not be representative of all segments of the population.

On-going aerial surveys may improve estimates of population size (Barlow and Forney, 1994). However, it is unlikely that we can say, unambiguously, whether porpoise populations are above or below their maximum net productivity level.

Our emphasis on estimating the status of a population relative to MNPL and *K* has been largely dictated by the wording and interpretation of the US Marine Mammal Protection Act prior to 1994. Our failure to obtain a precise, unambiguous estimate of the status of harbour porpoise in California illustrates the weakness in this management approach. A new management approach for marine mammals in the US was instituted in 1994 based on a conservative quota set as a percentage of the minimum population estimate. This quota (termed potential biological removal) is 37 harbour porpoises per year in central California (Barlow *et al.*, 1995).

Harbour porpoise mortality in central California declined from 200–300 in the mid-1980s (Table 2) to an average of 31 in the early 1990s (Barlow *et al.*, 1995). This decline resulted from a decline in total fishing effort in this region due to local (state) season and area closures which were instituted to protect sea birds, sea otters and harbour porpoise.

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Exploitation of Harbour Porpoises (*Phocoena phocoena*) in Danish Waters: A Historical Review

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ABSTRACT

Historically harbour porpoises have been taken at six major catch sites in Danish waters. The most important site, in the northern Little Belt at Middelfart, was first mentioned in 1357 and was operative until 1892, and again between 1916–19 and 1941–44. The overall average annual take may have been about 1,000 animals with a known minimum total of 59,028 animals for the years 1819–92. In the 1880s, the annual catch level increased to about 2,000 of a grand total of about 3,000 animals in all Danish waters, possibly initiating the decline of the Baltic population of the harbour porpoise. Figures for average and maximum daily catches declined from the 1880s to 1916–19 and again from 1916–19 to 1941–44. The actual catch may have been sustainable for several centuries until about 1870 and the initial population in Danish waters may have been as large as 25,000.

KEYWORDS: HARBOUR PORPOISE; NORTH ATLANTIC; DIRECT CAPTURE

INTRODUCTION

The harbour porpoise (*Phocoena phocoena*) is thought to have been hunted in inner Danish waters since the Stone Age (Möhl, 1970). The first written report of the hunt was from 1357 (Klausen, 1867). Organised guilds of porpoise hunters are documented for 1593 but may have existed much earlier (Ropelewski, 1957; Petersen, 1969). In the Danish straits harbour porpoises have been hunted both in spring and winter during the seasonal migrations of the species. An extensive bibliography, including newspaper articles, describing the various catch methods applied and the numbers of animals taken is provided at the end of this paper.

In the Little Belt area, the take consisted of migrating animals with summer ranges in the Baltic proper where the species nowadays is almost absent (Andersen, 1982; Skora *et al.*, 1988) due to a marked decline in the second half of the 20th century (Kinze, 1990). The hunt ceased in the first half of this century and whether the decline had already begun then has been a matter of speculation (Mitchell, 1975). A detailed examination of the available catch statistics is given and used to obtain an estimate of the order of magnitude of the original population size of the tentative Baltic stock.

MATERIAL AND METHODS

Information on harbour porpoise catches from 1767 to the present was obtained from books and journals covering natural history, fisheries or local history and from two newspapers from the Little Belt area, *Middelfart Avis* and *Fredericia Avis* for the period 1850–90.

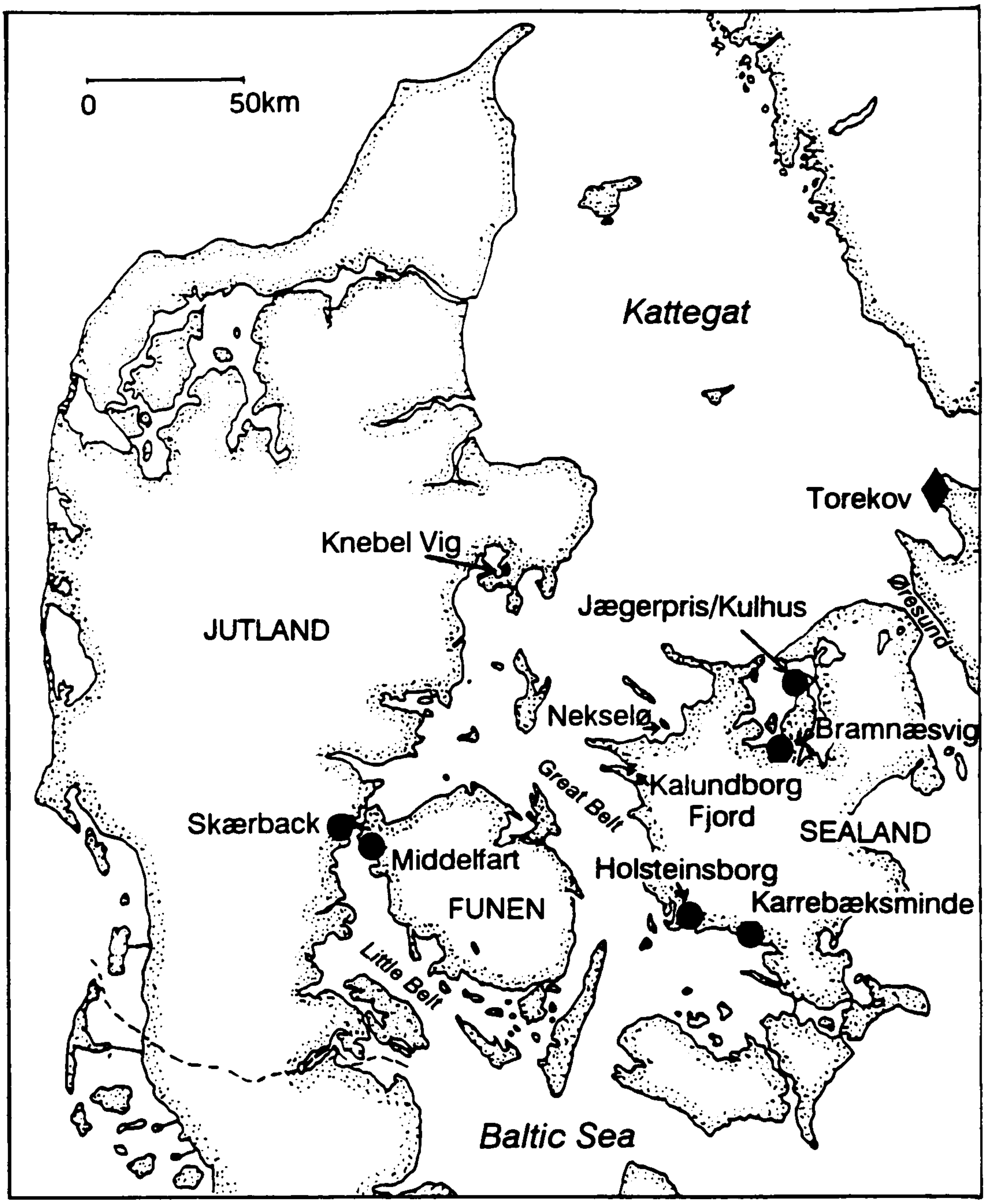

Fig. 1. Catch sites in Danish waters. Major Danish sites are Middelfart, Skærbæk, Bramnæsvig, Jægerspris/Kulhus, Karrebæksminde, 6. Holsteinsborg. Lesser Danish sites are: Knebel Vig, Kalundborg Fjord, Nekselæ. The black diamond indicates one of the Swedish sites at Torekov, the other two sites in the Laholm Bay and at Raflunda are just outside the map.

CATCH SITES

Harbour porpoises have been caught at six main localities (Fig. 1) in the inner Danish waters (Tauber, 1892; Möhl-Hansen, 1954): (1) Middelfart (Gamborg Fjord, Fig. 3); (2) Skærbæk (Kolding Fjord, Fig. 3); (3) Bramsnæsvig; (4) Jægerspris/Kulhus; (5) Karrebæksminde; and (6) Holsteinsborg. Sites (1) and (2) are in the Little Belt and sites (3) and (4) are in the Isefjord area. Harbour porpoises were also taken opportunistically all along the coast, e.g. at Nekselæ in 1529 (Brændegård, 1986), Kalundborg Fjord (Keldbjerg, 1961), and Knebel Vig (Møller, 1961).

Fig. 2. Photograph taken during the World War II catch at Svinæ (see Fig. 3).

(1) Middelfart

The catch was mentioned for the first time in 1357 (Klausen, 1867). The season usually lasted from Martinmass (11 November) and ended at Candlemass (2 February), although it occasionally started some weeks earlier. Catches after Candlemass were referred to as *gribsfangst* ('grabcatch') and were not under the jurisdiction of the guild of porpoise hunters (Petersen, 1969). Catches were discontinued in 1892 but resumed during the two World Wars in 1916–19 and 1941–44 (Berendt, 1921; Petersen, 1969; Brøndegård, 1986).

(2) Skærbæk

The catch at Skærbæk appears to have started in 1867. Catches took place during the same season as the catch in Middelfart and animals from both areas were delivered to the same oil factory in Middelfart. The hunt in both areas ceased in 1892 and the guild was officially dissolved in 1910 (Thomsen, 1991).

(3) Bramsnæsvig

Harbour porpoises were caught during the spring months. The catch was mentioned for the first time in 1402 (Møller, 1961) and continued until some years after World War II.

(4) Jægerspris/Kulhus

Harbour porpoises were caught from March to May (Eschricht, 1849). Although the practice is probably much older, catches are known since 1757 (Møller, 1961) and continued until some years after World War II (Jensen, 1946).

(5) and (6) Karrebæksminde and Holsteinsborg

These catch sites were operative in the 18th and 19th centuries, mainly during spring. By 1840, their importance was negligible (Smidt, 1861), although Tauber (1892) reported annual takes of 100 animals during the 1880s. Holsteinsborg is only mentioned by Möhl-Hansen (1954) and was probably never of great importance.

DESCRIPTION OF THE FISHERIES

The winter drive fisheries at Middelfart and Gamborg Fjord in the Little Belt have been described by several authors (Vilse, 1767; Pontoppidan, 1774; Erichsen, 1781; Bluhme, 1795; Begtrup, 1806; Anon., 1829; Poulsen, 1835; Irminger, 1846; Berendt, 1921 and Möhl-Hansen, 1954). Although there were slight differences in methodology, in general the pods were driven into shallow areas, enclosed by tow nets and pulled ashore (Fig. 3). Ten drive boats, each with a crew of three operated in Middelfart and eight boats with a crew of two operated at Skærbæk along with a three-man net boat (*garnbåd*).

The Skærbæk catch was dependent on the larger Middelfart catch, as all animals were delivered to the same oil factory at Middelfart. During weather conditions suitable for both guilds, the Middelfart guild took their catch first. Porpoises that escaped the Middelfart drive could be taken by the Skærbæk guild. Periods of easterly winds may have prevented catches at Middelfart, when catching was still possible at Skærbæk only (Thomsen, 1991).

The spring fisheries from Jægerspris/Kulhus, Bramsnæsvig, Holsteinsborg and Karrebæksminde used large meshed (6 × 6ins) cotton nets. The nets were mostly arranged as trapnets and examples of such arrangements are shown in Figs. 5A and B. In about 1840, approximately 70 nets were in use at Holsteinsborg and Karrebæksmind (Smidt, 1861).

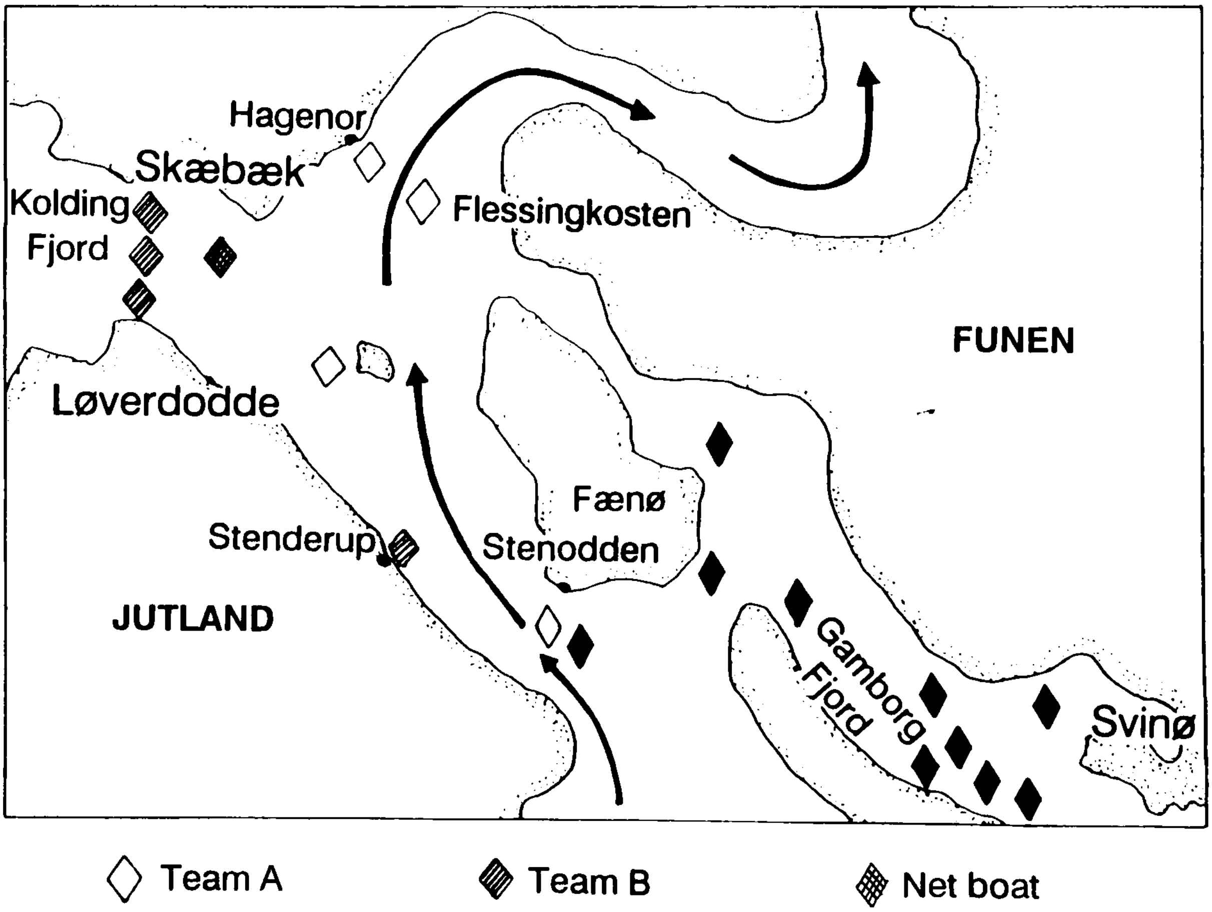

Fig. 3. The catch procedure in the northern Little Belt. Black diamonds indicate the positions of the boats of the Middelfart guild, other diamonds are the positions of the boats of the Skærbæk guild (see key to shading above for Team A, Team B and Net boat). The alternative catch sites of the Skærbæk guild are at Skærbæk and Loverodde respectivelye, the catch site of the Middlefart guild is at Svinø. Redrawn after Peterson (1969) and Thomsen (1991).

Fig. 4. Drawing by J. Mælgård showing the various phases of the catch at Middelfart (reproduced from Petersen (1969)).

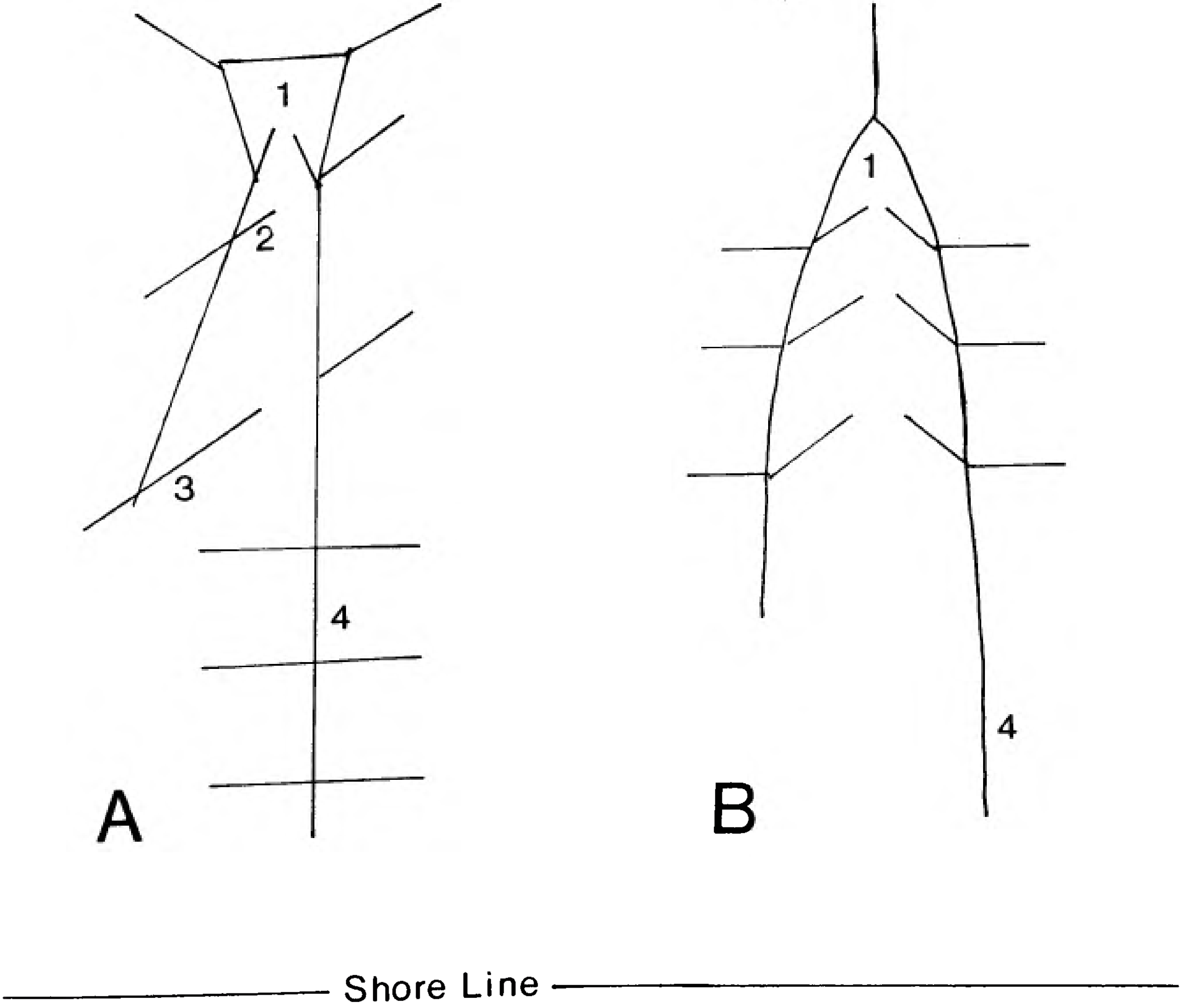

Fig. 5. Labyrinth nets used in the Isefjord area. The mouth of the nets faced the shore line. A = Jægerspris/Kulhus type. B = Bramsnæsvig type. Both types consist of the so-called 'head' (1) where the animals were caught and a left and right 'leg'. The left leg was at Jægerspris/Kulhus made of a series of 'hooks' (2, 3). The right leg (4) was longer and blocked the route of migrating harbour porpoises (redrawn after Møller, 1961)

CATCH DATA

Tauber (1880), presumably referring to the 1860s and 1870s, reported that the total annual take in Danish waters was about 1,400 (Little Belt 1,000; Isefjord area 300; Karrebæk and other places 100). A decade later, Tauber (1892) provided new estimates due to the increased take in the Little Belt and Isefjord areas. Of an estimated annual take of *ca* 3,000 animals, approximately 2,000 were taken in the Little Belt (Middelfart 1,500; Skærbæk 500), 800 in the Isefjord area, 100 in the Karrebæksminde Holsteinborg area and 100 animals as bycatches elsewhere. Exact figures extracted from fishery statistics have been published for the year 1885/86: 1,317 taken at Middelfart; 468 at Skærbæk; 29 at Bramnæsvig; and 103 at Jægerspris/Kulhus giving a total of 1,917 (Drechsel, 1890).

Little Belt

Middelfart 1545–1819

'Large catches' were reported around 1545. Initially tithes (1/6 of the catch) were paid to the local nobleman and later to the Danish king; one man's share (1/31) had to be delivered to the church. The season 1711–12 was poor and again in 1777 a substantial decline was reported with takes decreasing from 500–700 to 100–125 (Petersen, 1969). Erichsen (1781) reported weekly catches of 10, although sometimes up to 40–50; 1780 was mentioned as a fairly good season. According to Begtrup (1806), an average (weekly) drive yielded 30 animals during the best period. Catches ceased almost completely towards the end of the 18th century and up to 1819 (Berendt, 1921) due to a combination of severe ice conditions and lack of interest, although a contemporary German account (Schedel, 1799 cited in Klausen 1867) claiming that thousands of animals were taken with 'harpoons'. Schedel (op. cit.) probably confused the Middelfart catch with the contemporary Faroese take of pilot whales (*Globicephala melas*).

Middelfart 1819–92

Catch data have been compiled for the period 1819 to 1892 and are given in Table 1. The accumulated minimum take for all seasons was 53,092 animals.

Nilsson (1847) reported annual catches between 2,000 and 3,000 occurring, although the maximum attributed catch I could find was 1,684 for the period 1819–1845. According to Wulff (1881) the maximum annual take was 3,000 animals but he did not specify the season and according to Berendt (1921) the largest catch was 2,600. The maximum reported annual take specified to season was 2,200 (1857–58; Smidt, 1861).

The mean take for all seasons with known catch figures was 1,035 animals which is a little lower than earlier published means based on fewer catch figures (1,097, Berendt, 1921; 1,122, Andersen, 1982; Table 2).

Around 1880, a take of 1,000 animals would be considered a poor season, whilst a take of 1,500 was medium and only a season yielding 2,000 or more animals was profitable (Petersen, 1969), i.e. the take became more unprofitable with time.

According to Poulsen (1835) a good daily catch was 20 animals, but catches of up to 80, although uncommon, did occur. In 1833, 112 animals were taken in a single day. The largest daily catch witnessed by Irmiger (1846) was 79, but he reported daily catches of 100 to have taken place. Hofman (1843) reported a daily catch of 135 animals in April 1840. For the season 1857/58 the average daily catch was 40 and the maximum daily catch 92 (Smidt, 1861). The maximum daily take was 154 animals (1872/73 season; Petersen, 1969), but maximum daily takes of more than 100 animals are known from several seasons (Fig. 6).

Table 1

Catch statistics for Middelfart and Skærbæk for the period 1819-1892, 1916-19 and 1941-44. Footnotes: [1] 800 according to Klausen (1867); [2] 765 according to Melchior (1834) and Klausen (1867); [3] 1400-1500; [4] 800-900; [5] calculated from the total catch of the year 1875; [6] 450 according to Middlefart Avis 2nd March 1889; * Minimum take.

Season	Middelfart	Skærbæk	Min. total	Source
1819/20	244	-	244	Anon. (1829)
1820/21	478	-	478	ditto
1821/22	412	-	412	ditto
1822/23	789	-	789	ditto
1823/24	612 [1]	-	612	ditto
1824/25	354	-	354	ditto
1825/26	628	-	628	ditto
1826/27	654	-	654	ditto
1827/28	1,100	-	1,100	ditto
1828/29	739 [2]	-	739	ditto
1829/30	-	-	-	-
1830/31	1,000	-	1,000	Petersen (1969)
1831/32	855	-	855	Klausen (1867)
1832/33	999	-	999	Hofman (1843)
1833/34	1,286	-	1,286	Klausen (1867)
1834/35	1,684	-	1,684	Irmiger (1846)
1835/36	1,215	-	1,215	ditto
1836/37	1,416	-	1,416	ditto
1837/38	653	-	653	ditto
1838/39	886	-	886	ditto
1839/40	657	-	657	ditto
1840/41	683	-	683	ditto
1841/42	793	-	793	ditto
1842/43	1,395	-	1,395	ditto
1843/44	1,079	-	1,079	ditto
1844/45	330	-	330	ditto
1845/46	-	-	-	-
1846/47	-	-	-	-
1847/48	-	-	-	-
1848/49	-	-	-	-
1849/50	-	-	-	-
1850/51	-	-	-	-
1851/52	-	-	-	-
1852/53	-	-	-	-
1853/54	-	-	-	-
1854/55	1,742	-	1,742	Thomsen (1991)
1855/56	-	-	-	-
1856/57	-	-	-	-
1857/58	2,200	-	2,200	Smidt (1861)
1858/59	-	-	-	
1859/60	-	-	-	-
1860/61	-	-	-	-
1861/62	-	-	-	-
1862/63	700	-	700	Thomsen (1991)
1863/64	-	-	-	-
1864/65	-	-	-	-
1865/66	1,000	-	1,000	Thomsen (1991)
1866/67	1,450 [3]	-	1,450	ditto
1867/68	-	300	300	ditto
1868/69	-	-	-	-
1869/70	850 [4]	-	850	Thomsen (1991)

continued overleaf

Table 1 continued

Season	Middelfart	Skærbæk	Min. total	Source
1870/71	160 *	-	160	ditto
1871/72	156 *	-	156	ditto
1872/73	1,297	41 *	1,338	ditto
1873/74	2,031	60 *	2,091	ditto
1874/75	1,300[5]	-	1,300	This paper
1875/76	570	18 *	588	Thomsen (1991)
1876/77	1,135	-	1.135	This paper
1877/78	1,245	80 *	1,325	Thomsen (1991)
1878/79	544	-	544	ditto
1879/80	441	422	863	ditto
1880/81	1,831	476	2,307	Berendt (1921)
1881/82	1,814	353	2,167	ditto
1882/83	1,545	501	2,046	ditto
1883/84	1,505	399	1,904	ditto
1884/85	1,552	450	2,002	ditto
1885/86	1,318	468	1.786	ditto, Drechsel (1890)
1886/87	1,349	481	1,830	ditto, Anon. (1887)
1887/88	1.009	649	1,658	ditto, Thomsen (1991)
1888/89	1,589	317[6]	1,906	ditto
1889/90	992	415	1,407	ditto
1890/91	301	154	455	ditto
1891/92	525	202	727	ditto
1916/17	300	-	300	Berendt (1921)
1917/18	600	-	600	ditto
1918/19	700	-	700	ditto
1941/42	230	-	230	Petersen (1969)
1942/43	329	-	329	ditto
1943/44	421	-	421	ditto

Table 2

Calculated and published mean takes at Middelfart 1819-1892.

Period	Number of seasons	Range	Mean	Sources
1819-29	10	244 - 1,100	601	Anon. (1829)
1829-39	9	653 - 1,684	1,110	This paper
1839-49	6	330 - 1,395	823	ditto
1849-59	2	1,742 - 2,200	1.971	ditto
1859-69	3	700 - 1.450	1,050	ditto
1869-79	8	544 - 2.031	1,122	ditto
1879-89	10	441 - 1.831	1,395	ditto
1889-92	3	301 - 992	606	ditto
All years	51	244 - 2,200	1,035	ditto
All years	37	310 - 2,600	1,097	Berendt (1921)
All years (1982)	24	301 - 1,831	1,122	Andersen
Early 1830s	-	-	1,000	Poulsen (1835)
Late 1830s	-	-	1,000	Hofman (1843)
1850s	-	-	1,100	Smidt (1861)
Late 1870s	-	-	1,000	Tauber (1880)
Early 1880s	-	-	1,500	Tauber (1892)

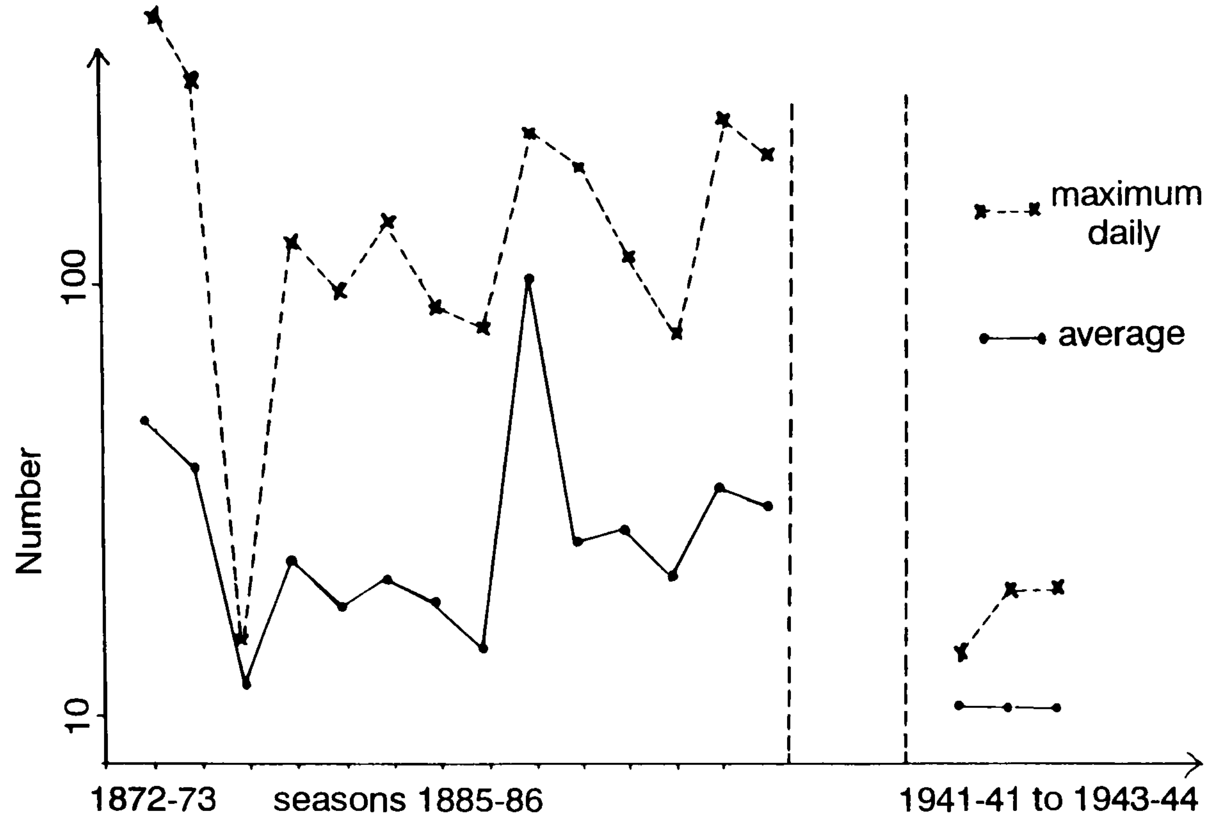

Fig. 6. Maximum and average daily takes at Middelfart during the season 1872/73 – 1885/86 and during World War II.

In seasons with severe ice conditions, the catch season was prolonged to compensate for the lower takes. Sometimes as much as half of the take derived from the grabcatch. During the final phase of exploitation the season was probably also prolonged because the stock was declining. Increasing proportions were taken as grabcatches: in 1881/82 only 7 out of 1,821 (0.4%) were taken outside the season; in 1888/89, however, 200 out of 1,589 (12.6%); in 1889/90 300 out of 992 (30.2%); and in 1890/91 103 out of 301 (34.2%). In the last season 1891/92 only 28 out of 525 (5.3%) were taken as grabcatch (Berendt, 1921; Petersen, 1969), but due to the decreasing profitablity, the catch effort had probably been reduced.

Skærbæk 1819–92

The catch from Skærbæk was smaller than the Middlefart catch, comprising about 25% of the total Little Belt catch for the years 1879–92, although daily catches of 150 animals are known (Berendt, 1921; Thomsen, 1991). For the period 1867 to 1892 catch figures are known for 15 seasons (mean take 382 porpoises) and partly known for another four seasons (1872/73, 1873/74, 1875/76 and 1877/78), giving a total take of 5,936 (Table 1).

Minimum total catch

The minimum total take in the Little Belt area (Middelfart and Skærbæk combined) for the period 1819–1892 was 59,028 porpoises.

Middelfart 1916–19 and 1941–44

During the First World War, 1,600 animals were caught with an annual mean of 533 (Table 1; Berendt, 1921). The resumed catch in the Second World War yielded 980 porpoises with an annual mean of 327 (Table 1; Petersen, 1969). In neither period did the takes reach the levels of the previous century. A comparison of the annual catch figures and maximum and average daily takes at Middelfart for the periods 1872–86, with the Second World War period, reveals a marked decline (Fig. 6).

The Isefjord area

For the period 1860–80, Tauber (1880) estimated a total annual take of 300 animals. In a later account he provided a new estimate for the 1880s of 800 animals annually (Tauber, 1892), showing a substantial increase in the last part of the 19th century.

Bramsnæsvig

In the 1880s, a mean of 60–70 animals were taken annually and this was reported to be only a third of the take of earlier decades (Brøndegård, 1986). The catch figure for 1885 was as low as 29 (Drechsel, 1890). In the years directly after the First World War catches again increased, reaching a maximum of 150 (Struberg, 1936).

Jægerspris/Kulhus

Maximum takes in the 1840s were between 300 and 400 animals per season (Eschricht, 1849). From 1861–1900, annual catches ranged from 70–429 (Smidth, 1864; Brammer, 1872; 1874; 1876; 1878; 1879a; b; 1881a; b; 1882; 1886a; b; 1892a; b; 1894; 1895; 1896; 1898a; b; 1900; 1901; Table 3) with no clear trend, although in 1889, a severe decline was reported from 4–5 porpoises per day during earlier decades to 4–5 porpoises per fortnight (Mortensen, 1889). For a presumed 63 day season (4.5 fortnights) this correlates to a drop from about 250 to 20 animals. During the Second World War (1942–44), the same area yielded only between 520 and 1,295kg per season (Jensen, 1946) or between 15–37 animals (assuming a mean weight of 35kg).

Liseleje to Kikhavn

An annual take of between 240 and 320 animals in the 1860s and early 1870s has been reported (Brammer, 1872; Brøndegård, 1986).

Karrebæksminde and Holsteinsborg

According to Smidth (1861) the catch was very small. For the 1880s, however, Tauber (1892) reported an annual take of about 100 animals. Drechsel (1890) reported no catches for 1885.

Table 3

Catch of harbour porpoises at Jægerspris 1861-1900.

Year	Number	Year	Number	Year	Number
1861	125	1881	180	1891	60
1860s	often >100	1882	-	1892	120
1873	80	1883	390	1893	-
1874	-	1884	200	1894	180
1875	>100	1885	103	1895	160
1876	70	1886	429	1896	212
1877	150	1887	156	1897	110
1878	150	1888	-	1898	120
1879	150	1889	-	1899	151
1880	150	1890	-	1900	300

Other areas

In the Sejræbugten at Nekselæ (Fig. 1), a porpoise catch yielded about 10 tons of oil every year in the 18th century corresponding to approx. 100 harbour porpoises annually (Møller, 1961; Brøndegård, 1986).

DISCUSSION

Kinze (1985) and Yurick and Gaskin (1988) suggested that there may be a separate Baltic stock of harbour porpoises. The original population size and range of such a stock is unknown, but it would probably include porpoises in the inner Danish waters as well as the Baltic proper. There is no information on possible substocks.

The available information reveals a three century long exploitation with mean annual catches of at least 1,000 porpoises in Danish waters. The total annual take from a tentative Baltic population would be even higher as catch sites are also known from the Swedish and the Polish coasts (von Linné, 1749; Nilsson, 1820; 1847; Liljeborg, 1874; Ropelewski, 1957).

There has probably also been a bycatch along the Baltic coast line. Along the southern coast of Sweden (Scania), harbour porpoises were caught during spring in large nets at Torekov (see Fig. 1), in Laholm Bay (Nilsson, 1847) and at Ravlunda (von Linné, 1749). No catch data are available, but the Swedish catch seems to have culminated in the middle of the 19th century, while the Polish catch continued with declining takes until the late 1930s.

Fluctuations have occurred in the Danish catch, both in the Little Belt and the Isefjord area, but a consistently increased take only occurred in the last half of the 19th century, when the catch level doubled in the Little Belt area and may have led to an overexploitation and initiated the decline of the population. In the Isefjord area, the fishery experienced a marked drop during the late 1880s as well, but the catch level increased again in the 1890s and catches may have continued until World War II. However, by 1944 the population had seemingly not 'recovered', as indicated by the information from the Little Belt and Isefjord areas.

An extremely crude estimate of 25,000 for the original population size in Danish waters can be made using the following assumptions:

(1) an average annual catch of 1,000 was sustainable;
(2) the animals can be treated as a single 'population';
(3) the tentative estimate of a sustainable yield level of 4% of the population for California harbour porpoises (Barlow and Hanan, 1995) is applicable.

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A Note on Catches and Exploitation of Harbour Porpoise (*Phocoena phocoena* L. 1758) Around the Faroe Islands

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ABSTRACT

This note provides information on harbour porpoises around the Faroe Islands based on interviews with islanders. The harbour porpoise hunt has never been of importance in the Faroe Islands although in time of food shortage catches did increase. It is not possible to estimate either past or present bycatch levels of harbour porpoises in Faroese fisheries but anecdotal information suggests that incidental catches are not a major problem.

KEYWORDS: NORTH ATLANTIC; HARBOUR PORPOISE; INCIDENTAL CAPTURE; DIRECT CAPTURE; DISTRIBUTION

INTRODUCTION

No systematic records of sightings, observations, bycatches or directed catches of harbour porpoises (*Phocoena phocoena*) have been kept on the Faroe Islands. Until 1986, recorded whaling statistics concerned only the great whales and the long-finned pilot whale. During the North Atlantic Sighting Survey in 1987 (NASS-87), 52 harbour porpoises were sighted in Faroese and adjacent waters but no estimates of abundance were made (Sigurjónsson *et al.*, 1989; Gunnlaugsson and Sigurjónsson, 1990). One harbour porpoise was reported taken at the Faroe Islands in 1987 and 11 in 1988 (Bloch and Hoydal, 1989; 1990). None have been reported since then (Bloch *et al.*, 1991; 1992; Bloch and Hoydal, 1994).

The intention of this note is to summarise the available information on harbour porpoise distribution, hunting and bycatches in Faroese waters.

MATERIAL AND METHODS

Enquiries and interviews concerning the former and present distribution of the harbour porpoise and any direct or incidental takes were made in 1987 in two towns, 25 villages and at all major harbours on the Faroe Islands. Among the 50 persons interviewed, ten had regularly or occasionally hunted porpoises; the remainder were fishermen or associated with the fishing industry. Interviewees were asked about the types of fisheries carried out, the possibility of harbour porpoises being incidentally caught, and whether they could provide past or present information on the distribution or catches of harbour porpoises.

RESULTS AND DISCUSSION

Distribution and abundance

Although harbour porpoises are known throughout the Faroe Islands (Fig. 1) most are seen in the northeastern area. On Fugloy, Borðoy and Eysteroy, 13 persons independently reported their perception that numbers of sea birds and harbour porpoises had declined since World War II, but of course this can neither be verified or quantified on the basis of the interviews.

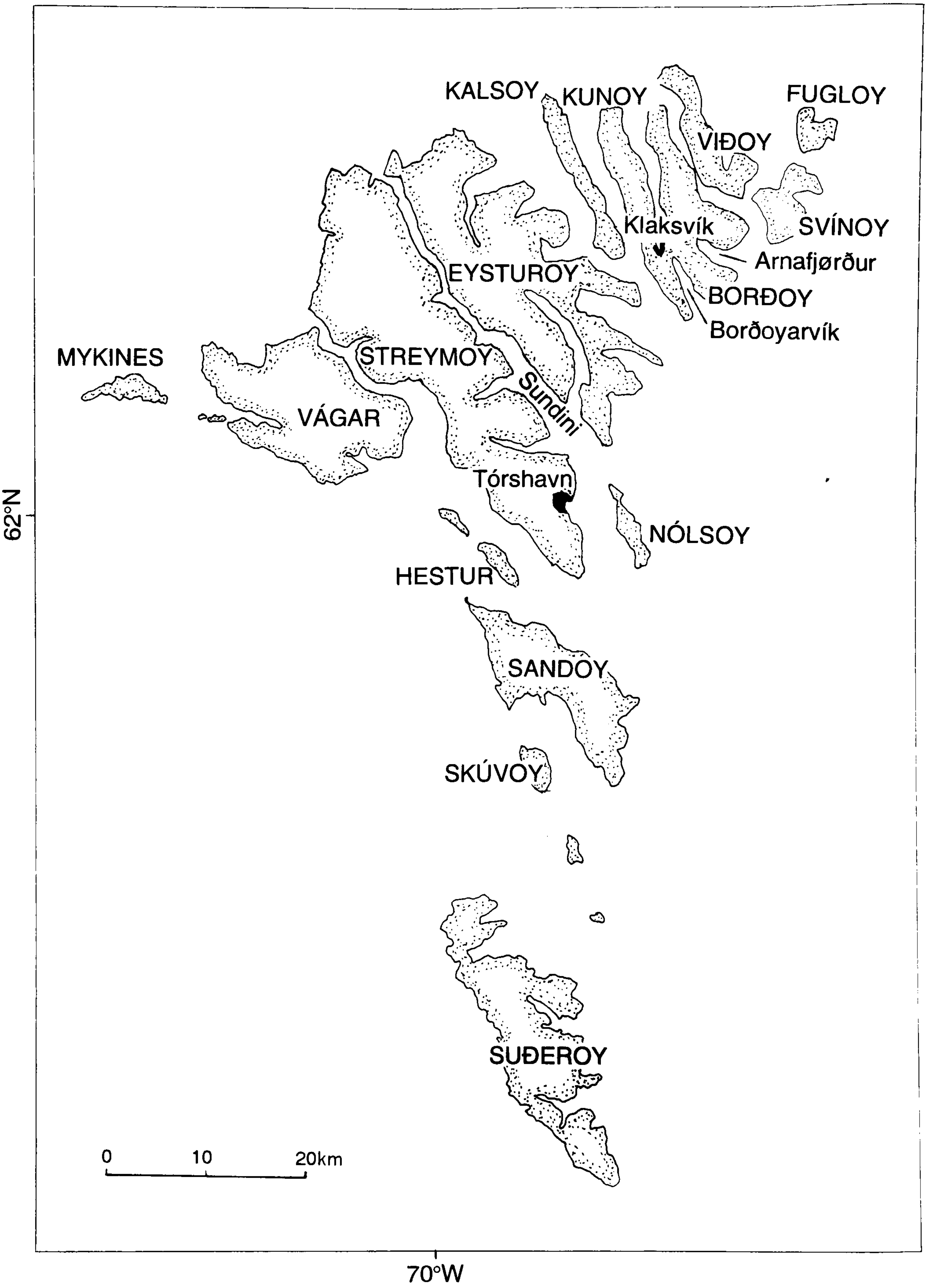

Fig. 1. Map of the Faroe Islands showing place names mentioned in the text.

Off the northern islands, harbour porpoises are most common from May to July-August in both coastal and offshore waters, although Bloch *et al.* (1992) reported year round sightings in Hostfjørður. Calves are seen in June-July. The animals are usually seen as singles or in groups of 2–3, although larger groups are sometimes seen in areas of concentration of the species the fishermen believe are prey species (herring, *Clupea harengus* and sandeel, *Ammodytidae*).

Hunting history and exploitation

Harbour porpoise meat is not as highly valued as pilot whale meat by the Faroese and therefore the harbour porpoise hunt has never been important. At occasional live strandings, the harbour porpoises are killed and the meat and blubber used for human consumption. Mass strandings do not occur.

Around the turn of the century, fishermen from the village of Anunum near Klaksvík went to fish in Iceland and were taught to hunt harbour porpoises using shotguns by the Icelanders; on their return to the Faroes, porpoises were taken when possible (Marius Joenslev, Nordskali; Robert Joensen, Klaksvík, pers. comm.) and the guts were used as bait in the longline fishery.

No harbour porpoises were reported shot near the Faroe Islands before 1935. However, in 1940, freezing facilities became available in Klaksvík and harbour porpoises were hunted and their guts stored for bait. After World War II, fish and squid became the predominant bait.

During the war, and at other times of food shortage, harbour porpoises were also hunted for human consumption. One of the interviewed fishermen from Klaksvík stated that he had raised his children on harbour porpoise meat during the war and reported annual takes of 20 to 40 animals (Hjalgrim Andreasen, pers. comm.). After 1945 the hunt declined. Recently it has been carried out almost exclusively from May-August around Klaksvík, i.e. in Arnafjørður and Borðoyarvík. Annual catches never exceeded 50. In the late 1980s about 10 hunters were involved, occasionally taking porpoises on fishing trips, with annual total takes of 10–20 animals (Otto Joensen, pers. comm.). Shotguns of 16 or 12 calibre and no. 2 or 3 shells were used (Robert Joensen, pers. comm.).

Harbour porpoises were taken in the straits of Sundini during the 1950s and 1960s. One fisherman reported taking 10–20 animals per year, which he noted was not unusual at that time. Harbour porpoises have become less common in the area since the 1960s (Marius Joenslev, pers. comm.).

On Eysturoy, porpoises are occasionally shot. However, there has been no regular hunt since the one hunter left in the 1970s. No hunting has occurred in other islands.

Fisheries and bycatches

Harbour porpoises were sometimes reported entangled and drowned in a driftnet herring fishery that operated from 1951–1969 in deep waters north of the Faroes. Nets drifted not far below the surface.

A fishery for cod (*Gadus morhua* L.) using driftnets has operated since the 1960s but has now been excluded from an area within 30 miles of the shore (Kjártan Hoydal, pers. comm.). Fishermen thought that the porpoises were entangled when the nets were either being set or hauled. The fishermen stated that such incidents were uncommon. Three fishermen interviewed at Eysteroy and Borðoy mentioned that bycatch has occurred in this fishery near the coast, but none were able to estimate its importance. They believed that there are only a few bycatches in the current offshore fishery.

A longline fishery operates for cod, tusk (*Brosme brosme* L.) ling (*Molva molva* L.), haddock (*Melanogrammus aeglefinus* L.) and whiting (*Merlangius merlangus* L.).

Harbour porpoises were reported to very occasionally have been taken on longlines off Fugloy and Eysturoy.

Trawl fisheries began in the Faroe Islands about a century ago but none of the interviewed fishermen knew of any bycatches. Bloch *et al.* (1994) reported a foetus collected from a trawl in 1992.

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Account of Harbour Porpoise (*Phocoena phocoena*) Strandings and Bycatches along the Coast of British Columbia

Robin W. Baird[1,2] and Tamara J. Guenther[1]

ABSTRACT

Little is known about the biology or status of the harbour porpoise (*Phocoena phocoena*) in British Columbia (BC), Canada. In this study, all available records of stranded and incidentally caught harbour porpoise are reviewed. Eighty-one records of stranded animals, or of animals caught in fishing gear along the BC coast, from the period 1934–1991, are presented. The harbour porpoise is the most frequently recorded cetacean stranding on the coast of BC. Stranding records are concentrated where there are large areas of water ranging in depth from 10 to 100m, usually associated with human population centres. Strandings have occurred throughout the year, but biases in effort preclude the determination of any seasonal or geographic trends. Records exist of animals taken incidentally in three commercial fisheries as well as in Canadian government test and research fisheries. Two animals taken incidentally in fisheries in adjacent US waters have also been recovered in BC. In addition, shark predation has been implicated in the death of one individual.

KEYWORDS: NORTH PACIFIC; HARBOUR PORPOISE; STRANDINGS; INCIDENTAL CAPTURE; PREDATOR-PREY; DISTRIBUTION; MOVEMENT; REPRODUCTION

INTRODUCTION

Throughout its range, many populations of the harbour porpoise (*Phocoena phocoena*) appear to be decreasing (Gaskin, 1984). In British Columbia (BC), Canada, little is known about this species, and no directed studies have ever been undertaken. Up until the beginning of this century, harbour porpoises appear to have been regularly taken by natives in this area (Boas, 1909; Drucker, 1951; Suttles, 1951; Barnett, 1955; Waterman, 1973). More recently, Cowan (1988) noted that the harbour porpoise population in BC appears to be decreasing. He suggested that this is most likely to be due to entanglement in fishing gear. Everitt *et al.* (1980) observed that in Puget Sound, Washington, the continual incidental take of this species in salmon gillnets is the most serious factor affecting the growth of the population. They also suggested that the harbour porpoise may be sensitive to pollutants, possibly accounting for its decline in these waters. In their analysis of pollutant levels in seven harbour porpoises from the Strait of Georgia, BC, Muir and Norstrom (1990) noted high levels of dioxins and furans relative to the other species of cetaceans tested. D.E. Gaskin (University of Guelph) recently reviewed the status of the harbour porpoise in Canadian waters and in 1990 recommended to the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) that both the eastern and western Canadian populations of harbour porpoise be listed as threatened (R.R. Campbell, pers. comm.). Although COSEWIC listed the eastern Canadian population as threatened, the Committee concluded that insufficient information was available to classify the western Canadian population (Gaskin, 1992). The purpose of this report is to summarise and present information on harbour porpoises that stranded or were caught incidentally to

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fishing operations on the BC coast. Information on distribution, seasonal movements, length at birth, sex ratio and calving seasonality are presented.

METHODS

Records were collected of animals that: (i) were found dead, either on shore or in the water; (ii) were live-stranded or moribund in the water; or (iii) were caught incidentally during fishing operations. Records of types (i) and (ii) are hereafter referred to as stranding records. All published records were tabulated and further records were obtained from several unpublished reports as well as from the Stranded Whale and Dolphin Program of BC, the Royal British Columbia Museum, the University of British Columbia, the Department of Fisheries and Oceans' (DFO) Pacific Biological Station and the Vancouver Public Aquarium. Whenever possible, sex was recorded, standard length was measured (American Society of Mammalogists, 1961), the ovaries and the uterus were examined for signs of past or current pregnancies, mammary glands were examined for the presence of milk and the testes were examined for the presence of sperm. Most animals were examined for signs of potential entanglement in fishing gear, as described by Hare and Mead (1987).

RESULTS AND DISCUSSION

Harbour porpoises are the most frequently reported cetacean stranding on the BC coast (Baird, unpublished data). A total of 81 records of stranded or incidentally caught animals was compiled, and these records are presented in Appendix 1, with locations shown in Fig. 1. Thirty-four of these records have not been previously reported and an additional nine were compiled from unpublished documents. The trend in the number of stranded and incidentally caught animals recorded annually since 1978 is presented in Fig. 2. The large increase in records since 1987 probably reflects increase in effort, rather than an increase in the number of occurrences. As has been reported elsewhere for this species (cf. Mead, 1979), all records were of single individuals and only a small proportion (7.5%) of the strandings were live animals.

Stranded and incidentally caught harbour porpoises have been recorded along the entire BC coast (Fig. 1). The records are concentrated near human population centres (again probably reflecting levels of effort), in areas where the shoreline is bordered by large areas of water greater than 10m but shallower than 100m in depth. Barlow (1988) noted that no harbour porpoises were seen in waters greater than 110m in depth during surveys off the California coast, and Watts and Gaskin (1985) observed that harbour porpoises appear to avoid narrow shelf regions with strong currents. Sighting records of harbour porpoises from around the southeastern tip of Vancouver Island similarly showed concentrations in broad areas of water ranging in depth from 20 to 100m, with few records in water outside that depth range, or in areas with a steep slope (Baird and Guenther, 1991). More effort is required in areas of the coastline where there is little or no human settlement yet extensive shallow habitat, presumably suitable for harbour porpoises.

Polacheck *et al.* (1995) note the value of using stranding records to examine seasonal migrations in the harbour porpoise. The seasonal distribution of stranding records for BC is shown in Fig. 3. The spring through fall peak in stranding records probably reflects a lack of effort during winter months. Records collected in this study do not indicate any North-South movement, as seems to occur in the western North Atlantic (Gaskin, 1992). The seasonal distribution of records in northerly areas in the province generally matches that of southerly areas, although this may possibly be due to the limited latitudinal range

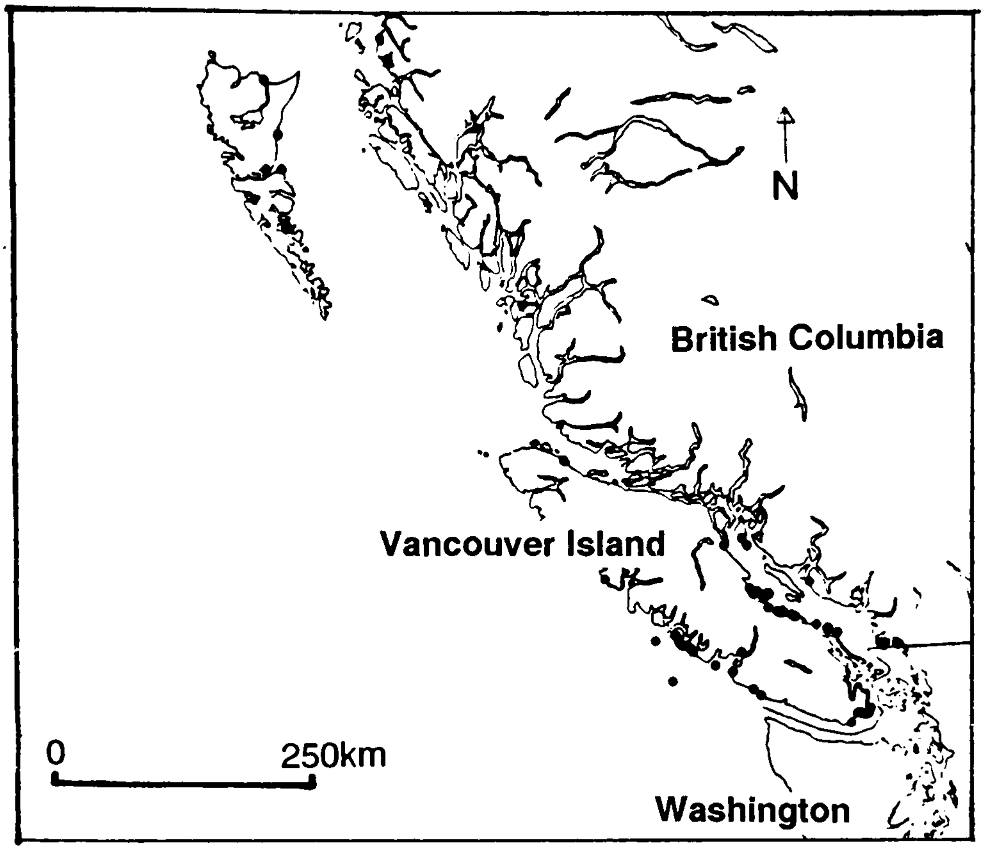

Fig. 1. Geographic distribution of stranding and incidental catch records of harbour porpoises in BC waters.

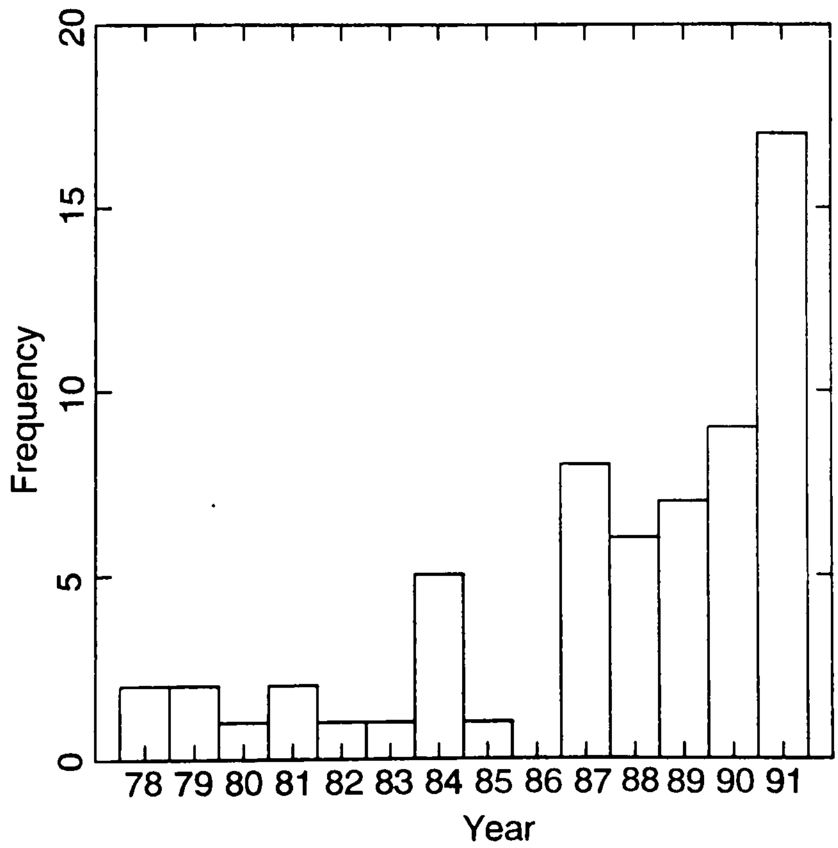

Fig. 2. Trend in the number of stranding and incidental catch records of harbour porpoise recorded annually since 1978 (n=62). Recent increases probably reflect increased effort.

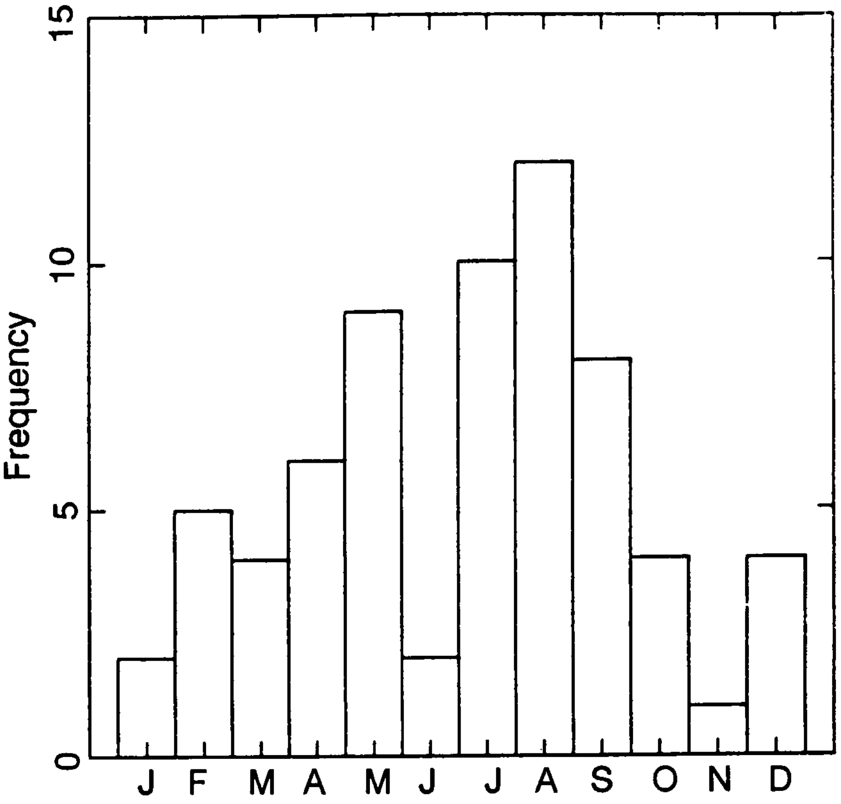

Fig. 3. Monthly distribution of 67 harbour porpoise stranding records in BC. Incidental catch records are not included here since all Canadian fisheries which have been conclusively recorded to catch harbour porpoises since 1981 take place between May and October.

covered by the records. Virtually all commercial fisheries are undertaken during the period from May through October, so the records of incidentally caught animals (not included in Fig. 3) are biased towards these months.

Total length was tabulated for 47 stranded and incidentally caught animals (Fig. 4). Total length was also noted for four foetuses. The smallest recorded neonate was 78.2cm, while the largest foetus was 77.0cm (Appendix 1). Gaskin *et al.* (1974) summarised information on length at birth in this species with neonatal lengths ranging from 70.0 to 99.1cm. Records from BC generally fall in the middle of this range. The size distribution in Fig. 4 indicates several peaks, with the first representing neonatal mortality. Such a neonatal peak was not apparent in the size distribution of 276 harbour porpoises stranded along the US northeastern coast (Polacheck *et al.*, 1994). Their data included animals killed in bottom set net fisheries off the US East coast. Read (1990a) noted that calves may be under-represented in this catch because they may not be able to dive to depths where the nets are set. The salmon drift gillnet fishery in BC is a surface fishery, and thus is unlikely to have a bias towards older animals as on the East coast. However, only one calf was recorded as being caught in fishing gear in BC. The mean length of stranded animals in BC was greater than that recorded by Polacheck *et al.* (1995). The largest animal recorded from BC was a 197cm female, which is close to the maximum recorded length for this species (Leatherwood and Reeves, 1983).

The sex for 61 harbour porpoises was noted (including two foetuses) from BC, with almost equal numbers of males (30) and females (31). Accurate determination of pregnancy rates in BC populations is not possible because of the small sample size and unequal seasonal distribution of records. Information derived from stranded animals however may help define calving seasonality, based on: (i) animals which had recently calved; (ii) the size of foetuses; and (iii) the presence of neonates (defined here as animals

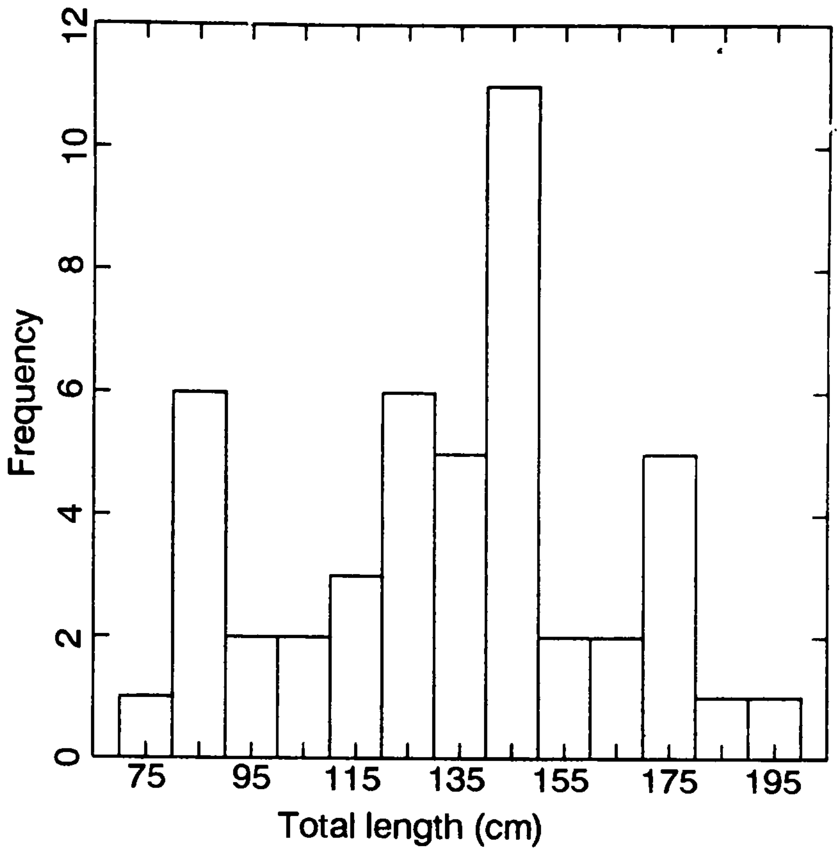

Fig. 4. Length distribution of 47 stranded and incidentally caught harbour porpoises in BC. X-axis labels represent the mid-point for each size class interval.

less than 100cm in length). Calving appears to extend from May through September, but one large (estimated 70cm) foetus was recorded from December, indicating that some calving must occur in early spring as well. Read (1990b) noted a distinct synchronisation of calving in May by the harbour porpoise in the western North Atlantic. Off California, calving appears to occur from May through July (Simons, 1984).

At least 12 animals were caught in fishing gear, ten of which were killed. More animals may have died from entanglement, since not all specimens were examined closely, and some may have died with no obvious signs of entanglement. In addition, external markings may become obliterated due to abrasion on a beach, decomposition or damage from scavengers. Mortality was noted in three commercial fisheries (salmon troll, salmon drift gillnet, hake trawl), as well as one research fishery (dogfish shark) and one test fishery (salmon drift gillnet) undertaken by the Canadian DFO. In addition, two harbour porpoises were recorded with signs of net entanglement which can be attributed to a monofilament set gillnet fishery for salmon by US native Americans in Semiahmoo Bay, Washington. These animals were recovered in the Boundary Bay-White Rock area in Canada, immediately adjacent to Washington State, in an area where no inshore or offshore Canadian fisheries were being undertaken.

Absolute levels of incidental mortality cannot be estimated using existing stranding data. Stacey *et al.* (1990) used data collected through a questionnaire survey of fisherman in BC to produce an estimate of incidental mortality of this and other species of small cetaceans. They estimated at least 43–59 individuals are killed annually, which is much greater than the number recorded through strandings or from occasional reports by fishermen. In addition, biases inherent in such questionnaire surveys typically result in a large underestimation of mortality levels (e.g. see Lien *et al.*, 1994).

One animal found dead had been attacked by a shark, judging by the wounds. Sharks have not previously been recorded as predators of harbour porpoises in British Columbia, although this has been noted elsewhere (Arnold, 1972). Harbour porpoise predation by transient killer whales (*Orcinus orca*) is regularly recorded in BC (Morton, 1990; Baird, unpublished data). One harbour porpoise specimen in the collection of the Royal British Columbia Museum was recovered floating at the surface after being partially eaten by two killer whales, so such remains may occasionally wash on shore and be recorded as stranded.

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Appendix 1

RECORDS OF STRANDED AND INCIDENTALLY CAUGHT HARBOUR PORPOISES WITHIN BC. ALL RECORDS ARE OF SINGLE INDIVIDUALS.

Date	Type[1]	Location	Sex	Source[2]	Length (cm)	Comments[3]
00/07/34	1	Nootka I	F	1		BCPM 3630
00/08/39	1	Hardy Bay, VI[4]	M	1		BCPM 4556
00/08/40	1	Victoria, VI	M	1		BCPM 4757, skeleton to UBC, immature
00/07/42	1	Herrando I	U	1		BCPM 4935, skeleton discarded
17/07/43	1	Cortes I, Mary I	U	2		BCPM 4999, mature
00/03/46	1	Qualicum VI	U	1		BCPM 5215, mature
11/05/46	1	Queen Charlotte City?	F	1		UBC 1880
12/07/48	1	Bella Bella, Denny I	F	1		UBC 2796
14/06/57	1	Massett, Graham I	U	2		UBC 13427, immature
10/02/62	2	Baynes Sound, VI	M	1	147	PBS, skeleton discarded, unspecified gillnet
11/10/64	1	Long Beach, VI	F	3	125.6	UBC 9055
Summ. 65	1	Long Beach, VI	U	4		Not recovered
21/02/69	3	Tofino Inlet, VI	M	3	134	
11/07/70	4	Pearl Harbour	U	2		Salmon gillnet
10/08/70	5	Nanaimo, VI	M	2	97.5	CMN, circling at surface
28/03/71	1	Long Beach, VI	F	3	159	Shot, not recovered?, foetus 53.5cm TL
26/02/74	1	Qualicum Bay, VI	M	2		Not recovered
25/07/75	1	Victoria, VI	F	2	176.5	BCPM 9249, mature
00/09/76	6	Pender Harbour	F	2	167.6	VPA, died
07/05/78	1	Qualicum Beach, VI	M	2	128.3	Not recovered, mature
Fall 78	1	Ten Mile Pt, VI	U	2		RBCM?, mature
00/05/79	1	Tofino, VI	F	2		Female not recovered, foetus male 75.5cm TL
07/08/79	7	Parksville, VI	F	2	80.7	Not recovered
00/07/80	1	Bamfield, VI	M	2		BCPM 10098, immature
30/07/81	1	Prince Rupert Harbour	F	2	124.5	Not recovered?, entanglement?
15/08/81	2	10 miles S Flores I	F	2	102.0	BCPM 12833, salmon troll fishery
07/04/82	1	Denman I	U	2		BCPM 11209, mature
05/08/83	7	Qualicum Beach, VI	F	5	170.0	BCPM 11767, recently calved
27/07/84	1	Crescent Beach	U	6		Not recovered?
02/08/84	1	Crescent Beach	F	6	182	Not recovered?
18/08/84	1	Gabriola I	M	6	81.5	Not recovered?, had breathed
23/08/84	1	Esquimalt, VI	F	2	102.0	BCPM 12694, immature
04/09/84	1	Long Beach, VI	F	6	177	PRNP, lactating
09/03/85	1	N of Qualicum, VI	M	2	149	Not recovered
17/02/87	1	Victoria, VI	F	7,8	167E[5]	BCPM 16042, foetus 31cm TL
29/04/87	1	Victoria, VI	F	8,9		BCPM 16118
01/05/87	1	Victoria, VI	F	8,9	118.5	BCPM 16119
11/05/87	1	Campbell River, VI	F	8,9	179	RBCM, had calved within days
25/08/87	1	Olibar Pt, Gabriola I	F	8,9	96	BCPM 16648
17/11/87	1	Sandspit, Moresby I	M	8,9	146	BCPM 16638, entanglement?
12/12/87	1	Long Beach, VI	M	8,9	147	BCPM 16647
12/12/87	1	Tsawwassen	F	8,9	161	BCPM 16650
23/05/88	1	Victoria, VI	M	10	144	BCPM 16655
23/05/88	1	Metchosin, VI	U	10	106E	Not recovered
00/07/88	1	Long Beach, VI	U	10		Not recovered
02/09/88	1	Union Bay, VI	F	10	84	Collected
23/09/88	2	La Perouse Bank	U	10		Not recovered, foreign bottomfish trawler
15/10/88	1,2	Hornby I	M	10	140	Sidney Mus. MM990.1, salmon? gillnet

Appendix 1—*continued.*

Date	Type[1]	Location	Sex	Source[2]	Length (cm)	Comments[3]
29/01/89	1	Boundary Bay	F	11	135	SWDP89-01
25/02/89	1	Tlell River, Graham I	U	11	124E	NPP
19/03/89	1	Tlell River, Graham I	U	11		CMN
12/05/89	2	Qualicum Beach, VI	F	11	197	SWDP89-09, DFO salmon gillnet test fishery
14/07/89	1	Wickaninnish Beach, VI	M	11	88.2	SFU, had breathed
20/09/89	1	Long Beach, VI	U	11		Not recovered
24/10/89	1	Tlell, Graham I	U	11		Not recovered
21/04/90	1	Clover Pt, Victoria, VI	M	12	119	UVIC
25/07/90	2	Qualicum River, VI	M	12	146	BMS, skeleton discarded, dogfish research sunken set gillnet
06/08/90	1	Clark I, Broken Group	U	12		Not recovered
00/09/90	1	Cox Bay, VI	U	12	122E	Not recovered
18/09/90	1	Wickaninnish Beach, VI	U	12	122E	Not recovered
25/09/90	1	Victoria, VI	M	12	86	RBCM
00/10/90	1	Loch Bay, Gabriola I	U	12	61E	Not recovered
11/10/90	1	Tofino, VI	U	12	122E	Not recovered
08/12/90	1	NE Side Vance I	F	12	190E	SFU, foetus 70E cm TL
14/01/91	1	Hornby I	F	2	128	Collected, entanglement?, immature
08/02/91	1	Kildonan, VI	M	2	134.6	Skeleton discarded, immature
08/04/91	1	Pedder Bay, VI	U	2		Not recovered
16/04/91	1,2	White Rock	F	2	143.0	SWDP91-07, native US salmon set gillnet, immature
18/04/91	1	White Rock	M	2	149.2	SIC
26/04/91	1	Victoria Harbour, VI	M	2	114.8	SWDP91-09
09/05/91	1	Esquimalt, VI	M	2	120.6	Sidney Museum MM991.1
14/05/91	1,2	Boundary Bay	F	2	159.0	VPA, native US salmon set gillnet, immature
15/05/91	1	Saxe Pt, Esquimalt, VI	F	2	143.4	UVIC, immature
15/06/91	1,8	Craig Bay, VI	M	2	134	AC, partially eaten by a shark
20/08/91	1	NE shore Hornby I	M	2	78.2	SWDP91-36, had breathed
23/08/91	1	NE shore Hornby I	F	2	88	RBCM, likely had breathed
07/09/91	1	N side Gabriola I	F	2	176.6	SWDP91-38, fetus UVIC male 77.0cm TL
07/09/91	4,6	Bamfield Inlet, VI	M	2	90E	Pt. Defiance zoo and aquarium, died
15/10/91	2	Qualicum, VI	M	2	131	NIWRA, DFO salmon drift gillnet test fishery
25/10/91	2	Off Nitinat, VI	M	2	149	SWDP91-43, salmon drift gillnet fishery, mature
30/12/91	1	Carmanah Pt, VI	M	2	120.1	RBCM, immature

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[1] Type: 1, found dead on beach or floating; 2, incidental catch, died; 3, live stranding, returned to water; 4, collided with fishing gear, not killed; 5, taken deliberately; 6, live stranded, taken into captivity; 7, live stranded, died; 8, killed by predators.

[2] Source: 1. Pike and MacAskie, 1969; 2. unpublished records collected from the Royal BC Museum, Department of Fisheries and Oceans, University of British Columbia, the Vancouver Public Aquarium and the Stranded Whale and Dolphin Program of BC; 3. Hatler, 1972; 4. Buffam, 1965; 5. Goodman, 1984; 6. Anon., 1985; 7. Cooper, 1987; 8. Baird *et al.*, 1988; 9. Anon., 1988; 10. Stacey *et al.*, 1989; 11. Langelier *et al.*, 1990; 12. Baird *et al.*, 1991. Note: Dates may differ from published sources if available unpublished details indicate the animal first stranded on an earlier date. Similarly, sex was occasionally misreported in earlier sources, and has been changed here based on available unpublished data.

[3] Comments: Locations of specimens noted where applicable. BCPM or RBCM = Royal British Columbia Museum, Victoria, BC. UBC = University of British Columbia, Vancouver, BC. PBS = Pacific Biological Station, Nanaimo, BC. DFO = Department of Fisheries and Oceans. PRNP = Pacific Rim

Appendix 1—*continued*

National Park, Ucluelet, BC. SWDP = Stranded Whale and Dolphin Program of BC, Victoria. NPP = Naikoon Provincial Park, Tlell, BC. CMN = Canadian Museum of Nature, Ottawa, ON. SFU = Simon Fraser University, Burnaby, BC. SIC = Stubbs Island Charters, Telegraph Cove, BC. VPA = Vancouver Public Aquarium, Vancouver, BC. BMS = Bamfield Marine Station, Bamfield, BC. UVIC = University of Victoria, BC. AC = Arctic College, Fort Smith, NWT. NIWRA = North Island Wildlife Recovery Association, Errington, BC.

[4] VI = Vancouver Island.

[5] E = estimated length.

Note: Canada (1988) reported a female harbour porpoise stranded in Sooke, BC on 27 August 1987, for which the skeleton was deposited in the Royal British Columbia Museum. However, this animal was misidentified, and was actually a Dall's porpoise.

SC/42/SM39

What Do Stranding Data Say about Harbor Porpoises (*Phocoena phocoena*)?

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ABSTRACT

The Smithsonian National Museum of Natural History maintains a centralized database on marine mammal strandings that occur along the eastern United States coastline. Data from this stranding database plus additional stranding data located from the state of Massachusetts are examined for information on harbor porpoises in the northwestern Atlantic. The data indicate that the winter distribution of harbor porpoises extends further south than previously reported and supports published studies which describe a seasonal north/south migration. Analyses of mature females indicates a high pregnancy rate and incidental kill records raise questions about the geographic extent of potential fishery interactions beyond those previously documented for bottom tending gillnet fisheries in the Gulf of Maine and Bay of Fundy.

KEYWORDS: HARBOUR PORPOISE; NORTH ATLANTIC; STRANDINGS; MIGRATION; INCIDENTAL CAPTURE

INTRODUCTION

Despite the growing concern about the status of the harbor porpoise (*Phocoena phocoena*) population(s) that inhabits the Bay of Fundy and waters off the eastern US coast, because of incidental takes in bottom tending gillnet fisheries (e.g. see summary in Read, 1994), relatively little is known about this population.

An extensive network of researchers coordinates data collection on stranded marine mammals from coastal areas of the United States. Most of the information is included in a single database maintained by the Smithsonian National Museum of Natural History in Washington DC. The harbor porpoise is one of the most common marine mammal species found stranded (usually dead) along the US east coast.

Prescott and Fiorelli (1980) reviewed the information on harbor porpoise strandings through 1979, but there were only a few years of systematically collected data available at that time.

The purpose of this paper is to analyze the information contained in the Smithsonian stranding database up to 1989, plus additional stranding data that we have located from

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Massachusetts, to form a basis to understand more fully the potential value of stranding data to provide information on the biology of harbor porpoises.

MATERIALS AND METHODS

A copy was obtained of all harbor porpoise records from the North Atlantic contained in the stranding database compiled by the United States Natural History Museum, Smithsonian Institute, Washington D.C. The information is derived from the Marine Mammal Events Program (MMEP) and the Scientific Event Alert Network (SEAN) of the Smithsonian. Our analyses include known stranded animals from 1975 to 1989. The first year of the broad-based SEAN program was 1975. Field data are supplied by Regional Stranding Networks, which coordinate the actual collection of field and laboratory data. Regional Stranding Networks comprise numerous dedicated individuals and institutions which respond to reports of strandings from Delaware to Canada. Participating institutions in the northeast United States include the College of the Atlantic, New England Aquarium, Mystic Marinelife Aquarium, The Okenos Foundation, New Jersey Marine Mammal Stranding Center, Smithsonian Institution and US National Parks Service.

The information stored in this database includes, where possible: the location of the stranding, the number of animals stranded, the stranding date, the length of the animal, sex, reproductive condition, and whether incidental fishery take was suspected as the cause of death. We have used the data from the Smithsonian database as supplied with a few minor corrections. For animals which were still alive when found stranded, data have not been consistently recorded; in some cases, date of death is recorded while in other cases it is the date of stranding. In one case that we are aware of, an animal stranded alive and lived for nearly three years in an aquarium. We have changed the date contained in the original database for this animal to the date of stranding and have treated the data on length for this record as missing since the recorded length refers to the length at the time of death and not at time of stranding. Three records were for strandings outside the USA and were excluded from our analyses.

Included within the Smithsonian database are records for animals for which the reported cause of death was fishery entrapment or entanglement. The actual number of incidental fishery take records for harbor porpoises is small (19 out of a total of 378). We have not included these records in our analyses of 'natural' strandings, but discuss these data separately (some of the 'natural' strandings may include animals which were incidentally killed in fisheries but which were not recognized as such).

Information for strandings in Massachusetts was supplemented by a review of the original stranding and necropsy reports collected by the New England Aquarium Stranding and Salvage Network, Boston, Massachusetts. Other sources of information include: Glover Allen Collection, Museum of Comparative Zoology, Harvard University; Col. E.S. Clark Collection, Greenbriar Nature Center, Sandwich, MA and the *Cape Cod Standard Times*. These sources provided greater detail and information about the stranded animals, particularly with respect to the animal's reproductive state and blubber thickness. In addition, they provided information on 59 strandings since 1975 which were not included in the Smithsonian database and 25 strandings prior to that year.

We have based our primary analyses on the information contained in the Smithsonian database since these data are representative of the entire US east coast. However, we also present results from the supplemental data for Massachusetts where the added detail or increased sample size was important. We distinguish these two sources of data in the results.

Most harbor porpoises strand singly. Only 13 out of the 358 stranding events in the Smithsonian database include more than a single individual. Nine of these instances involved two animals, three involved three and one included four. All but two of these multiple strandings occurred during February and March of 1977 along the North Carolina coast. We have based our analyses on the number of stranded individuals and not the number of stranding events. Annual results were not based on the calendar year but used the 12 month period running from 1 August of one year to 31 July of the following year. This was done because few strandings occur during the summer months and because the annual calving season ends in July (Gaskin *et al.*, 1984; Read, 1989).

RESULTS AND DISCUSSION

Spatial distribution

Harbor porpoise strandings have been reported in every state along the eastern coast of the United States with the exception of Rhode Island Delaware, South Carolina and Georgia (Fig. 1 and Table 1). The two strandings in Florida (one in 1984 and the other in 1985) represent a southern extension to the recorded limit for the distribution of this species in the western Atlantic. The latitude of the southernmost stranding was between 28° and 29°N. The previously reported southern limit was 34°N from strandings in North Carolina (Prescott and Fiorelli, 1980; Gaskin, 1984). Two strandings are clearly

Table 1

The number of reported stranded individual harbor porpoise in the Smithsonian stranding database by state and year of stranding. Note that years are not calendar years but run from August 1 for the year to July 31 of the following year.

	Year														
State	75/ 76	76/ 77	77/ 78	78/ 79	79/ 80	80/ 81	81/ 82	82/ 83	83/ 84	84/ 85	85/ 86	86/ 87	87/ 88	88/ 89[1]	Total
Maine	2	5	2	1	5	2	2	3	0	2	4	1	1	1	31
N.H.	0	0	0	0	2	1	2	1	1	1	0	2	0	0	10
Mass.	5	17	20	11	37	7	40	3	8	5	5	24	5	0	187
R.I.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Conn.	1	0	0	1	0	0	0	0	0	0	0	0	1	0	3
N.Y.	4	0	0	0	0	1	0	1	0	0	3	3	2	0	14
N.J.	0	0	1	1	2	0	2	0	0	4	2	2	3	1	18
Dela.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mary.	0	0	0	0	0	0	0	0	0	0	0	4	0	0	4
Virg.	1	3	1	2	2	0	0	0	0	2	1	9	3	0	24
N.C.	0	60	7	1	0	1	0	0	1	0	0	13	0	0	83
S.C.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Georgia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Florida	0	0	0	0	0	0	0	0	1	1	0	0	0	0	2
Total	13	85	31	17	48	12	46	8	11	15	15	58	15	2	376[2]

[1] Data for 1988/89 are incomplete.

[2] Note that total of 376 is not inconsistent with the total of 378 stranding records (19 of which were incidental takes) cited in the methods section since the total in this table represents number of individuals and 13 stranding records involve more than a single animal.

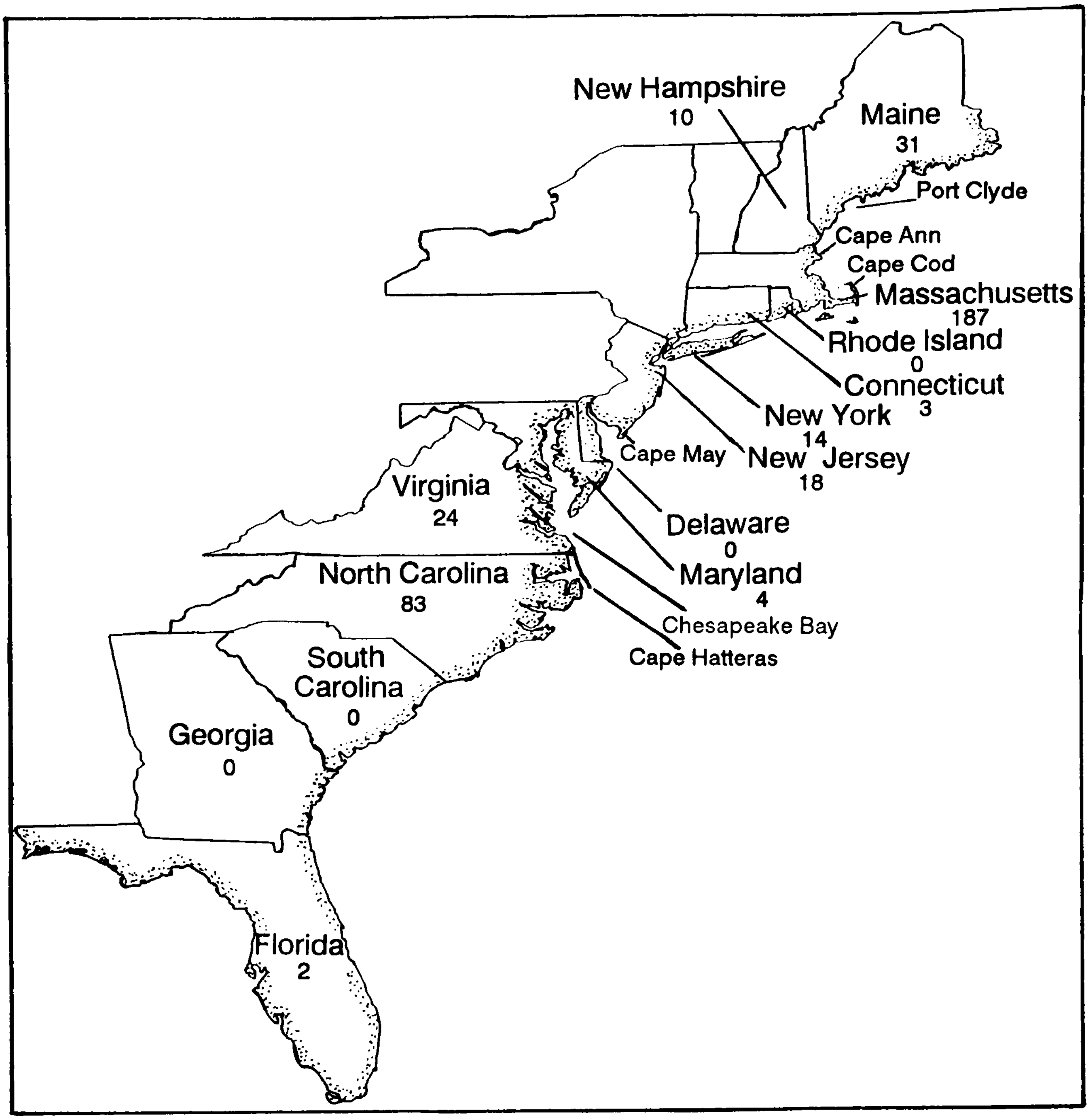

Fig. 1. Map of whole area (showing total number of reported strandings by state and names mentioned in the text).

insufficient to draw any conclusion about how common it is for harbor porpoise to occur this far south. However, it should be noted that the northerly Gulf stream current which flows along the Florida coast means that it is unlikely that these two strandings represent animals which had died a considerable distance to the north and drifted south.

The stranding data show that animals regularly occur in waters as far south as North Carolina and Virginia and that the coastal inshore waters of these two states should be considered as part of the normal habitat for harbor porpoises in the northwestern Atlantic. Thus, strandings have been reported for Virginia in 9 out of the 13 years with complete data and for North Carolina in 6 out of 13. Also, North Carolina has the second highest number of reported strandings ($n=83$) of any state after Massachusetts ($n=187$). Although over three quarters (60) of the strandings in North Carolina occurred in a single year (spring of 1977), excluding this year still results in North Carolina ranking fourth and

Virginia third in the total number of strandings after Massachusetts and Maine. The US National Park Service conducts regular and frequent surveys for stranded animals for over 100 miles of Cape Hatteras National Seashore, North Carolina (J. Mead, pers. comm.). These regular surveys may result in a higher rate of reporting and may account for the large number of strandings recorded from North Carolina. The inclusion of the waters off North Carolina and Virginia within the normal range of harbor porpoises also represents a southern extension. Previously, Cape May, New Jersey had been described as the typical southern limit of the range in the western Atlantic (Gaskin, 1984).

Five strandings and two incidental kills have been reported inside Chesapeake Bay. These strandings and incidental kills occurred during March to May in five different years (1976, 1977, 1987, 1988 and 1989) and indicate that this estuary system is part of the winter/spring habitat for harbor porpoises. However, the lack of any strandings between 1977 and 1987 raises some questions as to how regularly animals frequent this area. These strandings are consistent with an earlier report of regular sightings of harbor porpoises within Chesapeake in Prescott and Fiorelli (1980). M. Payne (pers. comm., Manomet Bird Observatory, Manomet, MA, USA) has also seen harbor porpoises in recent years inside Chesapeake Bay.

Seasonal distribution

Harbor porpoises have stranded each month of the year in Maine and Massachusetts, while no strandings have been reported during the six month period from July to December for states south of Massachusetts (Table 2). This pattern is consistent with earlier studies which have reported year round residents in the Gulf of Maine/Bay of Fundy region combined with a north/south and possible inshore/off-shore seasonal migration for a large portion of the population (Winn, 1982; Gaskin, 1984; Kraus and Prescott, 1984). The probability that a stranded animal is actually located and reported

Table 2

The number of reported stranded individual harbor porpoise in the Smithsonian stranding database by state and month of stranding.

	Month											
State	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
Maine	1	2	3	1	2	2	5	3	3	4	1	4
N.H.	2	1	0	3	0	2	0	0	0	1	1	0
Mass.*	13	27	55	25	9	7	6	1	3	7	15	18
R.I.	0	0	0	0	0	0	0	0	0	0	0	0
Conn.	0	0	2	1	0	0	0	0	0	0	0	0
New York	3	1	6	3	1	0	0	0	0	0	0	0
New Jersey	1	1	5	10	1	0	0	0	0	0	0	0
Delaware	0	0	0	0	0	0	0	0	0	0	0	0
Maryland	0	1	0	2	1	0	0	0	0	0	0	0
Virginia	1	0	7	13	2	1	0	0	0	0	0	0
N.C.	2	15	47	14	5	0	0	0	0	0	0	0
S.C.	0	0	0	0	0	0	0	0	0	0	0	0
Georgia	0	0	0	0	0	0	0	0	0	0	0	0
Florida	0	0	2	0	0	0	0	0	0	0	0	0
Total	23	48	127	72	2	12	11	4	6	12	17	22

* Note the month was not recorded for one stranding in Massachusetts.

would be expected to be greatest during the summer months, since this is the period when beaches are most used. Thus, the lack of summer strandings for states south of Massachusetts would appear to be convincing evidence that animals seasonally migrate from these southern coastal waters.

The strandings within Massachusetts (including the supplemental strandings) were divided into four finer scale spatial regions (Fig. 2) to examine the summer southern limits of distribution. The spatial distribution of these strandings appears to be relatively constant throughout the year with little evidence of a seasonal shift. From January to June, 59% of the strandings (*n*=201) occur in the regions of Cape Cod Bay and further south. From July to September, the percentage for these two regions is still 53%, although the sample size is small (*n*=17).

The occurrence and lack of change in the proportion of strandings in the summer months in southern Massachusetts is inconsistent with results from sighting surveys. Only a few harbor porpoises were sighted south of Cape Ann in summer months during the extensive aerial sighting surveys conducted by CeTAP (Winn, 1982). Although these sightings were all off-shore on Georges Bank, Kraus *et al.* (1983) saw no animals south of Port Clyde, Maine in July 1982 during a coastal sighting survey dedicated to harbor porpoises. In addition, sightings during July to September are extremely rare in the southern Gulf of Maine, Cape Cod Bay and Massachusetts Bay area despite large data collection programs based on extensive sighting effort from whale watch and research vessels (conducted by The Center for Coastal Studies, Provincetown, MA, Plymouth Marine Mammal Research Center, Plymouth, MA and Atlantic Cetacean Research Center, Glouster, MA; F. Wenzel, pers. comm.; and by CeTAP, Winn, 1982).

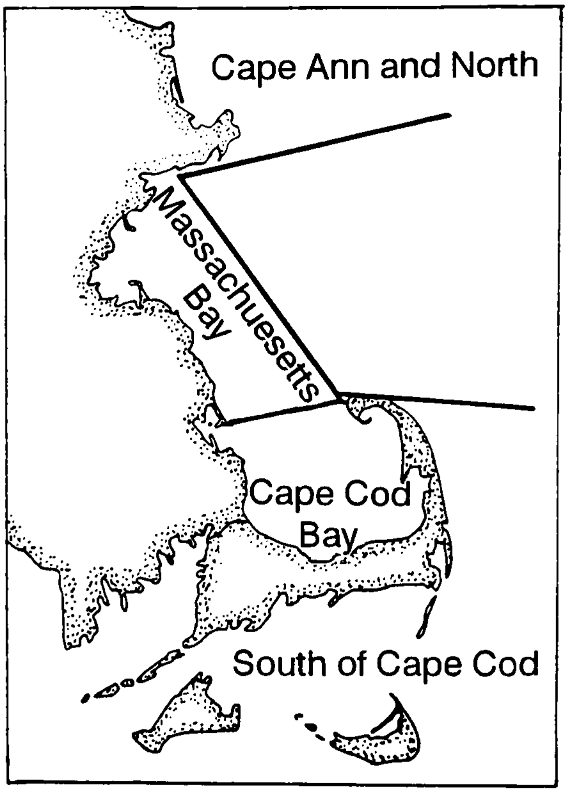

Fig. 2. Map showing the four regions used to look at the fine scale spatial/seasonal distribution of strandings within the state of Massachusetts (Table 3).

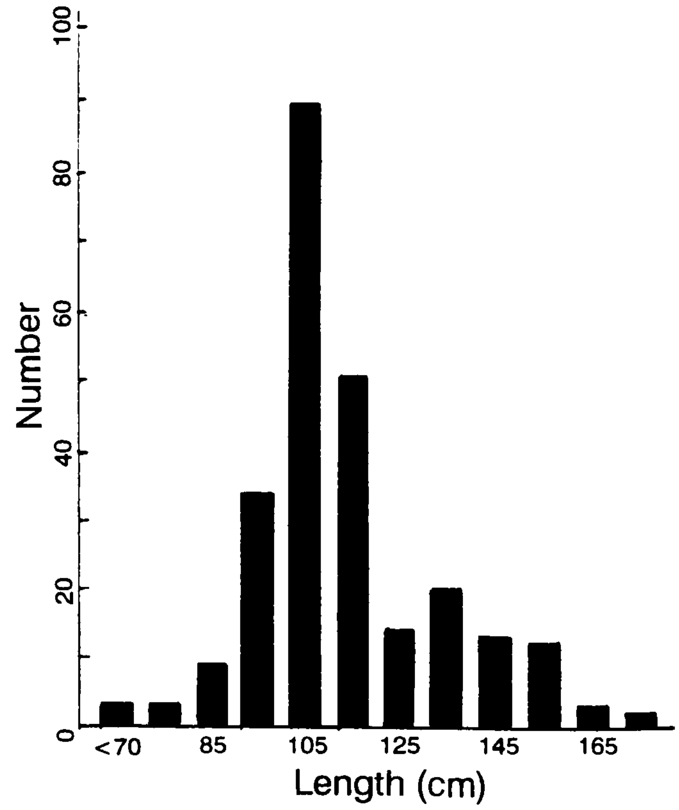

Fig. 3. Size frequency distribution for all harbor porpoises strandings with recorded lengths in the Smithsonian database (n=276). X-axis labels represent the mid-point for each size class interval.

Table 3

The location of strandings within Massachusetts by month of stranding. The data in this Table includes the supplemental information on Massachusetts strandings. As such, the numbers in this Table will not agree with those in Tables 1 and 2. (Note: specific location was not available for all strandings.)

Month	South of Cape Cod	Cape Cod Bay	Region Mass. Bay	Cape Ann and North	Total
January	3	12	3	0	18
February	1	26	6	3	36
March	3	38	37	11	89
April	2	18	13	3	36
May	2	7	3	1	13
June	0	7	1	1	9
July	3	4	0	2	9
August	0	1	0	1	2
September	1	0	2	3	6
October	0	5	1	1	7
November	1	12	2	4	19
December	4	16	3	0	23
Total	20	146	71	30	267

Reproductive state

Females mature between the ages of 3 and 4 which corresponds to a size of 135 to 145 cm (Read, 1989; Read, 1990). Thirty one females (17 in Massachusetts) were recorded as greater than 135cm in the Smithsonian database and only two of these reportedly had fetuses. However, a comparison with the more detailed Massachusetts information revealed that data on reproductive condition had not been regularly included, as 9 of the 17 animals had fetuses. Only the detailed Massachusetts data (including a further six animals) are considered in the following analysis (Table 4).

The carcasses from five of the 23 animals were reported as 'very decomposed' and no reproductive data were recorded. Eleven of the remaining 18 females (over 135cm) were carrying a fetus and a further two were lactating when they stranded in June or July. They had probably recently given birth as the calving season in this region is May to July (Gaskin *et al.*, 1984; Read, 1989). These results suggest a pregnancy rate of 0.72 (13 out of 18 animals).

This rate is slightly lower than published estimates for this population. Read (1989) estimated pregnancy rates for mature females from samples collected from incidentally killed animals in the gillnet fishery in the western Bay of Fundy. He found a pregnancy rate of 0.86 (43 out of 50) based on the presence of a corpus luteum and a rate of 0.74 (26 out of 35) based on the presence of a fetus from samples collected after the period of implantation. Read (1989) also reanalyzed the pregnancy rate data of Gaskin *et al.* (1984) to account for seasonality in reproduction and obtained a rate of 0.91 (21 out of 23) based on a corpus luteum criterium and 0.90 (9 out of 10) based on the presence of a fetus. The estimates based on the presence of a fetus are the most comparable to ours. Nevertheless, the pregnancy rates from either of these two studies, using either method for determining pregnancy, are not significantly different from our rate using Fisher's Exact *P* test (Sokal and Rohlf, 1969). It should be noted that the sample sizes in all the studies are small. The pregnancy rate from the stranding data would be expected to be slightly lower because the non-pregnant animals were collected much later in the reproductive cycle than the samples in the other two studies and some natural miscarriages may have occurred.

Table 4

Recorded information on all stranded female harbor porpoise greater than 135cm. The data in this table are based only on the supplemental information on strandings in Massachusetts (see text).

Month	Length (cm)	Foetus	Lactating	Condition/Comments
September	165	yes	-	-
	150	-	-	V. decomposed
October	164	-	-	V. decomposed
November	158	yes(14cm)	-	-
	174	yes(17cm)	-	-
	150	yes	-	-
December	161	yes	yes	-
	163	yes	-	-
	165	-	-	V. decomposed
	170	-	-	Hole in abdomen, pneumonia
January	162	-	yes	'Recently gave birth', miscarriage??
February	155	yes	-	-
	155	-	-	-
March	135	yes(49cm)	-	-
	151	-	yes	-
	167	yes	yes	-
	169	yes(39cm)	-	-
	140	-	-	V. decomposed
April	155	yes(64cm)	yes	-
	151	-	-	Emaciated, pneumonia
	150	-	-	V. decomposed
June	147	-	yes	-
July	149	-	yes	'Recently gave birth'

Comments and blubber thickness measurements for 4 of the 5 non-pregnant animals suggest that the animals were emaciated and/or sick or injured. One animal collected in January was reported as recently having given birth which may suggest a recent miscarriage, since May to July is the normal calving period (Gaskin, 1984; Read, 1989).

The fact that only 3 out of the 11 pregnant females were also lactating is not consistent with pregnancy rates of 0.7 to 0.9. However, it is not possible to determine what fraction of these animals were pregnant for the first time. Juvenile mortality would also be a factor in reducing the proportion of females both lactating and pregnant.

The length of the five measured fetuses showed a progressive increase from 14.5cm for the fetus from an animal that stranded in November to 64 cm for a fetus from a stranded animal in early April (Table 4). While the sample size is small, the change in length is consistent with the annual reproductive cycle described for harbor porpoises in the Gulf of Maine and Bay of Fundy region (Gaskin *et al.*, 1984; Read, 1989).

Mortality

Harbor porpoises strandings tend to occur in the spring. Thus, 32% of all strandings were reported in March and 64% during the three month period from February to April (Table 2). This suggests seasonally higher mortality rates, perhaps reflecting problems in locating food during the winter and early spring, a seasonal increase in entrapment, a closer inshore distribution during this season and/or more frequent on-shore winds. Summer sightings data indicate that harbor porpoises tend to be concentrated in inshore areas in the Gulf of Maine and the Bay of Fundy (Winn, 1982; Gaskin, 1984; Kraus and Prescott, 1984).

The strandings in 1977 and 1986 account for over 35% of the total and high numbers of strandings were reported in both North Carolina and Massachusetts in these two years. While some of the year to year variability in numbers is undoubtedly due to variations in on-shore currents and searching effort, the high proportions in 1977 and 1986 suggest considerable variation in natural mortality rates. Mead (1979) suggested that the large number of strandings in North Carolina in 1977 was related to an unusually cold winter.

The length distribution of all stranded harbor porpoises in the Smithsonian database shows that most stranded animals tend to be young with 75% (n=276) of the stranded animals less than 130cm (Fig. 3). Based on the growth curves developed by Read (1989), 130cm corresponds to an age of between two and three years. While a number of factors could skew the distribution of stranded animals towards younger ages and/or small sizes (e.g. spatial segregation by size), the results do suggest that natural mortality rates are higher for juvenile animals.

Incidental fishery takes

As stated earlier, 19 of the 378 harbor porpoises records in the Smithsonian database were either definitely, or most probably the result of animals being accidentally entangled in fishing nets. Twelve of these were from the Gulf of Maine (5 from Maine, 1 from New Hampshire and 6 from Massachusetts) and the remainder were from further south (1 from New Jersey, 3 from North Carolina and 3 from Virginia including 2 from inside Chesapeake Bay). While it is well documented that harbor porpoises become entangled in bottom tending gillnets in the Gulf of Maine and Bay of Fundy region, the occurrence of incidental takes south of Massachusetts is not well known and has usually not been included in concerns about the effects of incidental takes on this fishery (Gaskin, 1984; Gilbert and Wynne, 1987; Read and Gaskin, 1988; Polacheck, 1989; Read, 1994). Only one of the southern records can be attributed to a particular fishery – a gillnet fishery for shad in the York River flowing into Chesapeake Bay.

Information available currently is inadequate for evaluating whether or not significant takes of harbor porpoises are likely to be occurring in these more southerly areas (Read, 1994). A number of near and inshore fixed gear fisheries exist along the coast from New Jersey to North Carolina including gillnets, pound nets, weirs and fyke nets targeting shad, river herring and bluefish. These fisheries tend to be small in scale and levels of effort are poorly documented. Similarly, although the stranding data suggests that these coastal waters are a regular part of the winter habitat of harbor porpoises, the relative importance of this habitat is unknown. Moreover, while many of the fish species being targeted by these fixed gear fisheries might be appropriate prey, little is known about the harbor porpoises's feeding habits during the winter and spring seasons.

The detailed Massachusetts data provide six additional animals since 1975 that appear to be the result of accidental entanglement. Five were found with their flukes cut off, presumably by fishermen in the process of untangling them from their gear. These additional six animals suggest that information in the Smithsonian database can only be used as an indicator of the occurrence of fisheries interactions and is likely to be a poor measure of their magnitude.

Two further records in the Massachusetts database were reported as having been taken in fish traps and weirs during the first half of the century (1908 and 1936). Harbor porpoises are regularly taken in herring weirs in New Brunswick (Smith *et al.*, 1983). These observations and the fact that large numbers of fish traps and weirs were common in the Gulf of Maine during the early and mid 1900s raise the possibility that incidental fishery takes of harbor porpoises are not a recent phenomena.

Limitations of stranding data

While these stranding data appear to contain useful information on spatial/seasonal distributions and the mortality and reproductive processes for the harbor porpoises, they provide no direct information on abundance or trends in abundance for this species. Not only are the absolute number of strandings in most years relatively small, but the variation in numbers between years (Table 1) is too large to be considered a reflection of changes in abundance.

We encountered a number of problems when using the Smithsonian stranding database which limited our analyses. These included incomplete reporting of information and lack of standardized procedures. Based on the supplemental stranding data from Massachusetts, it is evident that part of the detailed information being collected in the field is not being entered into the centralized database. This was most apparent for the data on reproductive condition but was also true for information on incidental fishery takes and body condition. In addition, standardized procedures are not used for some data which are collected locally (e.g blubber thickness), while other information and analyses (e.g. age determination, blubber thickness) are not carried out consistently. The convention of recording data based on the time of death coupled with lack of information on live strandings introduces a potential for small errors in the type of analyses presented. The need for consistent, standardized and centralized data collection is well recognized, and substantial effort has gone into developing and improving the current centralized system (e.g. Geraci and St. Aubin, 1979; Harl and Mead, 1987; Winchell, 1990; Heyning, 1991; Hoffman, 1991). We again draw attention to the problem as an added impetus for further improvements so that the maximum potential information can be realized from these data in the future.

In conclusion, analyses of stranding data for harbor porpoises collected from animals found along the US east coast can provide useful insights into the biology of this species. The data indicate that the winter distribution of the harbor porpoises extends further south than previously reported and supports published studies which suggest a seasonal north/south migration. Analyses of mature females indicate a high pregnancy rate and incidental kill records raise questions about potential fishery interactions beyond those previously documented for bottom tending gillnet fisheries in the Gulf Maine and Bay of Fundy.

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The Bay of Fundy/Gulf of Maine Harbour Porpoise (*Phocoena phocoena*): Some Considerations Regarding Species Interactions, Energetics, Density Dependence and Bycatch

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ABSTRACT

The numbers of North Atlantic harbour porpoise (*Phocoena phocoena*) within the Bay of Fundy/Gulf of Maine were considered to be declining as a consequence of bycatch in the sink gillnet fisheries of both Canada and the United States. Evidence for a decline was based upon decreased sightings and a diminishing bycatch in areas considered to be a traditional habitat. Observed changes in the individual growth rates of porpoise, were also attributed to decreased density. By taking into consideration the dynamics of the habitat, as well as the possible effects of species interactions, an alternative interpretation is suggested, one which seems equally consistent with present observations: that changes in distributions and the growth response of porpoise reflects the strong coupling of this species to the distribution of herring (*Clupea harengus*). Furthermore, distribution of marine production affects the duration of the presence of herring and associated porpoise within the vicinity of sink gillnet fisheries. Recent surveys of porpoise numbers and distribution tend to support this hypothesis. Fluctuations in both the availability of herring and their energy content may also be a confounding factor affecting condition, previously used to argue for rapidly declining porpoise numbers. The probable reduction of shark predators through directed catches and bycatches in commercial fisheries over recent decades is considered here as a factor which may have enhanced the survival rate of this population of harbour porpoise, and that this larger population has been subjected to bycatch in an expanded gillnet fishery.

KEYWORDS: HARBOUR PORPOISE; NORTH ATLANTIC; INCIDENTAL CAPTURE; SHARKS; PREDATION; FEEDING; TRENDS; FISH; ENERGETICS; ASSESSMENT.

INTRODUCTION

The Atlantic harbour porpoise (*Phocoena phocoena*) of the Bay of Fundy/Gulf of Maine (BOF/GOM) has been classified as 'threatened' by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC). A threatened species classification is given to any indigenous species of fauna or flora which is likely to become endangered in Canada if the factors affecting its vulnerability are not reversed (Cook and Muir, 1984).

The first surveys for harbour porpoises in the BOF/GOM area were conducted during the 1980s and resulted in estimates ranging from 3,000 to 15,000 animals (Kraus *et al.*, 1983; Read and Gaskin, 1990b; IWC, 1991).

Gaskin (1989) proposed evidence of population decline based upon reduced sightings and the levels of bycatches in the traditional areas within the Bay of Fundy, as well as a detected change in the growth rates of adult and newborn animals (Read and Gaskin, 1988; 1990a). The decline was attributed to high levels of porpoise bycatch in the sink gillnet fisheries of Canada and the United States.

It is clear that high levels of porpoise bycatches in the demersal gillnet fishery can have a substantial effect upon the population. However, other ecological interactions should be considered when assessing the status of the harbour porpoise.

This study addresses the question of harbour porpoise trends in abundance within the context of energetics and species interactions (the harbour porpoise as both predator and prey), and explores several hypotheses with respect to possible density dependent growth and changes in the nutritive condition of harbour porpoises, as well as the potential for substantial changes to have affected their natural mortality.

The harbour porpoise is the smallest North Atlantic cetacean and is capable of annual reproduction which suggests a relatively high turnover of energy reserves compared to other species. This may require a greater year-round proximity to a reliable food base with the consequence that its distribution and nutritive condition may more strongly reflect the distribution and energy density of its prey than for other cetaceans. Any such year-round association between the harbour porpoise and its prey may confound attempts to assess population size, as well as interpretations of changes in growth and condition of individuals.

METHODS

Dynamics of harbour porpoise habitat and prey distribution

A full understanding of the harbour porpoise situation must take into account those factors that may influence its seasonal distribution, as well as information on the deployment of the demersal sink gillnet fishing effort.

For example, the variation in the frequency of harbour porpoise bycatches may be influenced by the feeding strategies of: (1) the pelagic, mobile herring stocks (*Clupea harengus*), the major prey species of the harbour porpoise (Recchia and Read, 1988) and (2) the demersal species (e.g. cod, *Gadus morhua*), whose distribution is more site-specific and which are the target of the sink gillnet fishery.

The BOF/GOM is influenced by the land mass which partially surrounds it (Fig. 1). This influence includes the discharge from a system of rivers, the watershed of which is approximately twice the area of the BOF/GOM. As in any such system, marine productivity will vary in accordance with the coastal influence (Wiggin and Mooers, 1992). The distribution of pelagic fish, such as herring, is dependent upon the distribution of mobile and shorter lived planktonic prey such as *Calanus* sp., which can vary in biomass by an order of magnitude between years (Gaskin, 1992). The distribution of herring reflects these interannual changes, as do the catches of herring by fixed gear fisheries such as coastal weirs. The fact that mobile fleets of herring seiners often search large areas for many days to detect schools, provides evidence of herring mobility and interannual variability.

Demersal species, such as cod, feed predominantly upon benthic prey whose distribution and density are largely defined by the quality of the bottom habitat (sand, gravel, etc.). The diversity of benthic prey species and their longer generation times (up to several years) result in relatively long term stability at these sites. The seasonal distribution of cod and their traditional fisheries using fixed gear such as gillnets are, therefore, remarkably site-specific (K. Frank, pers. comm.).

From this, it seems that the potential for bycatches of harbour porpoises in bottom-set gillnets will be greater during periods of overlap in the distributions of pelagic and demersal species. If this is indeed the case then interannual variation in the frequency of bycatches would be expected. Such variation has been indicated (Anon., 1992; Smith *et al.*, 1993).

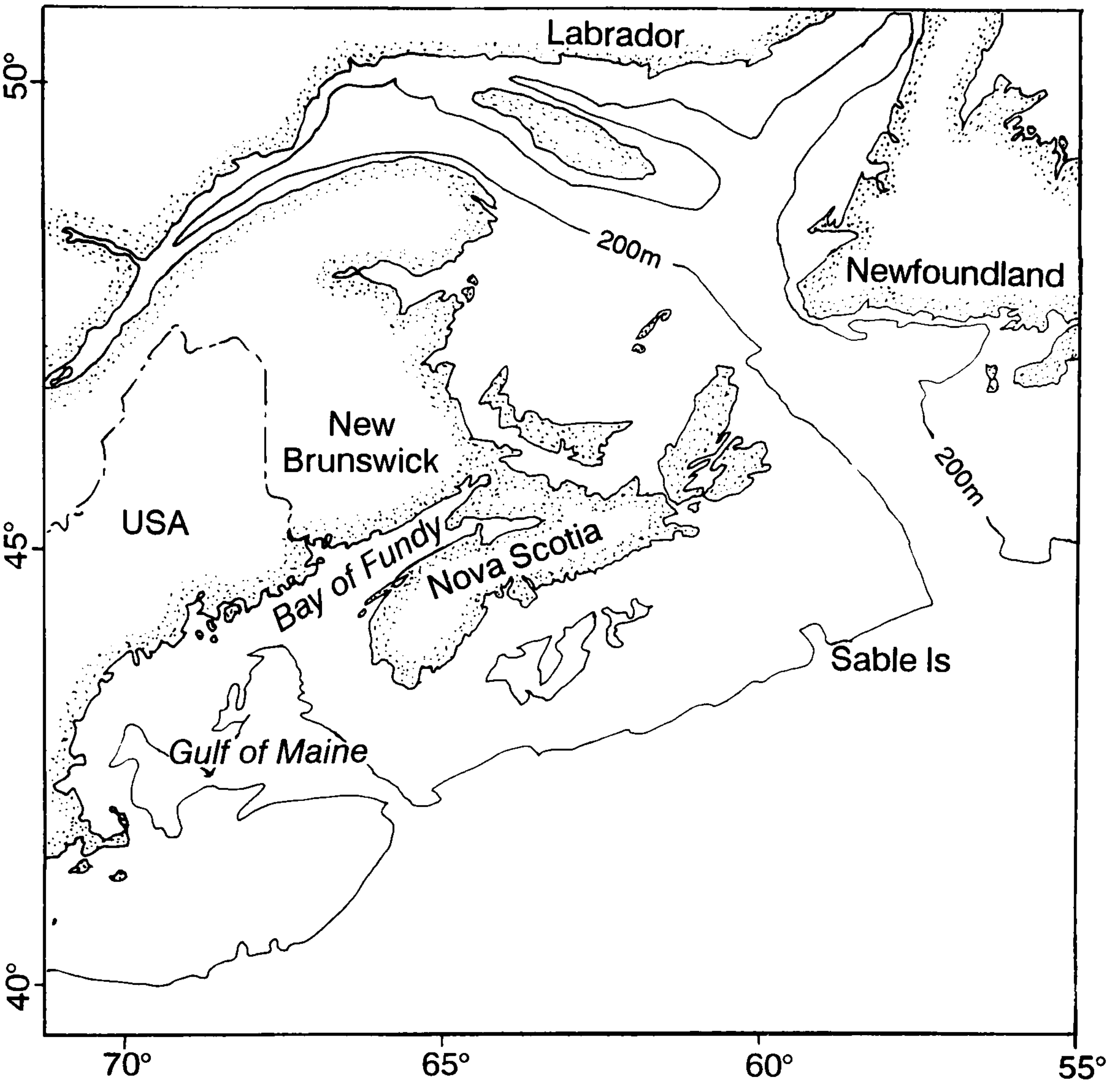

Fig. 1. The Gulf of Maine/Bay of Fundy is seasonal habitat for harbour porpoise and is also an area of intensive commercial fishing, using mobile and fixed fishing gear. Porpoises migrate annually after overwintering in waters south of Cape Cod, to spend the spring and late summer months in the northern Gulf of Maine/southern Bay of Fundy. The region of the Gulf of St. Lawrence, north of Nova Scotia and that of Newfoundland/Labrador also host populations of harbour porpoise. The degree of exchange of porpoise between these areas is unknown.

Changes in growth rates

Read and Gaskin (1988) examined data for animals collected during two time periods (1969–73 and 1981–86) and concluded that there were significant changes in the growth rates of harbour porpoises expressed as more rapid juvenile growth, earlier sexual maturation of females and larger newborn animals. This and a lack of large animals in the more recent sample, led them to propose that sustained levels of bycatch mortality have not only substantially reduced the size of the population[1] but also compressed the age structure of the population, perhaps reducing the reproductive lifetime of females. The

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[1] Unfortunately, it is not possible to estimate the level of population decline required to bring about detectable changes in for example growth rates. It is beyond the scope of this paper to review the controversy over the magnitude of density-dependent responses in cetaceans and whether they occur when the population has been only slightly or more heavily reduced. The interested reader is referred to Fowler (1984), Fowler and Baker (1991), de la Mare (1990) and Cooke and de la Mare (1994).

increased growth rates were considered to be the result of increased *per capita* food supply, i.e. classic density-dependence.

These changes were detectable over a relatively short time. It is worth examining whether changes in other components of the system might generate a similar response over the same period.

Any decline in the number of harbour porpoises due to gillnet bycatches over 13 years would be gradual over the time period. It follows that such a proposed density dependent growth response by harbour porpoises would have to be highly sensitive, implying a critical balance in *per capita* prey abundance over the period in question.

Herring is the major prey of the BOF/GOM harbour porpoise (Recchia and Read, 1988) comprising 80% of total caloric intake, with silver hake (*Merluccius bilinearis*) and cod comprising a further 17%.

An alternative hypothesis to a substantial decline in porpoise numbers for the changes observed in harbour porpoises is that the distribution, abundance or energy density of prey may have fluctuated over the 13 year period. This assumes that the prey biomass is of such magnitude that it does not limit harbour porpoise numbers. The observed growth rate increases would, therefore, be the result of changes in prey quality (energy density) or prey distribution. Recchia and Read (1988) reported that on a weight basis, the caloric value of herring is more than twice that of either silver hake or cod. Although herring sometimes comprised as much as 98% of the caloric intake, in the 1986 offshore sample of porpoises, silver hake contributed about the same caloric value as herring in the stomach contents. Silver hake are similar to herring in that they are found nearer the surface at night and at depth during the day, as well as being available in high concentrations (Waldron *et al.*, 1991). This suggests that the foraging effort required for silver hake will be similar to that for herring, thereby making feeding on herring more efficient. The equal caloric value found in stomach contents suggests that either hake may have been caught more readily and/or that foraging costs for herring may have increased in that area at that time.

The fat content of herring can range from 1%-25% on a wet weight basis, varying between seasons, years and area of sampling (Stoddard, 1968). Recchia and Read (1988) show that harbour porpoises can shift from herring to other prey species of lower specific caloric value. However, while porpoises may be sustained by shifting to prey species of lower energy density, additional energy beyond mere survival may not be available. This may be reflected by changes in their distribution, abundance, health and/or growth rates.

The change in migration timing and distribution of porpoise in 1992 compared to 1991 surveys (as reflected in quite different point estimates of abundance for the area (1991–37,500, 1992–67,500) although with wide confidence intervals – Smith *et al.*, 1993; Palka, 1995) may be related to the greater abundance and wider distribution of herring (R. Stephenson, pers. comm.; Kenny, 1994; Sherman, 1994). Harbour porpoise may presently have a greater choice of feeding options along the coast of Maine and southern Bay of Fundy due to the abundance of herring, compared to the more restricted distribution of past years.

Mortality through predation

While predation upon harbour porpoise is incorporated within the parameter of natural mortality in any modelling exercise, the potential for this component to have varied substantially with time and thus affect the age composition and possibly the growth rate of porpoises has been largely ignored.

Sharks have long been considered to be a predator of marine mammals along the eastern seaboard of North America (Arnold, 1972; Boulva and McLaren, 1979; Brodie and Beck, 1983; Casey and Pratt Jr, 1985). Arnold (1972) found direct evidence of white shark (*Carcharodon carcharias*) predation on harbour porpoises in the Bay of Fundy and postulated that sharks may be a significant predator on harbour porpoises in the area. A correlation between changes in the survival rate of Sable Island grey seals (*Halichoerus grypus*) and the large scale removal of shark predators through direct and indirect fishing, was proposed by Brodie and Beck (1983). Similarly, the harbour porpoise may have experienced varying levels of predation depending upon the standing stock of shark predators, particularly if such predation had been sufficient to maintain the population at lower levels. The substantial decrease in the numbers of shark predators in this area[2], as a consequence of directed shark fisheries (including sport fishing), as well as the high levels of bycatches in longline fisheries, might have substantially altered the level of shark predation upon harbour porpoise. If so, the effect might lead to an expanding population with a younger age distribution (assuming younger animals are more vulnerable to shark predation). Confirming or refuting such an hypothesis, however, is extremely difficult.

Our present understanding of the movements of BOF/GOM porpoises suggest that they range year-round through eastern seaboard fishing grounds, known to support stocks of sharks (Casey and Kohler, 1992). Whether this is a factor to consider with regard to other concentrations of harbour porpoises such as in the more northerly areas of the Gulf of St. Lawrence and off Newfoundland and Labrador is uncertain; the possibility that they could overwinter south from George's Bank would expose them to similar levels of predation for that portion of the year.

Depending on the level of exchange between the Newfoundland, Gulf of St. Lawrence and BOF/GOM populations, differences in the relative age distributions due to differential predation may be detectable and this warrants further analysis.

DISCUSSION

A major problem in assessing the situation of the harbour porpoise in this region is the lack of reliable estimates of trends in population size. The most comprehensive surveys of harbour porpoise in the BOF/GOM, conducted in 1991 and 1992, indicated a population of 47,200 (95%CI 39,500–70,600). Although this is substantially larger than previous estimates, they are not comparable due to the fact that earlier surveys covered smaller areas and had methodological short comings (Palka, 1995). The 1991/92 surveys were assumed to cover the population from which the bycatch is taken by both American gillnets and Canadian sink gillnets during June to September.

A further problem is the question of stock identity. If harbour porpoises from the Gulf of St. Lawrence and Newfoundland/Labrador areas migrate to common fall/wintering grounds on George's Bank and the New England coast, this would increase the 'population' subject to bycatches in US fishery.

The most recent assessment of the status of the BOF/GOM population of harbour porpoises suggests that the bycatches remain at levels which approximate the estimated potential rate of increase (*ca* 4% – Woodley and Read, 1991), based on a current population estimate of 47,200 (95% CI 39,500–70,600) and bycatches of 1–2,000 animals.

An alternative to the currently accepted hypothesis that the BOF/GOM harbour porpoise has substantially declined over the last 15 years is that, in fact, the population has been *increasing* at an unknown rate over the past 30–35 years as a consequence of decreased predation due to the increasing bycatch and directed catch of sharks in the area.

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[2] Exploitation of sharks off the US east coast has been at such a level that there is now regulation of direct and indirect catches, and large coastal sharks are considered to be over utilised (FMP, 1993).

A strong interaction with herring, the primary prey of the harbour porpoise, might result in changes in distribution according to the distribution of herring, and changes in growth rates and the 'condition' of porpoises due to changes in the abundance and energy density of herring in relation to other prey species. In effect, the abundance and bycatch levels of the harbour porpoises in certain areas, as well as their growth rates and nutritive condition, may be reflecting the relative abundance of herring rather than a substantial change in porpoise numbers.

The problem from a management perspective is that even if there is increased growth due to decreasing natural predation on porpoises, the balance (if any) between this and the bycatch of porpoise in an expanding sink gillnet fishery is unknown.

The thermoregulatory and energy storage capabilities of marine mammals provides them with sufficient stability, a strategy which has evolved in specific habitats. Fluctuations in their year to year energy requirements are difficult to determine, although we attempt to measure this as a 'condition factor'. Foraging costs and the degree to which they may fluctuate whilst maintaining a certain standard of condition, are difficult parameters to measure (Brodie and Påsche, 1982). As much as we may wish to emphasise the importance of density dependence as a factor in population dynamics, it is the removal through direct intervention by man or natural predator that is eventually the strongest signal.

CONCLUSION

This paper has shown that it is possible to interpret the same information regarding the BOF/GOM harbour porpoises in quite different ways and it is equally apparent that it is not possible to distinguish among hypotheses with our present knowledge. The most critical problem is the lack of direct information on any trend in harbour porpoise abundance. It is important that carefully designed regular surveys are undertaken and that effort is put into trying to understand the factors behind the interannual variation in harbour porpoise distribution, particularly with respect to prey distribution.

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Investigation of Aspects of the Life History of the Harbour Porpoise, *Phocoena phocoena*, in British Waters

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ABSTRACT

Specimens of harbour porpoises, *Phocoena phocoena*, from strandings and bycatches in fisheries around the British Isles between 1985 and September 1994 have been examined. Full autopsies were undertaken on most carcases, and measurements and samples taken. The date of finding, location, sex, total body length, body weight, reproductive organs and teeth of all specimens were collected during this period. A total sample of 234 individuals (including 114 males and 96 females) were aged, using decalcified thin stained sections of teeth. The sample included neonates through to animals age 24yrs. The modal age class was 0–1yr. Preliminary investigation of the age distribution indicated higher overall survival in females, with the lowest survival in the first year of life for both sexes. Birth size appeared to be 65–70cm length and 5kg weight (neonates with unhealed umbilicus range from 60–75cm length and weight of 3–9kg). The maximum body length in the sample was 163cm in males and 189cm in females. Maximum weights of 54kg and 81kg were recorded for males and females respectively. The inferred peak calving period is June, with high numbers of neonates and calves found stranded between June and September. Preliminary data suggest that age at sexual maturation in males is probably about 3yrs onwards. Peak testes weight was observed in June-August and peak births in June. This suggests a gestation period of approximately one year in harbour porpoise. Throughout the investigation, it has not been possible to distinguish reliably between bycatch and natural strandings.

KEYWORDS: HARBOUR PORPOISE; NORTH ATLANTIC; LENGTH/GROWTH; AGEING; BIOLOGICAL PARAMETERS; REPRODUCTION

INTRODUCTION

To date there has been no definitive study of harbour porpoise biology in British waters. Although this partly reflects relatively little interest in small cetaceans around the British Isles until recently, it is also due to the fact that the only available material is from strandings and bycatches. Bycatches have not been consistently reported, or recovered and so bycaught animals are usually discarded and tend to appear on beaches as strandings.

During the period April 1993-March 1994 inclusive, a total of 86 cetaceans was autopsied or examined by the Institute of Zoology, London, which estimated that 23% of porpoises recovered as strandings were the result of bycatch. For England and Wales, most (66%, n=86) species-identified cetacean strandings were harbour porpoises; in Scotland the equivalent value was 57% (n=127) (see Anon., 1995).

This paper collates the available age data and examines the age distribution of the sample to consider aspects of survival and growth and, in conjunction with information from gonads, age at sexual maturation. The results are compared with those from similar studies for other geographical areas.

MATERIAL AND METHODS

The material considered was obtained from harbour porpoise carcases autopsied and sampled between 1985 and September 1994, with the majority from 1990 onwards. The pre-1992 material was obtained from all around Great Britain. No data are available from Scotland since 1992 when a Scottish Strandings Scheme was begun.

The total sample comprised 234 harbour porpoises, including 114 males and 96 females. The following material/data for this study were collected from most individuals when feasible: total length (as measured in a straight line from the tip of the jaw to the notch in the tail flukes), sex, date of death, location found, teeth for age determination, gonads, foetal data and samples (if found) and body weight.

DATA AND METHODS

Age and biological parameters

Teeth were used for age determination, following the recommendations of Gaskin and Blair (1977), Nielsen (1972) and Perrin and Myrick (1980). The teeth were taken from the lower jaw (a string of teeth can be pulled free if manipulated with care using the tip of a sharp scalpel). Usually two teeth were selected for examination; the accepted criteria require that they be undamaged, straight and as little worn as possible. The teeth were cleaned (but never boiled) and fixed initially in 10% neutral buffered formalin. They were then treated, essentially following the method described in Lockyer (1995b), with a few minor changes in the method. Sections were stained with Erhlich's acid haematoxylin for approximately 30 minutes, 'blued' in weak ammonia solution, rinsed in distilled water, floated in water onto 5% gelatin-coated slides and then air-dried briefly on a slide warmer. The permanent mounting medium used was DPX, a clear resin. The sectioned and stained decalcified teeth were examined for counts of Growth Layer Groups (GLGs) (Perrin and Myrick, 1980) assuming 1 GLG equals 1 year, as described in Lockyer (1995b).

Testes were weighed and tissue samples removed from the middle of the testis and fixed in 10% neutral buffered formalin. Histological examination of these samples has not yet been completed. A study of ovaries is underway and will form the subject of a separate paper. Few foetuses have been recovered and no information regarding them is reported here.

Estimates of mean adult sizes have been calculated from data for animals older than 8yrs. No information on vertebral epiphiseal fusion is available but length and weight appear to have reached a plateau at this age. Length at birth has been estimated from restricting examination of carcases to those of less than 90cm length (see Lockyer, 1995a). The presence of an unhealed or recently healed umbilical scar and the absence of, or recent formation of, a neonatal line in the teeth, as well as milk in the stomach, suggests neonate status.

RESULTS

Age and biological parameters

Age composition of sample

Age data were available for 234 animals. Fig. 1 presents data for the 114 males and 96 females for which both sex and age were determined. The clearest difference in the age distribution of the sexes is in the numbers in the 0–1yr age group. This group comprised approximately 47% of males and 35% of females. The remaining numbers of individuals of age ≥2yrs were 60 males and 63 females.

A simple Heincke (1913) method for estimating annual survival from birth to the oldest age inclusive indicates 0.658 for males and 0.792 for females. If first year animals are

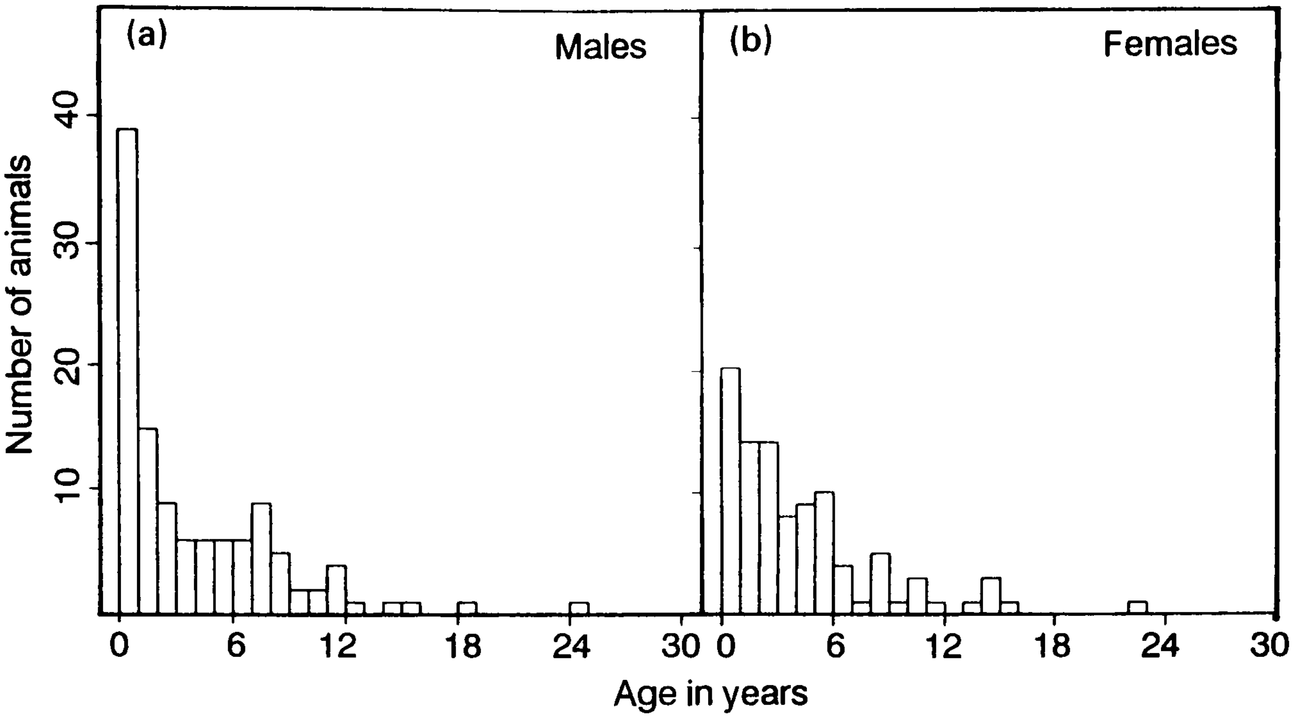

Fig. 1. Age frequency of (a) male porpoise; (b) female porpoise, in British waters.

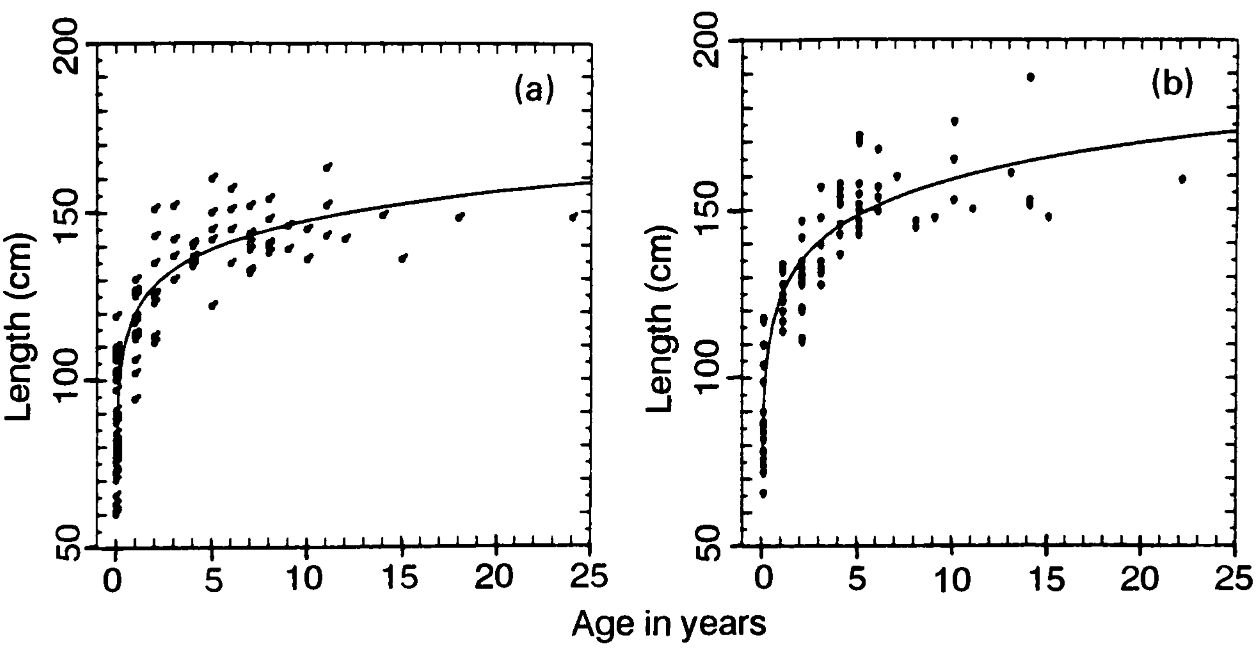

Fig. 2. Length (cm) at age for (a) male porpoise; (b) female porpoise, in British waters, with log-fitted curves.

excluded, estimates are 0.800 for males and 0.816 for females. The females appear to have a higher survival than males and this is mainly in the first year of life, although survival appears similar thereafter.

Length and weight at age

Body length against age is shown for each sex separately in Fig. 2. First year animals fall into the size range 60–118cm for males and 66–118cm for females. This age class comprises

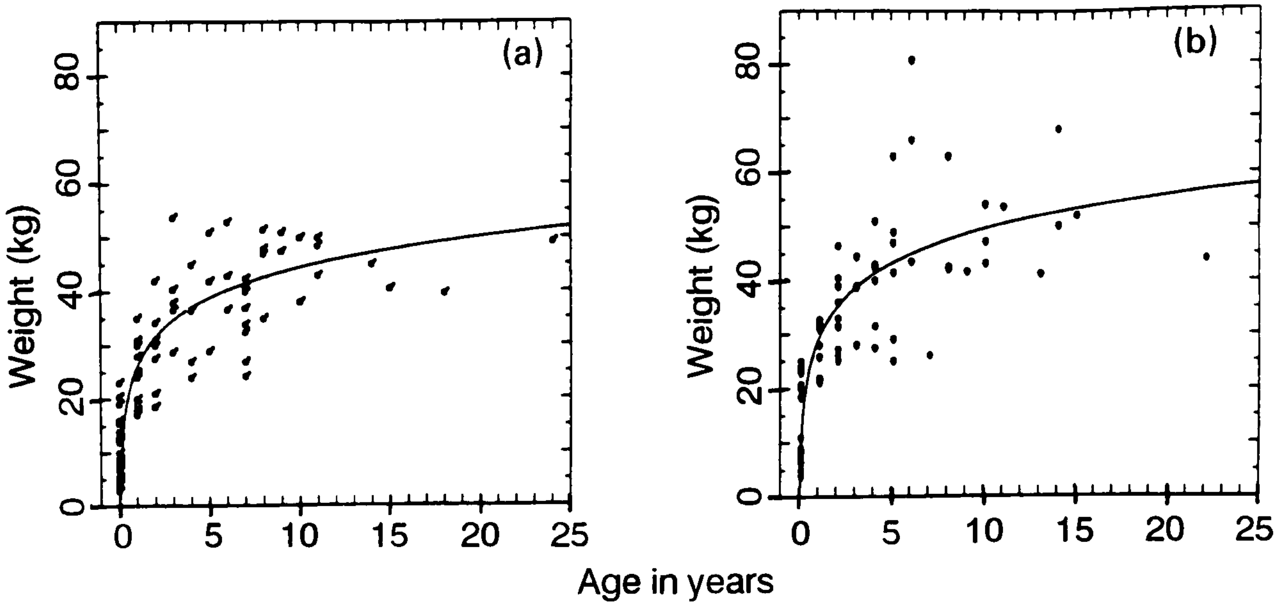

Fig. 3. Weight (kg) at age for (a) male porpoise; (b) female porpoise, in British waters, with log-fitted curves.

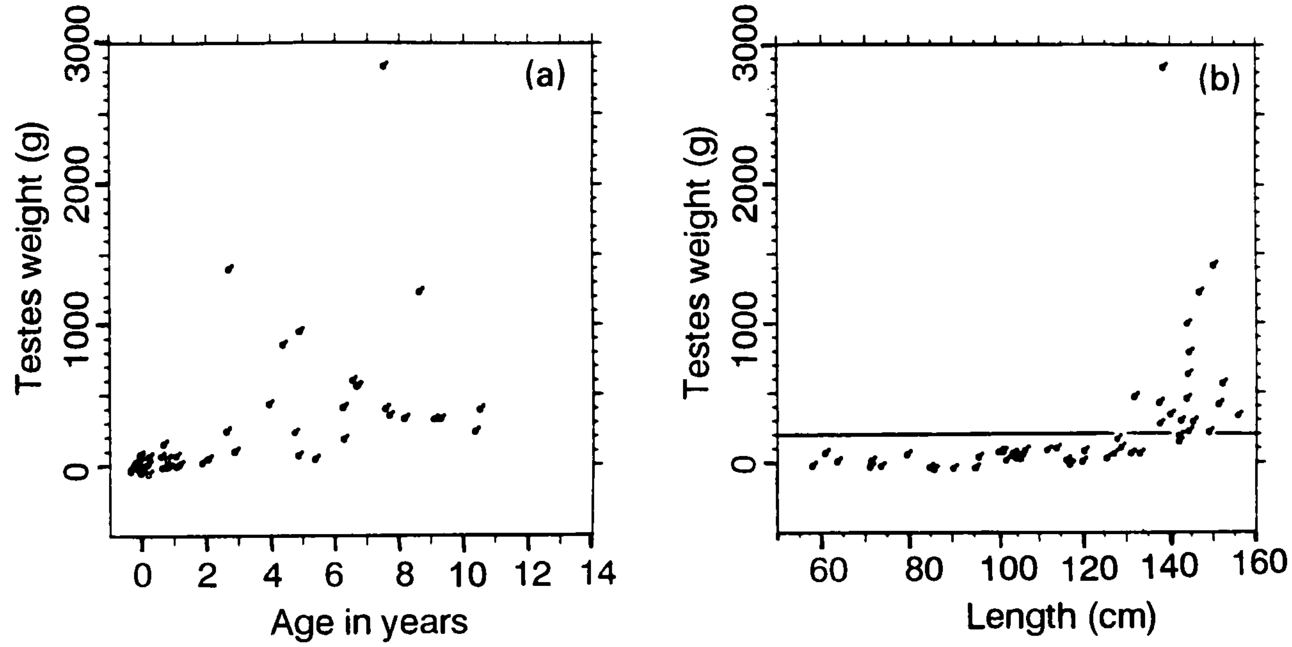

Fig. 4. Testes weight (g) at (a) age; (b) length, for male porpoise, in British waters.

both neonates and animals nearly one-year old. Using the criteria for determining neonates given in the Data and Methods section, neonates appear to fall in the range 60–80cm with a probable length at birth of about 65–70cm. The length at age data show that females grow larger than males and the maximum sizes recorded in the sample were 163cm in males and 189cm in females. Preliminary log curves have been fitted to the data, but there are insufficient data to determine when linear growth ceases and what asymptote can be assumed before detailed growth analyses can be attempted. The scatter around the mean is wide in all age classes, but if it can be assumed that the sample is from a single population, then it is likely that the mean adult lengths for males and females will be about 145cm and 160cm respectively.

Weight data plotted against age are shown separately for males and females in Fig. 3. The log curves fitted to the data in Fig. 3 are preliminary and again there is considerable scatter of data around the mean. However, it is clear that most animals have reached maximum size by the age of 8yrs. Females attain a greater weight than males. The maximum weights recorded were 54kg in males and 81kg in females. Both individuals were young adults. Mean adult weight, estimated from animals of 8yrs and older, is about 50kg in males and 55kg in females. The weight at birth is about 5kg for both sexes, with a range of 3–9kg for the 60–80cm group.

Reproductive data

Although no histological analyses have been carried out on testis tissue, weight data have been examined. The combined testes weights have been plotted against age in Fig. 4a and against body length in Fig. 4b. Testes weight increases sharply from age 3yrs (Fig. 4a) and from length 130cm (Fig. 4b). This suggests that onset of puberty occurs at about the age of 3yrs and at a length of 130cm. However, Fig. 4(a,b) shows that there is a wide variation in testes weight, independent of age or length. The pattern of the relationships of testes weight with age and body size suggests that maturation of the testes probably occurs only in tissue >200g (Fig. 4b). Tentatively, therefore, it seems reasonable to assume that testes <200g are immature, although no firm conclusion can be reached until histological examination of the testes is completed. The wide variation in testes weight can be explained by seasonal development as illustrated by plotting testis weight against month (Fig. 5). There is a rapid increase in testes size in the summer months June-August, with the heaviest testes observed in August. This indicates a strong seasonal reproductive activity in males.

This seasonal gonad activity in males implies a highly seasonal parturition period. In a plot of frequency of neonates (<90cm length), by month (Fig. 6), there is a rise in June-August with the peak in June. This is strongly indicative of a June-July birth for most porpoises in British waters.

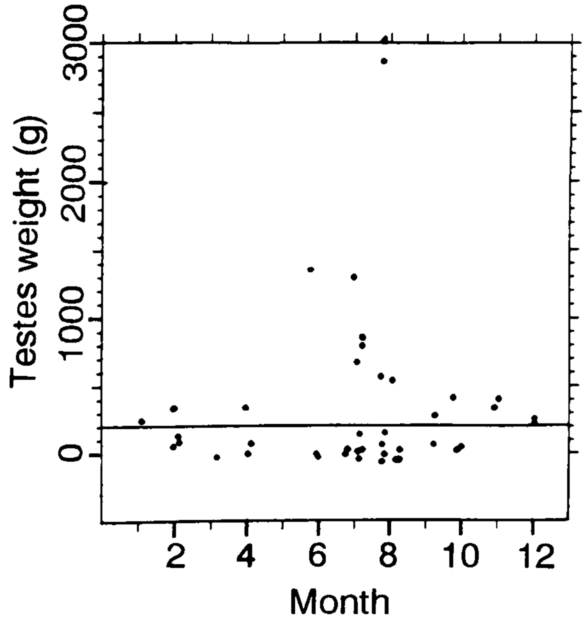

Fig. 5. Testes weight (g) by month for male porpoise, in British waters.

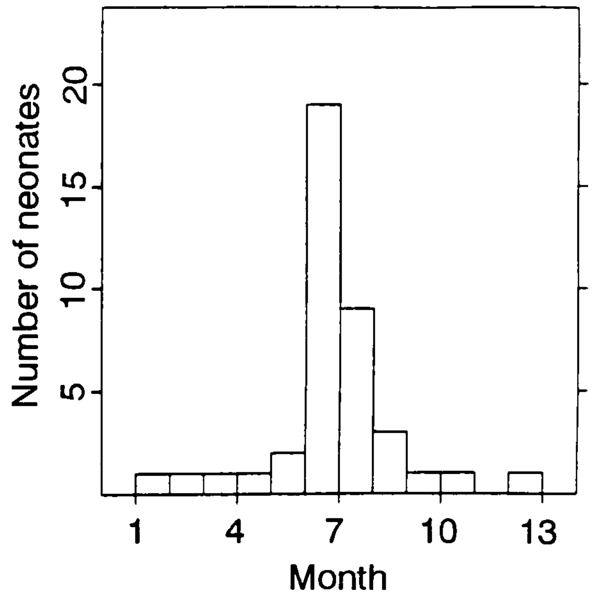

Fig. 6. Monthly occurrence of harbour porpoise neonates in British waters.

DISCUSSION

Age and biological parameters

Age composition of sample

The age frequency data which include animals up to 24yrs old, demonstrate that there are some old animals in the population of both sexes. This is in sharp contrast to the findings of Gaskin *et al.* (1984) and Read (1990a), who found no animals over the age of 13yrs; indeed few animals exceeded 8yrs of age. Read's (1990a) sample from the period 1985–1988 was entirely from a gillnet fishery and herring weir bycatch in the Bay of Fundy, eastern Canada and the sample size numbered 242 animals, of similar size to that examined here. Kinze *et al.* (1995) reported porpoises aged up to 15yrs off west Greenland. In contrast, Hohn and Brownell (1990) reported harbour porpoises up to 24yrs old off coastal California. These data indicate that individuals are capable of surviving to ages >20yrs and suggest that the Bay of Fundy data may be biased or that the population is depleted from continual incidental fishery exploitation.

Read and Gaskin (1990) reported a change in parameters between Bay of Fundy porpoises between 1967–73 and 1985–88. Body size and age at first reproduction appear to have changed in this population. Read and Gaskin suggested that this could be a response to an increase in prey availability per capita either *per se* or because of over-exploitation and a subsequent decline in population, although alternative interpretations of the data have been suggested by Brodie (1995).

One notable aspect of these details is the high incidence of neonate and first-year males while the full dataset suggests that longevity is similar for both sexes (although the oldest animal was a 24yr old male). It must be recognised that there are many problems in analysing these data: they cover several years, months and geographic areas and the cause of death is usually unclear. As noted above, over 20% of all strandings may be casualties of fisheries bycatch, whilst others may die from disease, predation or even aggression. Probably most carcases never wash ashore. Not only can biases not be ruled out – they must be assumed to occur. However, there is no information on foetal sex ratios from other studies that could explain why there are many more males than females in this early age group. A study on the body fat condition of these animals (Lockyer, 1995a) indicated that all neonates in the sample were thin and had a low mass of blubber, although males were thinner and had less blubber than females. June-July may be an environmentally favourable time for the birth of the thin newborn, because higher summer water temperatures result in less heat loss, although Lockyer (1995a) suggested that some neonatal deaths might be precipitated by unseasonably cold water in some summers. In such circumstances, the male neonates would be particularly vulnerable because of their low body fat mass. Ecologically therefore, females may have an advantage in survival at birth and this could explain the higher apparent mortality in male neonates. Data for this hypothesis could be monitored.

The suggested neonate size of about 70cm is smaller than that previously recorded by other researchers who give sizes within the range 70–85cm (Möhl-Hansen, 1954; Fisher and Harrison, 1970; van Bree, 1973; van Utrecht, 1978; Gaskin *et al.*, 1984; Hohn and Brownell, 1990; Kinze *et al.*, 1990). Although some 'neonates' may be the result of premature delivery (one record is of a stillborn animal with uninflated lungs) most small porpoises (60–75cm) had healthy lungs and stomach contents, suggesting that they were normal births. A few small animals had a healed umbilicus. Sørensen and Kinze (1990) reported harbour porpoise neonates in the size range 63–86cm off Denmark.

The only comparable source of survival estimates for the harbour porpoise is given by Kinze (1990). He produced a life-table model, assuming survival up to 23yrs of age, age of sexual maturation between 2–5yrs and a calving interval of 1–3yrs. If the first-year data in the British sample are ignored, then survival rates approach estimates from Kinze's model where an annual survival rate to age 23yrs could be as low as 0.867, depending on specific assumptions on breeding success, etc. However, the estimated survival from birth to age 1yr is extremely low in the present study suggesting that the numbers in this age group are biased, perhaps due to the impact of fishery interaction. One might surmise that although the survival estimates in themselves are inaccurate through sample biases, the differences in estimates between the sexes are not easily explained and may have some significance.

Length and weight at age

There appears to be wide variation in body size at age (Figs 2 and 3) which may be the result of several factors such as the inclusion of carcases from both healthy and near-starving animals, the inclusion of heavily pregnant females in the general female data and the inclusion of animals from different populations. Analysis of individual variation in size from the mean at any particular age might be helpful in examining whether or not outliers are indicative of the inclusion of more than one putative population in the sample, each with a different growth and maximum size characteristic. Four sub-populations in British waters were suggested by Gaskin (1984). However, the present sample size becomes very small if the overall sample is sub-divided for treatment. Further analysis of growth in size with age would be desirable, comparing von Bertalanffy (1938) and Gompertz (Laird, 1969) growth formulae, if other data show that the sample can be treated in its entirety.

The lengths of the British animals are generally similar to those reported elsewhere in the North Atlantic, North Sea and Baltic (Gaskin *et al.*, 1984). However, the largest male (163cm) and female (189cm) appear to be among the largest animals reported anywhere (Gaskin *et al.*, 1984). The length at age for each sex is similar to that for porpoises off California (Hohn and Brownell, 1990).

Reproductive data

There are many published reports of age at sexual maturity for female porpoises, with estimates in the range 3–5yrs, depending on the population and time period (van Utrecht, 1978; Gaskin *et al.*, 1984; Hohn and Brownell, 1990; Read, 1990a; Read and Gaskin, 1990; Sørensen and Kinze, 1990; Kinze *et al.*, 1995). At this stage it is anticipated that harbour porpoise from British waters will be similar, with a probable age of 3–4yrs. Probable size at maturity would be 140–145cm – similar to published reports for elsewhere and also compatible with data in Fig. 2b.

Reports of male sexual maturity give age and size as 3yrs and 130cm off west Greenland (Kinze *et al.*, 1995); 3yrs and 135cm off Denmark (Sørensen and Kinze, 1990); 3yrs and 132cm in coastal eastern Canada (Gaskin *et al.*, 1984 see p.137, fig. 1); and possibly about 4yrs and >140cm off California (Hohn and Brownell, 1990). The limited British data suggest maturation at age >3yrs and >130cm for males. Certainly, puberty is initiated at this age and size.

Data in this paper confirm the seasonal reproductive cycle in males reported by Gaskin *et al.* (1984), Read (1990b) and Sørensen and Kinze (1990). The data also support the existence of a mid-summer birth (June-July) and summer breeding (July) off Britain.

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Aspects of the Morphology, Body Fat Condition and Biology of the Harbour Porpoise, *Phocoena phocoena*, in British Waters

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ABSTRACT

Specimens of harbour porpoises, *Phocoena phocoena*, from both strandings and bycatch in fisheries around the United Kingdom between 1985 and 1994 have been examined. Full autopsies were undertaken on most carcases, and measurements and samples taken. The sex, date of finding, location, total body length, girth, body and organ weights, blubber thicknesses and blubber samples, reproductive organs and teeth were all collected during this period. A total sample of 303 individuals (including 144 males + 128 females), with data on most parameters, has been analysed. Small juvenile animals are both relatively and actually fatter than adults. The latter point may reflect the greater surface/volume ratios of young and their need for insulation. Blubber thickness and body size may also be important in thermoregulation for all animals. Length, cm (L) and mid-girth, cm (G) together provide the means of most accurate estimation of body weight, kg (W) for both sexes:

$$W = 0.000081.L^{1.2401}.G^{1.5524}.$$

Limited female data indicate that pregnant females are heavier and fatter, and that lactating females are lighter and leaner than anoestrous females. Blubber lipid content, determined from the blubber samples, averaged 83–87% wet weight tissue for all classes of animals except neonates (≤90cm), which appeared in the samples mainly during June and had a lower mean of about 68% wet weight tissue.

KEYWORDS: HARBOUR PORPOISE; NORTH ATLANTIC; MORPHOLOGY; PHYSIOLOGY; ENERGETICS; AGEING; REPRODUCTION

INTRODUCTION

From 1985, the Sea Mammal Research Unit (SMRU) received a small number of harbour porpoise carcases which have been processed and sampled. However, since 1990, the Department of the Environment (DOE) has funded the Institute of Zoology (IOZ) and the Natural History Museum (NHM), both in London, to collate strandings records throughout Great Britain and to undertake complete autopsies on every available cetacean carcase retrieved, as part of a broader study of disease and epidemiology in marine mammals.

This paper documents findings to date on aspects of the biology, growth and body fat condition of harbour porpoise, as determined from stranded and incidentally caught animals.

MATERIAL AND METHODS

The information discussed was obtained from porpoise carcases autopsied and sampled between 1985 and September 1994; the majority from the period 1990 onwards. Carcases were recovered from all around the United Kingdom, including Scotland until 1992 when the Scottish Strandings Scheme commenced (Lockyer, 1995). Therefore, the pre-1992 samples include material from Shetlands (mostly bycatch) and other areas of Scotland.

Post-1992 material comprises only data and samples from England and Wales.

In this study, a total sample of 303 porpoises, including 144 males and 128 females, has been examined. Only samples from fresh or frozen animals in good condition were utilised. Decomposed animals were not used. The following material/data for this study were collected when feasible: total length, mid-girth, sex, date of death, location found, teeth for age determination, gonads, foetal data and samples (if found), body and organ/tissue weights, blubber thickness along the mid-girth and blubber tissue for lipid analysis.

Age and reproductive data

Teeth were used for age determination and a description of the process is given in Lockyer (1995).

Testes weights >200g, body lengths >130cm and ages >3yrs were used collectively as criteria to determine sexual maturity in males (Lockyer, 1995). In females, evidence of ovulation (in the form of ovarian corpora), lactation, pregnancy and body lengths >140cm, were criteria used to ascertain sexual maturity (Lockyer, 1995).

Morphometrics

Total body length was measured in a straight line from jaw tip to notch between the tail flukes. Other measurements were made according to Fig. 1. However, only the girth measurement, G_3 and blubber thickness at position L_3, were taken consistently. Preliminary analyses recorded in Martin *et al.* (1990) indicated that mid-girth was the best measurement to take for body condition and weight determination, and mid-lateral blubber thickness was similarly determined as the best indicator of body fat condition. In addition this is consistent with the measurement used by Read (1990).

Body weight was measured for the intact animal while suspended from a *Salter* weigh-scale calibrated to the nearest 500g. Muscle and blubber were routinely weighed during autopsy when the tissues were stripped off the carcase. The muscle was removed as completely as possible although a small amount always remained around the ribs and

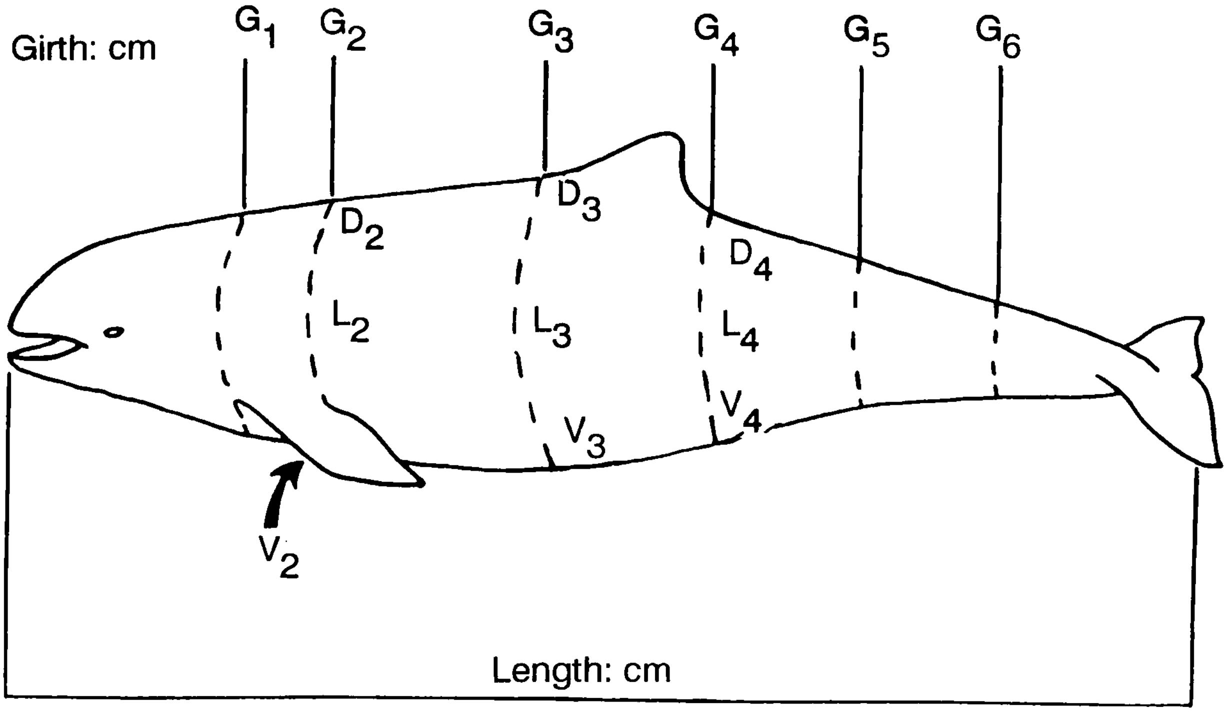

Fig. 1. Diagram of measuring and sampling sites on harbour porpoise.

vertebral column, despite careful cleaning of the bones. The blubber comprised all tissue from around the body and from the head, but excluded the tail flukes and pectoral flippers, both of which were classified as skeletal. Muscle tissue, blubber and skeletal material were weighed separately in tared buckets from the *Salter* weigh-scale. Individual organs, including the liver, kidneys, heart, lungs and testes were weighed to the nearest g on a digital balance and ovaries were weighed using a *Pesola* 5g balance to the nearest mg.

Various plots, curves and regressions, using software programmes SYSTAT and North West Analytical's STATPAK, were fitted to the data in an investigation of body weight prediction and correlations between various organ and tissue masses and dimensions. Differences with sex and age were examined.

Body fat condition

All blubber samples were taken as a strip from the mid-girth region, through to the underlying muscle. The blubber was frozen and stored at -20°C until analysed for lipid content. Then about 5g blubber was homogenised and lipid extracted using an automatic *Soxhlet* extraction process with hexane. All lipid contents were expressed as a percentage of wet weight of tissue. The lipid contents were subsequently examined in relation to girth and blubber thickness, and how these factors varied with sex, age and reproductive status. The overall sample was classified into the following groups defined broadly according to maturity criteria in Lockyer (1995): male and female neonates $\leq$90cm length, sexually immature males and females 91–130cm, sexually immature females 91–140cm, male and female mature adults and sub-adults $>$130cm but excluding all pregnant and lactating females, female adults $>$140cm but excluding all pregnant and lactating females, and separate categories of pregnant females, lactating females and simultaneously pregnant and lactating females. Mean ±SD was calculated for different characters, including length, weight, blubber mass, muscle mass, mid-girth (G_3), mid-lateral blubber thickness (L_3) and percentage blubber lipid content, in order to facilitate comparisons.

RESULTS

Age

Age composition of sample

Data on age were determined for a total of 234 animals including 114 males and 96 females (Lockyer, 1995) i.e. the majority of specimens considered in this study.

Length and weight at age

The lengths and weights of males and females have been examined in Lockyer (1995). In summary, the first year animals fall into the size range 60–118cm for males and 66–118cm for females. This age class comprises both neonates and animals of nearly one-year old. Neonates fall within the size range 60–80cm with a probable mean birth size of about 65–70cm. The length at age data show that females grow larger than males and the maximum sizes recorded in the sample were 163cm in males and 189cm in females. It is probable that the mean adult lengths for males and females will be about 145cm and 160cm respectively.

Weight data also indicate that females attain a larger size than males. Most animals have reached maximum size by age 8yrs. The maximum weights recorded were 54kg weight in males and 81kg in females, but mean adult weight is about 50kg in males and 55kg in females (Lockyer, 1995). The mean weight at birth is about 5kg for both sexes, with a range of 3–9kg for the 60–80cm group (Lockyer, 1995).

Morphometrics, body size and condition

Total body weight, length and girth relationship

Plots of body weight at length for males, females and sexes combined are shown in Fig. 2a-c, with fitted curves derived from log linear regressions. Regressions of weight (W) on length (L) are shown in Table 1. Correlation between weight and length is strong, and is

Table 1

Formulae for calculating body weight (W in kg) from body length (L in cm) of porpoise.

Sex	ΣN	Formula: $W = a.L^b$	±SE for b	r^2 correlation coefficient
Male	108	$0.000051.L^{2.7348}$	±0.0703	0.934
Female	87	$0.000216.L^{2.4338}$	±0.1097	0.851
Male and Female	200	$0.000083.L^{2.6323}$	±0.0585	0.910

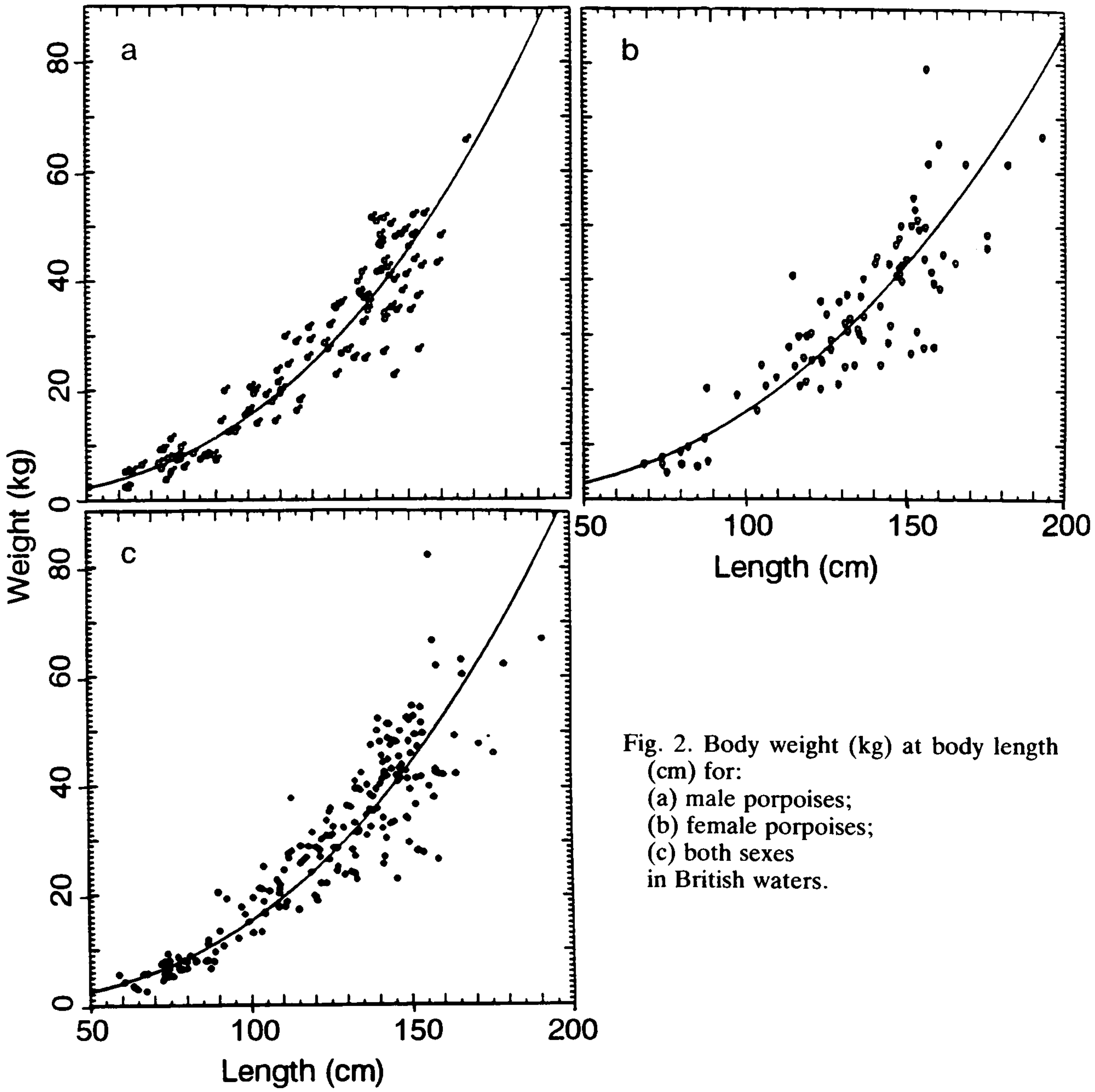

Fig. 2. Body weight (kg) at body length (cm) for:
(a) male porpoises;
(b) female porpoises;
(c) both sexes
in British waters.

greater in males than females. A plot of weight on mid-girth (G_3) for combined sexes in Fig. 3, demonstrates a close relationship. Table 2 shows regressions of weight on mid-girth for each sex and sexes combined. The actual correlation of weight with girth is higher than weight at length (Table 1) and the correlation remains greatest in males. Fig. 4 demonstrates that there is a linear correlation between mid-girth and length (both sexes combined), and in Table 3 formulae are shown for predicting weight from both length and mid-girth from log linear regressions. As anticipated, the correlation between weight and both linear measurements of size is strong in both sexes and is greater than weight with either length or mid-girth alone.

Table 2

Formulae for calculating body weight (W in kg) from mid-body girth (G_3 in cm) of porpoise.

Sex	ΣN	Formula: $W = a.G^b$	$\pm$SE for b	r^2 correlation coefficient
Male	65	$0.000211.G^{2.7004}$	±0.0615	0.968
Female	49	$0.000170.G^{2.7649}$	±0.1183	0.919
Male and Female	116	$0.000193.G^{2.7282}$	±0.0605	0.947

Table 3

Formulae for calculating body weight (W in kg) from length (L in cm) and mid-body girth (G_3 in cm) of porpoise.

Sex	ΣN	Formula: $W = a.L^b.G^c$	$\pm$SE for b	$\pm$ SE for c	r^2 correlation coefficient
Male	65	$0.000104.L^{0.8853}.G^{1.8862}$	±0.1709	±0.1656	0.977
Female	48	$0.000069.L^{1.4935}.G^{1.3053}$	±0.1525	±0.1597	0.970
Male and Female	115	$0.000081.L^{1.2401}.G^{1.5524}$	±0.1087	±0.1098	0.974

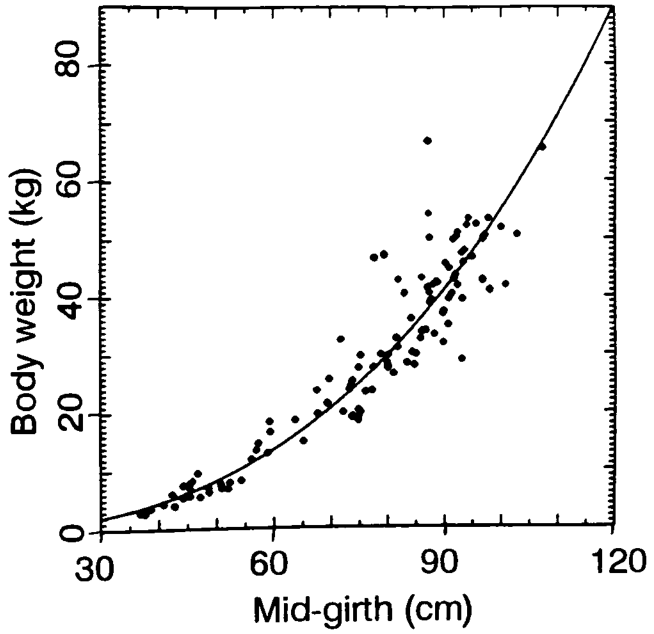

Fig. 3. Body weight (kg) on mid-girth (G_3), (cm) for both sexes of porpoise, in British waters.

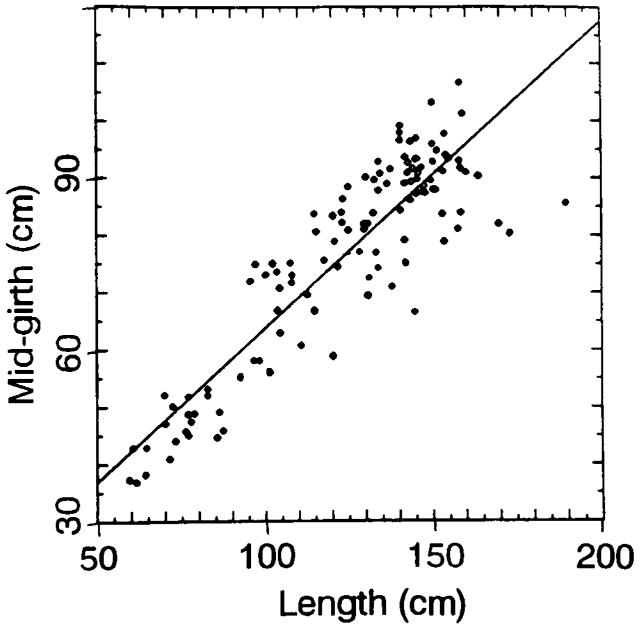

Fig. 4. Mid-girth (G_3), (cm) on body length (cm), for both sexes of porpoise, in British waters.

Tissue weight and length

The plots of muscle and blubber weights with body length are shown in Figs 5a and b. Muscle mass clearly increases greatly with increased body length (Fig. 5a) as a power curve fitted to the data demonstrate, whilst blubber mass does not increase as much as muscle (Fig. 5b). The blubber data appear to be served almost as well by a straight line plot (Fig. 5b) and it is certain that muscle mass becomes an increasingly important component of the body, whilst blubber becomes less dominant with general increase in body size.

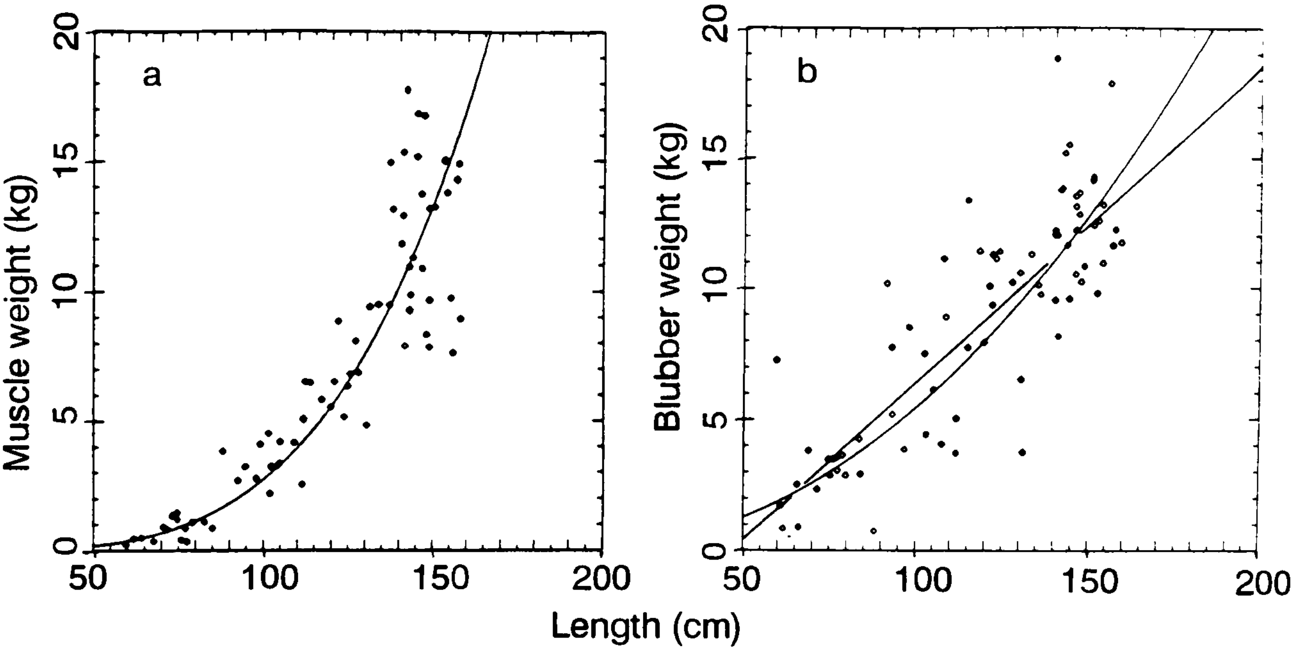

Fig. 5. (a) Muscle weight (kg) at body length (cm); (b) Blubber weight (kg) at body length (cm) – power-fitted and linear-fitted curves, for both sexes of porpoise, in British waters.

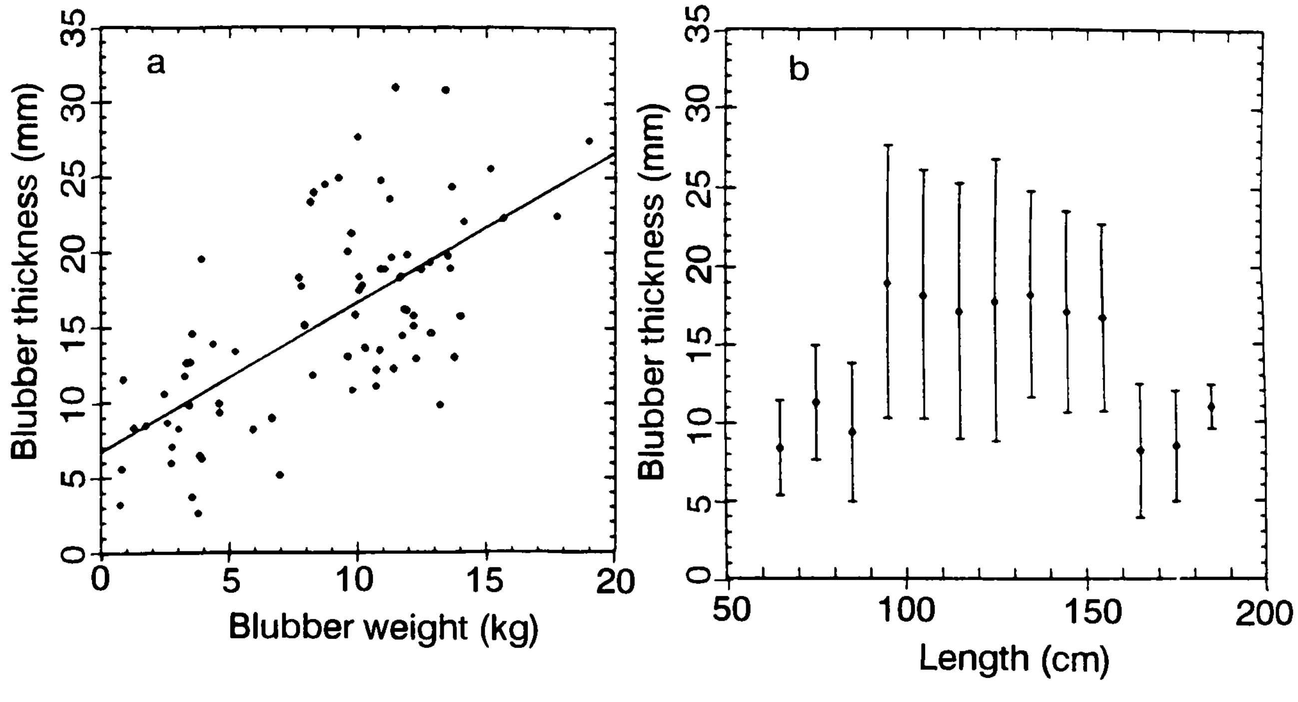

Fig. 6. (a) Blubber thickness (mm) at blubber weight (kg); (b) Mean blubber thickness (mm) ±SE at body length (cm), for both sexes of porpoise, in British waters.

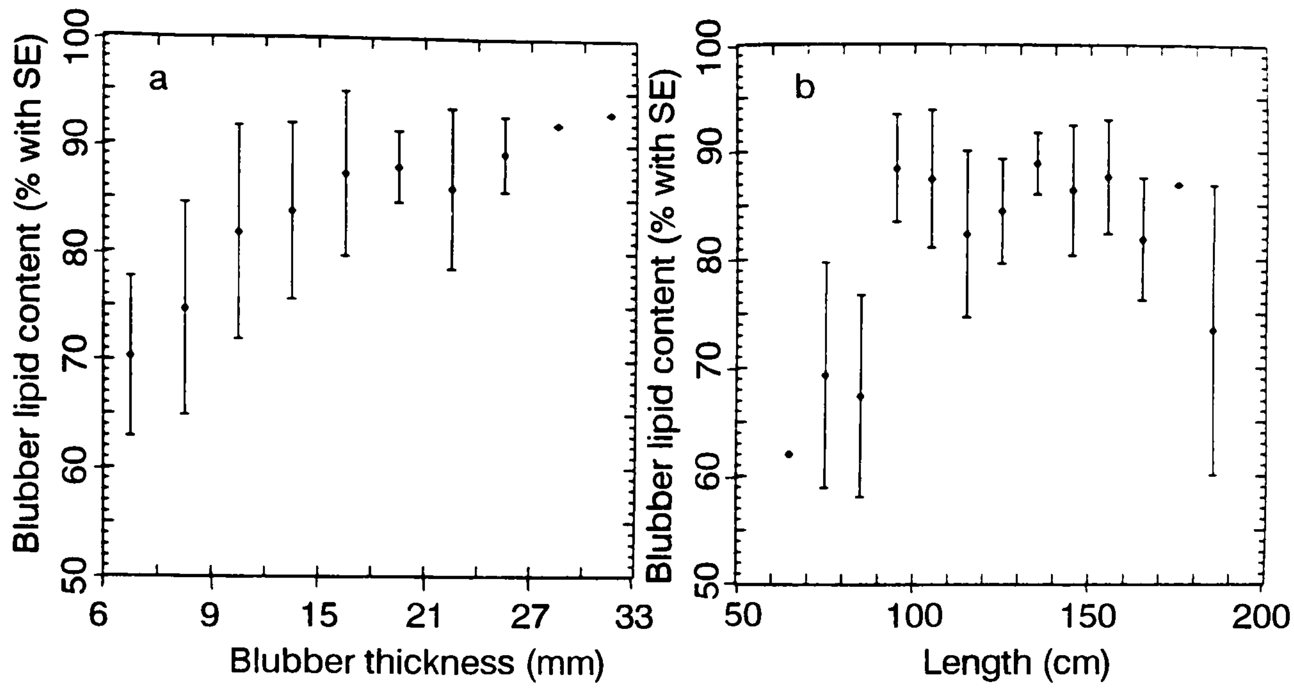

Fig. 7. (a) Mean percent blubber lipid content with blubber thickness (mm); (b) Mean percent blubber lipid content with body length (cm), for both sexes of porpoise, in British waters.

Blubber thickness

Blubber thickness has been plotted against blubber tissue weight in Fig. 6a for both sexes. There is much scatter to the data, as might be expected in combining sexes and different sizes of animals; but there is also a correlation, with a linear increase in thickness with increase in mass of tissue. In a plot of mean blubber thickness ±SE by 10cm increments of body length (Fig. 6b), again with both sexes combined, the variability is evident, particularly in the size ranges 90–150cm. The neonates and first year animals ≤90cm, as well as the very large animals >160cm (mostly females), all have relatively thin blubber. In fact there is a general decrease in mean blubber thickness throughout the size range 90–150cm. The pattern thus appears to be thin blubber in neonates and first year animals, thickest blubber in yearlings and juveniles 90–130cm, then thinner and decreasingly less blubber in adults as they become larger (and older).

Blubber lipid composition

Lipid content has been calculated as a percentage of wet weight of blubber tissue and represents the total lipid content of mid-lateral blubber (site L_3 on Fig. 1) throughout the depth of tissue from under-skin to muscle interface. Lipid content is plotted against blubber thickness in Fig. 7a, where the mean ±SE is shown for 3mm increments in blubber thickness. The lipid content appears to increase consistently with thickness of blubber from a mean of about 70% in blubber <6mm, to a maximum of 93% in blubber >30mm thick. The relationship between blubber thickness and body size is not simple (Fig. 6b) and, therefore, it is not surprising that in a plot of mean lipid content against body length in 10cm increments (Fig. 7b), we see a similar pattern as before (Fig. 6b) with low lipid levels in neonates, high levels in juveniles and adults, and a decline in lipid level in large adults which comprise virtually all females. A plot of mean blubber lipid content with age in years, demonstrates that the lowest lipid levels occur in neonates and first year animals (Fig. 8).

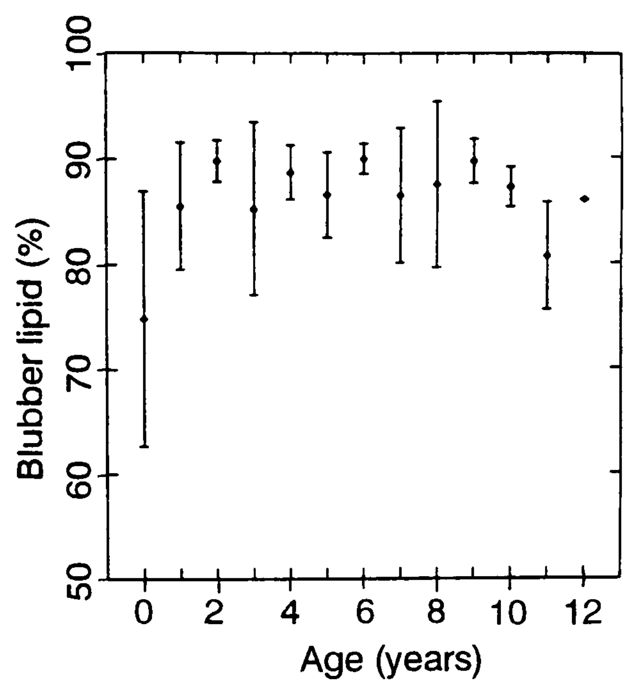

Fig. 8. Mean percent blubber lipid content ±SE at age (yr), for both sexes of porpoise, in British waters.

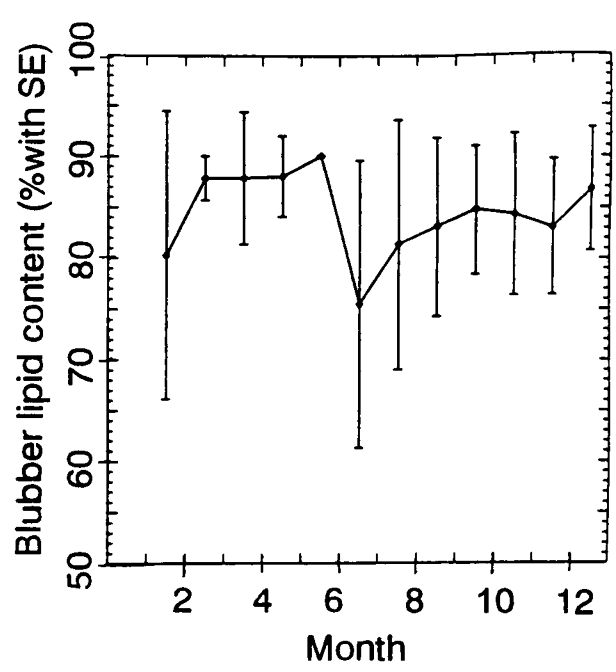

Fig. 9. Mean percent blubber lipid content by month, for both sexes of porpoise, in British waters.

Table 4

Numbers of neonates (< 90cm body length) of both sexes recovered in each month.

Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sept.	Oct.	Nov.	Dec.
1	1	1	1	2	19	9	3	1	1	0	1

A plot of mean blubber lipid content by month (Fig. 9), demonstrates some variability with a sharp dip in level during June. Table 4 indicates that the most plausible explanation for this is the high number of neonates recovered in June, which biases the mean lipid content downward.

Body fat condition and composition by age, sex and reproductive status

The overall sample was classified into the age and reproductive groups defined earlier in the Material and Methods section. Mean ±SD was calculated for different characters, including length, weight, blubber mass, muscle mass, mid-girth (G_3), mid-lateral blubber thickness (L_3) and percentage blubber lipid content, the results of which are shown in Table 5. Neonates (≤90cm) are slightly over half the adult mean length and about a sixth of adult body weight, whereas juveniles (excluding neonates) are about 54% (males) and 63% (females) adult mean body weight. The blubber: muscle ratios change as the animal grows and develops. In neonates, the ratio of blubber to muscle is 3.3:1 in females and 3.8:1 in males; in juveniles (excluding neonates) it is 1.5:1 in females and 1.7:1 in males; and in adults is 1.1:1 in females and 0.9:1 in males. Mean blubber mass as a percentage of total body weight in male neonates, juveniles and adults is 38%, 35.6% and 29% respectively, and in females is 49.4%, 32.2% and 26.4% respectively. The corresponding values of mean percentage muscle mass in males are 9.9%, 21.2% and 31.1% respectively,

Table 5

Mean values ±SD for various measurements of porpoise, by reproductive status. Sample sizes in parentheses.

Reproductive class	Length (cm)	Weight (kg)	Blubber weight (kg)	Muscle weight (kg)	Mid-girth (cm)	Mid-lateral blubber thickness (mm)	% Blubber lipid content
Neonates (♂) ≤90cm	76.2±8.0 (27)	7.1±2.0 (26)	2.7±1.8 (11)	0.7±0.4 (9)	45.6±5.2 (14)	9.9±4.1 (22)	67.3±8.6 (8)
Neonates (♀) ≤90cm	79.3±7.2 (13)	8.7±4.3 (11)	4.3±2.7 (7)	1.3±1.1 (7)	47.1±4.1 (7)	12.8±6.2 (10)	69.3±11.6 (4)
Neonates (♂+♀) ≤90cm	77.1±7.8 (45)	7.6±2.9 (40)	3.3±2.3 (18)	1.0±0.8 (16)	46.1±4.8 (21)	10.8±5.0 (32)	67.9±9.2 (12)
Immature less neonates (♂) 91-130cm	113.4±10.3 (43)	22.2±6.5 (33)	7.9±3.1 (18)	4.7±1.9 (19)	72.2±9.7 (24)	17.3±7.6 (32)	87.1±5.7 (17)
Immature less neonates (♀) 91-130cm	119.0±7.7 (37)	26.7±5.7 (27)	8.9±1.6 (6)	5.6±1.9 (6)	77.8±6.2 (10)	18.5±8.5 (27)	82.8±7.2 (11)
Immature less neonates (♂+♀) 91-130cm	115.8±9.8 (87)	24.2±6.5 (61)	8.2±2.8 (24)	4.9±1.9 (25)	73.4±9.4 (35)	17.6±8.1 (60)	85.4±6.5 (28)
Mature (♂) >130cm	144.5±7.8 (66)	41.1±8.5 (50)	11.9±3.3 (17)	12.8±2.9 (16)	90.5±6.8 (28)	17.7±6.9 (47)	87.2±5.2 (24)
Mature and sub-adult less pregnant and lactating (♀) >130cm	150.4±14.1 (61)	41.8±12.3 (42)	11.8±1.6 (10)	11.4±2.6 (10)	85.9±7.1 (25)	15.1±6.5 (38)	86.6±6.8 (23)
Mature and sub-adult less pregnant and lactating (♂+♀) >130cm	147.0±11.5 (133)	41.5±10.4 (92)	11.9±2.8 (27)	11.9±3.0 (26)	88.4±7.3 (53)	16.6±6.8 (85)	86.9±6.0 (47)
Immature less neonates (♀) 91-140cm	123.6±9.6 (53)	28.6±6.1 (38)	9.2±1.7 (7)	6.2±2.2 (7)	80.1±7.3 (16)	18.6±7.7 (36)	85.3±6.4 (19)
Mature less pregnant and lactating (♀) >140cm	156.9±11.6 (43)	45.0±13.0 (30)	11.9±1.7 (9)	10.5±2.7 (9)	86.6±6.9 (19)	13.4±5.9 (28)	85.5±8.1 (15)
Pregnant females	151.5±5.3 (6)	50.3±9.1 (6)	13.6±2.3 (6)	14.4±2.1 (6)	95.4±9.1 (6)	16.8±4.2 (6)	86.8±6.3 (5)
Lactating females	156 (1)	40.0 (1)	11.0 (1)	10.0 (1)	82.0 (1)	12.0 (0)	
Pregnant and lactating	150 (1)	49.0 (1)	11.0 (1)	8.0 (1)	96.0 (1)	14.0 (1)	83.0 (1)

and in females are 14.9%, 21.7% and 23.3% respectively. These findings confirm the interpretation of Fig. 5a-c earlier where muscle is observed to become a more dominant tissue in the body with increase in size. Also, females carry both actually and relatively more blubber and muscle mass than males (Table 5).

Mid-girth as a proportion of total body length remains stable throughout life, with the percentage being 59–65%, except for adult females >140cm with a proportion of 55%. The pregnant/pregnant and lactating females have a proportion of 63–64%. However, the only lactating female measured had a girth only 52% of body length. Blubber thickness varied considerably with developmental stage and body size. The juveniles generally had the thickest blubber of all with mean values of 17.3mm in males and 18.6mm in females. Other groups with thick blubber include adult males (17.7mm) and pregnant females (16.8mm). Adults generally have relatively thinner blubber than juveniles, but when 0.95 confidence intervals are calculated, there is overlap of actual values and the differences are therefore not significant between these groups. Neonates, however, have the thinnest blubber. There are too few data to conclude with certainty that the lactating female appears to have thinner blubber than other females and all other adults.

The mean lipid content for all groups (excluding neonates) is within the range 83–87% wet weight of tissue. The neonate group have less lipid than other groups at 67–69% wet weight of tissue.

DISCUSSION

Morphometrics, body size and condition

The analyses of body weight at length and mid-girth indicate that weight is strongly correlated with both these measurements. Moreover, body weight can be calculated from formulae derived by the log-linear regression of weight on either length or mid-girth, although a multiple regression involving both length and mid-girth is the most precise. It is clear that mid-girth is actually a more reliable predictor of body weight than length and this may be helpful when estimating body weight in instances where carcases are damaged and flukes or head is missing. These findings confirm earlier studies (Martin *et al.*, 1990).

The proportions of adult blubber and muscle mass expressed as a percentage of body weight (29.0% blubber and 31.1% muscle for males, and 26.4% blubber and 23.3% muscle for females) appear to differ from the findings of Yasui and Gaskin (1986) who report 33.4% blubber and 22.6% muscle for a ‘standard adult’ of 150cm length from the Bay of Fundy, Canada. The British porpoises have less blubber and rather more muscle. However, sample sizes were small (*n*=18 animals) in the Yasui and Gaskin study. Muscle becomes a more dominant tissue in adulthood, perhaps reflecting the extra power required by adults and greater levels of activity associated with reproduction. At the same time, blubber appears to diminish in the adult. Observations here that blubber thickness appears greater in juveniles and is relatively thinner in adults are similar to those of Read (1990). However, Read found that his calves were fattest amongst all groups, unlike findings here for neonates. However, Read measured blubber ventrally over the sternum, whereas measurement here was mid-lateral further back on the body; also there were differences in mean lengths of groups, mainly due to differences in classification. Read’s mean immature group size was larger by up to 16cm and his calf group was larger than the neonates by about 31cm. Read also observed a direct linear relationship between blubber mass and body length, as also found here (Fig. 5c). The mid-girths reported by Read (1990) for each group are similar to those in Table 5 excepting neonates, although his immature group is fatter – presumably because of the length incompatibilities of the data sets.

The neonates in the sample here were thin and had a low mass of blubber. Birth during June-July may be a favourable time environmentally because of higher water temperature, resulting in less heat loss. The greater blubber mass and blubber thickness in female neonates compared to male neonates (Table 5) might offer advantage to female survival at this stage of life, in the form of extra insulation and energy reserve. The slightly larger female body and muscle mass (Table 5) may also provide greater stamina. It is clear that juveniles rapidly acquire thick blubber and that lipid content also increases to adult level. Perhaps this takes place during the suckling phase in preparation for nutritional stresses at the time of weaning. Such a potential energy store coupled with increased thermal insulation may favour juvenile survival at a time when finding food may be a problematic and energetically demanding experience. Although lipid content remains fairly stable in adults at 83–87% wet weight of tissue, blubber thickness and mass declines relative to juveniles.

There is a suggestion that body fat condition may vary with reproductive state in females (Read, 1990), with increased fatness in pregnancy and depletion in lactation. Although differences in body fat condition are observed in several groups from the British sample, the picture may to a certain extent be confounded by the uncertainty about cause of death. Stranded animals may include a high proportion of sick and those in poor body condition, whilst bycatch animals may be more healthy. At present, because of the lack of formal bycatch reporting, the true significance of variation in body condition cannot be assessed. However, it may be concluded that general findings are similar to those elsewhere.

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Diet of the Harbour Porpoise (*Phocoena phocoena*) in Scandinavian Waters

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ABSTRACT

In this paper we report findings on the diet of the harbour porpoise (*Phocoena phocoena*) in Danish, Swedish and Norwegian waters. The study is based on stomach contents from 247 porpoises bycaught or stranded between 1985 and 1990. Fish otoliths were identified and counted and other stomach contents recorded. A minimum of 30 species of fish were identified, representing 16 families. Off northern Norway, capelin (*Mallotus villosus*) was an important species (62% frequency of occurrence). In Scandinavian waters as a whole, herring (*Clupea harengus*) was the single most important species in the diet. Clupeidae and Gadidae were the most common prey families. Pelagic and mesopelagic fish were more important in the diet of the harbour porpoises in Norwegian waters, while benthic species were more important in Danish and Swedish waters. Cephalopods occurred in only seven (3.8%) of the stomachs and in low numbers per stomach. The smallest porpoise with food remains other than milk had a total body length of 100cm. The differences between the diet in the northern and southern part of the study area are related to the geographical distribution of some of the prey species, but can also be related to differences in bathymetry in the Norwegian area and the Danish and Swedish area.

KEYWORDS: HARBOUR PORPOISE; FEEDING; NORTH ATLANTIC; FISH

INTRODUCTION

The harbour porpoise (*Phocoena phocoena*) is a coastal species usually found in water depths of less than 200m, occurring as single animals or in groups of up to 10 individuals (Klinowska, 1991). Adult males often tend to form separate groups as do young animals of both sexes (Tomilin, 1957; Gaskin, 1977). Females with calves also form separate groups and are particularly associated with shallow waters (Kinze, 1990). In the North Atlantic the harbour porpoise is known to feed on a wide range of pelagic and demersal fish species and, to some extent, on cephalopods (Collett, 1923; Tomilin, 1957; Lindroth, 1962; Rae, 1964; 1973; Andersen, 1965; Gaskin *et al.*, 1974; Källquist, 1974; Smith and Gaskin, 1974; Gaskin, 1977; Desportes, 1985; Recchia and Read, 1989; Lick, 1991). The different distribution of groups by age and sex may result in differences in diet between animals in the same population. Calves of harbour porpoises suckle for about eight months and then

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are gradually weaned (Gaskin *et al.*, 1984). In captivity they are able to feed on fish from 2–4 months of age (Andersen, 1974), but little information is available on the feeding habits of free ranging harbour porpoises during and immediately after the weaning period.

The purpose of this study is to assess the relative importance of the fish species found in the stomachs of harbour porpoises from Scandinavian waters. The occurrence of pelagic, mesopelagic or benthic fish species in the diet of the harbour porpoise is discussed in relation to bathymetry and differences in diet between sex and age groups are investigated.

MATERIALS AND METHODS

All 247 harbour porpoises (109 females, 133 males and 5 of unknown sex) used in the present study were incidentally caught in fishing nets or found stranded. The 109 harbour porpoises from Norwegian waters were all bycaught, while the 81 animals from Swedish waters and the 57 animals from Danish waters also included an unknown proportion of stranded specimens. About 65% (161 porpoises) of the Norwegian sample was caught in the salmon driftnet fishery in May–June 1988, while the rest of the animals were collected from other types of fish nets throughout the year (1989–90). All porpoises incidentally caught in Norwegian fisheries were frozen shortly after they were caught and shipped frozen to the laboratory in Oslo. Before dissection they were partly thawed. The porpoises from Swedish and Danish waters were collected during all months in the period 1985–89 and the frozen stomachs, or stomach contents, of these animals were shipped to Oslo for identification of prey species.

Teeth were collected and the age was estimated from dentine growth layer groups (Kvam *et al.*, 1989).

After dissection the stomachs were re-frozen (−20°C), until processing. The stomach contents were then washed through three interconnecting sieves with mesh sizes of 2.0, 1.0 and 0.25mm. Otoliths and other remains were preserved dry or in 70% ethanol. Fish species were identified using the otolith identification manuals of Breiby (1985) and Härkönen (1986). The number of individuals of each species found in a stomach was estimated as the highest number of either left or right otoliths. If the otoliths were severely eroded and difficult to determine as either left or right sided, the total number of otoliths was divided by two to determine the number of individuals. Otolith lengths and widths were measured to the nearest 0.01mm with a digital caliper and used to estimate fish lengths and weights following equations given by Härkönen (1986). No correction for erosion of the otoliths was made and otoliths from virtually undigested fishes were treated in the same way as more digested otoliths lying loose in the stomach. In most stomachs, however, the contents were well digested and a loss of valuable information would be the result if only undigested otoliths were used. The estimated weight and length of the fish will, therefore, only represent a minimum estimate of fish size.

The rows of ‘teeth’ located on the tongue of the Atlantic hagfish were used to calculate the number of individuals of this species, as most hagfish in the stomachs were no longer recognisable as individuals.

The importance of prey species was expressed as: (i) the percent frequency of occurrence (the number of stomachs found to contain the particular prey species divided by the total number of stomachs with identifiable remains and multiplied by 100); (ii) the percent numerical occurrence (the number of individuals of the particular prey species divided by the total number of prey individuals found and multiplied by 100); and (iii) the percent weight occurrence (the total weight of the particular prey species divided by the total weight of all prey species and multiplied by 100).

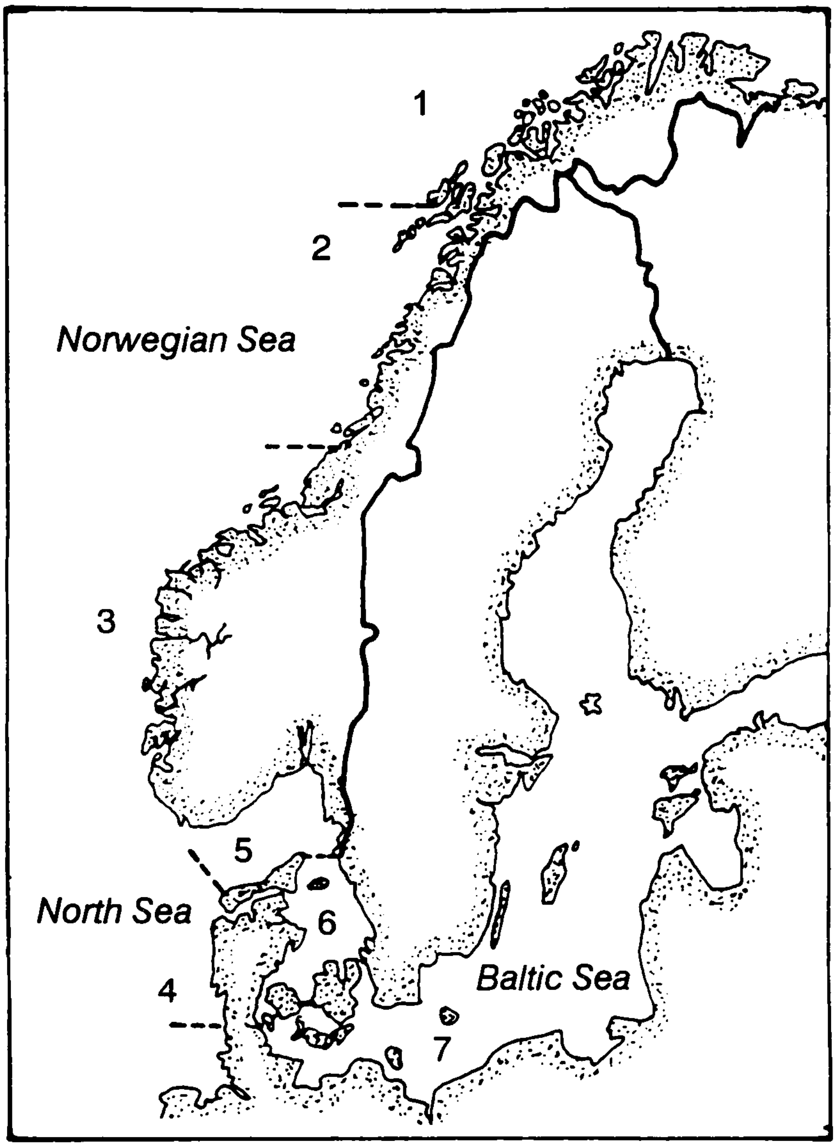

Fig. 1. Areas for sampling of porpoises in Scandinavian waters. The subareas are: (1) Finnmark and Troms counties; (2) Nordland county; (3) The Norwegian coast from Nord-Trøndelag county to the Swedish border; (4) Danish west coast; (5) Skagerrak; (6) Kattegat; (7) Baltic. Subareas 1–3 are pooled into the Northern area and subareas 4–7 are pooled into the Southern area.

The collected material was divided into seven geographical subareas (Fig. 1). Approximately the same number of males and females occurred in each of the areas. The seven subareas were also grouped into two larger areas (Northern and Southern) to reveal possible differences in the diet of harbour porpoises from relatively shallow southern waters and from the deeper northern waters. In the Northern area (subareas 1–3, Norwegian waters) the depths of coastal waters vary, but depths of 200–500m are most common (Anon., 1989). In the Southern area (subareas 4–7, Danish and Swedish waters) shallow waters (depths less than 90m) are most common.

RESULTS

Stomach contents

A total of 33% of the stomachs from the Southern area and 19% of the stomachs from the Northern area were without identifiable remains. In stomachs with identifiable remains, fish was the most important prey group. Otoliths from 8,101 fishes were recorded and 30 different prey species determined. In total, 16 fish families were present in the diet. The largest fish eaten (based on otoliths) was a cod estimated to have been 485mm long, but most of the fish species eaten (74%) had an average length of 250mm or less.

Cephalopod beaks were rare and occurred in only seven harbour porpoise stomachs (3.8%). Few beaks were found per stomach. Crustacean and polychaete remains were also rare. Hagfish eggs were found in two stomachs and plastic material was found in one stomach.

Fish species and geographical differences in the diet

The percent frequency of occurrence, percent numerical occurrence and percent weight occurrence of the fish species in the diet varied between areas (Tables 1 and 2; Fig. 2).

Table 1

Frequency of occurrence of fish species found in the stomachs of harbour porpoises collected during all seasons in the period 1985-1990. Coding of sampling areas: See Fig. 1. Prey categories are: P = pelagic, M = mesopelagic and B = benthic fish species (division following the species description of Pethon, 1989).

		Sampling areas						
Prey species	Prey cat.	1	2	3	4	5	6	7
Hagfish (*Myxine glutinosa*)	B					15		
Eel (*Anguilla anguilla*)	B					5		5
Capelin (*Mallotus villosus*)	P	62						
Smelt (*Osmerus eperlanus*)	P			3				
Herring (*Clupea harengus*)	P	33	59	35	18	70	54	62
Sprat (*Sprattus sprattus*)	P	5	4			25	15	10
Greater argentine (*Argentina silus*)	P	14	19	8				
Argentine (*Argentina sphyraena*)	P		11					
Pearlsides (*Maurolicus muelleri*)	M	10	11	23		5	8	
Gadidae sp.	-	19	26	18	36	15	21	
Trisopterus sp.	-		4	5				
Norway pout (*Trisopterus esmarkii*)	B	5	4	3		5		
Poorcod (*Trisopterus minutus*)	B		37	10	9	15	5	5
Blue whiting (*Micromesistius poutassou*)	M	14	19	30		5	3	
Whiting (*Merlangius merlangus*)	B		4	5	72	20	21	5
Silvery pout (*Gadiculus argenteus thori*)	B	5	7	3				
Haddock (*Melanogrammus aeglefinus*)	B	14	15	13		10	3	
Saithe (*Pollachius virens*)	P	19	15	43			5	
Cod (*Gadus morhua*)	B		4		26	5	8	29
Pollack (*Pollachius pollachius*)	P				9		3	
Hake (*Merluccius merluccius*)	B		4	5	27		10	
Ling (*Molva molva*)	B		4	3				5
Fb. rockling (*Rhinonemus cimbrius*)	B		4			20		5
Eelpout (*Zoarces viviparus*)	B							19
Scorpaenidae sp.	M		11					
Ammodytidae sp.	B		4	5	9	20	21	10
Gobiidae sp.	B		7	5	18	35	36	10
Houting (*Coregonus lavaretus*)	P							5
Pleuronectidae sp.	B							5
Long rough dab (*Hippoglossoides platessoides*)	B				18			
Mackerel (*Scomber scombrus*)	P			3				
Montagu's sea snail (*Liparis montagui*)	B					5	3	
Scad (*Trachurus trachurus*)	P					5		
Unidentified fish	-	10	7		9	5	5	5
Total number of stomachs:		21	27	40	11	20	39	21

Table 2

Numerical occurrence of fish species found in the stomachs of harbour porpoises collected during all seasons in the period 1985-1989. Coding of sampling areas: See Fig. 1. Prey categories are: P = pelagic, M = mesopelagic and B = benthic fish species.

Prey species	Prey cat.	Sampling areas						
		1	2	3	4	5	6	7
Hagfish (*Myxine glutinosa*)	B					3		
Eel (*Anguilla anguilla*)	B					0.1		2
Capelin (*Mallotus villosus*)	P	88						
Smelt (*Osmerus eperlanus*)	P			<0.1				
Herring (*Clupea harengus*)	P	2	7	1	1	10	7	28
Sprat (*Sprattus sprattus*)	P	0.3	2			5	1	12
Greater argentine (*Argentina silus*)	P	0.7	0.9	0.3				
Argentine (*Argentina sphyraena*)	P		1					
Pearlsides (*Maurolicus muelleri*)	M	3	35	78		6	2	
Gadidae sp.	-	0.8	9	0.8	0.7	5	1	
Trisopterus sp.	-		1	0.1				
Norway pout (*Trisopterus esmarkii*)	B	0.6	4	0.5		2		
Poorcod (*Trisopterus minutus*)	B		28	0.2	<0.1	3	0.7	0.9
Blue whiting (*Micromesistius poutassou*)	M	4	2	2		0.1	0.2	
Whiting (*Merlangius merlangus*)	B		0.2	0.1	91	3	1	0.9
Silvery pout (*Gadiculus argenteus thori*)	B	0.4	0.7	<0.1				
Haddock (*Melanogrammus aeglefinus*)	B	0.4	2	3		0.3	<0.1	
Saithe (*Pollachius virens*)	P	0.8	2	2			0.2	
Cod (*Gadus morhua*)	B		0.3		1	0.3	0.7	27
Pollack (*Pollachius pollachius*)	P				0.5		<0.1	
Hake (*Merluccius merluccius*)	B		0.2	0.4	0.2		1	
Ling (*Molva molva*)	B		0.2	<0.1				0.9
Fb. rockling (*Rhinonemus cimbrius*)	B		0.7			3		2
Eelpout (*Zoarces viviparus*)	B							13
Scorpaenidae sp.	M		0.9					
Ammodytidae sp.	B		0.2	0.2	0.3	1	0.1	4
Gobiidae sp.	B		2	11	2	57	83	7
Houting (*Coregonus lavaretus*)	P							0.9
Pleuronectidae sp.	B							<0.1
Long rough dab (*Hippoglossoides platessoides*)	B				2			
Mackerel (*Scomber scombrus*)	P			<0.1				
Montagu's sea snail (*Liparis montagui*)	B					0.2	<0.1	
Scad (*Trachurus trachurus*)	P					0.1		
Unidentified fish	-	0.3	0.9	0.2	<0.1	<0.1	0.3	0.9
Total number of stomachs:		713	587	2,554	1,902	706	1,522	117

Overall, herring was the single most important species and occurred in all areas. Some species (e.g. the greater argentine and capelin) were only found in the Northern area while others (e.g. the Pleuronectidae species) were found only in the Southern area. The Gadidae and Clupeidae families predominated in all areas. Gadidae species constituted 65% and 53% of the diet by weight in the Northern and Southern areas, respectively. Clupeidae species constituted 20% of the diet by weight in the Northern area and 39% in the Southern area.

Pelagic fish occurred more frequently in the stomachs of harbour porpoises collected in the Northern area while benthic fish occurred more frequently in harbour porpoises from the Southern area. The percent numerical and percent weight occurrence also showed the same tendency (Fig. 3).

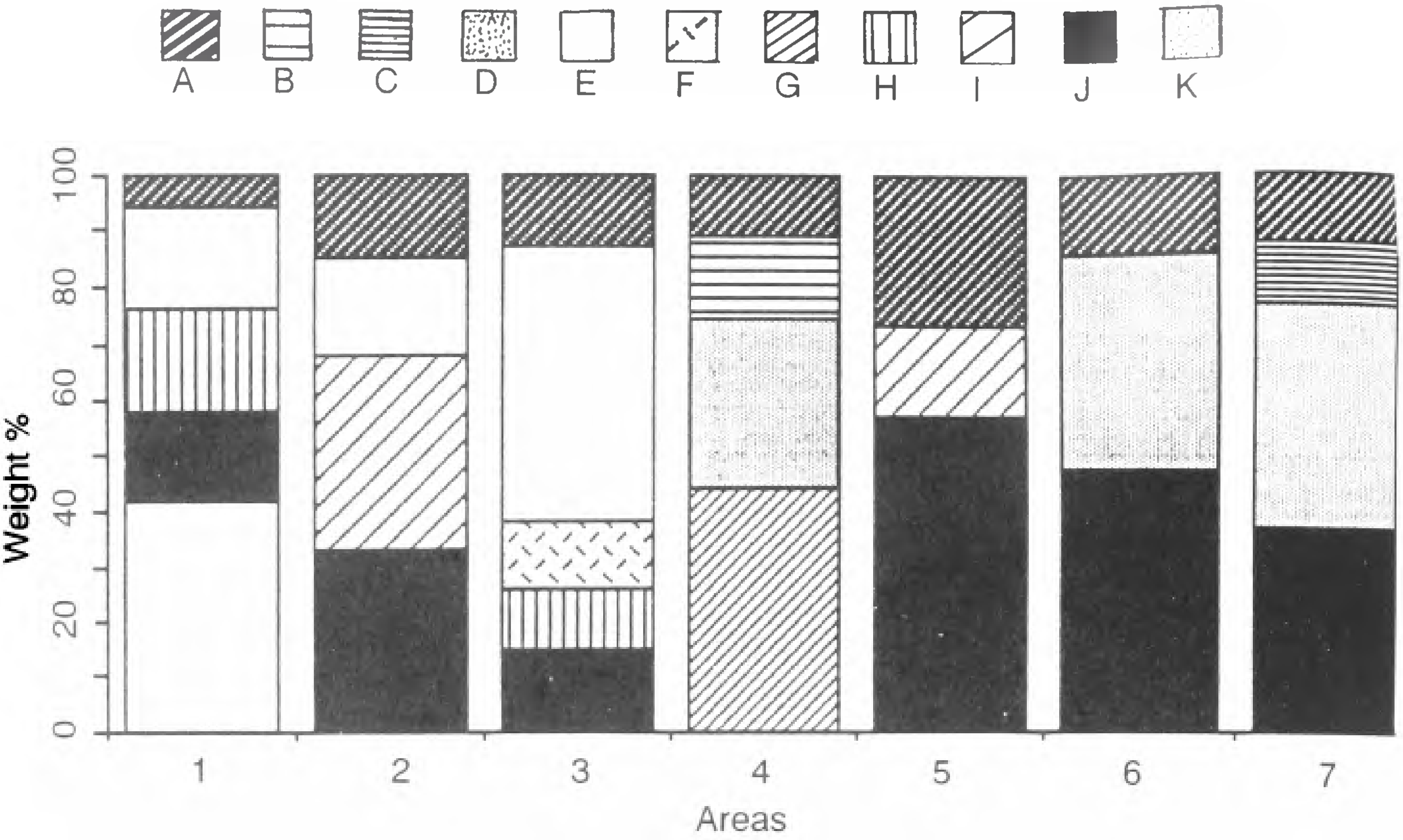

Fig. 2. Percentage by weight of fish species in the diet of harbour porpoise in Scandinavian waters (1985–1990). Coding of sampling areas: See Fig. 1. The fish species are: (A) Fish species contributing less than 10% of the diet; (B) Long rough dab; (C) Eel pout; (D) Cod; (E) Saithe; (F) Haddock; (G) Whiting; (H) Blue whiting; (I) Poorcod; (J) Herring and (K) Capelin.

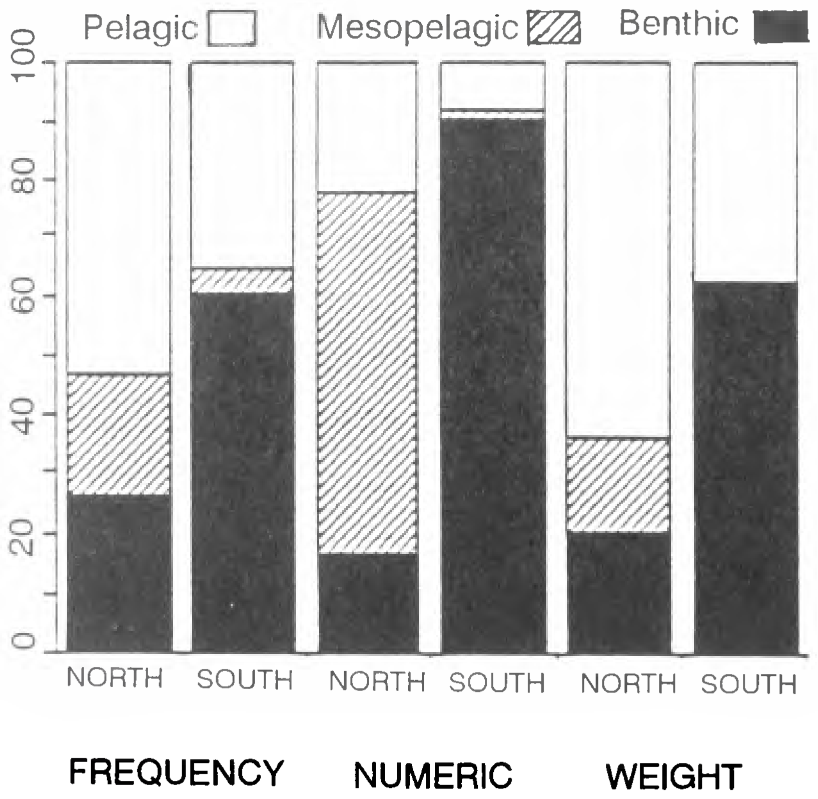

Fig. 3. Percent frequency of occurrence, percent numeric occurrence and percent weight occurrence of pelagic, mesopelagic and benthic fish species in the harbour porpoise diet in the Northern (Norwegian waters) and Southern (Danish and Swedish waters) area.

In all but the northernmost subarea (Finnmark-Troms) the number of benthic fish species found was higher than the number of pelagic and mesopelagic fish species. In that area, there were more pelagic fish species with capelin being the most frequently occurring.

Number of fish species and individuals per stomach

The number of individual fish found per stomach varied from 1 to 973 whilst the number of species recorded varied from 1 to 11. Of the 179 porpoises with identifiable remains in their stomachs, 82 (46%) contained only one species while an additional 41% of the porpoises had eaten two or three different species. Of those porpoises with only one fish species recorded, 77% had been foraging on pelagic or mesopelagic fish.

Seven porpoises, all adult females, had eaten more than five different species; two were pregnant, one was lactating, one was simultaneously pregnant and lactating whilst three were resting. The total sample included seven known pregnant or lactating females[1]; the remaining three had from 1–3 different species in their stomachs.

Age and sex related differences in diet

Of the seven pregnant or lactating females, only one (pregnant) had eaten cephalopods. All of the fish species found in the stomachs of the seven females were also found in the stomachs of sexually mature males. A comparison of the weight of stomach contents of the pregnant or lactating females to that of the 48 sexually mature males revealed no significant difference (t-test, $p=0.57$) although the number of females was low. The average weight of stomach contents for pregnant or lactating females was 691g (SD=585, $n=7$) and for sexually mature males of approximately the same body length, 507g (SD=806, $n=48$). The largest weight of stomach contents estimated was 7,601g, from a sexually mature female (not pregnant and with no information on lactation). As these estimates were based on all otoliths present in the stomach, they may comprise more than one single meal. The mean weight of stomach contents for all porpoises with identifiable remains was 499g (SD=851, $n=168$).

The smallest harbour porpoise with stomach contents other than milk had a total body length of 100cm. According to Kaarstad (1993) animals with total body lengths of 113cm or less were presumed to be younger than six months of age and therefore defined as calves in the suckling or weaning period. Of the 18 porpoises in this category, 16 were from the southern area. The weight of fish contents in the stomach of suckling calves appeared to increase during the weaning period, i.e. when calves increased their body length from 100 to 113cm (Fig. 4). The largest estimated weight of stomach contents found in a calf (based on otoliths) was 470g. At least 12 fish species were recorded from calves. The largest fish eaten by a calf was a 325mm blue whiting. Benthic fish occurred in 13 (72%) of the stomachs of calves. No difference in the diet composition of weaning calves and the older porpoises (>113cm) was found.

Male porpoises of one year or less ($n=30$) had greater numbers of fish in their stomachs than the females of the same age ($n=33$; t-test, $p<0.01$); Gobiids were the most common prey species in both sexes for these year classes. In the diet of harbour porpoises six years of age or older, pearlsides had the highest percent of numerical occurrence. Adult males in particular had eaten a large number of individuals of this mesopelagic species.

[1] The reproductive state of all sexually mature females in the sample was not known.

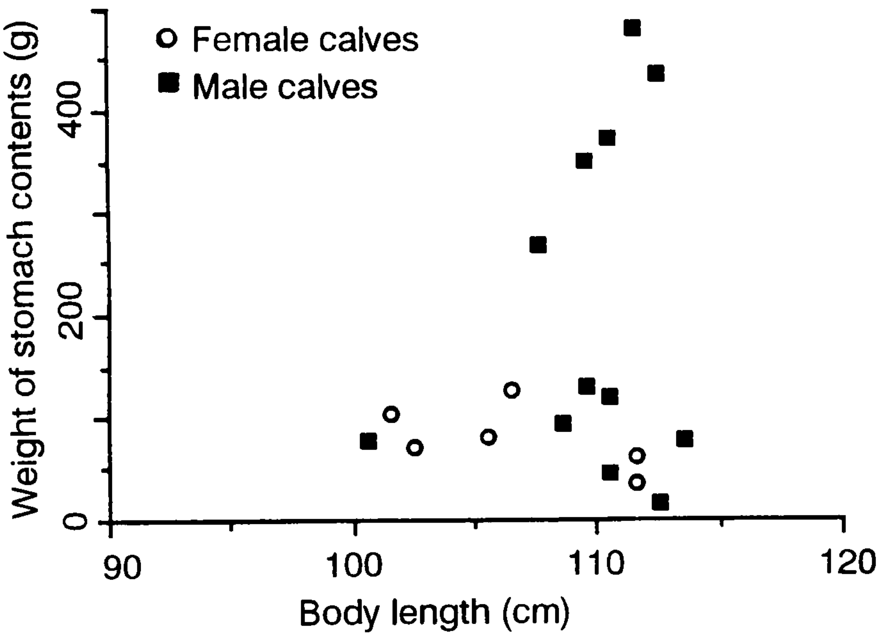

Fig. 4. The estimated weight of stomach contents of harbour porpoise calves with total lengths between 100 and 114cm. Harbour porpoise calves less than 100cm had only milk in the stomach. Harbour porpoises larger than 113cm had a mean weight of stomach contents of 542g (SD=890, *n*=150).

DISCUSSION

Bias caused by otolith erosion

It is important to remember that the observed stomach contents may be based on remains from one or more meals. Read and Gaskin (1985) suggested that harbour porpoises have one to two feeding periods during the day related to the tidal cycle, with little activity at night. Murie and Lavigne (1985) reported that herring otoliths were not retained in seal stomachs for longer than about 13 hours after feeding. The difference between species in otolith erosion rate and the differences in exposure time of otoliths to stomach acids may influence the recorded diet composition and the estimated weight of stomach content.

The problem of applying correction factors to back-calculate fish weights is discussed by Pierce and Boyle (1991). They concluded that unless the length of time prey have been exposed to digestion is known, correction is difficult since the degree of size reduction is unknown. The relationship between species in the diet will also be biased since some otoliths resist digestion better than others (da Silva and Neilson, 1985; Jobling and Breiby, 1986; Murie, 1987; Recchia and Read, 1989). Species without hard parts will also be underestimated.

Stranded versus bycaught porpoises

According to Evans (1990), stomachs of stranded cetaceans often do not contain identifiable remains. Collecting bycaught animals is, therefore, probably a more efficient sampling method for examination of diet composition. The harbour porpoises incidentally caught in fishing gear in the Northern area more frequently had identifiable food remains than the sample from the Southern area that included both stranded and incidentally caught porpoises. However, sampling incidentally caught cetaceans from fishing gear may select porpoises with a particular type of foraging behaviour (see IWC, 1994) and/or bias the diet composition towards the target species of the fishery in which the porpoises were caught. In this case, about two thirds of the porpoises sampled in Norwegian waters were incidentally caught in driftnets set for salmon, but no salmon was recorded in the stomach contents. This could indicate that salmon was not a preferred prey species, or that only soft parts of the salmon were eaten and thus not recorded in the stomach contents.

Important prey species and geographical differences in the diet

Herring was the most important single species in the harbour porpoise diet, ranging from 18 to 70% frequency of occurrence by subarea and forming a large part of the diet by weight in most subareas. The importance of herring in the harbour porpoise diet in the North Atlantic has been previously recognised by several authors (Tomilin, 1957; Lindroth, 1962; Rae, 1964; Gaskin, 1977; Recchia and Read, 1989). Read (1990) suggested a correlation between the amount of herring found in the stomachs and the body condition of the harbour porpoises.

Gadids formed an important part of the diet in all areas. Cod occurred frequently in harbour porpoise stomachs from the Danish North Sea and the Baltic, but despite its wide distribution and abundance in northern Scandinavian waters (Pethon, 1989; Anon., 1990), cod was only recorded in one stomach from the Northern area. Other Gadids, such as saithe and blue whiting occurred frequently in the diet of porpoises from the Norwegian coast, but occurred in few stomachs of porpoises from the Danish and Swedish coast. Whiting, Ammodytidae and Gobiidae species occurred frequently in the porpoises from the Danish and Swedish areas, but were of little importance in the diet in the Norwegian areas.

Capelin was the most important prey species of the harbour porpoises collected off the coast of northern Norway (the Finnmark-Troms subarea). Capelin has previously been identified as a prey species of harbour porpoises in northern Norwegian and Russian waters (Collett, 1923; Tomilin, 1957) and in harbour porpoise stomachs from the northeast Pacific (Scheffer, 1953).

Pleuronectidae species were not found in the stomach contents of the harbour porpoises collected along the Norwegian coast, but occurred in the porpoises from the Danish and Swedish area. Lick (1991) reported that Pleuronectids constituted 58% by weight in the diet of porpoises in the German North Sea. In our investigation from the adjacent Danish North Sea, Pleuronectids constituted 15% by weight, but our sample contained only eleven porpoises with identifiable stomach contents.

Diet composition and bathymetry

The number of fish eaten per porpoise varied, probably according to the relative body size and abundance of prey in the area. Pelagic fish species predominated in the diet of harbour porpoises from the Northern area whereas benthic fish species predominated in the Southern area. It may be that the water depths in some parts of the Northern area might exceed the preferred dive depth of the harbour porpoises and therefore reduce the availability of benthic fish species; the sea floor in the Southern area will, on the other hand, be within reach in most parts. The situation in the Southern area is comparable to the shallow parts of the Black Sea where benthic fish species were twice as important by weight as pelagic fish species in the harbour porpoise diet (Tomilin, 1957).

The large proportion of pelagic fish in stomachs containing just one species, suggest that if a pelagic fish species is encountered, it is available in large numbers of individuals typical of schooling species. In such circumstances porpoises do not forage on the sea floor. However, if pelagic fish species are not encountered during a dive the porpoises probably continue down to feed on benthic fish species. The higher frequency of a mixed diet when porpoises were foraging on benthic species may mirror the probability of encountering higher diversity of species at or just above the sea floor than in the water masses above due to the schooling behaviour of some pelagic fish species.

Age and sex related differences in diet

Calves apparently eat relatively large quantities of fish at an early age. No differences in the diet composition of calves (<113cm body length) and older porpoises was found. The number of different fish species found was high given the low number of weaning calves investigated and no preference for pelagic or benthic fish species was registered. This is in agreement with the findings of Smith and Gaskin (1974) who found no dietary differences between young and older harbour porpoises. Smith and Read (1992), however, found that calves in their first summer ate euphausiids while the adults ate herring. Lick (1991) also found different prey assemblages in the diet of young and adult porpoises, with adults feeding on a larger variety of prey species than young animals for which Gobiidae species predominated. However, benthic prey dominated the diet of both young and older animals in Lick's study, as was the case in our sample from the Danish west coast (subarea 4) which is adjacent to Lick's study area.

The stomachs of male porpoises, 0 to 1 year of age, contained a higher number of fish than the stomachs of females of the same age. A faster growth rate for males than females during the first two years of life is indicated by Kaarstad (1993) and this may imply a higher consumption rate by young males. Although no significant differences in diet composition between age groups were demonstrated, Gobiidae species were the most frequently occurring prey species in 0 and 1 year old porpoises.

In general, the porpoises were foraging on one or only a few prey species. The few porpoises which contained remains of more than five prey species were females of which four were pregnant or lactating. Our study does not, however, provide sufficient basis for a conclusion that pregnant or lactating females have a higher consumption, feed on larger fish or forage on different prey species, as indicated by other authors (Gaskin *et al.*, 1984; Yasui and Gaskin, 1986; Recchia and Read, 1989).

Other remains found in the stomachs

Few cephalopod, crustacean and polychaete remains were recorded. Cephalopods and possibly polychaetes have been reported as primary prey species, but they did not appear to be important in the diet of the harbour porpoises in our sample. The crustaceans found in the stomachs were most probably secondary prey. Plastic material was found in one of the harbour porpoises in our investigation. Man-made articles have previously been recorded in stomachs of porpoises held in captivity (Spotte *et al.*, 1978).

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Parasites and Pollutants in Seven Harbour Porpoises (*Phocoena phocoena* L. 1758) from the Faroe Islands, 1987–1988

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ABSTRACT

Parasite and pollutant loads, reproductive status and overall condition were recorded for seven harbour porpoise shot at the Faroes in 1987–1988. Four species of nematodes were found. A mixed infection of the lungworms *Pseudolius inflexus* with *Halocerus invaginatus* in two porpoises has not been reported from other areas. The lung worm *Torynumus convolutus* was not found in the Faroes porpoises. One species of liver fluke was found. Cd levels were high compared to those found in harbour porpoises from other North Atlantic areas, except for one from the Shetland Islands. This may be due to the vicinity of the North Atlantic ridge system. Generally, total DDT and PCB levels were between levels in porpoises taken in Denmark and in Greenland. *p,p*'-DDE had the highest contribution to total DDT, which corresponds to the fact that it is more persistent than *p,p*'-DDD and *p,p*'-DDT. Females can become mature from three years of age. The overall condition of the porpoises does not seem to have been affected by their parasite loads.

KEYWORDS: HARBOUR PORPOISE; PARASITES; POLLUTION; NORTH ATLANTIC

INTRODUCTION

A number of studies on parasites of the harbour porpoise from eastern Atlantic waters have been carried out: Wesenberg-Lund (1947) reported on lungworm species from Danish waters; Balbuena *et al.* (1987) and Clausen and Andersen (1988) reported on species of lungworms, ear worms, stomach worms and liver flukes from French Atlantic and Danish waters, respectively.

Pollutant burdens have been reported by Clausen and Andersen (1988), Granby and Kinze (1991) and Law *et al.* (1991). Aguilar and Borrell (1995) reviewed pollutants in harbour porpoises in the North Atlantic.

Although the sample size is small, this study provides the first information on the pollution and parasite burdens of the harbour porpoise off the Faroe Islands. The results are compared to those from Danish (Möhl-Hansen, 1954; Clausen and Andersen, 1988) and Greenlandic waters (Granby and Kinze, 1991).

MATERIAL AND METHODS

One porpoise shot in 1987 (Bloch and Hoydal, 1989) and six specimens shot in 1988, all near Klaksvík (Bloch and Hoydal, 1990), were necropsied (Table 1). The animal from 1987 was necropsied fresh, whereas the animals from 1988 had been stored frozen for 2½ months before necropsy.

Standard length was measured according to the American Society of Mammalogists (1961).

Table 1

Nutritional condition, reproductive status. Imm. = immature; Mat. = mature; CL = corpus luteum; CA = corpus albicans. A 'Yes' or 'No' indicates whether spermiae were found.

Porpoise	1	2	3	4	5	6	7
Shot	3/8 1987	18/5 1988	19/5 1988	20/5 1988	21/5 1988	28/5 1988	28/5 1988
Sex	M	M	F	F	M	F	F
Age (years)	10	9-10	3	5	5	8-9	4
Length (cm)	147	142	137	126	139	149	130
Nutritional condition	++	+++	+++	+++	+++	++	+++
Reproductive status							
Females			Imm.	Imm.		Mat.	Mat.
Pregnant or lactating						Lact.	
Corpora						CL6.8	
Measurements (mm)						CA2.9	CA2.9
Follicle measurements (mm)			<2.7	<1.8		<2.8	<5.2
Males							
Spermiae	Yes	Yes			No		

Age determination

Teeth were decalcified, sectioned using a microtome and stained with hematoxylin (Nielsen, 1972; Perrin and Myrick, 1980) and read in both transmitted and in polarised light (Norgaard and Larsen, 1991). It was assumed that one growth layer group is equal to one year (see Lockyer, 1995).

Nutritional condition

The nutritional condition of the animals was evaluated and registered according to the following scale: + for 'poor' (no fat around the lungs; blubber layer <1cm, weak-muscled), ++ for 'fair' (no fat around the lungs, well-muscled); and +++ for 'good' (fat around the lungs, well-muscled).

Reproductive status

Ovaries were examined according to standard methods (Perrin and Donovan, 1984). Epididymal smears were stained in giemsa (Larsen and Norgaard, 1991) and checked for spermatozoa. The reproductive status of the animals is listed in Table 1.

Parasite loads

Parasite loads in the various organs were evaluated and registered according to the scale: + (1–9 parasites), ++ (10–50 parasites) and +++ (>50 parasites) following Clausen and Andersen (1988). The condition of the bile duct walls (i.e. whether they were pathologically changed – thickened and with a whitish appearance due to increased amounts of connective tissue) was used to evaluate the load of liver flukes in the bile ducts.

Parasites were collected from the ear sinuses, lungs, stomachs and liver. Parasites in the intestines are not listed. Determination to species was performed at Institut für Meereskunde, Universität Kiel, Germany (Table 2).

Table 2

Parasite burden. Life history data are given in Table 1.

Porpoise	1	2	3	4	5	6	7
NEMATODES							
Earworms							
S. minor	+	+	+	++	+	+	+++
Lungworms							
P. inflexus	+				+	+	
H. invaginatus							
Eggs	+	+			+++		
Adults							++
Not identified							
Eggs				++			
Adults		+	+	+			
Stomach worms							
A. simplex	+	+	+	+ ulcer	+	+ ulcer	+
TREMATODES							
Liver flukes							
C. oblonga	++	+(+)	++	++	+(+)	+	No
Bile duct walls thickened	Yes	Yes	Yes	Yes	Yes	No	No

Pollutants

Samples for heavy metal analysis from liver and kidney were stored in plastic bags at –20°C. Analysis for mercury (Hg) in liver and kidney, and cadmium (Cd) in kidney were carried out using flameless atomic absorption spectrometric analysis (Magos, 1971; Anon., 1982) at the National Veterinary Laboratory, Copenhagen, Denmark. Results are expressed on a wet weight (WW) basis (Table 3).

Samples for organochlorine analysis from liver and blubber (at the sternum) were wrapped in aluminium foil and stored at –20°C. Organochlorine compounds were analysed at the Section of Zoology, Department of Biology, University of Barcelona, Spain, following the procedures described by Aguilar and Borrell (1988). The organochlorine concentrations are expressed on an extractable lipid basis (Table 3).

RESULTS

The female of eight or nine years of age had much thickened walls of the vagina and was lactating. None of the females were pregnant.

Parasites

Four species of nematodes were recorded: the earworm *Stenurus minor* (Kuhn 1829); the lungworms *Pseudalius inflexus* (Rudolphi 1808) and *Halocercus invaginatus* (Quekett 1841); and the stomach worm *Anisakis simplex*. Eggs of *H. invaginatus* were present in the lungs of three porpoises and adults were found in the lungs of another porpoise. Adult *P. inflexus* were found in the lungs of three porpoises. Adult *A. simplex* were found in the lumen of the stomachs, while larval stages were found attached to the bottom of a crater-like swelling (an 'ulcer') in the ventral part of the forestomach (Table 2).

Table 3

Pollutants. Concentrations of Hg, Cd and organochlorines. n.d. = not determined. EXTRA = amount of extractable fat (%). Life history data are given in Table 1.

Porpoise	1	2	3	4	5	6	7
Nutritional condition	++	+++	+++	+++	+++	++	+++
Total Hg mg/kgWW							
Liver	7.6	9.7	3.7	4.8	8.5	7.8	3.6
Kidney	1.5	1.9	1.1	1.2	1.3	1.3	1.2
Methyl-Hg mg/kgWW							
Liver	2.0	<1	1.0	0.3	1.1	3.0	<0.1
Kidney	0.3	0.5	0.3	0.3	0.2	0.2	0.4
Methyl-Hg in % of total Hg							
Liver	26.3	<10.3	27.0	6.3	12.9	38.5	<2.8
Kidney	20.0	26.3	27.3	25.0	15.4	15.4	33.8
Cd mg/kgWW							
Kidney	5.3	3.6	3.8	1.8	2.4	n.d.	2.8
% dry matter	21.0	21.3	19.1	20.2	23.8	n.d.	22.6
Concentrations of organochlorines (mg/kg) in blubber, expressed on an extractable lipid base							
p,p'-DDE	2.67	3.26	2.01	2.56	3.08	n.d.	1.80
p,p'-DDD	1.07	1.05	0.96	0.97	1.08	n.d.	0.88
o,p'-DDT	0.89	0.64	0.67	0.64	1.42	n.d.	0.66
p,p'-DDT	1.14	0.95	0.77	0.73	1.70	n.d.	0.65
tDDT	5.77	5.90	4.41	4.90	8.00	n.d.	3.99
tPCB	10.13	15.77	7.95	10.31	14.26	n.d.	8.22
EXTRA	85.48	88.09	89.60	96.10	85.85	n.d.	96.28
Concentrations of organochlorines (mg/kg) in liver, expressed on an extractable lipid base							
p,p'-DDE	0.70	1.21	0.59	0.54	0.67	0.55	0.92
p,p'-DDD	0.51	0.69	0.36	0.31	0.59	0.27	0.54
o,p'-DDT	0.05	0.06	0.05	0.05	0.05	0.08	0.18
p,p'-DDT	0.27	0.34	0.19	0.14	0.26	0.16	0.42
tDDT	1.53	2.30	1.19	1.04	1.57	1.06	2.06
tPCB	5.48	8.06	4.39	3.48	4.07	3.08	6.48
EXTRA	3.99	7.19	4.04	4.70	4.44	4.69	3.96

No parasites were found in the heart; no skin lesions from fungi infections were found and no ectoparasites were observed.

The liver fluke *Campula oblonga* (Cobbold 1858) had caused pathological changes in the walls of the bile ducts in five of six porpoises (Table 2).

Pollutants (Table 3)

Mercury (Hg)

The concentrations of total Hg (mg/kgWW) ranged from 3.6–9.7 with a mean of 6.5 in the liver and from 1.1–1.9 with a mean of 1.4 in the kidney.

Cadmium (Cd)

The concentrations of Cd (mg/kgWW) in the kidney ranged from 1.8–5.3 with a mean of 3.3. The animal with the highest value was taken at a different time of year than the others and may perhaps be from a different group of animals. Omitting this specimen gives values ranging from 1.8–3.8 with a mean of 2.9.

Organochlorines
The concentrations of total DDT (mg/kg) and total PCB (mg/kg) in blubber ranged from 3.99–8.0 with a mean of 5.5 and from 7.95–15.77 with a mean of 11.11, respectively. In the liver the concentrations ranged from 1.04–2.3 with a mean of 1.54 (total DDT) and from 3.08–8.06 with a mean of 5.0 (total PCB). Organochlorine concentrations are given on an extractable lipid basis.

DISCUSSION

Necropsy findings

The nutritional status of the animals were fairly similar to that found for Danish harbour porpoises by Clausen and Andersen (1988).

Although the small sample size precludes estimation of reproductive parameters, the finding of a four year old female taken in May with a corpus albicans shows that females may mature from three years of age. This was also found for animals in Danish waters (Clausen and Andersen, 1988) and from the Bay of Fundy, Canada (Read, 1990). The animals were killed prior to the breeding season if they follow the Danish seasonal pattern.

Parasites

All of the parasite species recorded in the porpoises from the Faroes have been recorded in porpoises from other regions.

The earworm *Stenurus minor* was found in 70% of animals more than one year old in Danish waters (Clausen and Andersen, 1988) and in the cranial sinuses of 25% (*n*=8) porpoises from the French Atlantic (Balbuena *et al.*, 1987). It was also found in lungs of harbour porpoises from the Bay of Fundy, Canada, by Arnold and Gaskin (1975).

Pseudalius inflexus was only recorded in the lungs of three Faroese specimens. However, Wesenberg-Lund (1947) found this species in the heart and in the large veins of the majority of 50 harbour porpoises examined for parasites in the Danish survey of Møhl-Hansen (1954). Clausen and Andersen (1988) found some specimens in the heart of one out of 149 examined harbour porpoises, in the lungs of 31% of porpoises younger than one year (n=55) and in the lungs of 97% of the older ones (n=94). The species has also been reported from harbour porpoise from the Bay of Fundy, Canada, from the North Sea off the Netherlands (Arnold and Gaskin, 1975) and from the French Atlantic region (Abeloos, 1982; Balbuena *et al.*, 1987). It was also found during a survey conducted in the Danish region from 1986–1989 (C.C. Kinze, unpubl. data, pers. comm.).

The mixed infection of *Pseudalius inflexus* with *Halocerus invaginatus* found in two porpoises in the present survey has not been reported from other areas. *H. invaginatus* was not found in any of the Danish surveys (Clausen and Andersen, 1988; Kinze, pers. comm.). Arnold and Gaskin (1975) reported *H. invaginatus* from harbour porpoise from the Bay of Fundy and Vancouver Island, Canada. Specimens were also reported from the Black Sea harbour porpoise by Skrjabin (1942) and from a harbour porpoise caught off Newfoundland (Smith and Threllfall, 1973) to be conspecific with *H. invaginatus*.

By contrast the mixed infection of *P. inflexus* with *Torynurus convolutus* reported for the French Atlantic (Abeloos, 1982; Balbuena *et al.*, 1987), Denmark in 1986–1989 (C.C. Kinze, unpubl. data, pers. comm.) and Canada (Arnold and Gaskin, 1975) was not found in this study; in fact *T. convolutus* was not observed.

All of the Faroese animals had *Anisakis simplex* present, two with ulcers. Clausen and Andersen (1988) had found *A. simplex* in 9% of animals <1 year (*n*=55) and 21% of older animals (n=94) in Danish waters including some with ulcers. Smith (1989) also reported such swellings in 70% (n=10) harbour porpoises from the Scottish east coast.

The finding of *Campula oblonga* in the livers of six of the seven Faroese specimens corresponds with the moderate to heavy infestation with this liver fluke in a proportion of about 65% of the Danish harbour porpoises examined in 1980–81 (Clausen and Andersen,1988). It was also recorded from British waters (Gibson and Harris, 1979) and from the French Atlantic region (Balbuena *et al.*, 1987).

Andersen (1974; 1978) and Clausen and Andersen (1988) reported fungal infection in the skin in Danish waters; this was not the case for the Faroese animals.

The nutritional data suggest that the overall condition of the Faroese harbour porpoises was not affected by their parasite loads. This was also found for Danish harbour porpoises (Möhl-Hansen, 1954; Clausen and Andersen, 1988).

Chemical analysis

The mercury levels in the kidney are similar to those found in Danish harbour porpoises older than three years (range 0.01–1.6; mean 1.3 mg/kgWW; n=40; mean age 6.3 years) (Clausen and Andersen, 1988). The levels in the liver are generally lower than found in 3+ year old animals by Law *et al.* (1991) from British waters.

However, cadmium levels were high compared to those found in other North Atlantic areas (see review by Aguilar and Borrell, 1995). The only animal with comparable levels was a one year old porpoise from the Shetland Islands (Law *et al.*, 1991) that had 1.2 mg/kgWW in the liver. This corresponds to 2.4–6.0 mg/kgWW in the kidney, as in cetaceans, concentrations of Cd are consistently higher by a factor of 2–5 in renal tissue than hepatic tissue (Wagemann and Muir, 1984). It is not known whether the relatively high concentrations of Cd at Klaksvík is of anthropogenic origin, or whether it originated from the volcanic activity of the North Atlantic Ridge system.

Granby and Kinze (1991) reported insignificant variations in pollutant concentrations in blubber samples from four parts of a harbour porpoise and hence considered results from different parts of porpoises comparable. If so, their results from their survey and those of Clausen and Andersen (1988) should be comparable with those of the present study (Table 4). The tDDT figures are considered comparable for monitoring purposes. However, as PCB mixtures vary in composition, the tPCB figures may not be directly comparable, but they may be used to expose overall tendencies (Granby and Kinze, 1991).

Table 4

Loads of total DDT and PCB in blubber (mg/kgWW) from porpoises older than three years, caught in Danish waters (DK) in 1980-81 and in 1986-89, from this study and at West Greenland (GR) in 1988.

	DK 80-81	DK 86-89	Faroes 87-88	GR 88		DK 80-81	DK 86-89	Faroes 87-88	GR 88
Females					**Females**				
tDDT	12	7.3	4.7	0.80	tPCB	54	8.1	9.4	0.7
	SD-8	SD-6.1	SD-0.3			SD-29	SD-6.0	SD1.2	
	n=18	n=4	n=3	n=1		n=18	n=4	n=3	n=1
Males					**Males**				
tDDT	40	17	7.6	9.2	tPCB	127	23	15.5	4.5
	SD-41		SD-1.5			SD-29		SD-3.2	
	n=19	n=1	n=3	n=1		n=19	n=1	n=3	n=1

In general, the further porpoises are taken from industrialised countries the lower the findings of total DDT and PCBs (Aguilar and Borrell, 1995). The loads in the blubber were lower in the Faroese porpoises than in porpoises caught in Danish waters in 1980–81 (Clausen and Andersen, 1988). They were also lower than, or similar to, loads in Danish porpoises caught in 1986–88 and, except for the tDDT loads in males, were much higher than loads in Greenlandic porpoises (Granby and Kinze, 1991).

In five samples, the relative contributions to tDDT are *p,p'*-DDT < *p,p'*-DDD < *p,p'*-DDE whilst in the remaining two the order was *p,p'*-DDD < *p,p'*-DDT < *p,p'*-DDE. This is in accordance with the fact that *p,p'*-DDE is the most persistent (EPA, 1980) and hence may dominate in more remote areas (Granby and Kinze, 1991).

Granby and Kinze (1991) and Duinker *et al.* (1989) found the latter order in blubber from harbour porpoises from Danish and Greenlandic waters and Dutch waters. Duinker *et al.* (1989) also found relatively large proportions of *p,p'*-DDE on blubber from cetaceans from the western North Atlantic respectively whereas Morris *et al.* (1989) found that *p,p'*-DDD provided the largest contribution to tDDT in blubber samples from Cardigan Bay.

The relatively small contribution of *p,p'*-DDD to tDDT in the Faroese animals is to be expected because *p,p'*-DDD has a tendency to votalize three times less than for *p,p'*-DDT and *p,p'*-DDE (HSDB, 1988) and hence the atmospheric contribution is low. And the relatively high contribution of p,p'-DDE can be explained by its persistence. Faroese waters are far from sources of input of DDT and the level of tDDT is lower than in Danish waters, but much higher than at West Greenland. PCBs are still in use, hence tPCB levels lower than or similar to the Danish levels, but much higher than the western Greenlandic levels are to be expected.

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Pollution and Harbour Porpoises in the Eastern North Atlantic: A Review

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ABSTRACT

Published data on concentrations of organochlorine compounds and heavy metals in tissues of harbour porpoises from the eastern North Atlantic are reviewed. The dynamics of pollutants in this population are poorly known because of lack of consistency and coordination between surveys. tDDT concentrations were of the same order of magnitude, or somewhat lower, than in conspecifics from other regions, but those of PCBs were usually higher. Therefore, tDDT/PCB ratios in eastern North Atlantic harbour porpoises were substantially lower than values estimated for other regions. Within the whole area surveyed, specimens from the Baltic Sea were different from the rest because they had proportionally more tDDT and less PCBs. During the period 1970–88, the overall tDDT/PCB ratio significantly decreased with time, indicating that tDDT decreased while PCBs remained constant or increased in the area. Levels of mercury, lead, copper, zinc and cadmium were not significantly higher in this population than in others from the same species or than those detected in other small odontocetes of similar body size and food habits from northern waters. Concentrations of other metals in North Atlantic harbour porpoises have seldom been reported but do not appear to be a matter of concern for the population. For reasons not yet clarified, overall levels of cadmium were substantially lower than reported for any other cetacean species. It was not possible to ascertain the current impact, if any, of pollutants on eastern North Atlantic harbour porpoises, but the levels of organochlorines especially PCBs were found to be high enough to cause concern about their possible effects on the maintenance of the population.

KEYWORDS: HARBOUR PORPOISE; NORTH ATLANTIC; POLLUTION-ORGANOCHLORINES; POLLUTION-HEAVY METALS

INTRODUCTION

Eastern North Atlantic harbour porpoises (*Phocoena phocoena*) inhabit one of the most heavily polluted marine environments in the world. As a result of human activity, persistent chemical pollutants such as organochlorine compounds and heavy metals have become abundant in the northern North Atlantic and the North Sea, and have been incorporated into the oceanic food webs, contaminating all the components of their biota. Harbour porpoises are no exception, and measurable quantities of pollutants have been detected in their tissues since the late 1960s. Moreover, harbour porpoises are common in coastal waters, feed at high trophic levels and have a small body size (and thus a high metabolic rate). These three factors combine synergetically to place the species in an ecological situation where they are most liable to be adversely affected by persistent chemical pollutants.

Pollutant surveys on eastern North Atlantic harbour porpoises have almost invariably focused on monitoring residue levels in local populations, and the information available is, in most cases, purely descriptive. Therefore, no comprehensive information is currently available to evaluate the significance of this pollution in relation to other cetacean species or populations of harbour porpoises, or to elucidate the effects of the contaminants on the population. The present paper reviews data published on concentrations of organochlorine compounds and heavy metals in tissues of harbour porpoises from eastern North Atlantic waters and examines their possible effect at the population level.

ORGANOCHLORINE COMPOUNDS

Organochlorines are synthetic chemicals consisting of a hydrocarbon molecule with a variable number of chlorine substitutions. Although many different types of organochlorines have been used on a widespread basis, only two groups highly resistant to biodegradation have entered the marine food webs in significant quantities and these represent the bulk of organochlorine loads in marine mammals: the DDTs, widely used as pesticides in agriculture until the late seventies; and most forms of PCBs (polychlorinated biphenyls), a group of chemicals that comprise 209 different congeners which have been extensively used in the electricity industry and in a variety of other industrial applications. Both groups of organochlorines are abundant in the eastern North Atlantic.

Other organochlorine compounds such as HCH, Lindane, HCB or Dieldrin have also been detected in harbour porpoises from European waters, but the concentrations reported were always very low (Holden and Marsden, 1967; Andersen and Rebsdorff, 1976; Harms *et al.*, 1977; Kerkhoff and de Boer, 1977; Duinker *et al.*, 1989; Bech *et al.*, 1990; Granby and Kinze, 1991). Residues of polychlorinated dibenzodioxins (PCDDs) and dibenzofurans (PCDFs) in one harbour porpoise collected in the North Sea were also reported to be low (Bech *et al.*, 1990).

Organochlorines are highly lipophilic chemicals. That is, they dissolve in fats and, consequently, are easily retained by lipid-rich layers and tissues, in which they reach the highest concentrations. This property explains many of the biochemical characteristics of organochlorines and is central to an understanding of their behaviour in marine ecosystems. Because blubber is the body compartment of marine mammals which contains the highest proportion of lipids and contributes significantly to the animal's body mass, it has typically been selected as the most representative tissue for monitoring organochlorine levels in cetaceans. This is fortunate because it facilitates comparisons between surveys, species and areas from data available in the literature. Other tissues from harbour porpoises such as the liver, brain, heart, kidney and muscle have also been analysed (Holden and Marsden, 1967; Andersen and Rebsdorff, 1976; Harms *et al.*, 1977; Alzieu *et al.*, 1983; Duinker *et al.*, 1989; Morris *et al.*, 1989) but they are not discussed here as, with the current knowledge and availability of data, they do not contribute towards a better understanding of the pollutant load in these cetaceans.

Table 1 details published organochlorine residue concentrations in the blubber of harbour porpoises. Although limited information is available on the organochlorine concentrations in tissues of foetuses (Duinker and Hillebrand, 1979; Alzieu *et al.*, 1983), it is not included here. The pattern of pollutant intake, the physiology, and the biochemical composition of the body of foetuses are completely different from those of adults and, consequently, their pollutant levels are not comparable.

The harbour porpoise was the first cetacean analysed for organochlorines. As early as 1965, Holden and Marsden (1967) determined the concentration of tDDT and Dieldrin in four specimens from Scotland and, since then, the organochlorine residue levels of more than one hundred harbour porpoises have been reported (Table 1). However, the data available are spread over a wide region with at least seven distinct sampling areas and over more than twenty years. In addition, analytical techniques have changed considerably over the period and have differed in accuracy among laboratories even in contemporary

Table 1

Concentration (expressed as ppm calculated on a fresh weight basis) of organochlorine compounds in the blubber of harbour porpoises from the eastern North Atlantic. When concentrations had been originally calculated on a lipid basis and the lipid content of the blubber was not given, a 60% lipid content value was used in all cases for the transformation (* indicates that concentrations were recalculated in this way).

Locality	N	Year	tDDT	%DDE	PCB	DDT/PCB	Reference
Baltic Sea*	4	1970	123.1	-	49.3	2.5	Otterlind (1976)
Baltic Sea*	1	1973	84.0	-	42.0	2.0	Otterlind (1976)
Baltic Sea*	3	1975	82.0	-	69.6	1.2	Otterlind (1976)
West Sweden*	2	1972	207.0	-	120.0	1.7	Otterlind (1976)
West Sweden*	2	1973	60.0	-	87.0	0.7	Otterlind (1976)
West Sweden*	1	1974	46.0	-	126.0	0.4	Otterlind (1976)
West Sweden*	1	1976	14.9	-	33.8	0.4	Otterlind (1976)
Denmark*	1	1974	4.4	-	90.0	0.05	Otterlind (1976)
Denmark*	3	1975	5.0	-	83.6	0.06	Otterlind (1976)
Denmark	4	1972-3	53.0	30.9	78.0	0.7	Andersen & Rebsdorff (1976)
Denmark	51	1980-1	23.2	-	82.4	0.3	Clausen & Andersen (1988)
Denmark	27	1986-8	15.92	46.1	34.9[1]	0.46[1]	Granby & Kinze (1991)
Scotland	4	1965-7	33.1	29.9	-	-	Holden & Marsden (1967)
West Wales	4	1988	13.4	31.3	55.6	0.2	Morris *et al.* (1989)
Germany	3	1976-7	25.9	48.1	81.3	0.3	Harms *et al.* (1977)
Germany*	1	1987	6.7	50.8	42.3	0.2	Beck *et al.* (1990)
Netherlands	1	1971	48.4	40.5	188.0	0.3	Kerkhoff & Boer (1977)
Netherlands	7	1970-1	40.7	-	85.7	0.5	Koeman *et al.*(1972);Koeman (1973)
Netherlands*	11	1977-9	149.7	43.1	84.8[2]	-	Duinker *et al.* (1989)
France*	1	1977	-	-	3.7	-	Alzieu *et al.* (1983)
France*	1	1979	-	-	9.1	-	Alzieu *et al.* (1983)
France*	1	1978	8.36	61.7	76.6	0.1	Alzieu *et al.* (1983)

[1] PCB levels recalculated from original values derived from the sum of seven PCB congeners only.

[2] PCB levels derived from the sum of 17 PCB congeners only. Because no transformation figure to convert this result to PCB mixture standards was given by authors, this value was not used in the calculation of the tDDT/PCB ratio.

surveys. Such a spread of effort and the variation in analytical techniques make any comparison of pollutant loads between localities and years extremely difficult. In fact our knowledge of the dynamics of organochlorines in eastern North Atlantic harbour porpoises is extremely poor.

A further problem is that the biological data from specimens sampled is seldom stated in published reports. As for most cetacean species so far studied (Aguilar, 1987), Granby and Kinze (1991) found that organochlorine levels in the blubber of harbour porpoises increased in both sexes until sexual maturity was reached, after which they continued to increase in males but decreased in females. Heterogeneous composition in the sex and/or age of specimens sampled may account for much of the unexplained variation in pollutant levels observed in different surveys.

Variation with time

From the data in Table 1, it is difficult to ascertain if overall organochlorine pollutant concentrations have varied over the period during which information is available (1965–88 for tDDT and 1970–88 for PCBs). As noted, the age and sex composition of the specimens studied is undoubtly a major factor of variability between surveys. However, the pattern between the two different groups of organochlorines does seem to differ and, while PCBs have remained at more or less constant (although very variable) concentrations, the highest levels of tDDT were invariably found in specimens sampled before 1975. This reflects the fact that, while PCBs have only had their use limited in relatively recent times, the production and utilisation of DDTs was already restricted in most countries bordering the North Atlantic in the early 1970s (Hayes, 1975). Therefore, despite some recent input in the waters around southern Europe and northern Africa, the DDTs currently present in North Atlantic marine ecosystems comprise mostly 'old' DDT. This is confirmed by the high percentage of metabolised forms, such as DDE, present in its composition (Aguilar, 1984). Unfortunately, information on DDE percentages in harbour porpoise tissues from the eastern North Atlantic is extremely limited (Table 1) and does not allow any reliable determination of trends with time.

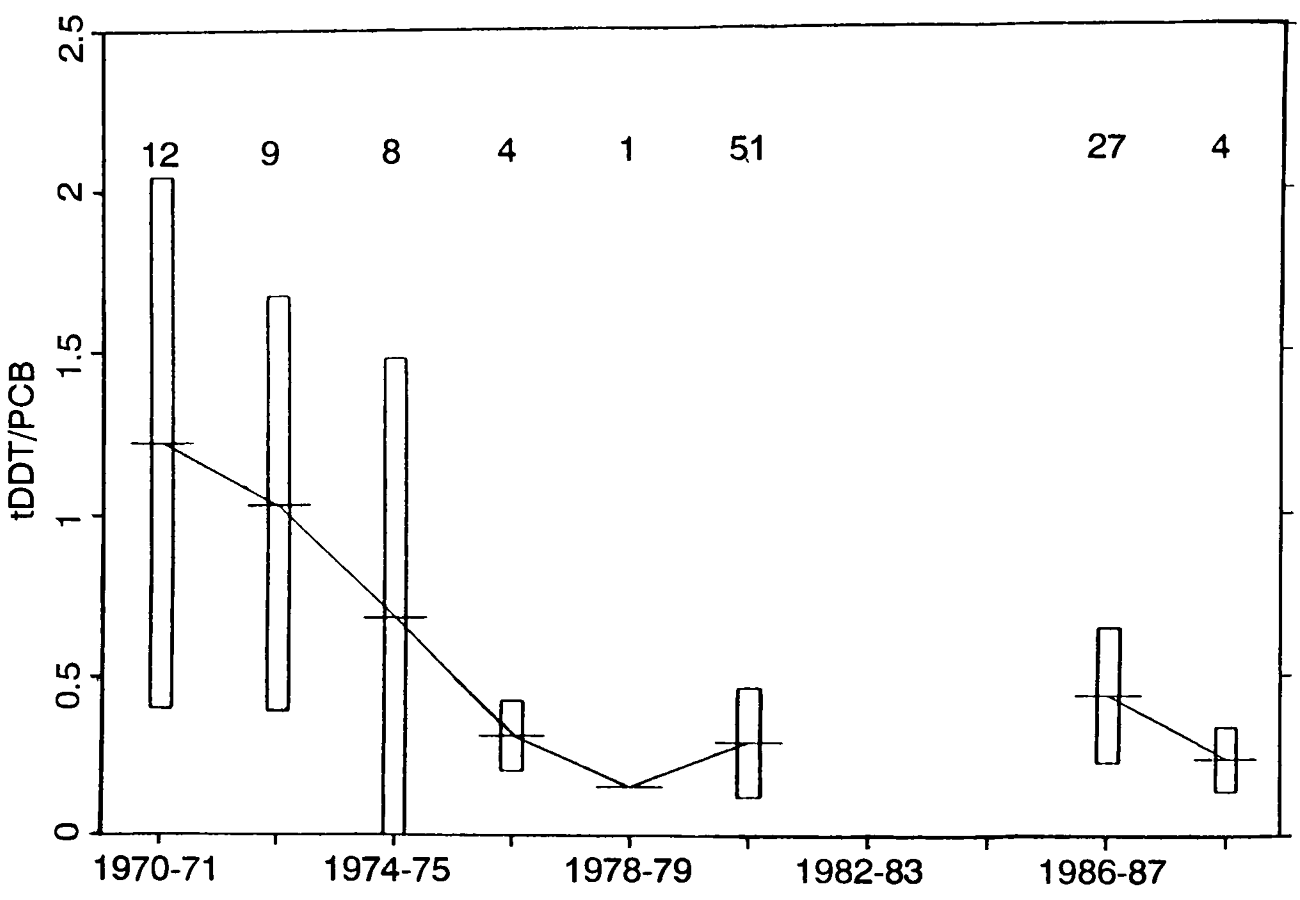

Fig. 1. Variation of the tDDT/PCB ratio in harbour porpoises from the eastern North Atlantic during the period 1970–88. Central points correspond to the means for the biannual period, and bars show the standard deviation of the means. The number above each bar is the sample size.

As a consequence of the diverging trend between tDDT and PCBs, the overall tDDT/PCB ratio in eastern North Atlantic harbour porpoises has decreased over time (Fig. 1). This suggests that, while DDTs are becoming less important as ecotoxicants for marine mammals, PCBs remain a standing health hazard for the smaller top predator species such as harbour porpoises. Although Granby and Kinze (1991) suggested that PCB levels in Danish harbour porpoises were lower at the end of the eighties than in previous decades, they calculated PCB concentrations as the sum of seven congeners, which significantly underestimates actual pollutant loads.

Variation between areas

The heterogeneity in year of sampling also hinders accurate comparison between localities. The magnitude of organochlorine concentrations is similar all over the region, but with large variations in individual concentrations within any given locality. However, Otterlind (1976) found that harbour porpoises from the Baltic Sea contained proportionally more tDDT and less PCBs than their conspecifics from other regions. This is reflected in the tDDT/PCB ratios, which in the Baltic Sea ranged from 1.8–3.3, as opposed to other areas, where they only ranged from 0.05–1.7 (Table 1). This pattern could be attributed to differences in the bioavailability of each group of compounds between the Baltic basin and the North Atlantic. However, the hypothesis cannot be corroborated because it relies on only eight specimens from the Baltic Sea studied by Otterlind (1976); no other data on harbour porpoises from this area are available. It should be pointed out, however, that the observed differences do not seem to be analytical artifacts because Otterlind (1976) applied the same laboratory techniques to specimens from three different areas which he studied, and in which this pattern could be observed.

Granby and Kinze (1991) have suggested that harbour porpoises from Danish waters had lower PCB concentrations than those from the Netherlands, but more Lindane than their conspecifics from Wales. However, this comparison again relies on a limited sample size and it is unclear whether heterogeneities in sample composition accounted for the observed regional differences.

Overall, the tDDT residue levels commonly detected in eastern North Atlantic harbour porpoises were of the same magnitude or somewhat lower than those found in conspecifics from eastern Canada (Gaskin *et al.*, 1982) or the western coast of the United States (O'Shea *et al.*, 1980; Calambokidis, 1986). Only harbour porpoises inhabiting the waters of western Greenland, an almost pristine environment, had blubber tDDT concentrations that were substantially lower than those characteristic of the eastern North Atlantic (Clausen *et al.*, 1974). Conversely, the PCB levels found in the eastern North Atlantic were in the upper range of those detected in both the Atlantic and Pacific waters of North America (O'Shea *et al.*, 1980; Gaskin *et al.*, 1983; Calambokidis, 1986). As a result of this proportionally higher PCB contamination, the tDDT/PCB ratio characteristic of the eastern North Atlantic harbour porpoises (weighted mean for the whole period surveyed: 0.54) is substantially lower than the values for this ratio estimated for other areas, where tDDT is typically more abundant than PCBs and the ratio reaches values greater than unity.

Comparison with other cetaceans

As said before, the biology of the harbour porpoise enhances the accumulation of high levels of persistent pollutants such as organochlorines. As a consequence of this, when compared to other cetaceans from eastern North Atlantic waters, the concentrations of these compounds in the blubber of harbour porpoises are many times those found in plankton-feeders such as large baleen whales (Johansen *et al.*, 1980; Borrell and Aguilar, 1987; Aguilar and Borrell, 1988), are substantially greater than those typical of the large and medium sized teutophagous odontocetes such as sperm or pilot whales (Holden, 1975; Harms *et al.*, 1977; Aguilar, 1983; Borrell and Aguilar, 1993), and are in the upper range of those detected in smaller, mostly icthyophagous dolphins and porpoises (Holden, 1975; Andersen and Rebsdorff, 1976; Alzieu and Duguy, 1979; Morris *et al.*, 1989). However, they are lower than those commonly found in small cetaceans from the neighbouring, even more heavily polluted Mediterranean waters (Alzieu and Duguy, 1979; Borrell and Aguilar, 1992).

HEAVY METALS

Heavy metals are natural components of sea water. However, the concentration of some of these in the marine environment has drastically increased in the last few decades as a consequence of human activity. Heavy metals enter the body of warm-blooded vertebrates mostly via food, and some of them are accumulative and increase progressively with age. Unlike organochlorines, heavy metals are not a homogeneous group, either by origin or biochemical/ecotoxicological properties. Moreover, different body tissues retain different heavy metals, and the appropriate sampling procedure for one element may not be suitable for another. As a result of this, information on heavy metals is even more fragmentary and less definite than for organochlorines. Table 2 details published results on heavy metal concentrations in tissues of eastern North Atlantic harbour porpoises.

Mercury

In addition to occurring naturally, mercury was released by industry and agriculture into North Atlantic waters in considerable quantities before many of its applications were banned or greatly restricted. Mercury is transformed by living organisms into organic derivatives (mainly methyl-mercury), and this is the most abundant form in which this metal is found in vertebrates. In most tissues of harbour porpoises, mercury was virtually all in the methylated form. However, the fraction of organic mercury in the liver of marine mammals heavily contaminated by mercury is much lower than in the rest of their body (Gaskin *et al.*, 1972; Thibaud and Duguy, 1973; Falconer *et al.*, 1983). This difference has been explained by a detoxification mechanism existing in pinnipeds and cetaceans through which organic mercury is demethylated to reduce its toxicity (Thibaud and Duguy, 1973; Koeman *et al.*, 1975; Roberts *et al.*, 1976).

So far, mercury has been the most studied metal in eastern North Atlantic harbour porpoises (Table 2). The tissues most commonly examined for this metal have been blubber, muscle, kidney, and liver, the latter having invariably the highest concentrations. By contrast, blubber, which is mostly composed of lipids, has a very low capacity for retaining metals and always has negligible mercury levels.

For any given tissue, the concentrations detected were extremely variable between localities and years. For example, concentrations in liver ranged from 0.62 – 70ppm and in muscle from 0.66 – 22ppm. Although data are available for the period 1970–88, the intrinsic high variation of the data make it impossible to test for temporal trends.

Overall mercury levels for harbour porpoises from the eastern North Atlantic are of the same order of magnitude as those detected in conspecifics from other regions. Thus, the weighed mean of mercury concentrations in liver for this population was 11.2ppm, an intermediate value in the range of liver concentrations reported for the well-studied eastern Canadian population (Gaskin *et al.*, 1972; 1979). In most tissues of the harbour porpoise, the concentration of mercury showed a progressive increase with age, and no significant differences between sexes seem to occur (Gaskin *et al.*, 1972; 1979; Falconer *et al.*, 1983; Clausen and Andersen, 1988). In relation to other cetacean species inhabiting the eastern North Atlantic, mercury levels of harbour porpoises are similar or lower than those of other small odontocetes (Koeman *et al.*, 1972; Thibaud and Duguy, 1973; Andersen and Rebsdorff, 1976; Harms *et al.*, 1977; Julshamn *et al.*, 1987).

Other metals

Tissue concentrations of other metals (e.g. lead, copper, zinc, cadmium, arsenic or selenium) have seldom been reported for eastern North Atlantic harbour porpoises (Table 2).

Table 2

Mean concentration (expressed as ppm calculated on a fresh weight basis) of some metals in different tissues of harbour porpoises from the eastern North Atlantic.

Locality	Tissue	N	Year	Hg	Pb	Cu	Zn	Cd	As	Se	Reference
Denmark	Blubber	4	1972-3	0.7	6	1.5	290				Andersen and Rebsdorff (1977)
	Liver	4	1972-3	22	3.5	4.5	59				Andersen and Rebsdorff (1977)
	Muscle	4	1972-3	1.9	3.3		19				Andersen and Rebsdorff (1977)
Denmark	Kidney	74	1980-1					0.31			Clausen and Andersen (1988)
	Kidney	89	1980-1	0.88							Clausen and Andersen (1988)
Denmark	Muscle	7	1987-8	0.93							Joiris *et. al.* (1991)
	Liver	6	1987-8	7.09							Joiris *et. al.* (1991)
	Kidney	7	1987-8	2.24							Joiris *et. al.* (1991)
Faroe Isl.	Liver	6	1989	6.5							Larsen (this volume)
	Kidney	7	1989	1.4							Larsen (this volume)
Germany	Muscle	3	1976-7	1.46	0.05	2.2	15.93	0.0033			Harms *et al.* (1977)
	Liver	3	1976-7	10.04	0.32	8.3	44.3	0.079			Harms *et al.* (1977)
	Kidney	2	1976-7		0.16	3.15	22	0.51			Harms *et al.* (1977)
North Sea	Liver	3	1970-1	70			51	0.44	0.76	58	Koeman *et al.*(1972)
	Brain	6	1970-1	0.56			9.4	<0.01	<0.01	0.59	Koeman *et al.*(1972)
Shetland	Liver	15	1989	3	<0.7	8.7	34	0.68			Law *et al.* (1991)
E. Scotland	Liver	23	1974	4.1	<0.5	7.27	43.33	0.18			Falconer *et al.* (1983)
	Kidney	23	1974	1.18	<0.5	3.77	23.62	1.52			Falconer *et al.* (1983)
	Brain	23	1974	0.56	<0.5	5.24	15.83	<0.05			Falconer *et al.* (1983)
E. England	Liver	3	1989	4.6	<0.7	11.73	34.3	0.09			Laws *et al.* (1991)
Irish Sea	Blubber	4	1988	0.07	<0.07	0.7	4.1	<0.07			Morris *et al.* (1989)
	Muscle	2	1988	0.66	<0.06	2.25	22.5	<0.06			Morris *et al.* (1989)
	Liver	2	1988	0.62	<0.07	7.65	37	<0.07			Morris *et al.* (1989)
	Liver	15	1988-9	17.08	<0.7	29.14	72.7	0.25			Law *et al.* (1990)
G. Britain	Liver	8	1989	3	<0.5	43.7	43.5	0.24			Martin *et al.* (this volume)
France	Blubbler	1	1972	0.77							Thibaud and Duguy (1973)
	Muscle	1	1972	4.9							Thibaud and Duguy (1973)
	Liver	1	1972	60.94							Thibaud and Duguy (1973)
	Kidney	1	1972	6.02							Thibaud and Duguy (1973)
	Brain	1	1972	2.53							Thibaud and Duguy (1973)
Belgium	Muscle	9	1987-8	1.84							Joiris *et. al.* (1991)
	Liver	6	1987-8	39.82							Joiris *et. al.* (1991)
	Kidney	5	1987-8	2.37							Joiris *et. al.* (1991)

Some of these, mainly cadmium, showed increasing concentrations with body length or age of specimens, while copper and zinc levels did not show any trend (Falconer *et al.*, 1983; Clausen and Andersen, 1988; Law *et al.*, 1991). However, in some cases these results may be unreliable because of inadequate sampling. For example, although lead accumulates in bone (Marcus, 1983), this tissue never appears to have been sampled for lead pollution surveys in harbour porpoises. In general, the above elements were detected in concentrations which were within the normal ranges of variation found in other small odontocetes from the Northern Hemisphere (Wagemann and Muir, 1984). There were, however, two noteworthy exceptions to this general trend.

The first concerns four harbour porpoises net-trapped in Denmark which, according to Andersen and Rebsdorff (1976) carried abnormally high concentrations of lead in their tissues (blubber, kidney and liver). The levels detected were about ten times those typically found in other surveys on harbour porpoises from the same region (Harms *et al.*, 1977; Falconer *et al.*, 1983; Morris *et al.*, 1989) so these concentrations were either wrongly determined or the specimens analysed had suffered some local contamination by lead and were not representative of the normal population.

The second exception is that overall levels of cadmium were substantially lower than those typical of any other cetacean species ever reported. For example, in eastern North Atlantic harbour porpoises the concentration of this element in the liver never exceeded 0.5ppm, while the levels usually found in other small cetaceans from northern waters typically range from 5 to 30ppm (Wagemann and Muir, 1984). Unfortunately, populations of harbour porpoises from other regions have not been examined for this element, so it is impossible to ascertain whether these abnormally low values are the consequence of a physiological peculiarity of the harbour porpoise, or reflect stable low levels of cadmium in their environment.

Research on harbour porpoises from European waters for other metals has been extremely limited. Falconer *et al.* (1983) searched for chromium, nickel and cobalt in porpoises from the UK, and found that the tissue levels of these elements were below analytical detection limits. Morris *et al.* (1989) and Law *et al.* (1991) analysed specimens stranded around the British Isles for chromium and nickel and found very low concentrations in all the tissues sampled, always at levels lower than 0.7ppm.

OTHER POLLUTANTS

There is no information available concerning contamination by other pollutants in eastern North Atlantic harbour porpoises. Indeed, data published for this species from other areas are also extremely scarce. In a survey on polycyclic aromatic hydrocarbons in the muscle of six cetacean and four pinniped species from the Northwest Atlantic, Hellou *et al.* (1990) found that harbour porpoises carried the highest concentrations of these compounds. This may reflect a higher susceptibility of the species to accumulate hydrocarbons, probably caused by their coastal distribution and diet composition, and deserves further attention. Some polycyclic aromatic hydrocarbons such as benzo(a)pyrene are highly carcinogenic and mutagenic and have been associated with the occurrence of tumors in white whales (*Delphinapterus leucas*) from the Gulf of St Lawrence in Canada (Béland and Martineau, 1988; Martineau *et al.*, 1988).

EFFECTS OF POLLUTANTS ON HARBOUR PORPOISES

With the current state of knowledge, it is impossible to ascertain the impact, if any, of pollutants on harbour porpoises. Heavy metals in this population do not seem to reach higher tissue concentrations than in other populations of harbour porpoises or in other small odontocetes of similar body size and food habits. The only exceptions to this general rule appear to be analytical artifacts or unusual contamination of particular specimens.

With respect to organochlorines, the situation is different. While tDDT residue levels, especially in specimens sampled in recent years (later than 1975), were medium or low in comparison to other harbour porpoise populations or to other cetaceans from adjacent waters, the concentrations of PCBs in the blubber of eastern North Atlantic specimens were extremely high.

PCBs are powerful inducers of the hepatic microsomal enzyme system and, under laboratory conditions, are known to affect mammal reproduction by interfering with several physiological processes (e.g. Kihlström *et al.*, 1973; Merson and Kirkpatrick, 1976; Aulerich and Ringer, 1977; Fuller and Hobson, 1986; Reijnders, 1986; Morrisey and Schwetz, 1989). However, the effect of chronic exposure on wild populations is difficult to evaluate. In several populations of pinnipeds and cetaceans, it has been claimed that these chemicals impair reproductive performance of females (Helle *et al.*, 1976; Reijnders, 1980; 1986; Martineau *et al.*, 1987; Addison, 1989) and reduce the testosterone levels of males (Subramanian *et al.*, 1987). Clausen and Andersen (1988) considered the reproductive activity of harbour porpoises from Denmark to be normal despite the fact that they carried high loads of tDDT and PCBs. However, they did not estimate critical parameters such as ovulation rates or calf survival, nor did they compare the reproductive fitness of this population of harbour porpoises with that of a non-polluted one.

It has long been known that organochlorines are depressors of body immune systems (Thomas and Hinsdill, 1978; Wassermann *et al.*, 1979; Vos and Luster, 1989) and these chemicals have been tentatively linked with the origin of recent viral epidemic diseases that led to the deaths of thousands of seals in the North Atlantic (Harwood and Reijnders, 1988; Simmonds and Johnston, 1989).

The levels of organochlorines especially PCBs in eastern North Atlantic harbour porpoises are high enough to cause concern about their possible physiological effects. Moreover, the capacity of small cetaceans for metabolizing some forms of PCBs seems to be extremely low when compared to birds and terrestrial mammals (Tanabe *et al.*, 1988) and, of the small cetaceans, harbour porpoises may be in the lower range of this capacity. Thus, Duinker *et al.* (1989) have suggested that the metabolism of certain PCB congeners is lower in harbour porpoises than in odontocetes inhabiting open sea waters. More research is clearly needed to evaluate the actual impact of these pollutants on harbour porpoise populations.

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Vaquita

Vaquita and shortfin mako shark (*Isurus oxyrinchus*) taken near El Quelele on 21 May 1991.
Photo by C. Navarro (Proyecto Vaquita)

Vaquita, *Phocoena sinus*

INTRODUCTORY REMARKS

In 1983, the Scientific Committee had somewhat optimistically noted that although the status of the vaquita was unknown, since the fishery for totoaba (itself an endangered species) had ceased, the vaquita was no longer at risk from gillnetting (IWC, 1984).

However in 1990, the Committee was informed there were still experimental as well as illegal fisheries for totoaba. In addition, the restriction on the totoaba fishery had led to development of a new fishery using large meshed nets for sharks in the upper gulf area. Records were available for 85 vaquitas taken incidentally between 1985 and 1990. This probably represented a small proportion of the total mortality from fishing operations, and available information indicated that at least 30–40 porpoises were killed each year. The Committee concluded that the vaquita was the most endangered marine cetacean, and that it was extremely vulnerable to further depletion. It recommended that further action be taken to stop the major cause of entanglement by fully enforcing the closure of the totoaba fishery and reconsidering the issuance of permits for experimental totoaba fishing, that immediate action be taken to stop illegal shipment of the totoaba across the US border, and that a management plan for the long-term protection of this species and its habitat be developed and implemented (IWC, 1991). As the vaquita was in immediate danger of extinction, the Committee advised that IUCN change the classification of this species from Vulnerable to Endangered.

In a major review carried out for UN Conference on Environment and Development (Bjørge *et al.*, 1994), the Scientific Committee reiterated its serious concern and the immediate need to develop an action plan if the vaquita was to be given a chance of survival.

The most recent consideration of the vaquita took place at the 1994 meeting in Mexico (IWC, 1995b). The Committee reviewed new information, including an abundance estimate suggesting that the population was in the low hundreds and the fact that, despite the declaration of the area as the Biosphere Reserve of the Upper Gulf of California, incidental catches were still continuing (a *minimum* of 15 deaths between January 1993 and March 1994). After welcoming the initiatives of the Mexican Government and USA/ Mexico research efforts, the Committee concluded as follows:

> Considering the low estimate of abundance, the limited distribution of the population, the low potential rate of increase, and levels of continuing incidental catches, the Committee expresses extreme concern over the status of this species. Although it recognises the utility of future research, in view of the precarious state of the vaquita the Committee recommends that immediate action be continued to eliminate incidental catches in the area. The available information indicates that present levels of incidental catches could cause the extinction of the vaquita (IWC, 1995a, p. 87).

Information provided at the 1995 meeting did not document any new actions to eliminate bycatches (IWC, 1996).

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SC/42/SM24 (Revised)

Population Biology and Incidental Mortality of the Vaquita, *Phocoena sinus*

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ABSTRACT

This paper reviews available information on the population biology and incidental mortality of the vaquita, *Phocoena sinus*. A re-examination of previous records and the collection of new records reveals that this porpoise has the most limited distribution of any marine cetacean, being restricted to the uppermost Gulf of California, México. Although no reliable abundance estimates are available, the population is very small, perhaps only in the low hundreds. Little is known of the life history of the vaquita. Twelve neonates examined ranged from 67cm to 78.2cm in length and a near-term foetus measured 71.5cm; parturition occurs in spring, with a peak in late March-early April. Sexually mature females ranged from 135 to 148.2cm in length and sexually mature males from 128.3 to 144cm. The largest immature female and male were 128.7cm and 127cm in length, respectively, and the largest adults were a 150cm female and a 145cm male. Vaquitas are taken incidentally in gillnets, especially those nets with mesh sizes of 15–30.5cm. There are records of 128 vaquitas captured incidentally between early March 1985 and early February 1992: 65% in illegal and experimental gillnets set for a sciaenid, the endangered 'totoaba' (*Totoaba macdonaldi*); 28% in gillnets for sharks and rays; and 7% in gillnets for mackerels (*Scomberomorus* spp.) and in shrimp (*Penaeus* spp.) trawls. These 128 captures certainly represent only a fraction of the total mortality from fishing operations. At least 35 vaquitas are killed each year by these industries. Considering the probable low population size, the relatively high rate of mortality in fishing operations and the difficulties and the costs of implementing and enforcing long-term conservation measures immediately, I conclude the vaquita is in immediate danger of extinction.

INTRODUCTION

Coastal small cetaceans are vulnerable to several adverse effects of human activities, including incidental mortality in fisheries (especially those using gillnets), habitat loss and degradation, direct exploitation for human consumption or for use as bait for other fisheries and culls if they are suspected of competing with fishermen (Perrin, 1989).

The Phocoenidae (sometimes called 'true porpoises') are generally inhabitants of marine coastal and shallow water areas. While two species (the Dall's porpoise, *Phocoenoides dalli*, of the northern North Pacific and the spectacled porpoise, *Australophocaena dioptrica*, of southern South America) are found regularly in the open sea as well as in coastal waters (Jefferson, 1988; Goodall, 1990), the remaining species (the harbour porpoise, *Phocoena phocoena*, vaquita, *P. sinus*, Burmeister's porpoise, *P. spinipinnis*, and finless porpoise, *Neophocaena phocaenoides*) are restricted to nearshore waters (Gaskin *et al.*, 1974; Brownell, 1983; Leatherwood and Reeves, 1983; Brownell and Praderi, 1984). As noted by Perrin (1989), coastal habitats are more restricted and more vulnerable to degradation and depletion. Moreover, all phocoenids are subjected to direct or accidental exploitation (e.g. Mitchell, 1975; Perrin, 1989) and indeed as a threatened group of small cetaceans they are second only to the river dolphins (superfamily Platanistoidea), being particularly vulnerable to incidental capture in gillnets (e.g. Bjørge *et al.*, 1994; Donovan, 1994).

The population biology of most phocoenids is still poorly understood. Most of the existing quantitative data relate to the harbour porpoise (about 90% of published literature) and to the Dall's and finless porpoises (Gaskin *et al.*, 1984). The population biology of the vaquita and the Burmeister's and spectacled porpoises is virtually unknown.

The purpose of this paper is to review briefly and discuss the available information on the population biology and incidental mortality of probably the least known of all porpoises, the vaquita, a species only found in the upper Gulf of California, México.

METHODS

In addition to reviewing the literature, additional information on incidental kills and fishing effort was obtained from: (1) personal interviews with local fishermen (who were familiar with the external appearance of the vaquita) conducted by experienced biologists in El Golfo de Santa Clara, Sonora, between 1985 and 1988; (2) personal communications from biologists who regularly visited the upper Gulf of California since 1985; (3) several field trips (conducted by the author) during 1990 to El Golfo de Santa Clara (February 18, 27–28; March 10–11, 24–25; April 6–14, 20–21; May 19–20, 26–27; September 1–2, 15; October 6) and Puerto Peñasco (February 17), Sonora, San Felipe and Puertecitos, Baja California (Norte) (BCN) (April 9–10; September 16; October 6–7), in an attempt to monitor the incidental mortality of the vaquita during commercial fishing activities; (4) data collected by biologists (principally C. Navarro of ITESM-Campus Guaymas) in semi-continuous residence in El Golfo de Santa Clara from early January to late May 1991 and in one field trip to this village on early October 1991 and four (31 January-1 February, 21–23 February, 10–12 April and 9 May) in 1992; and (5) statistics of fishing effort (i.e. numbers of boats, species exploited, dates and localities) for El Golfo de Santa Clara, Puerto Peñasco, San Felipe and Puertecitos, provided by local officials of the Mexican Secretariat of Fisheries (Secretaría de Pesca de México, SEPESCA), by the fishermen themselves and by direct observations by the author.

RESULTS AND DISCUSSION

Distribution and abundance

Geographical range

Locality data for all confirmed vaquita records are shown in Appendix Tables 1 and 2 and Fig. 1. These are based on: (1) osteological materials (mostly skulls and skeletons) and decomposed whole carcasses recorded on beaches (summarised by Brownell, 1986; Vidal, 1991; this paper); (2) specimens that had been captured incidentally during fishing activities (Brownell, 1982; 1983; Findley and Vidal, 1985; Brownell *et al.*, 1987; Pérez-D, 1987; Robles *et al.*, 1987; Silber and Norris, 1991; Vidal, 1991; this paper); and (3) sightings of free-ranging animals (Brownell, 1986; Vidal *et al.*, 1987; Silber, 1988; 1990a; b; Silber and Norris, 1991; Barlow *et al.*, 1993). These data clearly show that the vaquita is restricted to the upper Gulf of California, an area roughly defined as the region north of a line connecting Puertecitos in Baja California Norte and Puerto Peñasco in Sonora (approximately 5,000km^2 of mostly shallow waters), with most records near

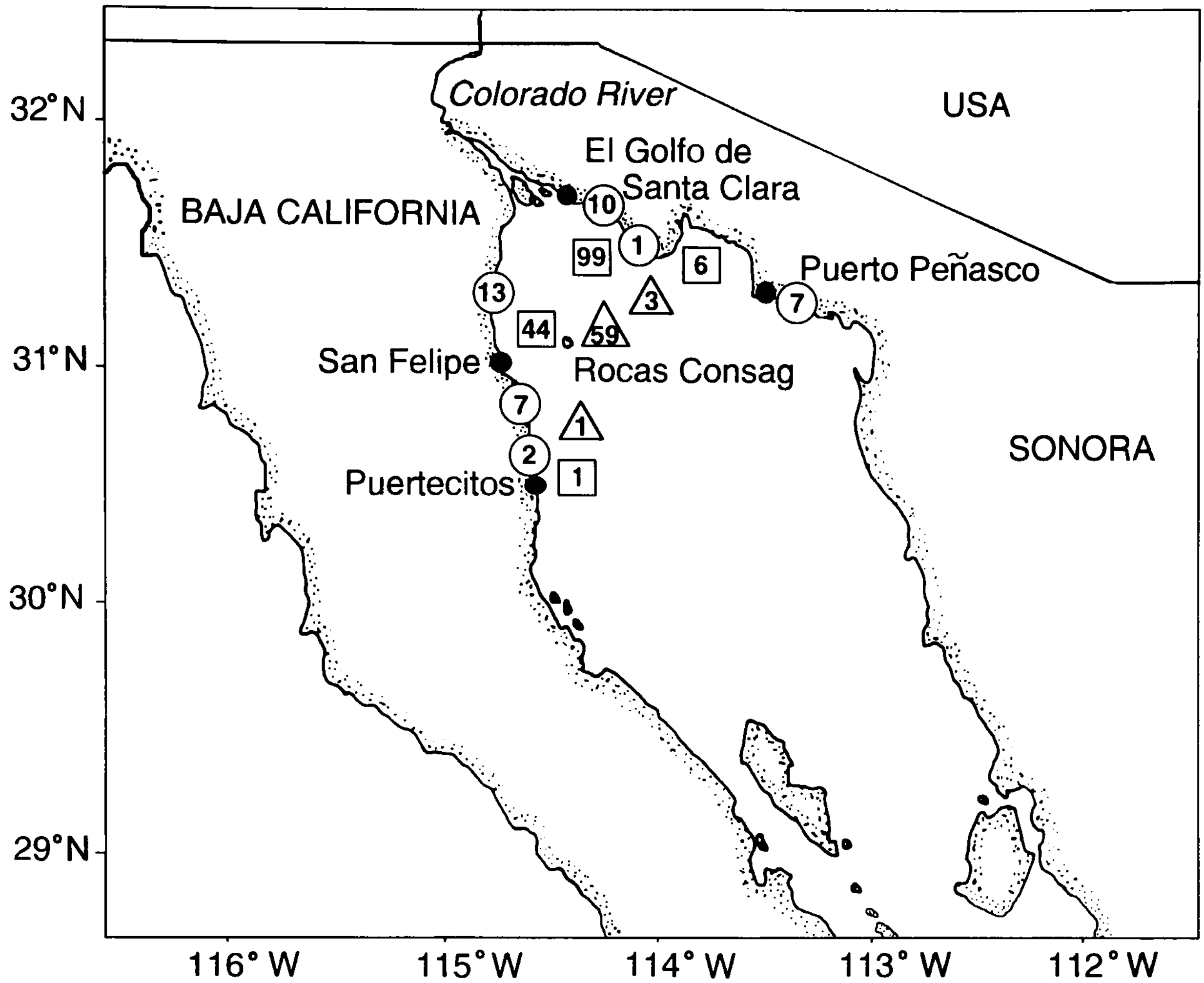

Fig. 1. Locality map of the northern half of the Gulf of California, México, showing the distribution of the vaquita, *Phocoena sinus*, based on confirmed records. Circles indicate beached specimens collected, squares indicate entanglements and triangles indicate sightings (see Appendix Tables 1, 2 and text; for more recent data, see D'Agrosa, 1995).

San Felipe, Rocas Consag and El Golfo de Santa Clara (Fig. 1). In fact, this species has the most limited distribution of any marine cetacean.

Two unconfirmed sightings near Isla Cerralvo, south of Bahía de La Paz, Baja California Sur (*ca* 850km south of the southernmost confirmed sighting) were reported by Silber (1990b). These sightings and a few previous reports for Bahía de Topolobampo, Sinaloa and Guaymas, Sonora (Norris and McFarland, 1958; Norris and Prescott, 1961), led Silber (1990b) to suggest that individuals may occur throughout the Gulf and that the species may have had a much greater historical range. However, Brownell (1986) discounted the unconfirmed sightings by Norris and his co-workers (see below).

From 12–25 June 1986, the author together with Alejandro Robles and Hugo Montiel surveyed both coasts of the Gulf to obtain information on the distribution of the vaquita and other cetaceans in the upper half of this sea. No physical evidence (i.e. osteological material) was found of the vaquita and of the more than thirty fishermen interviewed, only those in San Felipe and El Golfo de Santa Clara were familiar with the species. However, we found whole carcasses and osteological remains of other small cetaceans common dolphins, *Delphinus spp.*, and bottlenose dolphins, *Tursiops truncatus*) quite frequently along these same beaches. In addition to several of the small intermediate fishing camps, we visited Bahía de los Angeles, Punta Final, El Huerfanito, Bahía San Luis Gonzaga, Puertecitos and San Felipe, Baja California Norte; and El Golfo de Santa Clara, Puerto Peñasco, Puerto Lobos, Puerto Libertad, El Desemboque, Punta Chueca and Bahía Kino, Sonora. No records of the vaquita have been obtained by myself or colleagues (principally Lloyd T. Findley) in other parts of the Gulf since we began to work with marine mammals in 1979 (see Vidal *et al.*, 1993).

More than 1,400 physical records from 34 extant aquatic mammal species have been collected from México (mostly in the Gulf of California and along the Pacific coast of the Baja California peninsula) between 1868 and 1990 (Vidal, 1991), including 68 vaquita records. Together with the 29 additional specimens reported here, a total of 97 records exist, none of which were found south of Puertecitos and Puerto Peñasco (Table 2 and Appendix Table 1). This supports the view that the present geographical range of the vaquita is limited to the uppermost Gulf of California, as concluded by Brownell (1983; 1986). The two sightings reported near Isla Cerralvo (Silber, 1990b) were in 1983, a year with a strong *El Niño* Southern Oscillation event, when water temperatures in the region were unusually high (Cane, 1983). Therefore, these records, even if valid, do not necessarily imply a wider geographical range of the vaquita. In the absence of confirmed records (i.e. supported by voucher specimens or photographs) from the southern Gulf, it must be concluded that the species' range includes only the northernmost Gulf[1].

Population size

Little is known about the abundance of the vaquita. Most reported sightings are opportunistic and cannot be used to reliably estimate population size. Between 1985 and 1986 at least 24 sightings were made from commercial shrimp vessels and small fishing boats (*pangas*) near San Felipe (Pérez-D, 1987; S. Pérez-D, pers. comm., 10 January 1990).

Prior to 1986, only one dedicated vaquita survey was carried out but during 1,959km of effort, only two sightings were made (Wells *et al.*, 1981). Since then, Silber and co-workers have carried out a number of dedicated surveys (Silber, 1988; 1990a; b; Silber *et al.*, 1988). A total of 4,216km of boat and aircraft surveys conducted during 77 days in 1986–89 resulted in only 58 sightings, representing a total of 110 individuals (Silber, 1990a; b). Forty-three vaquitas (19 sightings) were recorded during 1,715km of vessel transects, a sighting rate of 2.51 individuals/100km surveyed (Silber, 1990b). The remainder of the sightings occurred while transect surveys were not conducted (Silber, 1990a).

Based on Silber's censuses for 1986 ('30 individuals in 11 sightings'; later amended by Silber, 1988, to 27 and 12, respectively) and on 14 specimens caught incidentally in gillnets during 1985–86 (Brownell, *et al.*, 1987; Robles *et al.*, 1987), Barlow (1986) estimated 50–100 individuals as a rough lower limit for the population, noting that it was not possible to estimate an upper limit from the available data.

Based on the four years of surveys, Silber (1990c) surmised, but did not quantify, an estimate of 200–500 individuals for the entire population. Given the nature of the surveys, the surfacing behaviour of the vaquita (see Silber *et al.*, 1988; Silber, 1990a) and the difficulty in identifying individuals, this total may well include some duplicate sightings both within and between surveys. The scarcity of sightings relative to survey effort and the limited geographical range of the vaquita make it clear that the population is very small, perhaps in the low hundreds[2].

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[1] Information made available since this paper was completed confirms this view (D'Agrosa, 1995; D'Agrosa *et al.*, 1995; Gerrodette *et al.*, 1995).

[2] Since this paper was completed, this view has been confirmed by a line transect survey carried out in August 1993; based on 22 sightings, Gerrodette (1994) estimated the population size to be 316 (95% CI 118–847).

Table 1

Twelve confirmed and four possible (reported by fishermen, indicated by an asterix) neonates and one near-term foetus of *Phocoena sinus* (see Table 2 and Appendix Tables 2 and 3).

Date	Sex	Length	Weight	Comments	Source
09/04/72	?	74cm			Brownell, 1983
13/03/85	F	70.3cm	7.8 kg		Brownell *et al.*, 1987
14/05/85	?	*ca* 75cm	?	A. Robles(pers. comm.)	This paper
06-09/04/88	M	74.3cm	11 kg	M. Románn (pers. comm.) this calf and the one below were incidentally killed with one large individual each (their mothers?)	This paper
06-09/04/88	M	70.8cm	10 kg	M. Románn (pers. comm.)	This paper
05/04/88	F	72.0c	?		Silber and Norris, 1991
mid 03/89	?	*ca* 50*cm	?	Captured ina gillnet	This paper
08/04/90	?	*ca* 80*cm	?	Captured in a shrimp boat	This paper
18/02/90	?	'Very small'*	?	Captured in a shrimp boat	This paper
02/04/90	M	78.2cm	12.5 kg		This paper
05/04/90	?	*ca* 80*cm	?	Found on the beach	This paper
11/04/90	M	75.8cm	11 kg		This paper
12/03/91	F	74.9cm	7.5 kg		This paper
09/04/91	M	77.5c	10.5 kg		This paper
11/04/91	F	72.8cm	8.5 kg		This paper
24/02/91	F	71.5cm	6.7 kg	Near-term foetus	This paper
13/05/94	M	67.0cm	5.0 kg	Stranded alive	CEDO, 1994

Life history parameters and population dynamics

Little is known about age at maturity, life span, reproductive cycle or population dynamics of the vaquita. The available information is summarised below[3].

Neonatal size and calving season

Twelve confirmed (as evidenced by umbilical scars and foetal folds) and four possible records of neonates exist and these are summarised in Table 1. These include a neonate (67cm long) with the umbilicus still attached, that stranded alive near Puerto Peñasco on 13 May 1994 (CEDO, 1994). A near-term pregnant female with a foetus (71.5cm long) was recovered from gillnets on 24 February 1991.

Silber (1988; 1990b) reported seven calves (8.18% of all individuals) during his surveys: six between 25–27 March 1986 and one 'very young, probably less than two days old' on 9 April 1987. Although the sample size is small, this suggests that parturition occurs in spring, between February and April, with a peak possibly in late March-early April.

Gaskin *et al.* (1984) reviewed estimates of gestation period for harbour, Burmeister's and Dall's porpoises and found that most were around 11 months. They also reported a mating season from June-August and parturition from May to early August for harbour porpoises from the Bay of Fundy, Canada and the northwest coast of the USA. Assuming

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[3] A paper on this subject is currently in press (Hohn *et al.*, In press). This is summarised in IWC (1995a); the vaquita life history appears similar to that of the highly exploited harbour porpoise population from the Bay of Fundy, Canada, except that calving does not appear to be annual.

similar values for the vaquita and that parturition occurs from February-April (smallest calf observed on 13 March), suggests that mating may occur between April and June. This is clearly a preliminary conclusion as taxonomic affinity does not necessarily imply similarity in life cycle (Gaskin *et al.*, 1984), especially when the habitats are so different.

Postnatal growth and maturity

Of the 54 individuals of known sex examined (28 males and 26 females), nine males and ten females were mature (Table 2 and Appendix Tables 2 and 3). Work is in progress with respect to the anatomical measurements and possible sexual dimorphism of the vaquita. A 145cm male and two females (139cm and 150cm, both decomposed) must have also certainly been mature (Brownell, 1983; Silber and Norris, 1991), making 22 mature specimens in all. The smallest mature female was 135cm and the smallest mature male was 128.3cm. Females were considered sexually mature if a *corpus albicans* was present on one or both ovaries. Sexual maturity for males was determined on the basis of testis weight and confirmed histologically (Hohn, In press). The largest immature female and male were 128.7cm and 127cm long, respectively. A male of 133.6cm was maturing (A. Hohn, pers. comm., 8 February 1993). Although the sample size is small, females appear to be larger than males, as suggested by Brownell *et al.* (1987) and as is found in the harbour porpoise (Gaskin *et al.*, 1984) and some other odontocetes, e.g. the franciscana, *Pontoporia blainvillei*, the baiji, *Lipotes vexillifer* and the tucuxi, *Sotalia fluviatilis* (Ralls, 1976; Best and da Silva, 1984; Brownell, 1984). Brownell (1984) noted that 'the only obvious common factor among the toothed cetaceans where the female is larger is an apparently simple social structure (i.e. small school size)'.

Ecology and behaviour

Habitat utilisation

Silber (1990b) reported that 86% of his sightings occurred in water depths from 21–35m, with water visibility from 0.9–12m. Most sightings were between 11 and 25km from shore. The two sightings by Wells *et al.* (1981) were in water depths of *ca* 19m and were about 18km from shore. All known incidental gillnet entanglements have occurred in water depths of 4–36m (estimated with some accuracy by the fishermen operating the nets, or by reference to nautical charts) and between 3 and 33km from the shore (Appendix Table 2).

All but two of Silber's sightings were less than 40km from San Felipe (mostly between this locality and Rocas Consag), but this may partially reflect the distribution of sighting effort (Silber, 1990b). Most of the documented vaquitas caught in gillnets have come from near El Golfo de Santa Clara (Table 3 and Appendix Table 2). In the upper Gulf nearly all the survey effort and thus the sightings have been in spring (Silber, 1990a; b; Silber and Norris, 1991). The picture is somewhat similar for the vaquitas caught in gillnets (Table 3).

Analysis of published reports and recent sightings in autumn, led Silber (1990b) and Silber and Norris (1991) to suggest that vaquitas occupy the upper Gulf year-round. They note that the vaquita distribution in the upper Gulf appears to be highly localised, with densities possibly highest near San Felipe (although this may be partly due to more survey effort in that area) and relatively high in the areas of Rocas Consag and El Golfo de Santa Clara. Data on incidental gillnet mortality summarised here and more recent data collected by D'Agrosa (1995) and D'Agrosa *et al.* (1995) tend to support this, as do more recent sightings data summarised by Gerrodette *et al.* (1995). It is important to carry out surveys throughout the upper Gulf at all times of the year and to monitor incidental mortality in San Felipe in order to define accurately the movements and seasonality of the vaquita within its range.

Text continues on p. 256

Table 2

Selected external measurements (following Norris, 1961) (in cm) of 36 specimens of *Phocoena sinus* incidentally killed in gillnet fisheries in the upper Gulf of California, México during February 1990 - May 1993. Footnotes: [1] Specimens ITESM900519, ITESM910313-2 and ITESM910313-3 were collected fresh but partially eaten by coyotes, therefore some measurements could not be taken; [2] Pregnant.

Catalog number (ITESM)	900227	900408	900408-2	900411	900412	900519	900421	900526	900902	910226	910312-2
Sex	Female	Female	Male	Male	Male	Male	Male	Male	Male	Male	Female
Sexually mature	No	Yes	No	No	Yes	No	Yes	No	Maturing	Yes	No
Physically mature	No	Yes	No	No	Yes	No	Yes	No	No	Yes	No
Weight (kg)	23.0	41.0	12.5	11.0	37.0	--	42.5	22.5	31.0	39.0	7.5
Total length	109.8	135.0	78.2	75.8	131.8	127.0	142.2	113.7	133.6	128.3	74.9
Tip of upper jaw to:											
Angle of gape	6.7	7.5	5.1	4.8	8.0	7.0	7.4	7.9	7.0	7.5	5.3
Center of blowhole	8.1	9.3	--	5.2	9.8	7.7	10.2	11.0	11.1	8.9	6.4
Center of eye	11.0	12.1	7.8	7.7	12.1	11.2	12.5	11.3	11.7	12.0	8.3
Auditory meatus	15.9	17.3	10.7	11.0	16.9	18.4	18.1	15.6	16.4	16.3	11.9
Ant. insertion of flipper	23.1	25.7	17.3	15.5	25.1	25.0	27.2	22.5	24.6	24.2	15.9
Umbilical scar	48.5	57.3	36.8	36.3	56.3	--	59.6	48.8	56.0	55.7	36.2
Tip of dorsal fin	64.7	76.0	48.7	47.4	70.5	*ca* 67.5	72.6	67.3	78.1	72.7	46.4
Center of genital slit	68.3	90.0	43.1	42.5	68.6	--	74.0	60.0	68.2	67.9	49.0
Center of anus	74.0	93.3	56.6	55.3	92.7	87.0	95.6	76.5	90.3	89.6	51.4
Ant. length of flipper	23.5	26.6	16.1	17.9	27.4	28.2	28.6	24.1	28.7	27.7	18.1
Axilla length of flipper	18.1	20.4	13.0	13.2	20.9	20.4	22.1	18.7	22.4	21.8	13.6
Max. width of flipper	9.1	10.1	6.7	6.6	8.6	10.8	10.9	9.4	10.7	10.3	6.8
Height of dorsal fin	12.5	15.1	7.5	8.0	18.5	--	18.5	12.3	16.4	16.2	7.6
Length of dorsal base fin	16.7	22.3	13.2	12.6	24.5	20.5	21.5	19.2	21.7	20.2	11.1
Width of flukes	32.8	40.0	20.7	21.8	39.8	--	46.3	33.4	--	43.0	20.0
Width of fluke, from notch to nearest point on anterior border	8.7	10.4	6.9	6.7	10.9	10.0	12.7	10.1	10.2	11.5	7.3
Depth of notch	2.0	1.2	1.2	1.2	1.7	1.7	2.2	1.9	1.8	1.5	0.9
Width of blowhole	2.1	2.5	2.1	0.8	2.6	2.6	3.0	2.1	2.9	2.6	--
Girth, at axilla	64.7	73.0	56.5	54.6	70.2	--	74.1	63.8	68.0	72.6	48.2
Girth, maximum	72.8	86.4	62.5	59.0	82.1	--	82.6	70.7	76.8	81.4	50.0
Girth, at anus	44.6	56.0	34.3	34.2	56.9	49.0	53.1	43.1	44.7	57.4	30.2

Table 2. (Continued.)

Catalog number (ITESM)	910313-1	910313-2	910313-3	910409	910411-1	910421	910519-1	910521	910207	910222-1
Sex	Female	Male	Male	Male	Female	Male	Female	Female	Female	Female
Sexually mature	Yes	Yes	Yes	No	No	No	No	No	No	No
Physically mature	Yes	Yes	Yes	No	No	No	No	No	No	No
Weight (kg)	47.5	--	>43	10.5	8.5	11.5	16.0	34.0	25.0	29.0
Total length	139.7	139.7	144.0	77.5	72.8	82.2	92.5	125.3	116.0	120.7
Tip of upper jaw to:										
Angle of gape	7.5	8.0	7.6	4.9	5.0	4.7	6.5	7.7	8.0	8.3
Center of blowhole	10.4	10.9	10.3	5.8	7.3	6.4	8.6	10.2	9.5	10.5
Center of eye	12.1	13.7	12.1	8.4	8.4	8.0	10.5	12.0	11.8	12.8
Auditory meatus	17.5	--	17.9	11.7	11.6	11.5	14.4	17.1	16.4	17.2
Ant. insertion of flipper	26.2	29.5	26.6	16.7	15.8	17.6	19.8	24.8	23.5	24.4
Umbilical scar	58.5	62.1	--	36.3	36.4	38.8	40.5	53.3	51.8	54.3
Tip of dorsal fin	78.6	--	76.0	48.0	46.1	49.0	54.0	73.2	67.2	70.0
Center of genital slit	89.7	75.1	76.8	43.8	50.7	46.5	58.5	83.1	72.1	76.5
Center of anus	94.0	97.8	100.0	55.5	53.0	58.0	62.0	87.0	79.4	81.6
Ant. length of flipper	27.6	26.1	27.3	16.7	15.1	18.0	18.5	27.4	24.9	27.2
Axilla length of flipper	22.0	22.0	21.2	13.1	11.2	13.3	14.0	20.3	19.1	20.7
Max. width of flipper	10.2	10.2	10.4	6.2	6.1	6.5	7.3	9.5	9.0	9.5
Height of dorsal fin	16.7	--	18.0	7.6	7.4	7.6	9.1	13.5	14.5	13.6
Length of dorsal base fin	22.0	20.2	24.2	10.5	10.1	11.0	13.5	21.5	21.2	21.5
Width of flukes	43.2	40.7	40.3	21.5	20.3	22.7	26.1	38.3	--	38.0
Width of fluke, from notch to nearest point on anterior border	12.0	10.5	11.1	7.0	6.5	7.9	7.5	10.1	8.8	10.1
Depth of notch	1.5	1.7	2.8	1.1	1.1	1.1	1.5	1.6	--	1.7
Width of blowhole	2.8	--	3.0	--	1.7	1.9	2.1	2.7	--	2.8
Girth, at axilla	77.0	--	72.1	53.5	50.0	53.7	60.0	73.8	67.6	70.2
Girth, maximum	87.5	--	--	58.0	53.2	61.0	64.0	86.5	73.1	76.4
Girth, at anus	57.5	--	63.4	34.1	29.5	36.4	41.4	53.7	45.2	49.7

Table 2. (Continued)

Catalog number (ITESM)	910312-1	910407	910224-1	910304	920202	910331	920120	920124	910224	930206
Sex	Male	Male	Female	Female	Female	Female	Female	Female	Female[2]	Female[2]
Sexually mature	No	Yes	No	No	Yes	Yes	No	No	Yes	Yes
Physically mature	No	Yes	No	No	Yes	Yes	No	No	Yes	Yes
Weight (kg)	23.0	43.0	6.7	31.0	44.0	46.0	26.3	24.7	57.5	55.0
Total length	109.1	135.8	71.5	128.7	148.2	140.5	116.6	113.2	140.9	145.2
Tip of upper jaw to:										
Angle of gape	7.0	7.7	4.9	8.2	8.1	8.5	8.2	6.5	7.5	8.5
Center of blowhole	9.2	10.5	7.1	10.7	11.1	10.2	9.5	9.5	9.6	11.2
Center of eye	11.5	11.9	7.7	13.0	13.0	13.2	12.6	10.8	12.5	13.4
Auditory meatus	16.0	17.7	11.5	17.8	18.5	18.3	17.3	16.7	17.5	18.7
Ant. insertion of flipper	21.9	25.7	16.5	25.5	29.7	27.0	23.0	23.8	25.7	27.1
Umbilical scar	50.8	55.3	34.3	54.5	61.5	58.5	51.4	51.4	61.4	--
Tip of dorsal fin	63.6	73.5	42.7	74.2	86.1	81.2	67.6	66.2	80.0	81.3
Center of genital slit	59.5	66.9	46.8	80.3	93.0	92.1	75.5	75.5	95.3	96.8
Center of anus	76.2	89.3	48.5	83.9	98.1	96.7	78.9	78.6	98.5	100.9
Ant. length of flipper	24.6	28.2	13.2	26.6	29.0	28.0	26.0	24.6	29.9	27.5
Axilla length of flipper	18.3	21.5	7.7	20.4	23.0	21.2	19.6	18.0	23.0	21.7
Max. width of flipper	9.0	10.2	6.6	9.7	11.3	10.4	9.3	9.1	10.9	10.7
Height of dorsal fin	13.8	17.8	9.0	12.6	14.8	15.1	12.8	13.8	16.0	13.7
Length of dorsal fin base						22.3	20.2	18.0	21.5	20.5
Width of flukes	35.4	43.8	21.1	37.4	40.0	41.0	34.8	32.2	44.2	39.7
Width of fluke, from notch to nearest point on anterior border	9.0	11.0	7.0	9.7	11.8	10.7	--	8.9	11.5	10.5
Depth of notch	2.2	1.8	1.4	2.0	2.0	1.0	2.2	2.5	2.6	1.9
Width of blowhole	2.5	2.6	1.7	2.8	3.0	3.2	2.6	2.4	2.7	2.4
Girth, at axilla	65.4	74.8	42.0	69.2	75.9	77.5	65.0	63.2	83.5	81.0
Girth, maximum	70.8	89.0	47.9	78.0	84.0	90.2	74.1	71.1	116.6	107.0
Girth, at anus	43.7	50.4	28.6	51.9	55.0	58.3	45.0	43.5	59.0	71.4

Table 2. (Continued)

Catalog number (ITESM)	930206-1	930331	930403	930502	930518
Sex	Female	Male	Female	Male	Male
Sexually mature	No (foetus)	Yes	No	No	No
Physically	No	Yes	No	No	No
Weight (kg)	4.3	41.0	24.0	25.0	20.0
Total length	*ca* 64.4	129.8	116.3	116.4	109.4
Tip of upper jaw to:					
Angle of gape	4.6	6.5	8.5	7.2	6.3
Center of blowhole	6.3	8.6	10.0	10.1	9.3
Center of eye	7.9	10.2	12.9	11.8	10.2
Auditory meatus	11.3	14.7	17.7	16.5	15.2
Ant. insertion of flipper	14.3	23.5	25.0	24.5	22.6
Umbilical scar	30.8	53.5	50.4	---	49.0
Tip of dorsal fin	40.4	72.0	69.0	---	66.0
Center of genital slit	42.5	67.5	75.7	---	58.0
Center of anus	44.0	88.9	80.0	80.0	75.0
Ant. length of flipper	14.4	26.1	25.0	24.1	23.0
Axilla length of flipper	10.8	20.2	19.5	18.9	16.6
Max. width of flipper	5.4	9.9	9.5	9.2	8.3
Height of dorsal fin	7.3	19.1	13.2	14.0	14.3
Width of flukes	20.1	42.0	34.3	35.8	35.2
Width of fluke, from notch to nearest point on anterior border	6.0	11.5	9.7	9.2	9.5
Depth of notch	0.8	1.6	2.7	1.7	2.2
Width of blowhole	1.5	2.8	2.5	2.6	2.9
Girth, at axilla	37.5	71.7	64.3	65.0	64.5
Girth, maximum	40.3	90.0	76.0	74.0	71.3
Girth, at anus	22.2	60.0	48.5	80.0	43.7

Social organisation

Like other phocoenids, the vaquita usually occurs in small groups. Silber (1990a; b) found that 91% of sightings were of 1–3 individuals, with a mean group size of 1.9 and a range of 1 to 7. Silber (1988) reported aggregations of single individuals or small groups (usually 2–4, maximum 8–10) throughout several hundred square meters. All previous sightings were of 1–3 individuals (Norris and McFarland, 1958; Norris and Prescott, 1961; Wells *et al.*, 1981; Vidal *et al.*, 1987) as well as the sighting by Barlow *et al.* (1993) and the more recent sightings summarised in D'Agrosa (1995) and Gerrodette *et al.* (1995).

Wells *et al.* (1981) suggested that the vaquita usually avoids boats, but Silber *et al.* (1988) noted no apparent directional response to their vessel when following two female/calf pairs for some hours at a distance of 40–200m, nor to the presence of several skiffs. In each case, however, abbreviated surfacing sequences were noted, possibly in response to the boats.

Feeding

Little has been published about the food habits of the vaquita. The remains of a bronze-striped grunt, *Orthopristis reddingi*, a croaker, *Bairdiella icistia* (Fitch and Brownell, 1968) and squid (Brownell, 1982) were found in the stomach of an adult female examined on a beach near San Felipe. Squid beaks, (of *Lolliguncula panamensis*) were also found in the stomachs of two porpoises collected by R.L. Brownell, Jr. in 1965 and 1984

Table 3

Summary of the incidental mortality of *Phocoena sinus* in fishing activities in the upper Gulf of California (for details see Table 2 and Appendix Table 2; for recent data see D'Agrosa *et al.* (1995) and D'Agrosa (1995)).

Year	Month	Number	Locality
1967-1984	Mar-Apr	At least 10	*ca* San Felipe
'Early 1970's'	?	'10'	'Around San Felipe'
1972	Apr	2	*ca* El Golfo de Santa Clara
1984	Sept-Oct	1	*ca* El Golfo de Santa Clara
1985	Jan, Mar, Apr, May, Jun, Nov	35	*ca* El Golfo de Santa Clara, Rocas Consag, San Felipe
1986	Feb, Mar, Jun	+2	*ca* El Golfo de Santa Clara, San Felipe
1987	Mar, Apr, Jul	6	*ca* El Golfo de Santa Clara, Rocas Consag
1988	Jan, Apr	9	*ca* El Golfo de Santa Clara
1989	Feb, Mar	13	*ca* El Golfo de Santa Clara, Punta Sargento, Baja California Norte
1990	Jan, Feb, Mar, Apr, May, Jun, Aug, Sept, Dec	36	*ca* El Golfo de Santa Clara, Punta Sargento, Rocas Consag, San Felipe
1991	Feb, Mar, Apr, Jul	22	*ca* El Golfo de Santa Clara, Rocas Consag, San Felipe
1992	Jan, Feb	5	*ca* El Golfo de Santa Clara

(Vidal *et al.*, In press). Two specimens collected in 1988 contained squid beaks, several whole fishes (probably *Anchoa nasus* or *Sardinops* spp.) and numerous unidentified fish otoliths (Silber, 1990a). Squid beaks, (of *L. panamensis* and *Loliopsis diomedeae*) were found in the stomachs of six vaquitas collected in 1985 (Vidal *et al.*, In press). The stomachs of 40 vaquitas incidentally killed in gillnets and recovered fresh by biologists and of two decomposed carcasses, all collected between 1985 and 1994, are currently under analysis. Silber (1990b) reported that during four vaquita sightings, the boat's depth sounder indicated concentrated layers at 15, 23 and 25m, representing schooling bait fish or squid upon which the vaquitas may have been feeding.

Diving and swimming

Silber *et al.* (1988) provided the only available information on the behaviour and respiration cycles of the vaquita. Two different female/calf pairs were observed for periods of about three hours each. Dive characteristics were similar to those reported for the harbour porpoise but mean dive times, roll intervals, surface times and rolls per surfacing reported for the harbour porpoise by Watson and Gaskin (1983) were somewhat higher.

Factors affecting natural mortality

Commensals and parasites

One to five individuals of the commensal pseudo-stalked barnacle, *Xenobalanus globicipitis*, were found attached on or near the trailing edges of the dorsal fins, flippers and flukes of 14 vaquitas incidentally caught in gillnets (Brownell, *et al.*, 1987; Vidal *et al.*, In press). Three parasitic trematodes, *Synthesium tursionis*, were found in the intestine of a male vaquita (Lamothe-Argumedo, 1988) and Vidal *et al.* (In press) reported two specimens of the nematode *Crassicauda* sp., one from the muscle connective tissue in the area of a mammary gland of one vaquita and the other from the blubber near the anus of another vaquita.

Predation

Several fishermen of El Golfo de Santa Clara, who regularly capture vaquitas in their nets, reported to the author that between February and May 1990 and 1991 they found whole or chewed parts of vaquitas in the stomachs of several species of large sharks. These were identified from photographs and/or jaws provided by the informants and they included at least six species: the great white, *Carcharodon carcharias*; the shortfin mako, *Isurus oxyrinchus*; the lemon, *Negaprion brevirostris*; the black-tipped, *Carcarhinus limbatus*; the bigeye thresher, *Alopias superciliosus*; and the broad-snout seven-gill, *Notorynchus cepedianus*. The great white and mako are both known locally as '*tiburones tonina*' ('dolphin sharks'). On 18 February 1990 a great white shark of *ca* 3m and 160kg (jaws now housed at ITESM, Campus Guaymas) was found to have in its stomach a vaquita cut into three pieces. Two more *tiburones tonina* caught in March 1985 and in early February 1990 also had a vaquita in their stomachs. These sharks may attack free-swimming vaquitas or perhaps pull them dead from gillnets. The flukes and/or flippers of several vaquitas incidentally killed in gillnets and examined by the author show notches or scars which could have been the result of (unsuccessful) shark attacks. Other large sharks that may be considered as potential predators includes the tiger, *Galeocerdo cuvier*, and the scalloped hammerhead, *Sphyrna lewini*. Arnold (1972) documented several records of predation by the great white shark on harbour porpoises and concluded that this shark was a potentially significant predator for this cetacean in the Canadian Atlantic. In the North Pacific, killer whales, *Orcinus orca*, have been reported as preying on finless, harbour and Dall's porpoises (see review in IWC, 1982).

It is important that attempts are made to determine the magnitude and impact of shark predation on the vaquita population. Killer whales are not uncommon in the Gulf of California (Vidal *et al.*, 1993) and they have been observed attacking and harassing other cetaceans (Vidal and Pechter, 1989; Silber *et al.*, 1990), but as yet there have been no reports of their predation on vaquitas although they must be regarded as potential predators.

Human effects

Incidental mortality

The vaquita is particularly vulnerable to incidental mortality in large-mesh gillnets. Table 3 (and Appendix Table 2) summarises all available data up to mid-1993 related to the mortality of this species during fishing activities. A detailed analysis of recent data is presented in D'Agrosa (1995) and D'Agrosa *et al.* (1995).

In the upper Gulf, gillnets are the most common and widespread type of fishing gear (Vidal *et al.*, 1994). They are used mainly to catch totoaba, *Totoaba macdonaldi*, a large sciaenid fish (which itself is endangered due to over-exploitation, Flanagan and Hendrickson, 1976; Anon., 1979; Lagomarsino, 1991), as well as smaller sciaenids and several species of large sharks and rays. However, the vaquita is also caught during other fishing activities, such as those for smaller fishes using smaller meshed-gillnets or trawls by shrimp boats. At least 35 vaquitas are incidentally killed each year.

GILLNETS

Vidal *et al.* (1994) summarise the history of the commercial fishery for totoaba with gillnets. The main fishing fleets (which included shrimp boats and small skiffs, both using gillnets) operated from San Felipe, El Golfo de Santa Clara and Puerto Peñasco. The main fishing areas were near these towns and near the mouth of the Colorado River. In fact, these cities developed principally as a result of the revenues generated by this fishery.

Due to a major decline in catches from a peak of 2,261 tons of meat in 1942 to 59 tons in 1975, the Mexican government declared a permanent ban on fishing the species, which was declared in danger of extinction (Flanagan and Hendrickson, 1976). Despite this, illegal gillnetting and poorly planned 'experimental' survey fishing (i.e. temporary permits issued by SEPESCA, since 1983, to assess [unsuccessfully] the population status of the totoaba) have continued in El Golfo de Santa Clara and San Felipe. It has been estimated that about 70 tons of totoaba were taken each year until 1992 e.g. Román-Rodriguez, 1990; Lagomarsino, 1991; J.C. Barrera, unpublished data for 1985–9; M. Almeida (Centro Ecológico de Sonora, Hermosillo), pers. comm., April 1991; pers. obs., 1990–92, and it was still possible to buy totoaba fillets in regional markets and restaurants in 1992 (Robles *et al.*, 1987; pers. obs., 1990–92). Although lacking any quantitative data, some fishing cooperatives in the northern Gulf claim that the totoaba stock has recovered and that the fishery should be opened (pers. comms to A. Robles of ITESM and Conservation International, and J. Balderas, the SEPESCA official in San Felipe). Although a majority of this catch is sold in cities of northwest México, it is believed that some of the totoaba meat is being smuggled out for markets in the USA, particularly in California (Lagomarsino, 1991; M. Lizárraga, Instituto Nacional de Pesca, SEPESCA, pers. comm., 1991). These markets (both in the USA and in México) are the major reason the fishermen continue fishing for totoaba. A gillnet fishery for several species of large sharks and rays has also been growing rapidly in the upper Gulf of California since the early 1940s, probably together with the totoaba fishery and continues to operate without control. This too threatens both the vaquita and totoaba populations.

The vaquita has probably been incidentally caught in gillnets since the mid-1920s. It can be assumed that the significant expansion of the fishing industry during the early 1940s further reduced the population. A minimum of 166 vaquitas are known to have been incidentally killed since the early 1970s (Table 3; D'Agrosa *et al.*, 1995; Appendix Table 2).

Table 3 summarises the available data until 1992. Most records begin after 1985, when the first fresh specimens were recovered by biologists (Brownell, *et al.*, 1987), particularly as a result of the increased awareness of regional biologists of the need to monitor incidental mortality. Between early March 1985 and early February 1992 at least 128 vaquitas were killed in fisheries: 65% in the totoaba fishery (nets with mesh size of 20–30.5cm), 28% in the shark and ray fishery (mesh size of 10–15cm), and 7% in the mackerel (*Scomberomorus sierra* and *S. concolor*) (mesh size of 8.5cm) and in commercial shrimp (*Penaeus californiensis* and *P. stylirostris*) trawl fisheries. This figure should be considered a minimum, since the monitoring effort was non-continuous (except for 1985 and 1990–91) and highly localised to the activities of fishermen of just one fishing town (the smallest, El Golfo de Santa Clara). The apparent absence of recorded dead vaquitas in October may be attributed, at least partially, to little or intermittent monitoring during this month.

However, the monthly numbers of dead vaquitas in gillnets correlated strongly with the seasonal fishing for totoaba (mostly from early February to early May) and to some extent that also for sharks and rays (mostly from early February to late July).

SHRIMP TRAWLS

Norris and Prescott (1961) briefly mentioned a report by a fisherman who had accidentally captured vaquitas in a shrimp trawl. The deaths of eight vaquitas in shrimp trawls in 1985 (2), 1988 (1), 1984–9 (2) and 1990 (3), with all but one referred to as 'very small' (probably calves or juveniles), were reported to the author, A. Robles and to H. Pérez-Cortés (pers. comms) (Centro Regional de Investigaciones Pesqueras, La Paz, BCS) by fishermen of El Golfo de Santa Clara (5), San Felipe (2) and by the San Felipe SEPESCA official (1). Considering the large number of shrimp boats operating in the uppermost Gulf of California, this fishery poses an additional threat to the vaquita population, particularly to the slow-swimming calves.

SUMMARY OF THREAT BY FISHERIES

The data presented in Table 4, although not complete, provide a general idea of the fishing effort for the fisheries that pose a threat to the survival of the vaquita. A similar approach was adopted by Turk-Boyer (1989). The urgent need to monitor the mortality in these fisheries and to determine ways to reduce the incidental mortality of the vaquita led to the study reported in D'Agrosa *et al.* (1995).

Pollution

As noted by several authors (e.g. see review by Reijnders, 1988), the reproductive potential of coastal marine mammal populations can be drastically reduced by the

Table 4

Summary of information (for 1990) of fisheries that may incidentally take vaquitas. Information provided by local SEPESCA officials, fishermen and direct observations by the author.

Species	Period	No. gillnets	Mesh size (km)	Length of net (m)	Total length (km)
El Golfo de Santa Clara (226 *pangas*)					
Sharks, rays	Feb.-July	126	15	680	86
Mackerels	Apr.-July	125	8.5	459	57
Totoaba	Jan.-May	at least 30	20-30.5	180	5.4
[Also 16 shrimp boats, most trawling locally, October-May]					
San Felipe (260 *pangas*)					
Sharks, rays	Feb.-July	300	10-15	680	204
Mackerels	Apr.-July	300	8.5	459	138
Totoaba[1]	Jan.-May	?	20-30.5	180	at least 5.4
[Also 33 shrimp boats, trawling locally, October-May]					
Puerto Peñasco (?? *pangas*)					
Sharks	Sept. 89-Jan 90	32	10		
Sharks	Sept. 89-Jan 90	88	15	*ca* 93	
Sharks	Sept. 89- Jan 90	16	25-30.5		
Small fish	Sept. 89-Jan 90	52	7.5-9	24	
[Also 204 shrimp boats, most trawling locally, October-May]					
Puertecitos (30 *pangas*, 40 fishermen)					
Sharks	Nov.-Aug.	30	10-15	900	27

[1] No accurate estimate available. Some local fishermen and those from El Golfo de Santa Clara believed at least similar to El Golfo de Santa Clara.

presence of high concentrations of organochlorine pollutants, particularly PCBs, DDT and DDE. Coastal odontocetes inhabiting waters near agricultural areas appear to be particularly susceptible to accumulation of these contaminants. Some coastal phocoenids have been found to have accumulated high concentrations of these pollutants (Holden and Marsden, 1967; O'Shea *et al.*, 1980; Gaskin *et al.*, 1982; 1983; Aguilar and Borrell, 1995). Although reproductive disorders and population declines in European harbour porpoises have been attributed by some authors to high PCB concentrations (Otterlind, 1976; Verwey and Wolff, 1981; both cited by Barlow, 1986), Reijnders (1992) concluded that this view was not supported by present information (and see IWC, 1995b).

After detecting high concentrations of DDT in bivalve molluscs near the Colorado River mouth, Guardado (1975) concluded that the Mexicali Valley, with all its agricultural activities, is an important source of pollutants in the upper Gulf of California. Pollutants could also have been carried to the region by the flow of this river after irrigating agricultural areas in the USA. However, samples of blubber from eight incidentally caught vaquitas (see Brownell *et al.*, 1987) analysed for chlorinated hydrocarbon concentrations (Calambokidis *et al.*, 1993), showed relatively low concentrations of DDT compounds, alpha-BHC and PCBs compared to those reported for odontocetes in many other areas. They concluded that chlorinated hydrocarbon pesticides do not apparently pose a threat to the vaquita population of the Gulf of California.

Vázquez-Cuevas *et al.* (1994) analysed four vaquitas (one adult female and three male calves) for heavy metals, and the highest concentrations (ppm) were of Zn(307–634), Fe (99–120), Hg (33–97), Al (50) and Pb (21–38).

Barlow (1986) reported that two drilling platforms were erected (and later removed) near Puerto Peñasco and El Golfo de Santa Clara in the early 1980s. Although it is not known if other explorations for fossil hydrocarbons are being planned in the upper Gulf, future development could pose a serious problem for the vaquita if a large oil spill occurs (Vidal *et al.*, In press).

RESEARCH NEEDS AND RECOMMENDATIONS

As pointed out by Barlow (1986), the most direct and probably the only sure way to promote the recovery of the vaquita would be to reduce the level of human-inflicted mortality. Several authors agree on what must be known and what must be done in order to ensure its survival (e.g. Brownell, 1982; Barlow, 1986; Silber, 1990b). In the original version of this paper, I summarised their suggestions and gave others for the rational management of this species. These are given below, along with a short summary (in italics) of any progress made.

(1) Eliminate incidental mortality of the vaquita in the illegal totoaba fishery by: (a) full enforcement of existing laws prohibiting this fishery; (b) elimination of the so-called 'experimental' permits to catch totoaba; (c) stopping the market of totoaba meat in México, particularly in Baja California Norte and Sonora; and (d) stopping importation of totoaba meat for USA markets and making the customers aware of the problem. *In February 1992, the Mexican Government banned the use of nets with mesh sizes >25cm and in June 1993 declared the Biosphere Reserve of the Upper Gulf of California and the Colorado River Delta mainly to protect the vaquita, totoaba and their habitat (see Vidal, 1993 and D'Agrosa et al., 1995).*

(2) Determine the magnitude of incidental mortality in other gillnet fisheries (i.e. for sharks and rays, sciaenid corvinas, mackerels, shrimp) by monitoring these fisheries. *Progress is reported in D'Agrosa et al. (1995).*

(3) Obtain accurate estimates of population size and more information on the total range and possible seasonal movements of the vaquita, by conducting census surveys. *Progress is reported in Gerrodette (1994) and Gerrodette et al. (1995).*

(4) Modify fishing effort, timing and technique for the shark and ray fishery by (a) restricting fishing areas; (b) restricting fishing periods; and (c) investigating alternative fishing methods or other economically viable alternatives. (*See numbers 1 and 10*).

(5) Analyse, as soon as possible, the information on food habits of the vaquita to determine if competition exists with commercial fisheries.

(6) Collect data on sources and magnitude of natural mortality.

(7) Determine the age at sexual maturity, calving interval and longevity of female vaquitas. *Progress is reported in Hohn et al. (In press).*

(8) Design and implement an educational program to increase the awareness of local fishermen and the general public of the plight of the vaquita. *NGO's and Government Agencies are working on this matter within the framework of a management plan which is being prepared for the Biosphere Reserve (see number 10).*

(9) Monitor plans for future oil exploration and development in the northern Gulf and assess the possible effects of oil spills.

(10) Design and implement a comprehensive management plan for the upper Gulf of California by multidisciplinary scientific and management effort. *The Mexican Secretariat of the Environment, Natural Resources and Fisheries, together with NGOs and academic institutions prepared a draft plan which is expected to be ready in late 1995.*

Status of the vaquita

P. sinus was listed as 'Vulnerable' in 1978 by the IUCN-The World Conservation Union [formerly the International Union for Conservation of Nature and Natural Resources (IUCN)] in their Red Data Book (IUCN, 1978) and also in the Mexican list of wild vertebrates in danger of extinction (Villa-Ramírez, 1978). The vaquita was also listed in Appendix I of the Convention on International Trade in Endangered Species (CITES) of Wild Fauna and Flora on 28 June 1979 (Brownell, 1983), and in February 1985 as an endangered species under the USA Endangered Species Act (Barlow, 1986). Recently, this porpoise was classified as 'Endangered' (a taxon in danger of extinction and whose survival is unlikely if the causal factors continue operating) in the IUCN Cetacean Red Data Book (Klinowska, 1991). Considering (1) the probable small population size and very limited range of *P. sinus*; (2) current levels of incidental (and potential) mortality in fishing activities; (3) the difficulties and the costs needed to implement and to enforce long-term conservation measures quickly; (4) the present lack of alternative means for fishermen to make a living; and (5) the several factors negatively affecting the upper Gulf ecosystem; I conclude that the vaquita is in immediate danger of extinction. If we do not succeed in reducing the incidental mortality soon, we will certainly face the extinction of the first cetacean species as a direct result of human short-sightedness and disregard for the ecological balance of the world in which we live.

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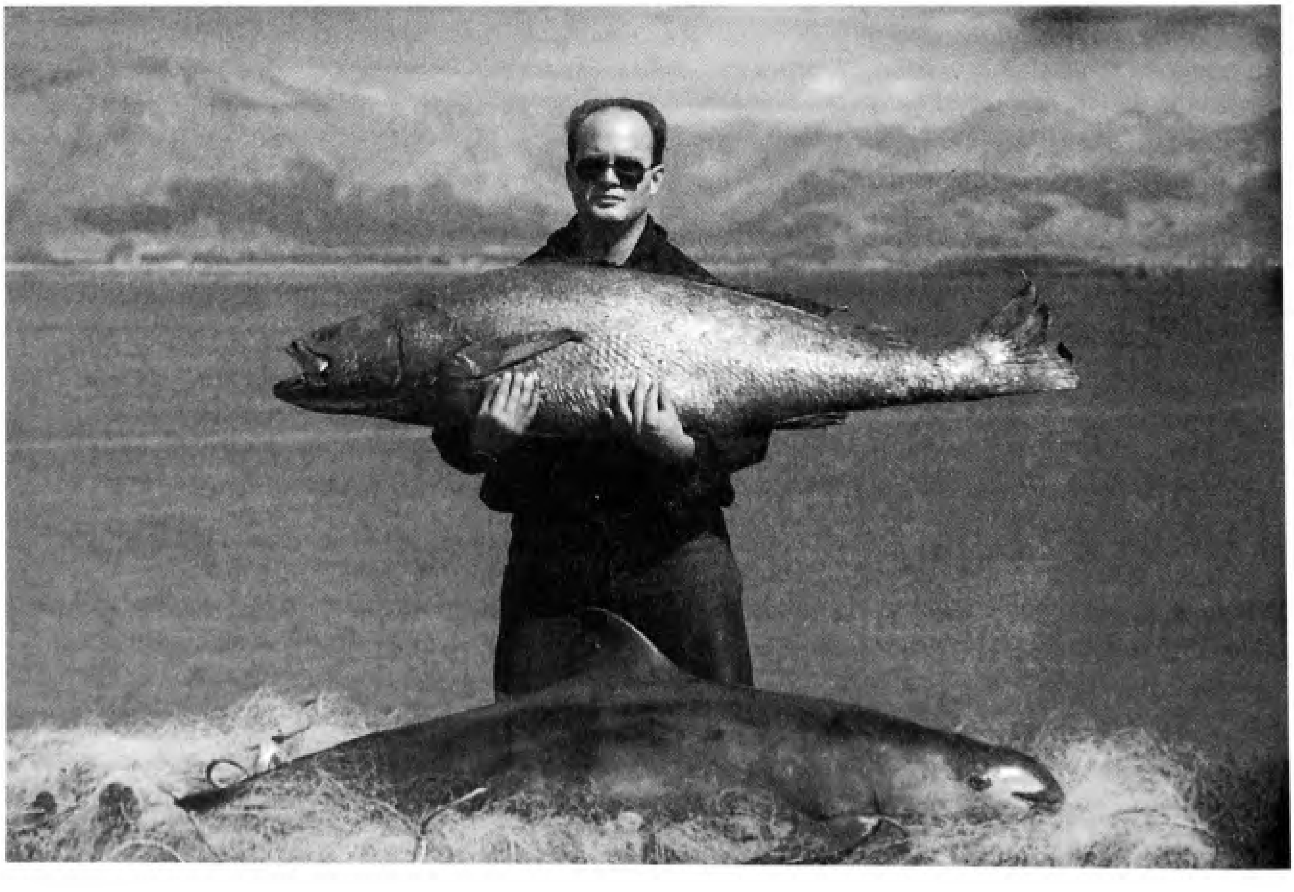

Plate I. C. Navarro with a vaquita and totoaba taken in totoaba nets at Golfo de Santa Clara (photo by O. Vídal).

APPENDIX

Table 1

Confirmed records of *Phocoena sinus* from the Gulf of California, Mexico (arranged from north to south) (SN=skeleton; PS=partial skeleton; SK=skull; PSK=partial skull; FP=fluid-preserved (complete specimen); F= frozen (complete specimen) OB=other bones, (e.g. vertebrae) (summarised by Brownell, 1986; Vidal, 1991; this paper) (see Fig. 1).

No.	Locality	Date of collection	Museum number	Nature of specimen	Reference
1	*ca* Isla Montague	26/02/91	ITESM910226	SN	This paper
2	5km N of El Golfo de Santa Clara	01/03/85	ITESM850301	SK,OB	This paper
3	3km N and 1km E of El Golfo de Santa Clara	05/02/71	LACM33496	PS	Brownell, 1983
4	*ca* El Golfo de Santa Clara	19/05/90	ITESM900519	SN	Vidal, 1991
5	*ca* El Golfo de Santa Clara	17/05/85	ITESM850517-01-'9'	SN	Brownell *et al.*, 1987
6	*ca* El Golfo de Santa Clara	20/05/90	ITESM900520	PS,SK	Vidal, 1991
7	*ca* El Golfo de Santa Clara	20/05/90	ITESM900521	PS,SK	Vidal, 1991
8	*ca* El Golfo de Santa Clara	24/02/91	ITESM910224	SN	This paper
9	*ca* El Golfo de Santa Clara	24/02/91	ITESM910224-1	FP	(A near term foetus of the above individual), this paper
10	El Golfo de Santa Clara	/02/69	UALP3408	PSK,OB	Brownell, 1983
11	El Golfo de Santa Clara	07/05/84	IBUNAM3839	SN	Brownell, 1986
12	El Golfo de Santa Clara	05/04/88	IBUNAM	SN	Silber and Norris, 1991
13	El Golfo de Santa Clara	21/04/88	IBUNAM	SN	Silber and Norris, 1991
14	El Golfo de Santa Clara	04/03/91	ITESM910304	SN	This paper
15	El Burro, *ca* El Golfo de Santa Clara	12/03/85	ITESM850312-01-'1'	SN	Brownell *et al.*, 1987
16	El Burro	12/03/85	ITESM850312-02-'2'	SN	Brownell *et al.*, 1987
17	El Burro	13/03/85	ITESM850313-01-'26'	SN	Brownell *et al.*, 1987
18	El Burro	13/03/85	ITESM850313-02-'27'	SN	Brownell *et al.*, 1987
19	El Burro	13/03/85	ITESM850313-03-'25'	FP	Brownell *et al.*, 1987
20	El Burro	13/03/85	ITESM850313-04-'24'	SN	Brownell *et al.*, 1987
21	El Burro	14/03/85	ITESM850314-01-'3'	SN	Brownell *et al.*, 1987
22	El Burro	21/02/86	IBUNAM	SN	Lamothe-Argumedo, 1988
23	El Burro	17/03/86	ITESM860317	SN	Vidal, 1991
24	El Burro	09/04/88	FCMM0123	SN	Vidal, 1991
25	El Burro	09/04/88	FCMM0124	SN	Vidal, 1991
26	El Burro	27/02/90	ITESM900227	SN	Vidal, 1991
27	El Burro	11/04/90	ITESM900411	FP	Vidal, 1991
28	El Burro	12/04/90	ITESM900412	SN	Vidal, 1991
29	El Burro	21/04/90	ITESM900421	SN	Vidal, 1991
30	El Burro	22/02/91	ITESM910222-1	SN	This paper
31	El Burro	12/03/91	ITESM910312-1	SN	This paper

Table 1 (cont.)

No.	Locality	Date of collection	Museum number	Nature of specimen	Reference
32	El Burro	12/03/91	ITESM910312-2	FP	This paper
33	El Burro	31/03/91	ITESM910331	F	This paper
34	El Burro	07/04/91	ITESM910407	SN	This paper
35	El Burro	11/04/91	ITESM910411-1	FP	This paper
36	El Burro	21/04/91	ITESM910421	FP	This paper
37	El Burro	19/05/91	ITESM910519	FP	This paper
38	El Burro	02/02/92	ITESM920202	SN	This paper
39	Between El Burro & El Tornillal, *ca* El Golfo de Santa Clara	13/03/91	ITESM910313-1	SN	This paper
40	Between El Burro & El Tornillal	13/03/91	ITESM910313-2	SN	This paper
41	Between El Burro & El Tornillal	13/03/91	ITESM910313-3	SN	This paper
42	Between El Tornillal & La Salina, *ca* El Golfo de Santa Clara	14/05/85	IBUNAM3947	SN	Brownell *et al.,* 1987
43	El Tornillal	14/05/85	IBUNAM3948	SN	Brownell *et al.,* 1987
44	El Tornillal	27/04/86	ITESM860427	SN	Vidal, 1991
45	El Tornillal	26/05/90	ITESM900526	SN	Vidal, 1991
46	El Tornillal	07/02/91	ITESM910207	SN	This paper
47	El Machorro, *ca* El Golfo de Santa Clara	12/05/85	ITESM850512-01-‘4’	SN	Brownell *et al.,* 1987
48	El Machorro	20/08/90	ITESM900902	SN	Vidal, 1991
49	El Quelele, Baja California	08/04/90	ITESM900408-2	FP	Vidal, 1991
50	El Quelele	08/04/90	ITESM900408	SN	Vidal, 1991
51	El Quelele	20/01/92	ITESM920120	F	This paper
52	El Quelele	24/01/92	ITESM920124	F	This paper
53	*ca* El Moreno, *ca* El Quelele	09/04/91	ITESM910409	FP	This paper
54	El Macho, *ca* El Quelele	21/05/91	ITESM910521	SN	This paper
55	Playa Estación, Puerto Peñasco	20/11/79	IBUNAM17057	SN	Magatagan *et al.,* 1984
56	Playa Estación	20/11/79	IBUNAM19588	SN	Magatagan *et al.,* 1984
57	Las Conchas, Puerto Peñasco	/12/80	IBUNAM19589	SK	Magatagan *et al.,* 1984
58	Las Conchas	27/06/91	IBUNAM	SN	CEDO News, 1991
59	Las Conchas	28/06/91	IBUNAM	SN	CEDO News, 1991
60	Puerto Peñasco	10/05/84	IBUNAM3840	PS	Brownell, 1986
61	Puerto Peñasco	30/04/87	CEDO0007	SN	Silber and Norris, 1991
62	18km NE of Rocas Consag	/06/85	FCMM0067	SN	Vidal, 1991
63	18km NE of Rocas Consag	/06/85	FCMM0068	SN	Vidal, 1991
64	*ca* Rocas Consag	14/05/85	ITESM850514-01-‘5’	SN	Brownell *et al.,* 1987
65	*ca* Rocas Consag	14/05/85	ITESM850514-02-‘6’	SN	Brownell *et al.,* 1987
66	*ca* 24.5km off Punta Felipe	07/07/87	ITESM870707	SN	Vidal, 1991
67	*ca* 24km N of San Felipe	24/04/66	SDNHM20688	SN	Brownell, 1983
68	*ca* 24km N of San Felipe	01/04/67	LACM28259	SN	Brownell, 1983

Table 1 (cont.)

No.	Locality	Date of collection	Museum number	Nature of specimen	Reference
69	*ca* 24km N of San Felipe	01/04/67	----	OB	Brownell, 1986
70	*ca* 24km N of San Felipe	/10/67	USNM395722	PSK	Brownell, 1986
71	20km N of San Felipe	10/07/70	LACM51138	PSK	Brownell, 1986
72	*ca* 20km N of San Felipe	/11/67	USNM395723	PSK	Brownell, 1986
73	*ca* 19km N of San Felipe	06/02/66	SDNHM20689	OB	Brownell, 1986
74	*ca* 19km N of San Felipe	/64	BMNH69.678	PS,SK	Noble and Fraser, 1971
75	*ca* 17km N of San Felipe	23/09/66	LACM27407	PSK	Brownell, 1986
76	*ca* 16.5km N of San Felipe	03/02/64	MCZ51490	PSK	Brownell, 1986; Vidal, 1991
77	15km N of San Felipe	23/04/66	SDNHM20690	OB	Brownell, 1986
78	NE shore of Punta San Felipe	18/03/50	MVZ120933	SK	Norris and McFarland, 1958
79	5km N of San Felipe	/06/82	NMFS(NMML)	SK	Brownell, 1986
80	San Felipe	/60	SDNHM20697	PSK	Brownell, 1986
81	San Felipe	11/04/88	IBUNAM	SN	Silber and Norris, 1991
82	Bahía de San Felipe	/12/51	MVZ120934	PSK	Norris and McFarland, 1958
83	Bahía de San Felipe	/12/51	USNM303308	PSK	Norris and McFarland, 1958
84	S of Bahía San Felipe	26-28/11/64	LACM	PSK	Brownell, 1986
85	S of Bahía San Felipe	22/11/62	LACM	PSK	Brownell, 1986
86	S of San Felipe	/04/66	----	PS,PSK	Brownell, 1986
87	27km S of Punta Diggs	Easter 1966	SDNHM21555	PSK	Brownell, 1986
88	*ca* 10km N Puertecitos	18/08/68	CAS14631	PSK	Orr, 1969
89	*ca* 3km S Puertecitos	Spring 61	USNM395892	PSK	Brownell, 1986
90	Gulf of California	89	SWFC0113	SK	Vidal, 1991

Collection acronyms: BMNH, British Museum (Natural History), London; CAS, California Academy of Sciences, San Francisco, USA; CEDO, Centro Intercultural para el Estudio de Desiertos y Océanos, Puerto Peñasco, Sonora, México; FCMM, Facultad de Ciencias, Universidad Nacional Autónoma de México, México, DF; IBUNAM, Instituto de Biología, Universidad Nacional Autónoma de México, México, DF; ITESM, Instituto Tecnológico y de Estudios Superiores de Monterrey-Campus Guaymas, Sonora; LACM, Natural History Museum of Los Angeles County, California; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA; MVZ, Museum of Vertebrate Zoology, University of California, Berkeley; NMFS (NMML), National Marine Fisheries Service, National Marine Mammal Laboratory, Seattle, Washington; SDNHM, San Diego Natural History Museum, California; SWFC, Southwest Fisheries (Sciences) Center, National Marine Fisheries Service, La Jolla, California; UAZLP, University of Arizona, Laboratory of Paleontology, Tucson, Arizona, USA; and USNM, National Museum of Natural History, Smithsonian Institution, Washington, DC.

Table 2

Incidental mortality of *Phocoena sinus* in fishing activities in the Gulf of California, México (arranged from north to south) (EGSC = El Golfo de Santa Clara; GT = gillnet for totoaba, with a mesh size of 20-30.5cm; GS = gillnet for sharks and rays, mesh size of 10-15cm; OG = other gillnet, mesh size of 8.5cm; SB = shrimp boat; SM = sexually mature; PM = physically mature) (see Fig. 1)[1].

No.	Locality	Date	Cause of death	Dist. from shore(km)	Depth(m)	Sex	Length (cm)	Weight (kg)	SM	PM
1	*ca* Isla Montague	26/02/91	GT		*ca*. 14	M				
2	EGSC09	09-10/84	GT	*ca* 3.6	*ca* 14			*ca* 20		
3	EGSC	05/04/88	G?			F	72.0		No	No
4	EGSC	10/90	SB							
5	EGSC	01/03/91	OG			F				
6	Offshore from EGSC	09/04/72	GT			F				
7	Offshore from EGSC	09/04/72	GT				74.0			
8	Offshore from EGSC	06/90	GS							
9	Offshore from EGSC	17/12/90	GT						No	No
10	Offshore from EGSC	24/02/91	GT	*ca* 27	*ca* 13	F			Yes	Yes
11	El Machorro, *ca* 8km S of EGSC	21/04/88	GT				*ca* 100			
12	El Machorro	21/04/88	GT				*ca* 100			
13	El Machorro	12/05/85	GS	*ca* 10	*ca* 27	F	110.0	23.7	No	No
14	El Machorro	10/06/90	GS		*ca* 16		*ca* 115			
15	El Machorro	20/08/90	OG			M	133.6	31.0	No	No
16	Between El Tornillal and La Salina, *ca* EGSC	14/05/85	GS	*ca* 33	18-22	F	90.3	14.7	No	No
17	La Salina, *ca* EGSC	1-5/11/85	SB	*ca* 3.3						
18	La Salina	1-5/11/85	SB	*ca* 3.3						
19	La Salina	08/04/90	SB		27		'calf'		No	No
20	La Salina	07/09/90	OG		36					
21	El Tornillal, *ca* EGSC	14/05/85	GS	6	22-27	M	94.5	17.7	No	No
22	El Tornillal	08/05/85	?	*ca* 4.5	*ca* 30			*ca* 18	No	No
23	El Tornillal	04/87	GS							
24	El Tornillal	04/87	GS							
25	El Tornillal	25/02/90	GT							
26	El Tornillal	mid 02/90	GT		*ca* 14					
27	El Tornillal	16/04/90	GT		*ca* 16					
28	El Tornillal	24/05/90	GS	*ca* 18	18	M				
29	El Tornillal	*ca*10/06/90	GS							
30	El Tornillal	*ca*07/02/91	GT		*ca* 16	F				
31	El Tornillal	13/03/91	GT		*ca* 14	M				
32	El Tornillal	13/03/91	GT		*ca* 14	M				
33	8km off El Tornillal	13/05/85	GS	*ca* 8	*ca* 31		*ca* 110	*ca* 20		
34	Between El Tornillal and El Burro, *ca* EGSC	03-06/89	GS		*ca* 14					
35	Between El Tornillal and El Burro	03-06/89	OG		*ca* 14					
36	Between El Tornillal and El Burro	26/02/91	GT		*ca* 14					
37	Between El Tornillal and El Burro	13/03/91	GT		*ca* 13	F				
38	El Burro, *ca* 20km ESE of EGSC	12/03/85	GT	7	12.6	M	103.0	21.7	No	No
39	El Burro	12/03/85	GT	7	12.6	F	108.6	23.7	No	No
40	El Burro	13/03/85	GT	4	12.6	F	135.0	42.7	Yes	Yes

Table 2 (cont.)

No.	Locality	Date	Cause of death	Dist. from shore(km)	Depth(m)	Sex	Length (cm)	Weight (kg)	SM	PM
41	El Burro	13/03/85	GT	4	12.6	F	135.0	43.7	Yes	Yes
42	El Burro	13/03/85	GT	4	12.6	F	70.3	7.8	No	No
43	El Burro	13/03/85	GT	4	12.6	M	134.5	46.7	Yes	Yes
44	El Burro	14/03/85	GT	4	12.6	F	106.9	22.2	No	No
45	El Burro	04?/85	GT	*ca* 10	*ca* 22					
46	El Burro	21/02/86	GT	*ca* 3	*ca* 11	M	114.0	20.5		
47	El Burro	24/03/86	GT	*ca* 4	*ca* 13	M	131.5	41.0	Yes	Yes
48	El Burro	03/87	GT							
49	El Burro	03/87	GT							
50	El Burro	6-9/04/88	GT		*ca* 18	M	74.3	11.0	No	No
51	El Burro	6-9/04/88	GT		*ca* 18	M	70.8	10.0	No	No
52	El Burro	6-9/04/88	GT		*ca* 18	F(?)				
53	El Burro	6-9/04/88	GT		*ca* 18	F(?)				
54	El Burro	late/02/89	GT							
55	El Burro	mid/03/89	GT				*ca* 50		No	No
56	El Burro	03/89	GT							
57	El Burro	03/89	GT							
58	El Burro	03/89	GT							
59	El Burro	03/89	GT							
60	El Burro	03/89	GT							
61	El Burro	10/02/90	GT		*ca* 11					
62	El Burro	14/02/90	GT		*ca* 14		*ca* 150			
63	El Burro	14/02/90	GT		*ca* 14		*ca* 150			
64	El Burro	20/02/90	GT		10.5	F	109.8	23.0	No	No
65	El Burro	25/02/90	GT		*ca* 11					
66	El Burro	02/03/90	GT		*ca* 11					
67	El Burro	11/04/90	GT		*ca* 11	M	75.8	11.0	No	No
68	El Burro	12/04/90	GT		*ca* 11	M	131.8	37.0	Yes	Yes
69	El Burro	19/04/90	GT		*ca* 16	M				
70	El Burro	22/02/91	GT	2	*ca* 15	F				
71	El Burro	12/03/91	GT		*ca*16	F				
72	El Burro	12/03/91	GT		*ca* 4					
73	El Burro	31/03/91	GT		*ca* 13	F				
74	El Burro	04/04/91	GT		*ca*14				No	No
75	El Burro	07/04/91	GT		*ca* 14					
76	El Burro	11/04/91	GT		*ca* 13					
77	El Burro	11/04/91	GT		*ca* 13					
78	El Burro	12/01/92	GT							
79	El Burro	02/02/92	GT			F	148.2	44.0	Yes	Yes
80	El Quelele, 10km off Punta Sargento, Baja California	17/05/85	GS	*ca* 14	9	M	110.0	23.2	No	No
81	El Quelele	12/05/85	GT	*ca* 10	*ca* 14		*ca* 100	*ca* 18		
82	El Quelele	12/05/85	GT	*ca* 10	*ca* 14		*ca* 100	*ca* 18		
83	El Quelele	09/05/85	GT	*ca* 10	*ca* 14			*ca* 20		
84	El Quelele	03-05/89	GS		*ca* 8					
85	El Quelele	03-05/89	GS		*ca* 8					
86	El Quelele	mid/03/89	GT	*ca* 10	*ca* 14					
87	El Quelele	02/04/90	GT		*ca* 12.6	F	135.0	41.0	Yes	Yes
88	El Quelele	02/04/90	GT		*ca* 12.6	M	78.2	12.5	No	No
89	El Quelele	01/92	GT							
90	El Quelele	20/01/92	GT			F	116.6	26.3	No	No
91	El Quelele	24/01/92	GT			F	113.2	24.7	No	No
92	*ca* El Quelele	09/04/91	GT		*ca* 7				No	No

Table 2 (cont.)

No.	Locality	Date	Cause of death	Dist. from shore(km)	Depth(m)	Sex	Length (cm)	Weight (kg)	SM	PM
93	Off Pta Borrascoso	26/01/88	GT	*ca* 3	*ca* 8					
94	30 km N of Rocas Consag	14/05/85	GS		*ca*22		*ca* 75	*ca* 12		
95	18km NE of Rocas Consag	06/5	GS				F	140.0	Yes	Yes
96	As 95	06/85	GS				M	95.0	No	No
97	*ca* 10km N of Rocas Consag	14/05/85	GS		18-22	M	93.5	16.7	No	No
98	As 97	14/05/85	GS		18-22	F	143.5	45.7	Yes	Yes
99	NW of Rocas Consag and NE of San Felipe	07/07/87	GS	*ca* 24.5	16	M	109		No	No
100	5km N of Rocas Consag	01?/85	GT		*ca* 36					
101	N of Rocas Consag	11/05/85	GS	*ca* 20	*ca* 22			*ca* 13		
102	N of Rocas Consag	13/05/85	GS	*ca* 20	*ca* 22		*ca* 100	*ca* 20		
103	N of Rocas Consag	17/05/90	GS							
104	N of Rocas Consag	19/05/90	GS		*ca* 23					
105	*ca* Rocas Consag	18/05/90	GS			M	127.0		No	No
106	*ca* Rocas Consag	06/90	GS							
107	*ca* Rocas Consag	08//90	GS							
108	*ca* El Cantiloso, *ca* 9km S of Rocas Consag	18/02/90	SB		*ca* 72				No	No
109	El Chinero, *ca* San Felipe	12/04/85	GT	*ca* 7	*ca* 9	M	*ca* 110			
110	El Chinero	10/05/85	GS		*ca* 7					
111	El Chinero	04/90	GT		16					
112	El Chinero	04/90	GT		16					
113	*ca* Campo Don Abel, San Felipe	03-04/ 1967-84	GT,GS, SB	('at least 10 vaquitas caught')						
114	Campo Don Abel	1985-86	GT							
115	Campo Don Abel	1985-86	GT							
116	Campo Don Abel	1985-86	GT							
117	Campo Don Abel	1985-86	GT							
118	Campo Don Abel	1985-86	GT							
119	San Felipe	11/04/88	G?			F	129			
120	Near San Felipe	1985-87	GT							
121	Near San Felipe	06/90	GS							
122	Near San Felipe	07/90	GS							
123	'Around San Felipe'	early 1970s	GT	(10 vaquitas caught)						
124	Isla Salvatierra, Islas Encantadas	01/90	GS							
125	'Upper Gulf'	early 05/85	GS							
126	'Upper Gulf'	03/89	SB				*ca* 110			
127	Upper Gulf	02-05/90	GT?							
128	Upper Gulf	02-05/90	GT?							

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[1] Reported by: Brownell (1982): No. 123; Brownell (1983): 6, 7; Brownell *et al.* (1987): 13, 16, 21, 38-44, 80, 97, 98; Pérez-D (1987): 95, 96; Silber and Norris (1991): 3, 119; Present paper: pers. obs. by Vidal and/or communications of reliable fishermen (1, 2, 4, 5, 8-10, 14, 15, 19, 20, 22-32, 34-37, 46, 54-79, 84-92, 103-113, 120, 121, 124, 126-128); and pers. comms of A. Robles (17, 18, 33, 45, 81-83, 94, 100-102, 125), J.C. Barrera (11, 12, 47-49, 93), S.A. Pérez (114-118), M. Román (50-53) and F. Maldonado (99).

SC/46/SM7

Distribution of the Vaquita, *Phocoena sinus*, Based on Sightings from Systematic Surveys

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ABSTRACT

Sightings of 37 groups of vaquitas, *Phocoena sinus*, with an estimated total of 62 individuals, are reported from six major systematic surveys and four small boat surveys in the Gulf of California, México, carried out between May 1992 and December 1993. All vaquita sightings but one occurred on the western side of the northern Gulf of California, where nearly all previous confirmed sightings have occurred. Furthermore, vaquitas have been seen in this area in all seasons, suggesting year-round occupancy. Stranding data, mortalities in fishing nets and sightings of live animals all confirm that the present distribution of *P. sinus* is concentrated in a small area near Rocas Consag in the northwestern Gulf of California.

KEYWORDS: VAQUITA; NORTH PACIFIC; SIGHTINGS SURVEY; STRANDING; INCIDENTAL CAPTURE

INTRODUCTION

Phocoena sinus, the vaquita or Gulf of California harbor porpoise, is the only cetacean known to be endemic to México (Vidal *et al.*, 1993). In the original description of the species, Norris and McFarland (1958) described the geographic range as the northern Gulf of California and probably extending south along the Mexican coast. However, based on skeletal remains found in the northern Gulf of California, the lack of skeletal remains at other locations in the Gulf and a few confirmed sightings of live animals, Brownell (1986) concluded that the range of the vaquita was limited to the upper Gulf of California. Subsequent sightings (Silber, 1988; 1990; Silber and Norris, 1991), stranding data and deaths in fishing nets (Vidal, 1995) have supported this conclusion. There are some reports, of questionable reliability, of vaquitas occurring outside the upper Gulf of California (reviewed in Brownell, 1986; Silber, 1990; Barlow *et al.*, 1993; Vidal, 1995).

This paper presents the results of surveys carried out in the Gulf of California during 1992 and 1993 and addresses the question of current vaquita distribution. The surveys took place during different months of the year and the question of possible seasonal migration of vaquitas is also addressed.

METHODS

In the late summer and early fall of 1993, the Southwest Fisheries Science Center (SWFSC) of the US National Marine Fisheries Service conducted a marine mammal line-transect survey jointly with the Mexican Secretaría de Pesca (SEPESCA) along the coast of California and Baja California. As part of the SWFSC cruise, the 52m research vessels *David Starr Jordan* and *McArthur* conducted transects in the Gulf of California between 3 August and 2 November 1993 (Table 1). North-south primary transect lines were spaced 30 minutes of longitude (about 26 n.miles) apart from the northern end of the Gulf to the south, ending at a line connecting Cabo San Lucas and Cabo Corrientes (Fig. 1). Some secondary east-west transect lines at intervals of 60 n.miles were traversed after the primary transects were completed. Transect lines ended at a depth of 20m; thus, some potential vaquita habitat in shallow water was not searched.

In normal searching mode, three observers searched by eye with the additional use of hand-held 7X binoculars and pedestal-mounted 25X binoculars; however, while in the area where vaquitas had previously been seen, additional observers were used and a stratum of more closely spaced transect lines was added (Gerrodette, 1994). The eye height of the observers was 10.7m above the water. The location of a sighting was calculated from the position of the ship, determined by the ship's Global Positioning System (GPS), and the bearing and distance from the ship to the sighting. Distance from ship to sighting was measured with calibrated reticles in the 7X and 25X binoculars.

Five seasonal line-transect surveys were carried out by the Programa Nacional de Investigación y Conservación de Mamíferos Marinos de México (PNICMM) of SEPESCA between July 1992 and October 1993 (Table 1). Each survey used two identical 34m Mexican Navy patrol vessels and a 24m research vessel from the Instituto Nacional de la Pesca, except for the last cruise (no.5 in Table 1), which had only two Navy vessels. Each survey covered from the northern end of the Gulf to the 28th parallel (Figs 2–6). On each vessel 4–6 observers were located approximately 5.5m above the water and searched by eye and with 7X and 10X binoculars. The first of these surveys in July 1992 concentrated search effort in the northern Gulf of California, with scattered effort elsewhere (Fig. 2).

Table 1

Cruise dates and transect lengths (n. miles) for cruises conducted by the Southwest Fisheries Science Center (SWFSC), the Programa Nacional de Investigación y Conservación de Mamíferos Marinos (PNICMM) and the Instituto de Biología of the Universidad Nacional Autónoma de México (IBUNAM) in the Gulf of California, México.

Cruise	Dates	Transect length
SWFSC	3 August - 2 November 1993	2,369
PNICMM #1	16-26 July 1992	1,438
PNICMM #2	18-30 October 1992	1,755
PNICMM #3	15-26 March 1993	1,868
PNICMM #4	23 June - 3 July 1993	1,660
PNICMM #5	15-24 October 1993	1,140
IBUNAM #1	May-June 1992	200
IBUNAM #2	November-December 1993	154
IBUNAM #3	May-June 1992	220
IBUNAM #4	November-December 1993	69
	Total	10,873

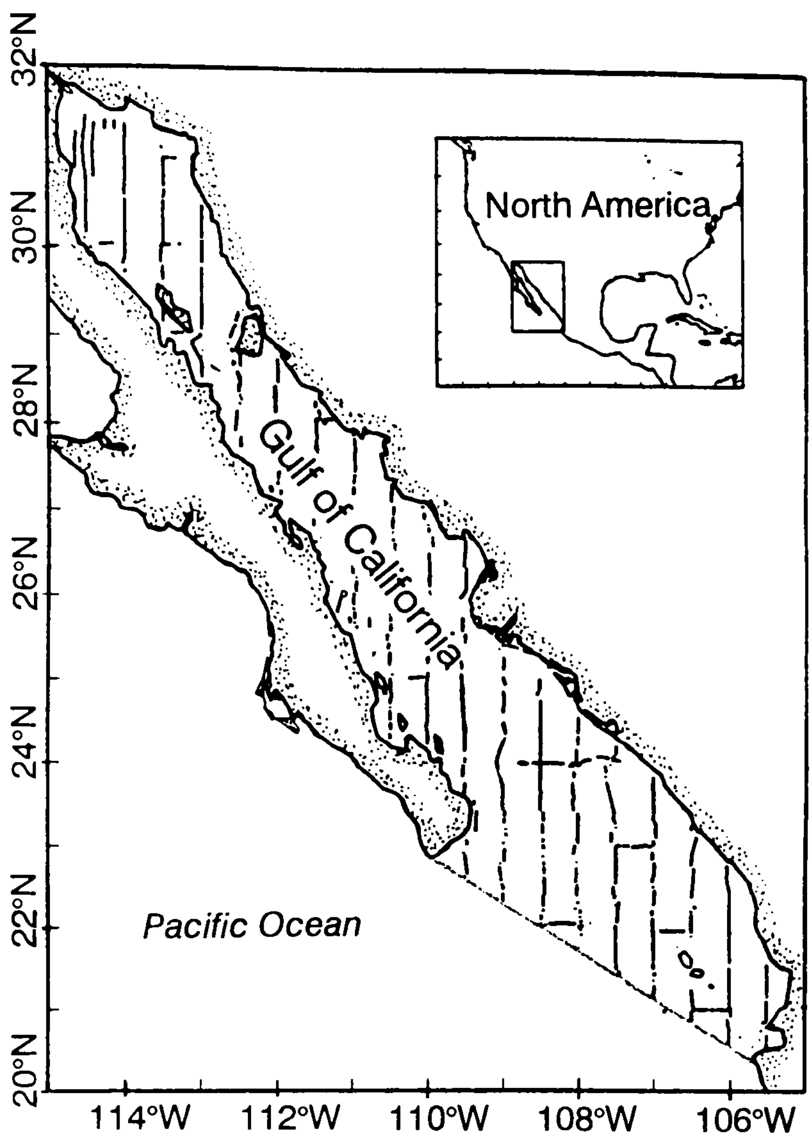

Fig. 1. Map of the Gulf of California, México and trackline surveyed on the Southwest Fisheries Science Center cruise, 3 August-2 November 1993.

For the other four surveys, 35 east-west transects, 20 n.miles long, were pre-selected at random in each of the three sub-areas from a grid of parallel lines separated by 5 minutes of latitude, but coverage during each cruise varied depending mainly on weather conditions (Figs 3–6). Location of the ship was determined by triangulation, portable GPS units or dead reckoning.

Four small boat (4.5–7m) surveys were carried out by the Instituto de Biología of the Universidad Nacional Autónoma de México (IBUNAM) between May 1992 and December 1993 (Table 1). Each survey used 3–4 observers in a boat with an outboard motor to search near the shore and out to the vicinity of Rocas Consag, offshore from the town of San Felipe. The eye height of observers was 1–2m above the water. Location was determined by triangulation and in the last survey (no.4 in Table 1), by GPS. The small boats surveyed areas closer to shore than was possible with the larger vessels, but searching did not cover a systematic grid and search effort time was much less than for the SWFSC and PNICMM cruises. Therefore, the cruise tracks are not shown in the figures. Also in contrast to the previously described line-transect surveys, searching during the IBUNAM cruises was confined to 50m on each side of the vessel.

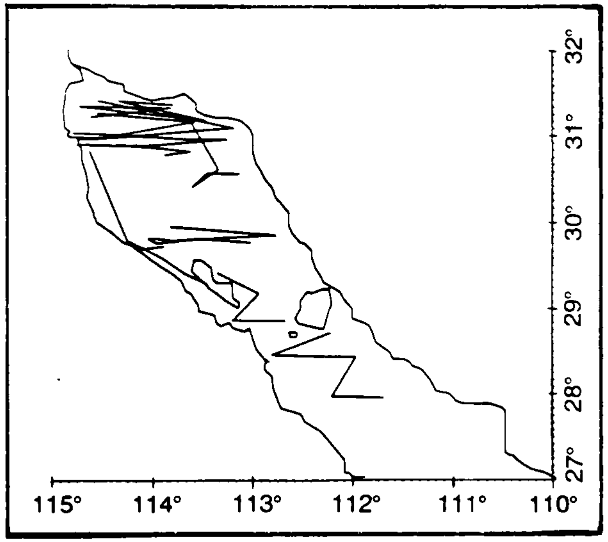

Fig. 2

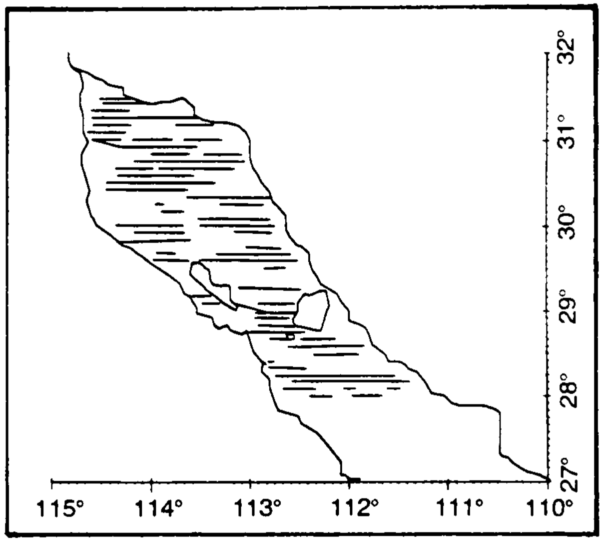

Fig. 3

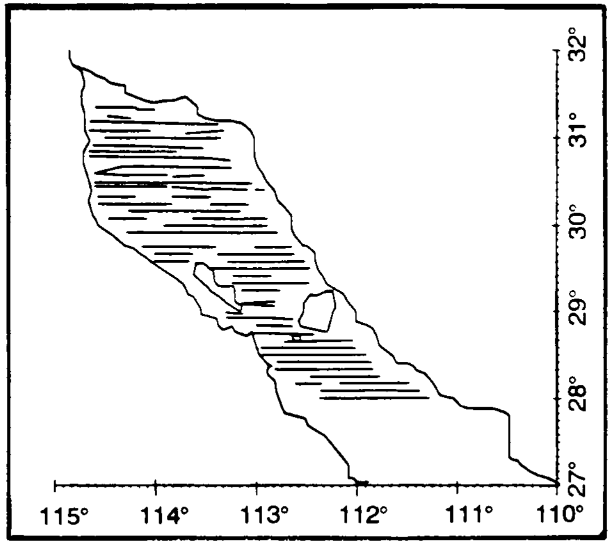

Fig. 4

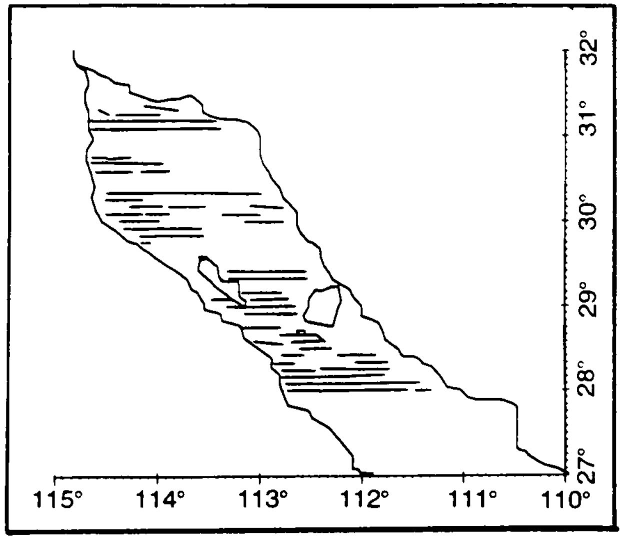

Fig. 5

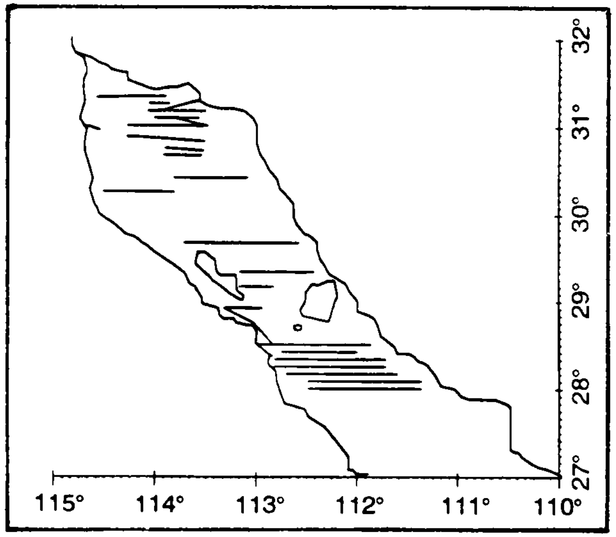

Fig. 6

Figs. 2–6. Trackline surveyed on the first to the fifth Programa Nacional de Investigación y Conservación de Mamíferos Marinos cruises.

Fig. 2: 16–26 July 1992.

Fig. 3: 18–30 October 1992.

Fig. 4: 15–26 March 1993.

Fig. 5: 23 June–3 July 1993.

Fig. 6: 15–24 October 1993.

Phocoena sinus was identified on the basis of body size, coloration (if seen) and dorsal fin shape and size. Vaquitas have a maximum length of 1.5m and a distinct triangular dorsal fin which is large in proportion to the size of the animal, with a convex leading edge and a vertical or slightly concave trailing edge (Brownell *et al.*, 1987; Leatherwood *et al.*, 1988). Other small odontocetes in the area (*Delphinus capensis* and *Tursiops truncatus*) are larger and have distinctly different dorsal fins.

RESULTS

Total trackline searching effort was 10,873 n.miles, 2,369 n.miles on the SWFSC cruise, 7,861 n.miles on the PNICMM cruises and 643 n.miles on the IBUNAM surveys (Table 1). Fig. 1 shows transects completed on the SWFSC cruise and Figs 2–6 show transects completed on the PNICMM cruises. There was a total of 1,749 marine mammal sightings, 508 on the SWFSC cruise, 1,168 on the PNICMM cruises and 73 on the IBUNAM surveys.

A total of 37 groups of vaquita, comprising of an estimated 62 individual animals, was recorded (Table 2). All but one sighting occurred in a small area in the northwestern part of the Gulf of California (Fig. 7). The other sighting occurred approximately 50 n.miles to the east of the others, south of the town of Puerto Peñasco. All vaquita sightings on the

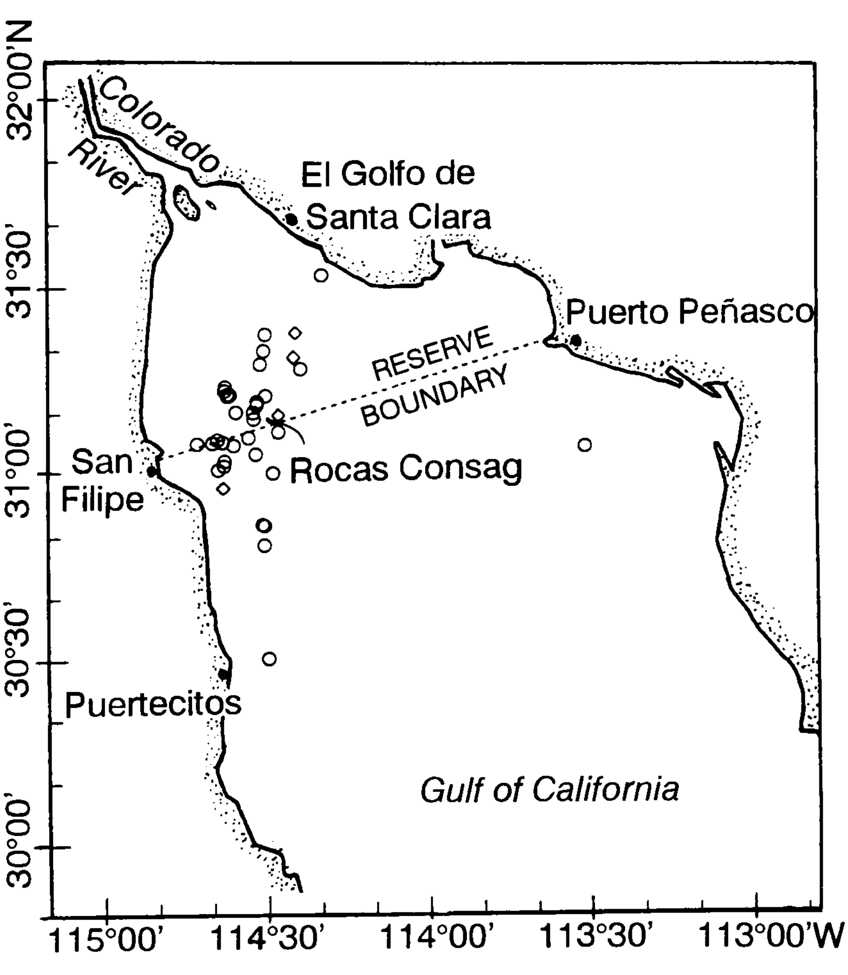

Fig. 7. Locations of the 37 vaquita sightings during 1992–1993 reported in this paper. Sightings with smaller-than-adult-sized animals are indicated with a diamond symbol. The boundary of the Upper Gulf of California and Colorado River Delta Biosphere Reserve is also shown as a dashed line.

SWFSC cruise were made during August. Vaquita sightings on PNICMM cruises were made in March, June, July and October, while sightings on the IBUNAM surveys were made in May and November (Table 2).

The number of vaquitas in each group ranged from one to three (Table 2). The mean size of the observed groups was 1.68, with a standard deviation of 0.70. Four sightings involved animals smaller than adult size (Fig. 7). The SWFSC sighting on 11 August 1993

Table 2

Date, time, position and group size for sightings of vaquitas, *Phocoena sinus*, for (a) the Southwest Fisheries Science Center (SWFSC) cruise, (b) the Programa Nacional de Investgación y Conservación de Mamíferos Marinos (PNICMM) cruises and (c) the Instituto de Biología of the Universidad Nacional Autónoma de México (IBUNAM) cruises.

Date	Time	Latitude (°N)	Longtitude (°W)	Group size
(a) SWFSC cruise				
08 August 1993	16:37	31°04.39'	113°31.18'	2
09 August 1993	06:41	31°22.46'	114°30.53'	1
09 August 1993	07:33	31°19.15'	114°30.83'	1
09 August 1993	08:09	31°17.69'	114°31.41'	1
09 August 1993	08:45	31°11.67'	114°32.03'	2
09 August 1993	08:53	31°11.20'	114°32.05'	1
09 August 1993	08:57	31°10.00'	114°32.67'	1
09 August 1993	09:05	31°08.97'	114°32.59'	2
09 August 1993	09:33	31°03.34'	114°32.19'	1
09 August 1993	10:39	30°51.84'	114°30.98'	1
09 August 1993	11:07	30°48.50'	114°30.71'	1
11 August 1993	06:22	31°14.07'	114°37.83'	1
11 August 1993	06:24	31°13.48'	114°37.97'	2
11 August 1993	06:26	31°12.63'	114°37.39'	2
11 August 1993	06:30	31°12.81'	114°36.99'	2
11 August 1993	06:30	31°12.87'	114°37.48'	2
11 August 1993	06:44	31°10.06'	114°35.88'	1
11 August 1993	07:08	31°05.26'	114°38.29'	1
11 August 1993	07:11	31°05.66'	114°39.24'	2
11 August 1993	07:21	31°01.43'	114°38.02'	1
11 August 1993	07:44	31°00.80'	114°39.13'	2
11 August 1993	07:59	30°57.85'	114°38.21'	3
11 August 1993	09:15	30°51.66'	114°30.61'	1
11 August 1993	13:07	31°16.87'	114°23.93'	2
11 August 1993	13:23	31°18.83'	114°25.24'	3
11 August 1993	13:56	31°22.70'	114°24.91'	3
(b) PNICMM cruises				
19 July 1992	09:27	31°05'	114°43'	2
20 October 1992	13:19	30°30'	114°30'	2
23 March 1993	12:22	31°00.24'	114°29.03'	1
29 June 1993	16:11	31°02.21'	114°37.94'	2
29 June 1993	16:54	31°05.11'	114°40.20'	2
29 June 1993	17:14	31°04.77'	114°36.27'	3
(c) IBUNAM cruises				
13 May 1992	13:30	31°32'	114°20'	1
23 May 1992	13:00	31°06'	114°33.5'	1
29 November 1993	14:20	31°12.65'	114°30.42'	3
29 November 1993	14:53	31°09.56'	114°28.01'	1
29 November 1993	15:27	31°06.92'	114°28.01'	2

at 0759 included a calf swimming close to an adult animal, another (on 11 August 1993 at 1323) contained a juvenile, while a third (on 11 August 1993 at 1356) contained a small animal, possibly a calf. The IBUNAM sighting of 29 November 1993 at 1453 was a young animal. No small animals were noted among the PNICMM sightings.

DISCUSSION

The comprehensive survey effort of the cruises reported here has resulted in a significant increase in the total number of reported vaquita sightings. Brownell (1986) was critical of many sighting records and considered only four, all in the upper Gulf of California, to be reliable. However, descriptions of the vaquita's external appearance and morphology (Brownell *et al.*, 1987) has made field identification more reliable. Since the sightings reviewed by Brownell (1986), there have been two sightings (probably of the same individual) reported by Vidal *et al.* (1987), 51 by Silber (1990), seven by Silber and Norris (1991) and one by Barlow *et al.* (1993), all of which have been in the same area as the sightings reported here. Almost all vaquita sightings have occurred on the western side of the northern Gulf, west of 114°20'W. The majority of sightings have been in the vicinity of a rocky island named Rocas Consag (Fig. 7). However, shallow water near the delta of the Colorado River was not surveyed as systematically as deeper water (Figs 1–6). One sighting occurred on the eastern side of the northern Gulf, south of the town of Puerto Peñasco (Fig. 7) and on 13 May 1994 a new-born vaquita calf stranded on the beach near Puerto Peñasco (Boyer, 1994).

It is also important to consider the lack of vaquita sightings at other locations. The SWFSC cruise and four of the five PNICMM cruises surveyed large areas of the Gulf in a systematic manner and did not encounter vaquitas elsewhere, although many other cetaceans were seen. Vaquitas represented only 1.9% of all marine mammal sightings on the SWFSC and PNICMM cruises. Other recent surveys, although less systematic than those reported here, have also failed to find vaquitas in other locations (Wells *et al.*, 1981; Vidal *et al.*, 1987; pers. comm. of L. Ballance, L.T. Findley and B. Tershy reported in Silber, 1990).

Vaquitas, like harbour porpoises (*Phocoena phocoena*), are difficult to detect because they are small, surface inconspicuously and occur singly or in small groups. Therefore, it is unlikely that vaquitas were detected in those parts of the SWFSC and PNICMM cruises which were undertaken in conditions of Beaufort 4–5. However, calm conditions (Beaufort 0–2) under which vaquitas could be detected did occur in each survey. In particular, very calm conditions prevailed during the SWFSC cruise in the northwestern Gulf of California: 98% of searching effort took place in Beaufort 0–2 (Gerrodette, 1994).

Vidal (1995) has summarized all available stranding data. All skeletal material has been found in the upper part of the Gulf and none found south of the town of Puertecitos. As with sightings, the lack of vaquita skeletal material on other beaches, despite extensive collections of other species (Brownell, 1986; Vidal, 1995), is significant.

Vidal (1995) has also summarized fishing-related mortality. All confirmed incidental mortality has been from the northern Gulf, principally from the fishing towns of San Felipe, El Golfo de Santa Clara and Puerto Peñasco (Fig. 7). Fleischer *et al.* (1994) and D'Agrosa *et al.* (1995) have reported rates of vaquita mortality in various types of fishing nets.

Thus, the sightings of live animals, collections of bones on beaches and incidental mortality in fishing nets all support the conclusion that the distribution of *Phocoena sinus* is limited to a small area in the northwestern Gulf of California, with a majority of sightings of live animals occurring north of 30°45'N and west of 114°20'W. Vaquita sightings were made in the same area in all seasons. Thus, vaquitas appear to occupy this area throughout the year (Silber and Norris, 1991) and do not migrate to other areas of the Gulf. However, this does not preclude the possibility that vaquitas may undergo seasonal movements on a small scale within the northwestern Gulf of California.

The mean group size of 1.68 from the sightings reported here is somewhat smaller than previous observations of about 1.9 (Silber, 1988; 1990; Silber and Norris, 1991), primarily due to the large number of single– animal sightings on the SWFSC cruise (Table 2). However, the majority of Silber's observations were made in the spring, while all SWFSC sightings took place during August. Group size may change during the year. Furthermore, it is probable that the observed mean group size on any survey is positively biased because of the greater probability of detecting larger groups. Hence the true mean group size is probably less than 1.68. There appears to be a tendency for smaller-than-adult-sized animals to be seen in groups. For the SWFSC sightings, each of the three sightings of smaller-than-adult-sized animals occurred in a group of three vaquitas. Moreover, these three sightings were the only groups of three animals among the SWFSC sightings. The sightings of Silber (1988) showed a similar pattern of calves occurring in the larger groups.

Both the US and Mexican governments have recognized that the vaquita is in danger of extinction and the vaquita is classified as endangered by the IUCN in its Red Data Book (Klinowska, 1991). A recovery plan for the species has been prepared (Villa Ramírez, 1993). The Mexican government established the Upper Gulf of California and Colorado River Delta Biosphere Reserve on 10 June 1993, with the objective of conserving various biological resources within the area, including the vaquita (Vidal *et al.*, 1993). The range of the vaquita is partly contained within this reserve, but 40% of sightings reported here have occurred outside the southern boundary of the reserve (Fig. 7).

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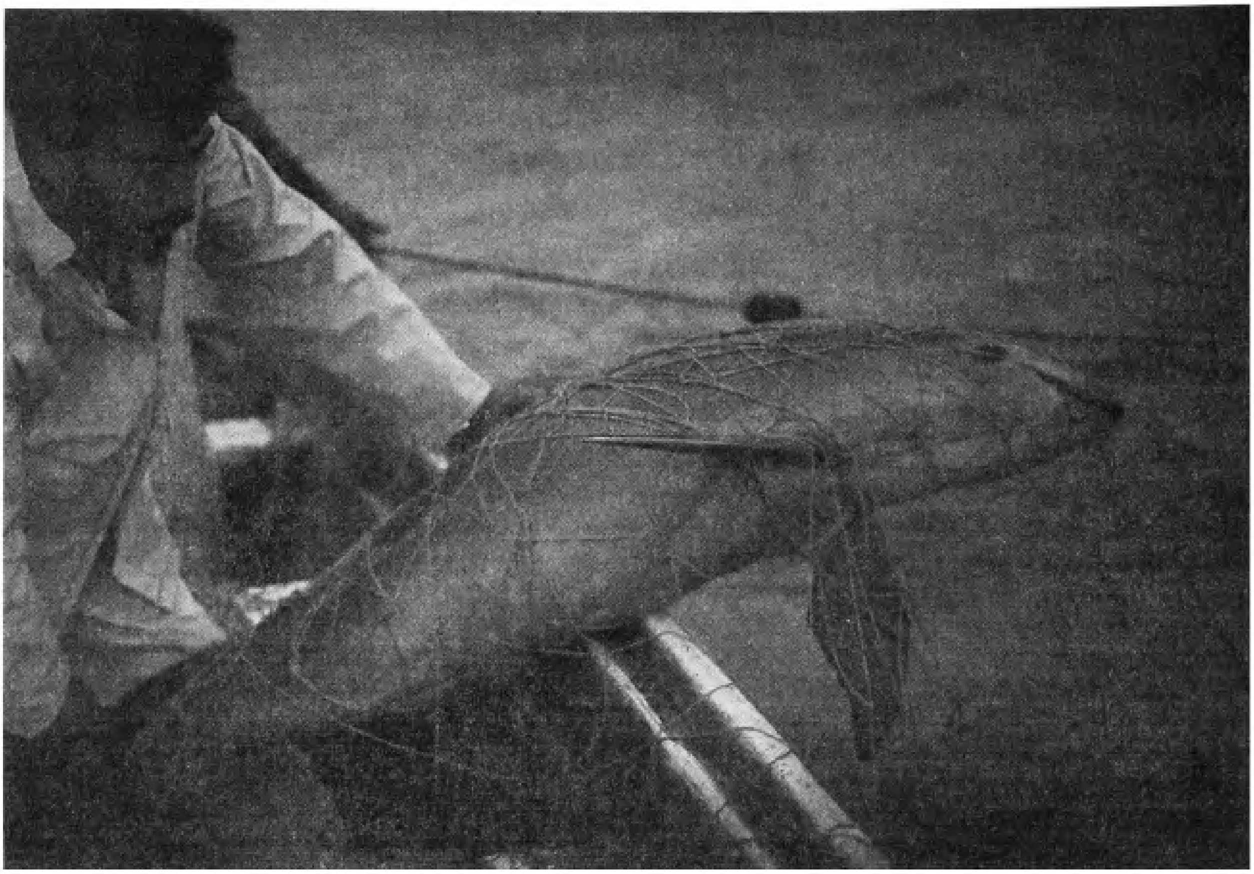
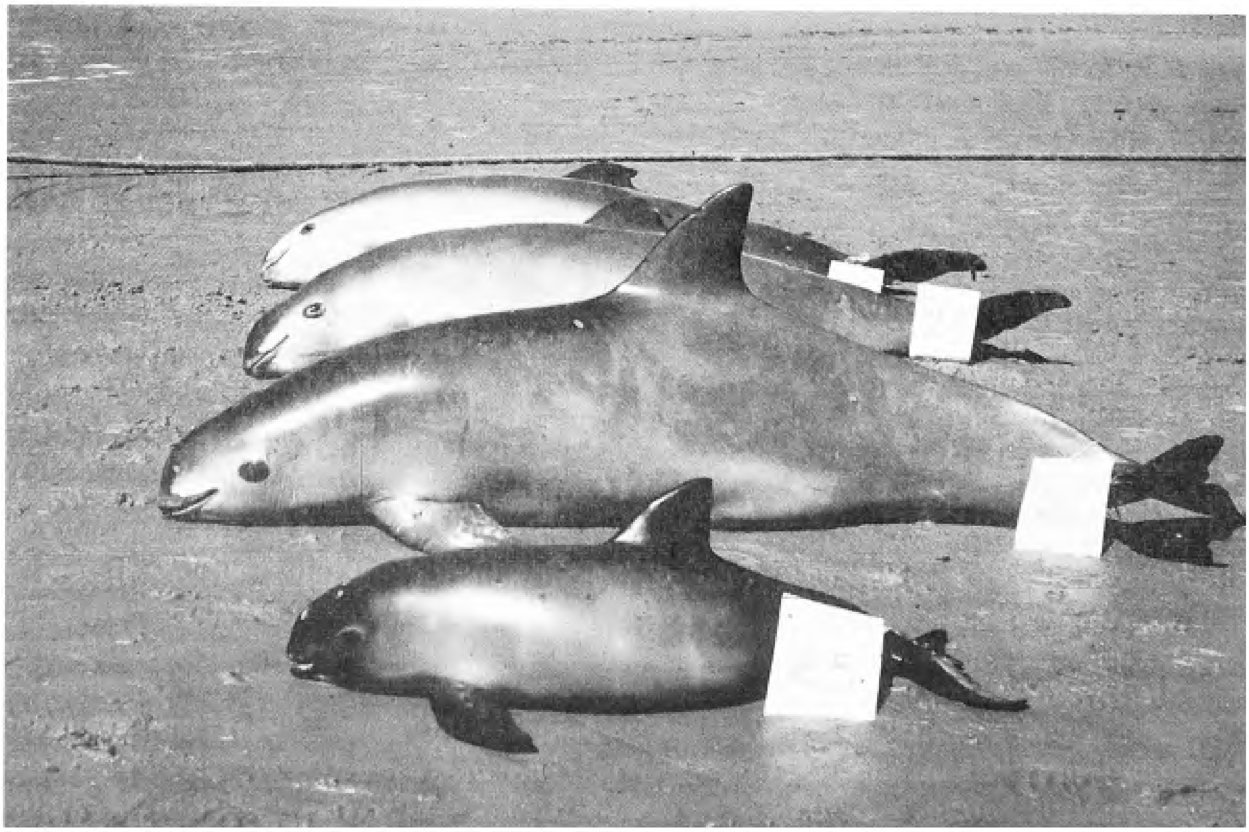


Vaquita taken in totoaba nets at Golfo de Santa Clara in February 1992. Photo by C. Faesi (Proyecto Vaquita).



Four vaquitas taken in totoaba nets at Golfo de Santa Clara in 1985. Photo by A. Robles.

SC/46/SM8

Mortality of the Vaquita (*Phocoena sinus*) in Gillnet Fisheries During 1993–94

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ABSTRACT

Gillnet fisheries in El Golfo de Santa Clara, Sonora and neighboring fishing camps, in the upper Gulf of California, México, were monitored for 114 days, from 23 January to 7 August 1993, and on nine 1–6 day visits from 15 September 1993 to 29 March 1994, to estimate the rate of incidental mortality of the vaquita (*Phocoena sinus*). Data on fishing effort and vaquita deaths were collected by interviewing fishermen on the beach when they had returned from fishing and by placing observers on different vessels each working day. The deaths of 15 vaquitas were documented during 1993–94. Twelve vaquitas were killed in *ca* 16,000 hours of fishing effort between January and October 1993: 5 in gillnets (mesh size 10–11cm) set for chano (*Micropogonias megalops*); 3 in gillnets ('chinchorro de línea', mesh size 7cm) for shrimp (*Penaeus* spp.); 2 in gillnets (mesh size 15cm) for sharks; 1 in a gillnet (mesh size 7.6cm) for mackerel and sierra (*Scomberomorus* spp.); and 1 in either a gillnet set for chano or for sharks. Two more vaquitas were killed in October 1993 and January 1994 (the last one in a gillnet set for shrimp) and another in a commercial shrimp trawl in February 1993. Most vaquitas were caught in nets set on the bottom; some were caught in driftnets.

KEYWORDS: VAQUITA; INCIDENTAL CAPTURE; NORTH PACIFIC

INTRODUCTION

The vaquita (*Phocoena sinus*), an endemic species only found in the upper Gulf of California, México, has the most limited distribution of any marine cetacean (Brownell, 1986; Vidal *et al.*, In press) and is in danger of extinction due to its incidental capture in gillnets (Vidal, 1993; IWC, 1995). Based on recent surveys, Gerrodette *et al.* (1994) estimated that the total vaquita population is 400–500 individuals. Genetic studies based on samples taken at different times and locations in the upper Gulf found no sequence polymorphisms (i.e. no genetic variability) in a 400 base pair segment of the control region of the mtDNA molecule, which may represent the results of a population 'bottleneck', founder effect, or severe inbreeding in the species (Rosel and Rojas-Bracho, 1993).

Gillnets are the most widely used fishing gear within the habitat range of the vaquita and these nets, particularly of large mesh sizes, are the most important factor in vaquita incidental mortality (Vidal, 1995). Until recently, they were mainly used to catch totoaba (*Totoaba macdonaldi*), a large sciaenid fish which is also endangered, although they are also used to catch sharks and rays. The totoaba fishery, once one of the most important fisheries in the upper Gulf of California, has been responsible for most vaquita deaths, at least during the last decade (Vidal, 1995). Although this fishery was banned in 1975 (Flanagan and Hendrickson, 1976), fishermen in the upper Gulf continued to fish totoaba at least until February 1992 (Vidal, 1993). In February 1992, the Mexican authorities banned the use of gillnets with a mesh size greater than 25cm (Diario Oficial de la Federación, 1992). However, this still permitted the use of nets with smaller mesh sizes (i.e. for sharks and rays) previously proven to catch vaquitas. Renewed enforcement of the ban in 1993 and 1994 probably kept all, or most, totoaba fishermen from fishing this species. As the totoaba population decreased, fishermen turned their attention to other species such as shrimp, sharks, rays, corvinas and mackerel.

On 10 June 1993, the Mexican government declared the Biosphere Reserve of the Upper Gulf of California and the Colorado River Delta, mainly to protect the vaquita, the totoaba and their natural habitat (Vidal, 1993).

Although the information to date on fishing effort is not adequate to allow an estimation of the total pressure on the vaquita, data presented by Vidal (1995) provide a general idea of the potential impact of fishing activities. He documented a minimum of 128 vaquitas incidentally drowned in gillnets between March 1985 and February 1992: 65% died in gillnets with mesh sizes between 20–30.5cm set for totoaba; 28% in nets with mesh sizes between 10–15cm set for sharks and rays; and 7% in nets of a mesh size of 8.5cm set for mackerel and sierra (*Scomberomorus* spp.). Vidal (1995) estimates that a minimum of 35 vaquitas were killed every year between 1985 and 1991 in these fisheries. However, to date monitoring efforts have been non-continuous and highly localized to the activities of just one fishing town, El Golfo de Santa Clara, Sonora. Data on the life history of the vaquita indicates that there is some bias in those animals caught in gillnets (Hohn *et al.*, In press). There is a bimodal age structure in the sample, comprised mostly of animals incidentally killed by fishermen from El Golfo de Santa Clara, of less than three years and greater than ten years of age. Although monitoring effort of fishing activities has concentrated along the Sonoran coast and efforts to find live vaquitas have concentrated in the area between San Felipe and Rocas Consag, most of these data were collected in the spring (Silber, 1990; Vidal, 1995).

Until now, no attempt has been made to relate the mortality rates of vaquitas with fishing effort. This paper examines the rate of incidental mortality of the vaquita in gillnets during 1993–94 and provides a general description of these fisheries. However, these analyses are preliminary.

METHODOLOGY

Monitoring concentrated on fishing from El Golfo de Santa Clara, a small town of about 1,600 people of whom almost all depend on fishing (McGuire and Greenberg, 1993) and where daily contact with the fishermen was possible. Monitoring took place from 23 January to 7 August 1993, and on nine 1–6 day visits between 15 September 1993 and 29 March 1994. Data on fishing effort and vaquita deaths were collected by D'Agrosa and at least two field assistants by non-systematically interviewing the greatest number of fishermen possible on the beach when they returned from fishing. These data include hours that the nets were in the water, kilograms of product caught per net, net size, mesh size, fishing depth, fishing location, number of boats, number of nets, and the incidental catch of vaquitas and other non-target species. Over the data collection period, a total of 48 field assistants were placed on small outboard motor boats (called *pangas*), which were also selected non-systematically, in order to corroborate the data provided by the fishermen and to collect additional data on the fishing activities (including latitude and longitude of fishing grounds using a global positioning system satellite navigation device, and climatological and oceanographical conditions). Data collected during the last two weeks of February and during two visits in March 1994 are not included in this analysis. No fishing (and thus monitoring) took place during neap tides, bad weather or during holidays.

Participant observation, a tool frequently used by anthropologists and which implies direct involvement in community life (Agar, 1980), such as helping deploy and collect the nets, attending social events and getting to know the families, was encouraged among field assistants to establish the trust of the fishermen and thus increase the reliability of the data obtained.

The rate of incidental mortality of the vaquita in gillnets was estimated by dividing the number of vaquitas caught by the number of hours the nets were in the water for each fishery. Vaquita mortality is standardized in this way so that we are able to make direct comparisons of incidental mortality by fishery, net mesh size, depth and geographic location. This also lays the groundwork for future statistical analyses.

RESULTS

Monitoring effort

From 23 January to 7 August 1993, 104 days of fishing activities were monitored, 9.5 days were monitored between 15 September 1993 and 29 March 1994 (Table 1). We sampled 322 (61%) of the estimated 525 trips to fish shrimp with gillnets during 1993, 367 (25%) of 1,486 trips to fish chano, 215 (46%) of 470 trips to fish sharks and rays, 30 (60%) of 50 trips to fish corvina and 232 (59%) of 390 trips to fish mackerel and sierra (see below) (Table 2).

Fisheries

Although the fishing activities monitored covered the area from Punta Borrascoso, Sonora, across the Gulf, to San Felipe, Baja California (Fig. 1), only fishermen from El Golfo de Santa Clara were monitored. This included five fisheries using *pangas* with 55 and 75hp outboard motors and crews of 2–3. The percentage of hours of fishing for each

Table 1

Monitoring of gillnet fisheries in El Golfo de Santa Clara, Sonora, 23 January 1993 - 29 March 1994 (DF = days in the field; DM = days monitored; NA = number of field assistants) (see text).

Month	DF	DM	NA	Fishery
1993				
January	15	2	3	Shrimp
February	28	14	6	Shrimp
March	31	17	8	Chano
April	30	19	6	Chano
May	18	12	2	Corvina/Shark
June	30	26	6	Shark
July	31	10	4	Mackerel/Sierra
August	8	4	2	Mackerel/Sierra
September	2.5	1	1	Shrimp
October	2.5	2	2	Shrimp
November	1.5	0	0	Shrimp
December	1.5	0	1	Shrimp
1994				
January	1.5	0	1	Shrimp
February	5	2.5	4	Shrimp
March	6	4	2	Shrimp/Chano
Total	211.5	113.5	48	

Table 2

Survey effort in El Golfo de Santa Clara, 23 January 1993 - 15 February 1994.

Fishery	Total trips observed	No. trips sampled	% total trips sampled	Total hours sampled	% total hours sampled
Shrimp	525	322	61	3,826	25
Corvina	50	30	60	23	0.1
Mackerel/Sierra	390	232	59	2,677	17
Shark/Ray	470	215	46	6,218	40
Chano	1,486	367	25	2,787	18

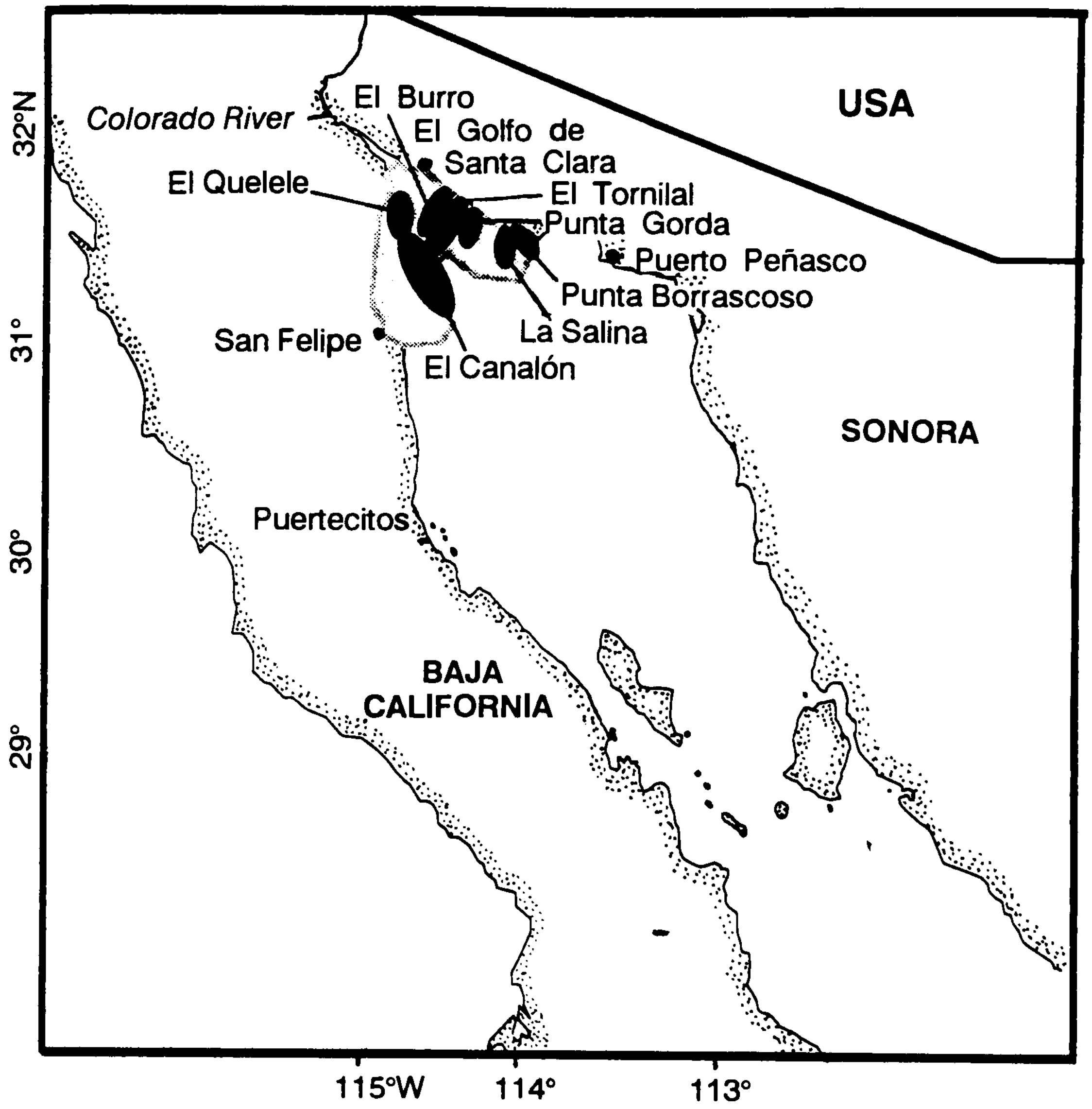

Fig. 1. Study area. Preferred fishing grounds in black, 23 January 1993–29 March 1994.

fishery from 23 January to 16 October 1993 are given in Table 2, with a total of *ca* 16,000 hours of effort monitored. These range from a high of 40% for the shark and ray fishery to a low of 0.1% in the corvina fishery. A general description of these fisheries follows (see also Table 3).

Table 3

General information of gillnet fisheries in El Golfo de Santa Clara during 1993-94 (dates are for both years unless otherwise specified).

Fishery	Dates	Average net length (m)	Average net depth (m)	Net mesh size (cm)	Net type	Target species
Shrimp	Jan.-Mar. 1993; Sept. 1993-Mar. 1994	402	26	7	Demersal, drift	*Penaeus stylirostris*, *P. californiensis*
Chano	Mar.-May	342	17	10-12	Demersal, drift	*Micropogonias megalops*
Shark	May-Jul.	399	15	12-15	Demersal, anchored	*Carcharhinus* spp., *Sphyrna* spp., *Rhizoprionodon* spp., *Mustelus* spp.
Corvina	May	320	9	7-15	Demersal, drift	*Cynoscion* spp.
Mackerel, Sierra	Jul.-Aug.	504	0	7-10	Surface, drift	*Scomberomorus sierra*, *S. concolor*
Ray	May-Jul.	219	10	12-23	Demersal, anchored	*Myliobatis*, *Rhinobatus*, *Dasyatis*, *Mobula*

Shrimp

Brown (*Penaeus californiensis*) and blue shrimps (*P. stylirostris*) were fished from January to March 1993 and from September 1993 to mid-March 1994 using demersal monofilament gillnets (called *chinchorro de línea*) with a mesh size of 7cm or less. The nets are left to drift with the currents from 0.5 to 1.5 hours. They are cast and retrieved continually from sunrise to sunset. The nets are an average 402m long, 2.5m wide and drift at an average depth of 26m.

Chano

Fishing for chano (*Micropogonias megalops*), an endemic species of croaker, apparently increased in 1991 due to the decrease in shrimp yields, but also probably because of the renewed enforcement of the totoaba ban by the Mexican authorities, which forced some fishermen to look for other sources of income. In particular in 1993, the chano fishery was economically important for the people of El Golfo de Santa Clara, hence the large increase in fishing effort in that year. Chano were fished using demersal monofilament gillnets from mid-March to early May. These nets, which usually have a mesh size of 10–12cm, are left to drift with the current from 0.75 to 2hrs, usually beginning in mid-morning and ending in the late evening. The nets for chano are an average 342m long, 2m wide and drift at an average depth of 17m. The 1994 fishing season for chano began in late March.

Elasmobranchs

Various species of shark, including *Carcharhinus* spp., *Rhizoprionodon* spp., *Mustelus* spp. and *Sphyrna* spp., as well as skates and rays, such as *Rhinobatus* spp. and *Myliobatis* spp., the stingray (*Dasyatis brevis*) and mobulas (*Mobula* spp.), were fished from May through July 1993. These nets are demersal anchored monofilament gillnets with mesh sizes ranging from 12–23cm, which are deployed in the late morning or early afternoon, checked the next morning and left in the same location if catch was good. If not, they are relocated and checked the next day. The nets most commonly used are an average of 400m long, 2m wide and set at an average of about 15m deep. During 1993, some fishermen fished only for skates and rays, using nets with an average length of 219m and set about 10m deep. These nets have the larger mesh sizes previously mentioned. Since July 1993, the only elasmobranchs fished have been caught on long-lines (from January to March 1994).

Corvinas

During 1993, various species (*Cynoscion* spp.) of sciaenid corvinas (sea trouts) were fished, mainly in the shallow channels of the Colorado River Delta, but for only four days in early May. This accounts for the small percentage of hours for this fishery as compared to the other fisheries. The nets used for corvinas were primarily 7–15cm mesh monofilament gillnets, with an average length of 320m and set at an average depth of 9m. According to fishermen from El Golfo de Santa Clara, corvinas were also exploited by the upstream agricultural community, who fished in this area as well as farther up the river using similar gillnets. As far as we know, between May 1993 and mid-March 1994 no corvinas had been intentionally fished, although they appear to be abundant as bycatch in most of the other fisheries. The fishermen again reported fishing corvinas within the main channel of the Colorado River beginning 22 March 1994.

Mackerel and sierra

From July to August, Monterey Spanish mackerel (*Scomberomorus concolor*) and sierra (*S. sierra*) were caught in monofilament gillnets set near the surface in the early evening. These nets are anchored to the *panga* and both drift with the current all night. The fishermen check them once during the night and then at dawn. The most common mesh sizes range from 7–10cm, and the average net dimensions are 504m long and 3m wide.

Totoaba

We know that at least nine *pangas* fished totoaba during January, February and March 1993, although the fishermen would not admit it, so there is no relevant information. However, during our first two visits to El Golfo de Santa Clara in 1994 (January 21–24, February 11–15), two fishermen admitted that they had fished totoaba in early January 1994. We do not know if the fishermen of this town are presently fishing totoaba.

Incidental mortality of the vaquita

Between 23 January 1993 and 29 March 1994 there have been 15 observed vaquita deaths due to fishing activities (Table 4). Of these, seven fresh carcasses were given to us by the fishermen and eight more were reported, including one which died in a commercial shrimp trawl. Twelve of these vaquitas died in *ca* 16,000 hours of fishing effort between 23 January and 16 October 1993: 5 in gillnets with a mesh size of 10–11cm set for chano, 3 in gillnets with a mesh size of 7cm set for shrimp, 2 in gillnets with a mesh size of 15cm set for sharks, 1 in a gillnet with a mesh size of 7.6cm set for mackerel and 1 in a net set either for chano or for sharks. In addition to these 12, two more vaquita deaths (in early October 1993 and in late January 1994) were reported by fishermen. We do not know for certain in which fishery the animal reported in October was taken, but it is possible that it was a gillnet for shrimp since that was the predominant fishery at that time. The animal reported in January was taken in a shrimp gillnet. Two decomposed carcasses, for which the cause of death is unknown, were found on the beach and collected in 1993. Table 5 shows the results for basic capture-rate computations for January-October 1993, which range from

Table 4

Incidental mortalities of vaquitas in fishing activities in the upper Gulf of California, 23 January 1993 - 29 March 1994[1].

Date	Mesh size (cm)	Fishery	Locality	Length (cm)	Maturity	Sex
02/02/93	7	Shrimp	El Tornillal, Sonora	-	-	-
02/05/93	Trawl	Shrimp	Rocas Consag	-	-	-
02/06/93	7	Shrimp	Punta Gorda, Sonora	140.0	M	F
02/22/93	7	Shrimp	El Tornillal	106.3	I	F
03/31/93	11	Chano	El Quelele, Baja California	129.8	M	M
04/03/93	10	Chano	'Canal6n de la Baja' Baja California	116.3	I	F
04/16/93	10	Chano	El Quelele	110.0	I	F
05/02/93	10	Chano	El Quelele	115.3	I	M
05/01-15/93	10	Chano	Unknown	-	-	-
05/15-20/93	10, 15?	Chano/Shark?	El Tornillal	-	-	-
05/15-20/93	15	Shark	Rocas Consag, Sonora	-	-	-
06/15/93	15	Shark	Rocas Consag	109.4	I	M
07/19/93	9	Mackerel	El Burro, Sonora	-	-	-
10/15/93	7	Shrimp?	El Machorro, Sonora	-	-	-
01/22/94	7	Shrimp?	El Tornillal	-	-	-

[1] Also, two beached specimens (cause of death unknown) were found *ca* 6km south of El Golfo de Santa Clara: a 110cm long immature male on 05/18/93 and a 128cm long mature male on 05/28/93.

Table 5

Capture rates of vaquitas for fisheries in El Golfo de Santa Clara, 23 January - 16 October 1993.

Fishery	Number of vaquitas caught[1]	Total hours sampled	Vaquitas caught/hour
Chano	5	2,787	0.0018
Shrimp	3	3,826	0.0008
Shark/Ray	2	6,218	0.0003
Mackerel/Sierra	1	2,677	0.0004
Corvina	0	23	0.0000

[1] There is one animal which could have been caught in either the chano fishery or the shark/ray fishery, for a total of 12 (see Table 4).

zero in the corvina fishery to 0.0018 vaquitas per hour in the chano fishery. The percentages of total effort monitored for each fishery, followed by the percentages of the total number of vaquitas caught is: chano (25; 55), shrimp (61; 20), shark/ray (46; 15), mackerel/sierra (59; 10), and corvina (60; 0).

DISCUSSION

The data presented here, plus those obtained by Vidal (1995) during 1990–1992, demonstrate that vaquitas are not only being killed in large mesh totoaba gillnets, but in virtually all mesh sizes. It also seems that no matter whether the nets are anchored or drifting, or whether they are demersal or on the surface, they catch vaquitas. Some 92% of the vaquitas killed in 1993 were caught in nets set on the bottom, 8% in surface nets. In total, 75% were caught in driftnets and 25% in set nets.

The figure of 15 vaquitas caught in fisheries between early 1993 and early 1994 is clearly a minimum, both for El Golfo de Santa Clara and for the whole range of the species, since we only monitored part of the fishing effort in the smallest (El Golfo de Santa Clara) of the three fishing ports with activities in the range of this porpoise.

Spatio-temporal distribution of the vaquita

Vaquitas were caught almost year-round during 1993, as has been the case in previous years. Monitoring effort for the months of January and August-December 1993 and January-March 1994 was regular but reduced to a few days each month. It appears that vaquitas are caught almost everywhere that fishermen from El Golfo de Santa Clara fish in the upper Gulf. A preliminary analysis of vaquita distribution based on catch records and confirmed sightings (reviewed by Brownell, 1986; Silber, 1990; Vidal, 1995) indicate that in the spring (March-May) vaquitas are concentrated along the Sonoran coast, between El Golfo de Santa Clara (31°41'10'N, 114°29'59'W) and Punta Gorda (31°30'00'N, 114°10'31'W), just outside of La Salina (31°29'34'N, 114°03'37'W), in the outlet of the left channel of the Colorado River Delta (*ca* 31°31'20'N, 114°40'39'W), in the middle region of El Canalón (31°26'29'N, 114°22'38'W) and in the area between San Felipe, Baja California and Rocas Consag. In the summer (June-August) there are records of vaquitas between El Machorro (31°40'N, 114°30'W) and El Tornillal (31°33'42'N, 114°17'45'W), Sonora, and in the area between San Felipe and Rocas Consag. In the fall (September-November) vaquitas have been reported in and just south of the area between San Felipe and Rocas Consag and along the Sonoran coast from El Machorro to La Salina. In the winter (December-February), they have been reported from El Burro (31°32'51'N, 114°22'38'W) to Punta Gorda, in the outlet of the left channel of the Colorado River Delta, in the middle region of El Canalón, and in the area between San Felipe and Rocas Consag. However, these conclusions are preliminary. The spatio-temporal distribution of the vaquita is not clear because: (1) there is almost no information on incidental mortality for the San Felipe and Puertecitos areas; (2) there has been limited survey effort along the northernmost coasts of Sonora and Baja California; and (3) most surveys and monitoring effort have been conducted in the spring.

In summary, the mortality of the vaquita in gillnet fisheries not previously monitored (chano, corvinas, mackerel/sierra and shrimp) suggest that overall incidental mortality may have been higher than previously estimated (i.e. >35 individuals/year), because these nets are utilized throughout the range of the vaquita in the upper Gulf of California and because previous estimates were based mostly on totoaba and shark nets. About 40% of the sightings by Silber (1990) and of those obtained by the Southwest Fisheries Science Center of the US National Marine Fisheries Service during an August 1993 survey were made outside of the boundaries of the recently declared Biosphere Reserve of the Upper Gulf of California and the Colorado River Delta (IWC, 1995). This was also the case for sightings made in surveys by the Programa Nacional de Investigación de Mamíferos Marinos of the Mexican Secretariat of Fisheries (Gerrodette *et al.*, 1995; IWC, 1995). The low population estimates and the preliminary analysis of data on incidental mortality presented here support previous conclusions that the vaquita is in danger of extinction. Every effort must be taken to decrease or eliminate incidental mortality throughout its range.

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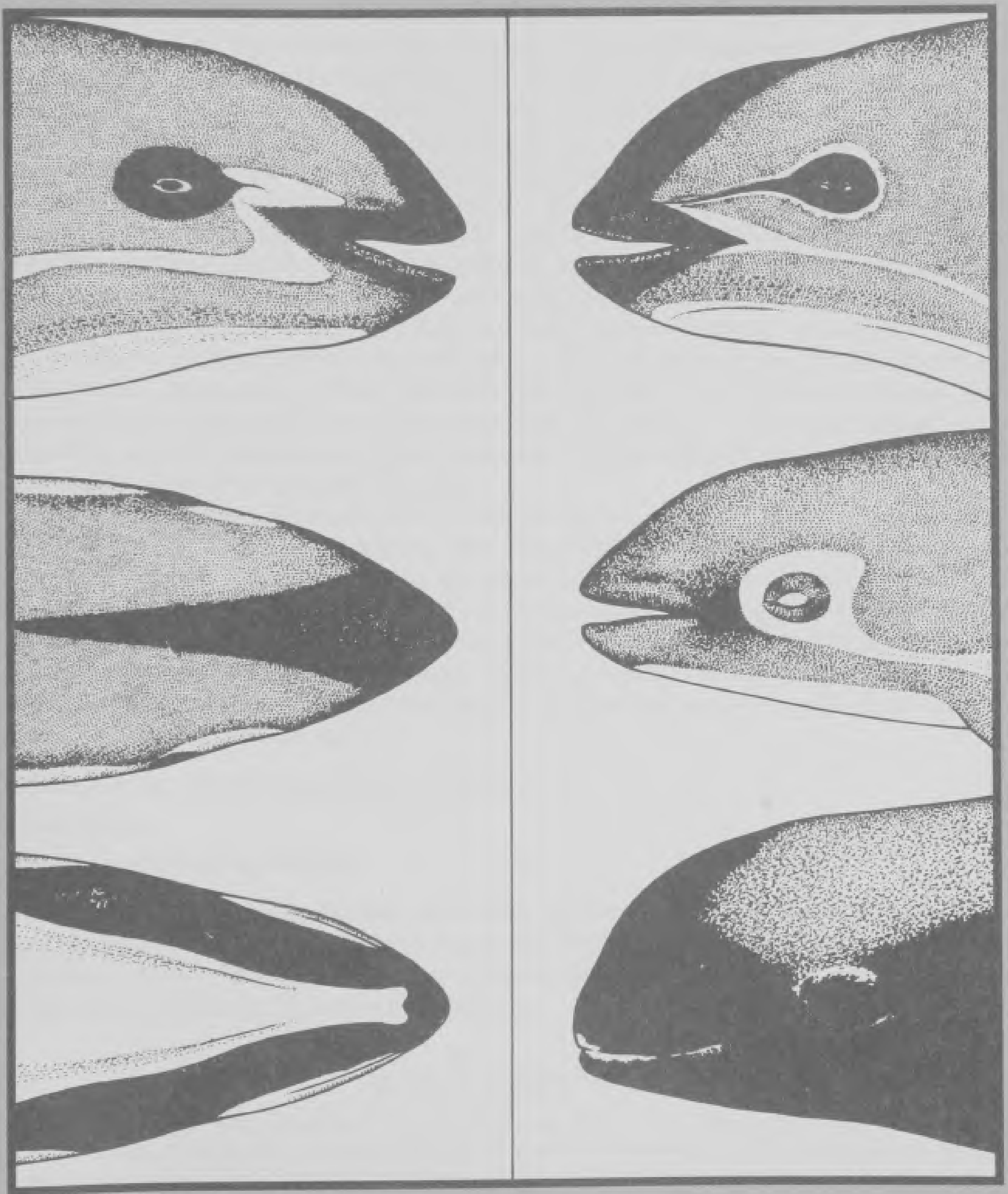
Burmeister's Porpoise



Schematic representations of the pigmentation of the head in Burmeister's porpoise. *Illustration courtesy of R.N.P. Goodall.*

Burmeister's porpoise, *Phocoena spinipinnis*

INTRODUCTORY REMARKS

In its first examination of this species in 1983, the IWC Scientific Committee had little information other than that there were some animals taken in nets along the west coast of South America (IWC, 1984)

Considerably more information was available at the 1990 meeting (IWC, 1991) and the Workshop on Mortality of Cetaceans in Passive Fishing Nets and Traps (IWC, 1994). The Committee learned that there were incidental takes in Brazil, Uruguay, Argentina, Chile and Peru. Although the extent of these catches was poorly documented, it was believed that the takes were likely to be significant in Peru. Directed takes were reported from Peru and Chile. In Peru, the meat was used for human consumption and in southern Chile the Burmeister's porpoise was shot and harpooned for use as crab bait. Given the high levels of mortality of Burmeister's porpoise in Peruvian fisheries, the Committee recommended that estimates of abundance be obtained for this population, better estimates of the number of porpoises killed be obtained, and that catch statistics collected by the Ministerio de Pesquería in Peru be recorded by species and in number of animals taken rather than by tonnage. Furthermore, the Committee recommended that the history of this exploitation, including fishing effort and historical catch levels, be compiled.

In a major review carried out for the UN Conference on Environment and Development (Bjørge *et al.*, 1994), the Scientific Committee considered the Burmeister's porpoise in the context of the Peruvian fisheries. It repeated its recommendations that catches be properly documented, that abundance estimates be obtained and that attempts to reduce or eliminate bycatches be made.

The most recent examination of this species was at the 1994 meeting (IWC, 1995). Although there is no direct evidence, the Committee noted that it was possible that Burmeister's porpoises might still be occasionally taken for use as crab bait in Chile. However, most attention focussed on the Peruvian situation. Despite a ban on cetacean exploitation and utilisation in 1990, it was clear that considerable mortality of several species, including Burmeister's porpoises, was continuing. The Committee expressed its concern and once again re-iterated the need for research on a number of factors to enable an assessment to be carried out:

(1) distribution, migration and stock identity;

(2) abundance;

(3) demography and life history.

A number of scientists have worked extremely hard with limited budgets to address the issue of incidental catches, particularly Koen van Waerebeek, Julio Reyes and colleagues. In addition to the information in this section, the most important recent papers are included in the following selected bibliography.

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Sightings of Burmeister's Porpoise, *Phocoena spinipinnis*, off Southern South America

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ABSTRACT

Although thought to be fairly common off the western and southeastern coasts of South America, Burmeister's porpoise (*Phocoena spinipinnis*) has seldom been seen alive by cetacean researchers. Published sightings are reviewed and new observations described. Animals seen in the wild appear light brown to brownish black; the most notable field characteristic is the low, backward-leaning dorsal fin with tubercles along its forward edge. Swimming is unobtrusive, with little of the body exposed and little water disturbance, making the animals almost impossible to see in rough weather. In calm weather the porpoises can be located by their short 'puff-puff' respirations. All sightings were in inshore waters, but incidental captures occur to at least 50km offshore. The porpoises enter bays, fiords and rivers and are sometimes found within the kelp line. Most sightings were of less than six individuals. Calves thought to be less than a month old were seen in Tierra del Fuego in January and April. Burmeister's porpoises are often seen near but not directly associated with other species. At Golfo San José, Chubut, Argentina, porpoises were studied from 1974–76, 1981–1988 and again in 1990, in inshore waters in spring and summer. Sightings were much more numerous in 1990 and the animals occupied a wider area of the bay, possibly occupying niches left by bottlenose and dusky dolphins, which have been much less numerous in the area in recent years. As in Chile, animals may move offshore following prey in winter. Opportunistic sightings in Canal Beagle, Tierra del Fuego, indicate that there is a resident group(s) near Ushuaia/Lapataia, seen all months except August and September. These animals may be filling a niche left by Peale's dolphins which were exploited by the *centolla* industry. Little is known about the biology and ecology of this species.

KEYWORDS: BURMEISTER'S PORPOISE; SOUTH PACIFIC; SOUTH ATLANTIC; SURVEYS; SIGHTINGS-INCIDENTAL; DISTRIBUTION; INCIDENTAL CAPTURE

INTRODUCTION

The Burmeister's porpoise, *Phocoena spinipinnis*, occurs only off South America, from southern Brazil to northern Peru. Although once thought to be 'probably the most abundant coastal small cetacean in southern South American waters' (Brownell and Praderi, 1982), other species are now thought to be more abundant in coastal waters in these areas: dusky dolphins, *Lagenorhynchus obscurus*, off Peru and northern Patagonia (Würsig and Würsig, 1980; Reyes and Van Waerebeek, 1995), the franciscana, *Pontoporia blainvillei*, off northern Argentina and Uruguay (Praderi *et al.*, 1989; Corcuera, 1991); the Chilean dolphin, *Cephalorhynchus eutropia*, and Peale's dolphin, *L. australis*, off central and southern Chile (Norris, 1968; Oporto and Brieva, 1994) and the Commerson's dolphin, *C. commersonii*, and Peale's dolphin near the Strait of Magellan and northern Tierra del Fuego (Goodall, 1978; Goodall *et al.*, 1988a).

Recent studies have shown that Burmeister's porpoise is taken incidentally in all these areas, but little is known of its abundance, habitat preference, behaviour or ecology (Goodall *et al.*, 1990; 1995; Corcuera, 1991; Corcuera *et al.*, 1995; Reyes and Van Waerebeek, 1995). Only one account (Würsig *et al.*, 1977) has been published on its behaviour. Few people, other than the fishermen who catch them, have seen this animal alive. This paper is a review of published and new sightings and observations of the behaviour of this species.

METHODS AND MATERIALS

In addition to a review of the literature, information is provided from the studies summarised below.

In 1968, KSN carried out sighting and collecting expeditions in several areas along the coasts of the eastern South Pacific from northern Peru to central Chile. He was also the chief scientist in an expedition aboard the R/V *Hero*, which carried out a cetacean survey from Valparaiso to Cape Horn and back to Punta Arenas from 12 November to 10 December 1968. Several experienced observers were on board.

During a long-term cetacean stranding programme begun in southern Argentina in 1974, RNP collected specimens on the beach and distributed sighting forms to numerous ships and volunteers (including participants in bird surveys). A.C.M. Schiavini trained the boat captains to search for and identify cetaceans. The returned forms have been compiled by species and reviewed for pertinent information. Two catamarans that take tourists to see the wildlife on the islands off Ushuaia accounted for many sightings. The *Ana B* began operating in the 1990–91 season and makes daily trips to the islands in winter and twice a day in summer. The *Ezequiel MB* began in the 1993–94 season and makes daily trips to the islands and then eastward to Harberton or westward to Lapataia (Fig. 2). Sightings reported earlier (Goodall and Polkinghorn, 1979) are also detailed.

From June 1974 through March 1976, BMW studied bottlenose dolphins in Golfo San José, Península Valdés, Argentina (42°23'S, 64°04'W), either from shore or from small boats (Würsig *et al.*, 1977). In 1990 they returned to Golfo San José to undertake observations from 15–21 November (Würsig and Harris, 1990; Würsig, 1992b).

GH formed part of an observation team studying southern right whales, *Eubalaena australis*, at Golfo San José from February 1981 to March 1988. Observations from a beach camp or cliff observation hut equipped with telescope and theodolite were made daily except for three months per year (usually July, November and March). Observations were more intensive from June to December, when right whales were in the bay, somewhat less intensive through March, with least effort from March to July. Except for one sighting from a kayak, all other sightings were made using a Bushnell spotting scope.

SIGHTINGS

All sightings of *P. spinipinnis* from the literature, our records and those from colleagues are listed in Table 1 and mapped in Figs 1 and 2. Few published accounts were found (Aguayo, 1975; Donoso-Barros, 1975; Würsig *et al.*, 1977; Goodall and Polkinghorn, 1979; Beade *et al.*, 1988; Van Waerebeek and Reyes, 1990). New sightings were included only if the observer was sure of the field marks of the species, such as the dark upper body and the unusual backward-leaning dorsal fin with tubercles on its upper edge, set well back on the body (Brownell and Praderi, 1984). Nevertheless, several sightings are suspect because they were not made by trained observers.

Burmeister's porpoises are difficult to see; this is due to a combination of their quiescent surfacing and unobstrusiving swimming habits, small size and long (to over two minutes) submersions. Even experienced observers can not see Burmeister's porpoises unless the sea is fairly calm (Würsig *et al.*, 1977; Van Waerebeek and Reyes, 1990).

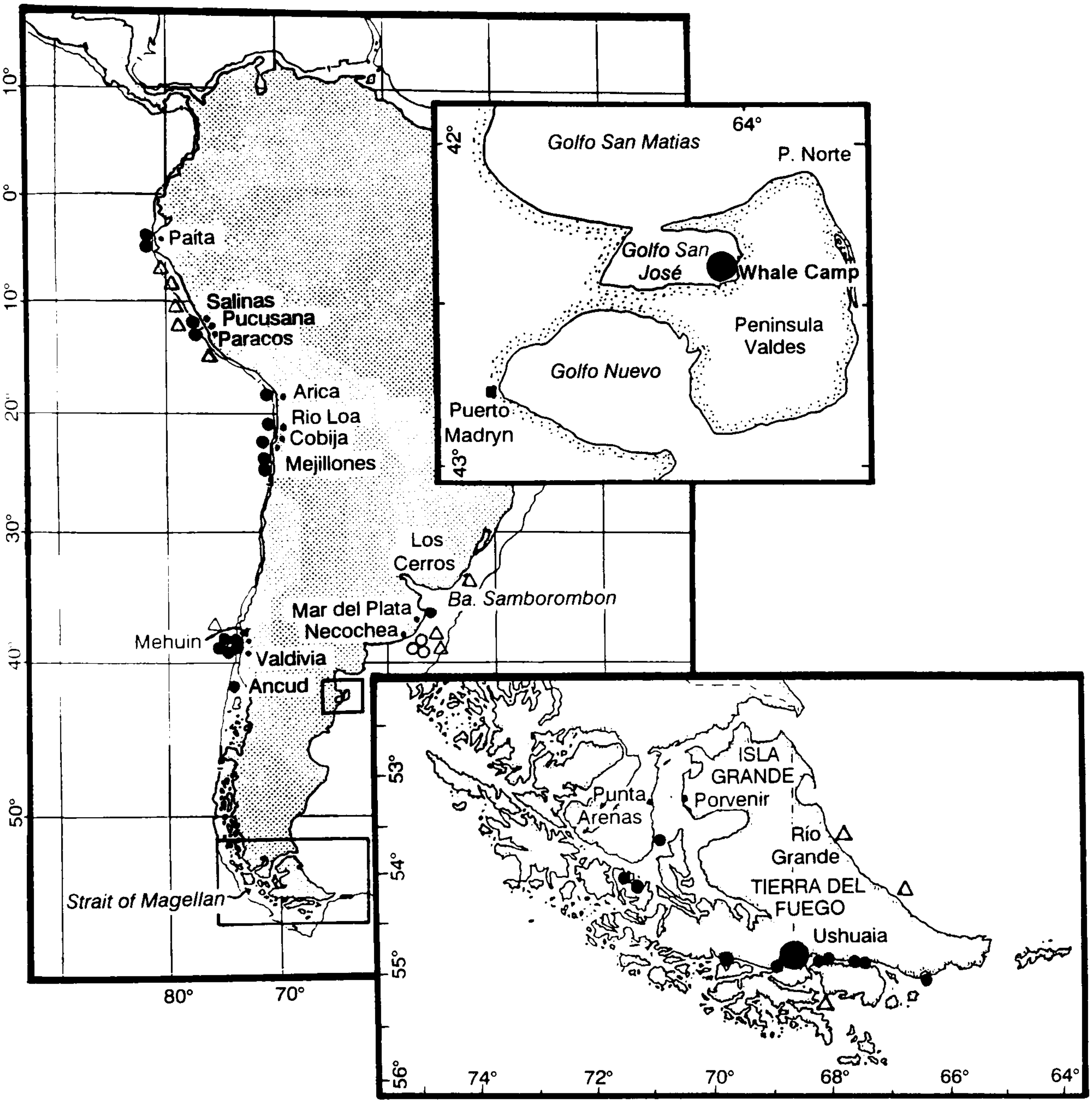

Fig. 1. Map of South America showing sightings of Burmeister's porpoises, with insets of Península Valdés and Tierra del Fuego. Closed circles are confirmed sightings; open circles, reported but unconfirmed sighting; open triangles indicate major areas of incidental or deliberate capture. The circles indicate number of sightings, but do not represent distance from shore.

Text continues on p. 305

Table 1

Sightings and other observations of Burmeister's porpoise, *Phocoena spinipinnis*. Notes on captures are included because they indicate the areas where the porpoises occur. nm = nautical miles, m = metres.

Date	Location	Details	Platform	Reference or observer
Southeastern South Pacific				
Peru				
10 Sep. 1968	Balneario Esmeralda N of Paita	Two animals in 10m of water. 1/2km offshore, water temp. about 18°C. Could not get close.	M/L *Estrella Luminosa*	K.S. Norris
10 Sep. 1968	Balneario Esmeralda N of Paita	Later, crossing the bay, three more animals observed. All fled.	M/L *Estrella Luminosa*	K.S. Norris
22 Jan. 1988	1-2km off Salinas	2 animals with SA sea lions. Porpoises dove & fled on approach.	Boat	Van Waerebeek & Reyes, 1990
09 Mar. 1988	Bahía Paracas & E of Chinchas Islands	22 in loose scattered groups perhaps feeding & mating.	Boat	Van Waerebeek & Reyes, 1990
1988-1989	Pucusana, Cerro Azul	Taken mostly in demersal gillnets set for bottom-dwelling rays & sharks, up to 55km (30nm) from shore.	-	Van Waerebeek & Reyes 1994; Reyes & Oporto, 1994
Chile				
I Región				
-- -- 1948	Near Bahía de Arica	A group seen by R. Donoso-Barros	-	Donoso-Barros, 1975
II Región				
10-11 Oct.	Mouth of Río Loa 21°25'S	School of 8 animals, dark, knobs on anterior border of fin, 170cm.	-	Aguayo, 1975: 1139
22 Jan. 1982	Interior of Bahía de Mejillones, 23°06'S	School of 70 animals, swam very near shore.	-	Guerra *et al.*, 1987
10 Feb. 1983	Cobija, 22°33'S	Two animals seen 800m from coast.	-	Guerra *et al.*, 1987
26 Aug. 1986	23°21'S, 70°35'W	Only one animal seen during over 26hrs of survey in good condition.	PAM *Guanaye*	Guerra *et al.*, 1987; Van Waerebeek & Reyes, 1990
X Región				
-- -- --	Mehuín, 39°26'S, 73°13'35"W	Seen by fishermen, a gravid female captured.	-	R.P. Schlatter
31 Jan. 1979	Golfo de Ancud, Isla Chiloé 42°33'S, 73°10'W	One animal seen at 1810hrs. Sketch. Exposed only dorsal fin, surfaced differently from *L. australis*.	M.N. *Isabella*	J. Perkins Goodall & Polkinghorn, 1979

Continued

Table 1 continued

Date	Location	Details	Platform	Reference or observer
24 Apr. 1980	Puente Pedro de Valdivia, Valdivia	1450hrs, two animals swimming under bridge on Río Valdivia	Shore	J. Pinela Oyarzún
15 May 1980	Mehuín near Valdivia	1430hrs. 12-15 individuals in three groups. Surf-riding to the beach; one jumped free of water.	Shore	Carlos Bertran
03 Oct. 1980	San Carlos, Bahía de Corral, Valdivia	1200-1300hrs. 5-6 animals behind or beside boat, only show dorsal fin.	*Caranco*	Wladimir Steffen R.
Nov.-Apr. 1989-1991	Off Queule 38°40'S-39°27'S	Caught from 1-55km from shore. 1/2-18.5km in summer, 18-37km in winter, when sardines & *corvina* move offshore.	-	Reyes & Oporto, 1994 Oporto & Brevia, 1994
XII Región				
19 Feb. 1968	Strait of Magellan South of Punta Arenas	Two animals seen, sketched.	*Navarino*	Sir Peter Scott Goodall & Polkinghorn, 1979
-- Jan. 1986	Seno Lyall, Isla Capitán Aracena, S of St. of Magellan	One with darkly pigmented calf, 10m from kayak. Tranquil dives under kayaks. Seen on way out two days later	Kayak	Adrian Domines
-- Jan. 1986	West side of Canal Pedro, South of St. of Magellan	One animal, black body & fin seen at a distance.	Kayak	Adrian Domines
Oct.-Nov. 1985	Isla Navarino to Cabo de Hornos, 55-56°S	Occasionally harpooned or shot with shotgun for crab bait.	-	Cárdenas *et al.*, 1987
Southwestern South Pacific				
Uruguay				
1972-1984	Off Los Cerros	No sightings published; taken in shark fishery 40km (20nm) east.	Fishing boats	Pilleri & Gihr, 1972
Argentina - Provincia de Buenos Aires				
02 Aug. 1985	South part of Bahía Samborombón, off Canal Gen. Lavalle	One animal 5km from coast, 6m depth. Passed near boat, ignored it. Water 18°C, calm. Killer whales in distance.	*Viene Sur Mar*	Beade *et al.*, 1988 Gloria M. Cabrera, J. Loureiro pers. comm.
1989-1992	Mar del Plata	One animal taken in nets for Antherinids	-	Bastida *et al.*, 1992
Sep.-Jan. 1989-1990	Off Necochea & Claromecó	Captured in shark nets up to 50km from coast in waters of 60m. Not taken inshore.	Fishing boats	Corcuera, 1991

Continued

Table 1 continued

Date	Location	Details	Platform	Reference or observer
Argentina - Provincia del Chubut, Península Valdés				
The following 12 observations are by M. & B. Würsig at Campo 39, Golfo San José, 42°23'S, 64°83'40"W. Most observations were from a zodiac or kayak. Würsig *et al.*, 1977.				
15 Oct. 1974	Whale camp	4-6 animals 1,000m from coast.		
13 May 1975	WNW of camp	5 animals 3,000m from shore.		
06 Nov. 1975	NW Pta Observatorio	Three sightings of 4 animals 300-800m from shore.		
05 Dec. 1975	Playa 39	6 animals 750-1,000m from shore; breathing times taken.		
29 Dec. 1975	-	4-5 animals, 375m from shore; slow movements.		
30 Dec. 1975	-	Group 1,800m from shore.		
15 Jan. 1976	-	6-8, breathing times taken.		
31 Jan. 1976	-	6 animals 1,500m from coast.		
05 Feb. 1976	NW of camp	3 animals 100-1,500m from shore.		
11 Feb. 1976	-	Two sightings of groups of 3-4; the second ignored a Commerson's dolphin nearby.		
17 Feb. 1976	-	Two sightings of 3 & 2-3 animals 800-2,500m from shore.		
19 Feb. 1976	-	Group 100-1,500m from shore.		
The following continue the observations at Whale Camp & are within 2miles of the station. All but one sighting were made with a spotting scope from the observation platform 1/2km south of the camp.				
03 Oct. 1983	Cliff hut	1200-1340hrs. 5 porpoises 200m from shore.		G. & P. Harris
11 Oct. 1983	Cliff hut	0745-0900hrs. Flat calm. 6-7 animals 200m from shore.		G. & P. Harris
19 Sep. 1984	Whale camp	0940-1110hrs. 5-6 animals 1.8km from shore; water calm to ripples.		G. & P. Harris
-- Dec. 1984	Golfo San José	Seen on several occasions.		Peter O. Thomas
10 Mar. 1985	20m-1km offshore	08-10hrs, flat calm. 5-6 animals 20m-1km offshore, depth 5m. With them in two kayaks for 2 hrs. Colour brownish.		G. & P. Harris Gustavo Ramirez
18 Nov. 1985	Cliff hut	Calm & sunny, 10 individuals near shore.		G. & P. Harris
27 Nov. 1985	Whale camp	0930hrs. 2 in 5-10m depth. 200m offshore; breathe 7-8 times, disappear 1-2min. Pale brown.		G. & P. Harris
02 Oct. 1987	Whale camp	1700-1900hrs. 3 animals 50-100m off, 5-10m depth. Dark brown. South right whales nearby; no interactions.		G. & P. Harris

Continued

Table 1 continued

Date	Location	Details	Platform	Reference or observer
B. and M. Würsig returned 15-21 November 1990 and found Burmeister's porpoises more common at Golfo San José, while there were fewer dusky and bottlenose dolphins.				
15 Nov. 1990	50-200m of shore	Groups of 1, 2 & 3, 2-6m depths, surfacing on waves, wind W 60-75km/hr.		
18 Nov. 1990	Same	2 pairs & 2 singles, same depths, calm to35km/hr winds.		
19 Nov. 1990	Boat	1 animal 4km from shore, 50-60m depth.		
20 Nov. 1990	Boat	Groups of 1,2,2. Surface temp. 14°C, 16km/hr N wind, depth less than 5m, 200-300m from shore.		
Tierra del Fuego				
03 Dec. 1975	Bahía Lapataia, Canal Beagle	Large animal incidentally caught in *centolla* net, thrown overboard.	*Siempre Republicana*	Crab fishermen. Goodall & Polkinghorn, 1979
26 Jul. 1978	Bahía Sloggett 55°01'S, 66°22'W	1500hrs, about 30 seen for over two hours by crab fishermen.	*Wapisa*	J. Perez L., Goodall & Polkinghorn, 1979
-- Jul. 1978	Paso MacKinlay, Canal Beagle	Seen twice in the narrows.	*Wapisa*	J. Perez L.,
27 Dec. 1984	Bahía Lapataia	1140hrs. 3-4 in loose school, 100m from ranger's house, milling in circles.	Shore	Peter O. Thomas
-- Jan. 1986	Estancia Túnel, Canal Beagle E. of Ushuaia	One animal near shore inside the kelp, going west.	Shore	A.C.M. Schiavini
14 Apr. 1988	Mouth of Río Pipo Canal Beagle	Calf caught in net, mother at 50m; on release of calf she joined it & they moved off.	Zodiac	Alvar P. Sobral
31 Dec. 1988	Bahía Lapataia, west coast	1500hrs, 2-3 animals in view 20 minutes, near shore, high waves.	Shore	Nestor Sucunza
-- Jan. 1989	Bahía Lapataia	Seen several more days in the same area as on 31 Dec.	Shore	Nestor Sucunza
30 Oct. 1989	Caleta Chica, SW of Bahía Lapataia	3 animals feeding near shore at low tide; respirations audible.	Shore	Jim & Carolyn Gove
19 May 1990	Bahía Ushuaia	1200hrs. Calm. One animal passed 10m of yacht. Brownish with white marks on back. Swam SE while a Peale's dolphin accompanied boat.	*Ayne*	A.C.M. Schiavini
17 Nov. 1990	Paso Chico	2 near islands.	Catamarán *Ana B*	R. Gramuglia
Summer 1990 -1995	Islas Bridges, Isla H, near Baliza Iturrieta	Groups of 2-3 or 4-6, shy of boat but ignore tourists walking on island.	*Tres Marías*	Hector Monsalve

Continued

Table 1 continued

Date	Location	Details	Platform	Reference or observer
17 Mar. 1991	Caleta Chica, SW of Bahía Lapataia	2 animals near shore.	*Yagán II*	Julio Brunett to ACMS
11 Nov. 1991	Near Ea Túnel	4 near shore, 1020hrs.	Catamarán *Ana B*	R. Gramuglia
17 Jan. 1992	Near mouth of Río Olivia	4 animals, 1000hrs.	Catamarán *Ana B*	R. Gramuglia
17 Jan. 1992	Faro Les Eclaireurs	3 animals, 1100hrs.	Catamarán *Ana B*	R. Gramuglia
21 Nov. 1992	Paso Chico	1 animal sighted.	Catamarán *Ana B*	R. Gramuglia
26 Nov. 1992	Between Faro W & Isla Despard NE	2 animals seen.	Zodiac	A.C.M. Schiavini
31 Mar. 1993	Paso Chico	1430hrs 2 animals surfaced closely together. Wind SW 20-25kts, sea rough.	*Tapara* (zodiac)	A.C.M. Schiavini
10 Nov. 1993	Near Ea Túnel	4 animals, 1030hrs.	Catamarán *Ana B*	R. Gramuglia
15 Jan. 1994	Islas Bridges, Isla H Baliza Iturireta	1500hrs, 6 animals, dove, appeared 200m away. Seen earlier the same day by Esteban Curruchet.	Shore	A.C.M. Schiavini
12 Feb. 1994	Faro Les Eclaireurs	1 animal at 1100hrs.	Catamarán *Ana B*	H. Gallardo
20 Mar. 1994	Puerto Túnel	2 animals, dove rapidly. 1515hrs. Wind 3, 6knts; water depth 70m.	Catamarán *Ana B*	Marcela Peréz
13 Apr. 1994	Near Ea Túnel	5 animals, 1515hrs.	Catamarán *Ana B*	H. Gallardo
15 Jun. 1994	Paso MacKinlay, Isla Gable	1 animal, fled. Water 3°C, wind W 1/2 knots; water muddy from rivers, thaw.	L/M *La Pampa*	D. Kuntschik
Oct. 1994-Apr. 1995	Paso Romanche, E of Islas Bridges	Porpoises seen often.	Catamarán *Ezequiel MB*	R. Gramuglia
08 Dec. 1994	Faro Les Eclaireurs	1 animal, 1600hrs.	Catamarán *Ana B*	H. Gallardo
01 Apr. 1995	Paso Chico	1 animal at 1100hrs.	Catamarán *Ana B*	H. Gallardo
10 Apr. 1995	SW mouth of Bahía Lapataia	3 seen, then 2 more in a different group.	Campsite on shore	F. Bugnest
-- May 1995	Near Ea Túnel	6-7 with many seabirds & sardines jumping on water surface.	Catamarán *Ana B*	A.C.M. Schiavini

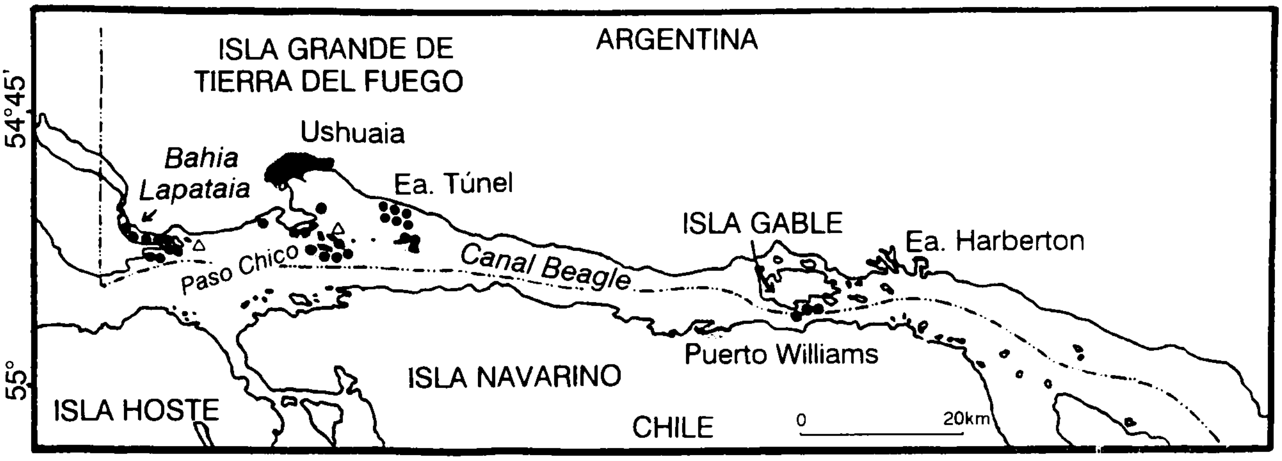

Fig. 2. Map of Canal Beagle, Tierra del Fuego, showing sightings of Burmeister's porpoises (dark circles) and incidental capture in *centolla* nets from 1974–1976 (open triangles).

Southeastern South Pacific

In Peru, although Burmeister's porpoises were reported to be hunted extensively for bait and sale (Brownell and Praderi, 1984), at least all recent specimens have come from incidental entanglement in nets and were not seen alive by the fishermen or scientists (Van Waerebeek and Reyes, 1989; J. Reyes, pers. comm.). The nets are set legally up to 55km from the coast, but some fishermen may go farther. This incidental capture takes place from Paita (0.5°S) to southern Peru. The distance from shore is not noted in the many publications on this fishery (e.g. Reyes and Oporto, 1994; Van Waerebeek and Reyes, 1994).

In 1968, KSN made sightings in the Bay of Paita. He observed two and later three Burmeister's porpoises within 500m of shore, but could not get close to them (Table 1, Fig. 1). During recent Peruvian studies, two porpoises were sighted in January off Salinas and 22 in March off Paracas (Van Waerebeek and Reyes, 1990). There are no other sightings reported for Peru.

In Chilean waters, sightings have been recorded by several authors (e.g. Aguayo, 1975; Donoso-Barros, 1975; Goodall and Polkinghorn, 1979; Guerra *et al.*, 1987; Van Waerebeek and Reyes, 1990), ranging from Africa in the north to the Strait of Magellan in the south. Burmeister's porpoises are taken in gillnets, especially off the Valdivia region (Oporto and Brieva, 1994; Reyes and Oporto, 1994) and were reportedly taken for crab bait near 55°10'S near Cape Horn (Cárdenas *et al.*, 1987). It is not clear if these authors actually observed living animals. We report six new sightings for Chile, four in the Valdivia region collected by R. Schlatter and two south of the Strait of Magellan observed at close range from a kayak.

During the 1968 R/V *Hero* cruise there was only one unconfirmed sighting (by A. Aguayo) at the mouth of Seno Aguila, 52°30'S. No Burmeister's porpoises were seen during expeditions through the Chilean channels from November 1983-February 1984 in the yacht *Tortorore* or from January-March 1988 aboard the *Southern Cross* (Oporto, 1992). Likewise, no porpoises were seen during daily watches held aboard tourist ships traversing the channel region from 1986–1994 (M. Rumboll, pers. comm.; RNP, pers. obs.). Despite difficulties in observing porpoises from a large ship, they should have been visible in the often calm channel waters.

Southwestern South Atlantic

Burmeister's porpoises have stranded as far north as Santa Catarina State, Brazil at 28°48'S (Simöes-Lopes and Ximenez, 1988). Low numbers are taken in shark nets set about 40km off the coast of Uruguay (Pilleri and Gihr, 1972; Brownell and Praderi, 1982; 1984). Animals were taken in nets off Mar del Plata and Necochea up to 50km from the coast of Argentina (Corcuera, 1991; 1994; Bastida *et al.*, 1992; Corcuera *et al.*, 1995).

The northernmost sighting in the South Atlantic was off the southeast coast of Bahía Samborombón, Argentina (36°25′S), where a young animal was also stranded (Beade *et al.*, 1988). We consider as doubtful a sighting of over 50 animals 10–15km off Miramar (about 38°30′S), thought by A. Messidoro to be this species.

Golfo San José

BMW made 16 sightings of Burmeister's porpoises during their bottlenose dolphin study from 1974–1976 and one porpoise stranded during that time (Würsig *et al.*, 1977). At least ten sightings were made there between 1981 and 1988 (GH). In November 1990, BMW made 11 sightings in seven days.

Tierra del Fuego

Specimens of Burmeister's porpoise were taken incidentally in nets set in Canal Beagle for *centolla* from 1974–1976 and for fish along the northeast coast of Tierra del Fuego (Goodall, 1978; 1989; Goodall *et al.*, 1995). Two sightings were recorded (Goodall and Polkinghorn, 1979). Since then, over 30 sighting events have been reported, as a result of work on bird surveys and the training of boat captains. A sighting of over 30 animals off southeast Tierra del Fuego (about 55°S), made by J. Pérez, is included but with reservations, although the observer drew a sketch of a backward-inclined dorsal fin with bumps along the upper surface.

The number of sightings is fairly small in comparison to effort. Most of the sightings came from the catamarans which take passengers to see the wildlife on the islands off Ushuaia. An additional captain who takes small groups of tourists to the Islas Bridges, says he has seen these porpoises 'often', but did not take notes (H. Monsalve, pers. comm).

HABITAT

Burmeister's porpoise has been assumed to be a coastal species which prefers shallow waters, and indeed most of the sightings have been near shore. In central and northern Chile the porpoises were found in bays, near shore, in river mouths and up to 18km upstream. KSN (pers. obs.) found them in less than 10m of 18°C water near shore.

The northernmost sighting in South America was about 5km from shore but in water only 6m deep. However, incidental captures in nets set for fish occurred farther from shore in all areas: up to 40km from shore in Uruguay, 50km in northern Argentina and 55km in Peru and Chile. The only water depth recorded was about 60m, off Argentina. The most common inshore species in this area was the franciscana (*P. blainvillei*) with the Burmeister's porpoise being found just offshore (Corcuera, 1991; Corcuera and Monzón, 1992), while off Peru the Burmeister's porpoises seemed to use the waters inshore of the dusky dolphins. These habitat preferences are similar to those of the harbour porpoise, *P. phocoena*, which occurs shoreward of the 100 fathom curve, and seems to prefer protected inland waters (see review in Szczepaniak and Webber, 1985).

In Golfo San José Burmeister's porpoises were usually observed in waters of 5–25m depth and 300–1,000m offshore in spring and summer when surface waters were no colder than 12.5°C. They were most common in summer temperatures of 17.5°C to 19.5°C (the highest temperatures recorded in the study area; see Würsig and Würsig, 1980). The temperature during the November 1990 sightings averaged 14°C.

In Tierra del Fuego, one sighting was in open waters near shore, but the others were close to shore in the bays of Canal Beagle or narrow fjords, sometimes within the kelp. The porpoises were often seen along the sides of open channels (Paso Chico, Paso Romanche) or to the east (lee) side of islands in Canal Beagle. The lowest water temperate recorded during a sighting was 3°C in June; the average summer temperature is about 9°C.

ABUNDANCE

There are no estimates of abundance of this species anywhere in its range. Although large numbers may be taken (e.g. off Peru and Chile) in all areas Burmeister's porpoises are sighted less often than other species. Even at Golfo San José, where the station has been manned almost continuously year-round since 1972, sightings of this species are exceptional and not the norm (Würsig *et al.*, 1977; P.O. Thomas, pers. comm.; GH, pers. obs.). This may be due, in part, to the difficulties in sighting small, unobtrusive animals (see below) in an area famed for its high winds and rough seas.

SEASONALITY

Little is known about seasonal movements in this species. Off Valdivia, Chile, there is a seasonal movement in captures. Fishermen set their nets from 0.5 to 18.5km from shore in summer and move them farther off, from 18–37km offshore in winter because the target fish, *corvina*, are no longer in the coastal waters. Perhaps both the *corvina* and the porpoises follow a winter offshore movement of sardines (Oporto and Brieva, 1994).

Almost all sightings at Golfo San José were in spring and summer, indicating a possible seasonal pattern in these temperate nearshore waters (Würsig *et al.*, 1977; GH pers. obs.). Because diligent observations from shore on the rare calm days almost always discovered small groups of these porpoises, BMW gained the unquantified impression that about 3–6 animals were present within 1,000m of shore throughout spring and summer. This seasonal occurrence pattern suggested that these porpoises may prefer warmer temperatures (see 'Habitat' above). Temperature may have a direct or indirect effect on occurrence; for example by influencing distribution patterns of prey. Fig. 3a shows the seasonal occurrence of porpoises during long-term studies at Golfo San José.

Farther south, Commerson's dolphins (*C. commersonii*) are seldom seen in coastal waters in winter (Goodall *et al.*, 1988a). They probably follow local migrations of fish, such as sardines, *Sprattus fuegensis*, and *róbalo*, *Eleginops maclovinus*, which are inshore from October-November to March-April (Bastida *et al.*, 1988). This dolphin has been sighted about 7km offshore in winter off Tierra del Fuego (J.M. Fraguiero Frias, pers. comm.) and Chubut (M. Iñiguez, pers. comm.).

Nevertheless, sightings of Burmeister's porpoises in Canal Beagle have been made in every month except August and September. This may merely reflect less sightings effort during August and September when there are fewer tourists. These animals probably represent a resident group or groups (Ushuaia, Lapataia) which probably remain there year-round, as does *P. phocoena* in certain parts of its range (Szczepaniak and Webber, 1985).

BEHAVIOUR

Field characteristics

The Burmeister's porpoise seems to be an unobtrusive, almost furtive animal in the wild, exposing little of its body in swimming. The pigmentation of recently dead animals has

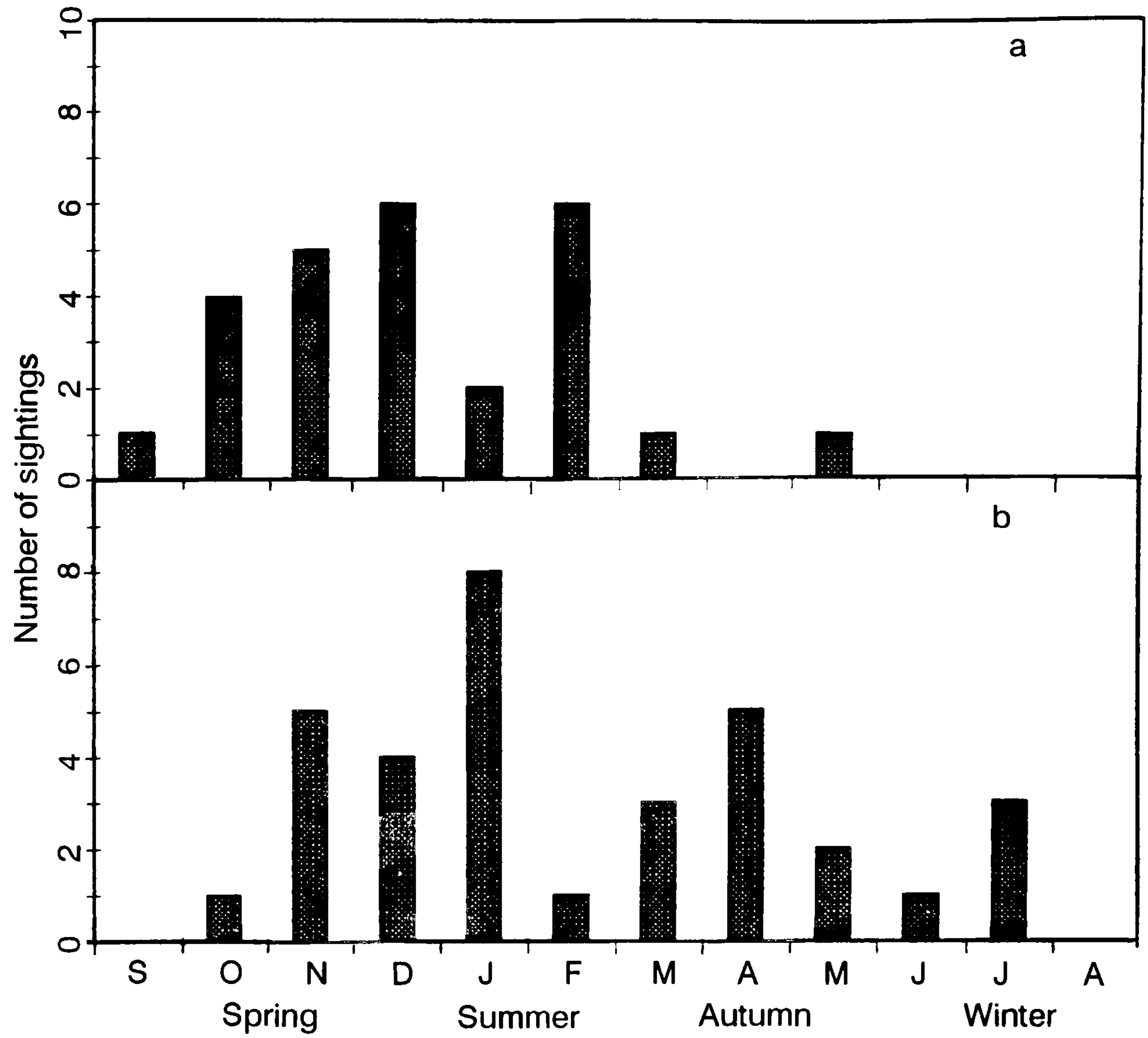

Fig. 3a. Number of sighting events of Burmeister's porpoises by month and season in Golfo San José, Provincia del Chubut, Argentina. 3b. Number of sighting events by month and season off Tierra del Fuego, Argentina.

been described by Reyes and Van Waerebeek (1995). Once dead, the skin darkens quickly, so that earlier descriptions were not reliable (Goodall *et al.*, 1995). At sea, the animals may appear a light to medium brown, dark brown, gray, or grayish black depending on the reflection of the water itself, which might be dark in the southern channels or clear blue in the northern parts of the range (Goodall *et al.*, 1988b). The dark eye patch was noted in only one sighting. In the water, the lighter streaks are not noticeable and the animal may appear uniformly dark or brown; especially since so little of it is visible. GH, in watching animals at close range in a kayak, could not see the eye patch or flipper stripe. One animal sighted in Canal Beagle had white spots or streaks of unknown cause on the dorsal surface.

The best field mark is the unusual dorsal fin. As P.O. Thomas (pers. comm.) described his sighting at Lapataia: 'The most notable [characteristic] is the far back dorsal fin that rises very gradually and in an elongated form from the line of the back. The tip of the dorsal is finely pointed and seems to point upward....'. The 'retroussé' shape of the dorsal fin and the row of tubercles along its forward edge, from the front of the insertion to the tip, are diagnostic and can be seen in the field on close approach (Aguayo, 1975).

Swimming and respiration patterns

At Golfo San José, Burmeister's porpoises could usually only be seen on calm days. They would typically surface in an unhurried smooth motion at a shallow angle, producing a slight forward bobbing motion of the head and then slide beneath the surface again. Their swimming is described as a slow roll, exposing the blowhole and then the dorsal fin, barely disturbing the surface of the water. The dorsal fin appears as the head begins its downward journey. KSN wrote of the animals off Paita as having a quick movement 'with much flexing of tail stock. Only once did I observe a blow.' The animals at Golfo San José characteristically leaned to the left, with the dorsal fin 20–30° to the left during emersions (Würsig *et al.*, 1977).

The surfacing pattern was similar in all sightings. All the animals in a group would surface 7–8 times in a small area and then would disappear for one to three minutes, to reappear 50+ft (17+m) away. Breathing frequency of a stranded calf (obviously under stress) in an aquarium pool was seven breaths per minute (Loureiro, 1986).

The porpoises are difficult to follow as their course under water is often irregular. Measurements with a theodolite on one occasion gave an underwater swimming speed of 4kmhr^{-1}, surprising as the animals appeared to surface only slowly.

Two animals were sighted in the Río Valdivia 18km from the river mouth. They swam perpendicular to the shore, crossing the river opposite each other, showing their dorsal fin and sometimes the flukes on surfacing.

Near Mehuín, 12–15 animals in three groups surfed on waves breaking on the shore, retreating with the waves and following them in again. One animal jumped out of the water, entering head first. BMW also saw porpoises at Golfo San José surfing on waves and observed one leap. No porpoising or acrobatic displays were seen by GH in his years at Golfo San José.

Sounds

No underwater sounds have been recorded for this species. Both BMW and Thomas used the porpoises' 'puff-puff' noise on blowing to locate animals in calm weather, and these respiration sounds have been recorded. Although not loud, exhalation and inhalation are of about the same volume, tonal quality and time length, giving a short 'puff-puff'. The animals could always be heard in calm weather, but could not be located when there were rough seas.

School size

The maximum group size observed in the Golfo San José was eight animals. In Canal Beagle, the maximum confirmed school size was seven, but a possible group of 30 was reported just offshore to the east (see above). Off Mehuín, three groups of 12–15 have been observed (C. Bertran, pers. comm.). A 'loose' group of 22 was seen off Paracas, Peru (Van Waerebeek and Reyes, 1990) and 70 animals were reported in northern Chile (Guerra *et al.*, 1987). In most sightings, group size was from 1–6, the most common being two (Fig. 4). It may be that this porpoise, like *C. commersonii*, forms larger groups at certain times of the year (Goodall *et al.*, 1988a).

Interactions with boats

The little information available is summarised below. Off the Bahía Corral, a group of 5–6 porpoises moved along with the boat without approaching it and the observers were unable to get close. The mother and calf pair seen by A. Domines near the Strait of Magellan dived tranquilly under the kayaks. In the Golfo San José, porpoises would often

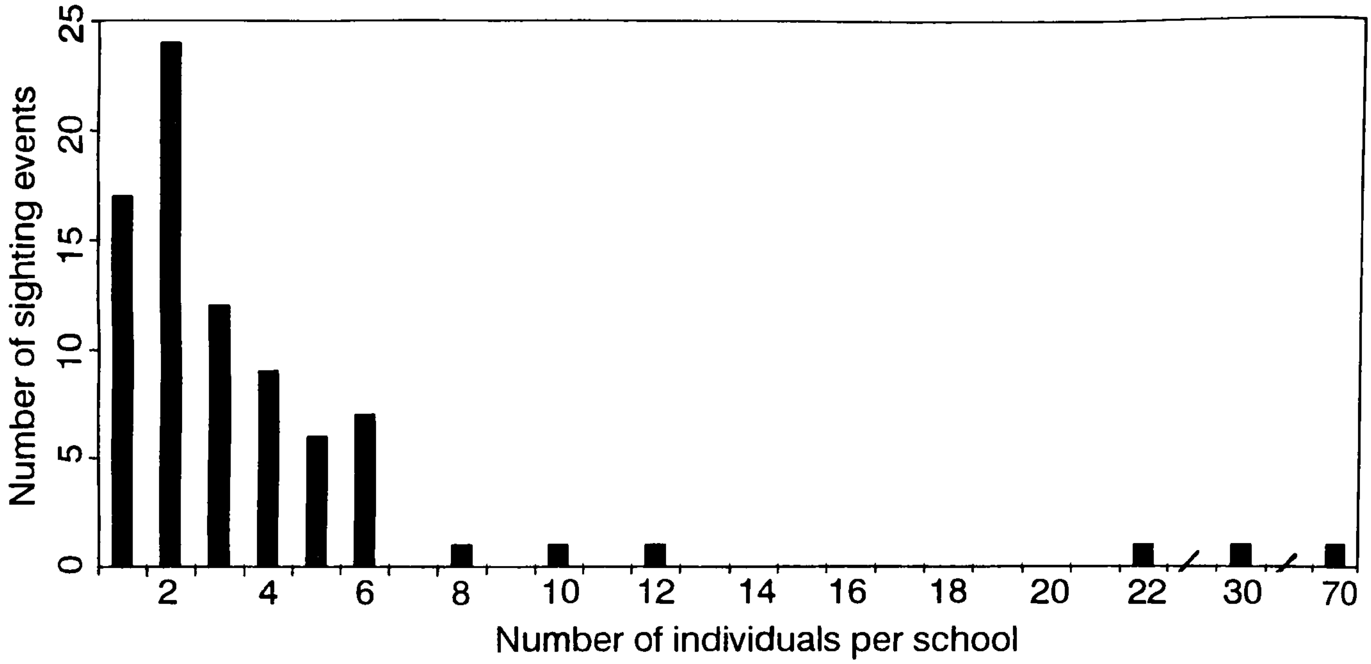

Fig. 4. Number of individuals seen in sightings of Burmeister's porpoises, pooled for all areas and using lowest estimates.

dive under the boat and come up behind it while it was moving, in an apparent (but tranquil) attempt to evade the vessel. When the vessel was stopped, the animals often milled, coming up in different areas and directions on each surfacing. GH was able to get close enough in a kayak to see the ring around the eye and the porpoises occasionally surfaced within two meters of the kayaks but paid no attention to them. In this case the observers stayed with the group for two hours, with no apparent reaction from the animals.

Interactions with humans

The only information was supplied by Enrique Berron of the ship *San Mateo* of Iquique, Chile, who told KSN that the porpoises swim with bathers at Playa Cavancha and are tame. However, this sounds more like *Tursiops* (bottlenose dolphin) behaviour and may be a result of misidentification.

Reproduction

Reproduction in this species has been reviewed by Reyes and Van Waerebeek (1995) and Goodall *et al.* (1995). Mating behaviour has not been described, but Van Waerebeek may have observed a mating group (Van Waerebeek and Reyes, 1990). Porpoises with small calves were seen in late January in a fiord south of the Strait of Magellan and in the Canal Beagle in mid-April. The latter calf was about 80cm long with no visible scars or fetal folds and was probably less than a month old. These two calves were evidently born in summer and fall in Tierra del Fuego. Birth size in this species is thought to be about 86cm.

Parent-calf interactions

A calf of *ca* 80cm caught in a net set by ichthyologists near the Río Pipo in Tierra del Fuego was released alive. As the boat approached the net with the entangled but still floating infant, the mother moved off slowly, keeping 20–50m away and submerging only briefly. When the calf, which had no wounds but was visibly tired, was released, it remained beside the boat until the mother approached from below and the pair went off some 100–150m without submerging and then were lost to sight. The observers thought that the mother may have been entangled but escaped as the 8cm mesh net had been pulled out of the position in which it had been left (A.P. Sobral, pers. comm.)

Epimeletic behaviour

As far as we know, no observations have been reported or published.

Interaction with other species

Burmeister's porpoises were caught in nets with franciscanas off Uruguay (Pilleri and Gihr, 1972) and with dusky dolphins off Peru (Van Waerebeek and Reyes, 1988). Off Salinas, Peru, two porpoises were seen near southern sea lions (Van Waerebeek and Reyes, 1990). In the sighting off Bahía Samborombón, killer whales were seen in the distance, but appeared to produced no reaction in the porpoise (G.M. Cabrera, pers. comm.). In Canal Beagle, one Peale's dolphin accompanied the boat but was 'ignored' by the Burmeister's porpoises in the area.

In the Golfo San José, a group of 3–4 porpoises passed near a solitary Commerson's dolphin without any reaction from either species (Würsig *et al.*, 1977). In the same area, GH observed three porpoises near southern right whales, also with no reactions from either group.

The porpoises in Golfo San José were not seen to associate with the more numerous dusky and bottlenose dolphins; the peak of Burmeister's porpoise occurrence in December-February of 1975–76 coincided with a low period of bottlenose dolphin occurrence in the waters within 1,000m of shore (Würsig *et al.*, 1977; Würsig and Würsig, 1979; 1980). Furthermore, Burmeister's porpoises frequented waters 300–1, 000m from shore, over depths of 5–15m. This preferred habitat overlapped only partially with the nearshore movements of local bottlenose dolphins (generally less than 10m depth; Würsig, 1978; Würsig and Würsig, 1979) and the further offshore movements of foraging dusky dolphins (at mean depths of 34–46m during spring-summer feeding; see fig. 10 of Würsig and Würsig, 1980). There thus appears to be some spatial habitat separation between the three species. This niche separation may be similar to one described for the intermediate-water vaquita *(Phocoena sinus)*, the more nearshore bottlenose and more offshore common dolphins *(Delphinus delphis)* in the northern Gulf of California, Mexico (Silber, 1990).

Feeding

There has been no confirmed published observation of feeding behaviour in the wild. A loosely associated group of about 22 animals was thought to be feeding (Van Waerebeek and Reyes, 1990). Other animals seen milling or moving back and forth across a small area have been assumed to be feeding. However, A.C.M. Schiavini (pers. comm.) reported that six or seven porpoises joined many sea birds in feeding on jumping sardines in Canal Beagle.

In the aquarium, the 126cm stranded calf (see above) was tube fed a formula of fish, cream and vitamins, from 720–1,500g per day. It lived nine days, dying of bronchial pneumonia (Loureiro, 1986).

Changes in distribution patterns

When BMW returned to the same site in Golfo San José in November 1990, 14 years after their original studies, they found from personal observation and discussion with local naturalists, that bottlenose dolphins rarely visited the southeastern shore any more

(Würsig and Harris, 1990; Würsig, 1992a) and that in recent years, dusky dolphins had also become scarce (Würsig, 1992b). The marine bird life which had been closely associated with dusky dolphin feeding activity in the 1970s had also dwindled to less than 20% of the 1970s activity by spring 1990. No explanation for this apparent drastic ecological change has been found.

However, during the seven days of observations in November 1990, Burmeister's porpoises were observed 11 times compared to only 16 sightings in the earlier 21 month period (Table 1). On 15 November they were within 50–200m of shore (2–6m depths), often surfing on large whitecapped waves induced by a 60–75km/hr westerly wind. Never before had BMW seen these porpoises so active and observable in windy conditions. They were seen in similar conditions three days later and on 19 November, by boat, 4km from shore in waters 50–60m deep. On 20 November they were back inshore in shallow waters.

Although this brief census effort does not allow for far-reaching conclusions about seasonal use or habitat shift of Burmeister's porpoises, it suggests a number of possibilities. First, use of the southeast portion of Golfo San José by Burmeister's porpoises had increased. Second, they now utilised a more wide-ranging habitat, from very shallow to relatively deep water, than in the more comprehensive earlier study. Third, the apparent increase in numbers and habitat range coincided with a paucity of both bottlenose and dusky dolphins in the area. This in turn raises the possibility of competitive exclusion of Burmeister's porpoises by the larger groups of dusky and bottlenose dolphins (as possibly for the vaquita; Silber, 1990). However, it is just as likely that the possibly complicated changes in ecological conditions which affected occurrence patterns of the two dolphin species allowed more porpoises to utilise the nearshore area. A thorough study of this phenomenon, based at least in part on prey patterns of Burmeister's porpoise in Golfo San José, would help shed light on the ecological (and perhaps behavioural) interactions between dusky dolphins, bottlenose dolphins and Burmeister's porpoises.

A parallel situation may have occurred in Tierra del Fuego. Although parts of a skull and vertebrae of Burmeister's porpoises were found in aboriginal kitchen middens carbon-dated 6,500 and 2,400 years before the present (Piana *et al.*, 1985), there have been no other records of the species in Fuegian waters, even by the earliest European residents, until recently. These porpoises are now seen frequently in the interior waters of Canal Beagle. This may just be an artifact of better observations or may reflect a filling of the inshore niche left by the exploitation for *centolla* bait of Peale's dolphin, which was formerly the most frequent cetacean in the channel, especially on the south (Chilean) side. Peale's dolphins are now only occasionally seen in these inland waters (Goodall, 1978; Goodall and Cameron, 1980; RNP, pers. obs.).

CONCLUSION

The study of this species has only just begun. Now that several localities have been identified as places where the animals can be found, there is a great opportunity for new research on behaviour, sound, abundance, seasonal movements and ecology of the Burmeister's porpoise.

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ADDENDUM

R.N.P. Goodall

As the above work was in press, we received new information and publications on *Phocoena spinipinnis.*

New specimens have appeared. A second animal stranded recently at Río Grande do Sul, Brazil (M.C. Pinedo, pers. comm.). A young 145cm female died in a net set in the Río de la Plata off Uruguay in September 1995 (R. Praderi, pers. comm.). A 170cm, 55kg female stranded south of Playa Bengoa, Golfo San José, Chubut, Argentina on 3 Sep. 1995 (S. Pedraza, pers. comm.). This animal had recently given birth as evidenced by the enlarged uterus and abundant milk. This birth was in early spring in northern Patagonia. The animal had trematodes in the lungs and diseased spots in the skin and blubber.

Yáñez *et al.* (1994) describe a fossil cranium of this species in the Colección Paleontológica del Museo Regional de Concepción (MRC 26.0287). Of unknown precedence, the cranium is incomplete but easily identified as *P. spinipinnis.* Although three species of foramifera were found in the sediments inside the cranium, the exact age of the skull was not determined. The only other Phocoenid fossil known for the Pacific coast of South America is the extinct *Piscolithax longirostris* from Peru.

The full text of the paper by Pinedo (1989) was not available to me earlier. It describes a 139cm male (MORG 1015) stranded on 12 Dec. 1986. The vertebral formula was C7, Th14, L15, Ca31 = 67, with 17 chevron bones. The first three cervical vertebra were fused. The skull and complete skeleton, including hyoids and pelvic bones, is illustrated and measurements given for most elements. The stomachs contained remains of Pelecypoda, *Mactra* sp., fish bones and 29 otoliths of *Cynoscion striatus* (Sciaenidae). The latter is a principal food of franciscana (*Pontoporia blainvillei*).

The gastrointestinal parasites of *P. spinipinnis* are described by Torres *et al.* (1992). The Helminths *Pseudoterranova* sp., *Polymorphus cetaceum, Synthesium tursionis* and *Anisakis simplex* were found in 83% of 18 porpoises taken in gillnets off Queule, Chile from 1989–1990. The prey (99.2% fish of 8+ species, 0.8% *Loligo gahi*) include species which are hosts of larvae of *Anisakis* and *Pseudoterranova.*

Torres *et al.* (1994) report the occurrence of the nematode *Sterurus australis* in 33 Burmeister's porpoises taken off Queule in 1990–1991. The mean length for seven mature females was 170 ± 8.5cm, the weight 78 ± 17.3kg. The mean for 15 mature males was 174 ± 5.2cm and weight 80.4 ± 10.4kg. All mature animals were infected, as were 80% of the immature females and 66% of the immature males. All those infected had parasites in the auditive ducts and pterygoid sinuses; only three had them in the nasal sinuses. The life cycle of *Sterurus* spp. are unknown. *S. australis* has been recorded previously only from Peru.

I appreciate the information on new specimens given by M.C. Pinedo, R. Praderi and S. Pedraza, and thank J.A. Oporto for sending the publications.

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Notes on the Biology of the Burmeister's Porpoise, *Phocoena spinipinnis*, off Southern South America

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ABSTRACT

Published and new fresh and museum specimens of Burmeister's porpoise, *Phocoena spinipinnis*, collected prior to the recent research in Peru, Chile and Argentina, are listed and described. Distribution is from southern Brazil (28°48′S) to the southern tip of the continent near Cape Horn (56°S) and to Paita, Peru (05°S). Most specimens are from captures, with few known strandings. Lengths of nine unpublished females ranged from 134–185cm, with sexual maturity reached by 164.5cm. An animal of 164.5cm was also physically mature, but one female of 185cm was not. Teeth of this largest female had four GLGs. Total length in nine males ranged from ±80cm to 175cm; none were physically mature. Foetuses of 37, 81 and 86cm were recorded; the smallest neonate was 80+cm. Young calves were found in January and April in Tierra del Fuego, a near-term foetus in November in Chile. An animal of 126cm had partially erupted teeth and one of 131cm may still have been suckling. One female was simultaneously pregnant and lactating. A 181cm female had given birth in July. Animals have dark eye patches, dark lips with occasional whitish margins, a white or light stripe from eye to above flipper, a darker wide stripe from lower lip to flipper, a white chin and distinctive curves and stripes on the lighter ventral region. Stomach contents included anchovies and other fish. Parasites were present in some animals. An analysis of milk colostrum is given for a recently calved female, which had the maximum weight of any animal, 67kg. Incidental capture in nets set for fish occurs throughout the range; direct exploitation (harpooning) for bait may take place in southern Chile. Only one young calf has been kept in captivity (eight days). Nothing is known of the abundance, seasonal movements and stocks of this animal.

KEYWORDS: BURMEISTER'S PORPOISE; SOUTH PACIFIC; SOUTH ATLANTIC; REPRODUCTION; DISTRIBUTION; ANATOMY/MORPHOLOGY; AGEING; INCIDENTAL CAPTURE; STRANDINGS; FEEDING; PARASITES; REVIEW; EXPLOITATION

INTRODUCTION

For many years it was thought that there were two populations of the Burmeister's porpoise (*Phocoena spinipinnis*) in temperate waters of South America: an eastern population off Uruguay and north-central Argentina in the southwestern South Atlantic;

and a western population off Peru and north-central Chile in the southeastern South Pacific (Brownell and Praderi, 1984). However, the species was then found in sub-Antarctic waters of the Canal Beagle of Tierra del Fuego, at nearly 55°S at the tip of the continent (Goodall, 1977; 1978). The species is heavily exploited throughout much of its range, but little has been published on its basic biology. Recent studies in Peru, Chile and central Argentina have produced considerable new information on the species (see below).

The present paper does not attempt to review these recent papers, but rather presents unpublished information obtained from specimens collected prior to the Peruvian research, particularly in the southern part of the range (Table 1), and details specimens found in museum collections. It updates Goodall *et al.* (1989; 1990b).

MUSEUM OR COLLECTOR CODES USED

BMNH, British Museum of Natural History, London; CAS, California Academy of Sciences, San Francisco; CNP, Centro Nacional Patagónico, Puerto Madryn, Chubut, Argentina; IZUA, Instituto de Zoología, Universidad Austral, Valdivia, Chile; JFM, Jorge F. Mermoz, Buenos Aires; KSN, Kenneth S. Norris; MACN, Museo Argentino de Ciencias Naturales B. Rivadavia, Buenos Aires; MCNO, Museo de Ciencias Naturales y Oceanográficas, Puerto Madryn, Chubut, Argentina; MCZ, Museum of Comparative Zoology, Harvard; MHN-V, Museo de Historia Natural, Valparaíso, Chile; MNHN-M, Museo Nacional de Historia Natural, Montevideo, Uruguay; MNHN-S, Museo Nacional de Historia Natural, Santiago, Chile; MVZ, Museum of Vertebrate Zoology, Berkeley; RLB, Robert L. Brownell, Jr.; RNP, collection of R.N.P. Goodall, Ushuaia, Tierra del Fuego; RP, Ricardo Praderi, Uruguay; UA, Instituto de Investigaciones Oceanológicas, Universidad de Antofagasta, Antofagasta, Chile; UCMZ, Universidad de Concepción, Museo Zoológico, Concepción, Chile; USNM, United States National Museum, Washington D.C.

METHODS AND MATERIALS

Data on specimens were obtained through a literature review, a series of beach surveys for stranded animals, salvage of incidental captures, visits to museums, interviews with colleagues and personal observations in the area.

Norris (KSN) carried out coastal expeditions in Peru and Chile (Norris, 1968), during which time, he examined specimens in many museums, obtained or captured (when this was still possible) seven fresh animals and picked up several beach-cast skulls. Data on these specimens are published here for the first time. The skeletal material from this expedition is stored in USNM.

The Goodall (RNP) team carried out regular beach surveys for stranded smaller cetaceans in Tierra del Fuego, Argentina, beginning in 1974 (Goodall, 1978; 1989) and found ten cranial and four post cranial specimens of *P. spinipinnis*. Goodall and I.S. Cameron (ISC) also studied specimens of this species in Chilean and Argentine museums in 1978, 1980 and 1986.

Harris (GH) was part of a cetacean observation team at Golfo San José, Península Valdés, Argentina from 1981 to 1988 and continues to work in the area. He provides information on specimens from Chubut including those deposited in MCNO and CNP.

Oporto (JAO) salvaged specimens taken by fishermen off Valdivia, Chile. Six specimens collected between 1976 and 1979 are listed here; they are deposited at IZUA. Burmeister's porpoises studied after that date are reported in Brieva and Oporto (1990).

(*Text continued on page 326*)

Table 1

Specimens and other records of the Burmeister's porpoise, *Phocoena spinipinnis*. Dates marked with an asterisk are date of death; those unmarked are date of collection. 'Skull' means both cranium and mandibles (as opposed to 'cranium' only). For museum codes, see Methods.

Stranding* or collection date	Locality	Details	Where deposited	Reference or source
SOUTHWESTERN SOUTH ATLANTIC				
Brazil				
Santa Catarina				
12 Oct. 1986*	2km S of Río Urucanga 28°48'S, 49°12'W	One 180cm animal found dead on beach. Perhaps attacked by sharks. Stomachs empty; CBL 288mm.	UFSC 1025	Simões-Lopes & Ximenez 1988, 1989
Rio Grande do Sul				
12 Dec. 1986	Lago Patos 32°40'S	One specimen found, stomach contents.	MORG	Pinedo, 1989
Uruguay				
Departamento de Rocha				
12 Jan. 1968	Cabo Polonio 34°24'S, 53°47'W	Incomplete cranium. Col. A. Ximenez.	MNHM-M 1307	Praderi, 1971 Ximenez *et al.*, 1972
-- Dec. 1970	Los Cerros Punta del Diablo	Adult of unknown sex caught in shark net. Col. Dardo da Costa; skeleton.	Pilleri T 474	Pilleri & Gihr, 1972
-- Oct. 1972	Los Cerros	Skull, collected by Dardo da Costa and O. Romang.	Pilleri T 532	Pilleri & Gihr, 1974
24 Feb. 1973*	Punta del Diablo 35°22'S, 53°46'W 4kms offshore	44cm male foetus, fluid preserved. (RLB 901)	USMN 501,068	USMN Database Brownell & Praderi 1976; 1982; 1984
		183cm female (with foetus) above). Captured by fishermen.	MNHN-M	
24 Feb. 1973*	Punta del Diablo	180cm sexually mature male. AO 1974-23.	-	Brownell & Praderi 1976; 1984
24 Feb. 1973*	Punta del Diablo	±179cm male; stomach contents col. Measurements published.	RP 301	Brownell & Praderi 1976; 1984
24 Feb.1973*	Punta del Diablo	±180cm.	-	Brownell & Praderi 1976
-- -- --	Punta del Diablo	'We examined several adults ... that ranged from 180-200cm.'	-	Brownell & Praderi, 1982; 1984
-- -- --	Punta del Diablo	Animal of 190cm.	-	R.L. Brownell *in* Mitchell, 1975

Stranding* or collection date	Locality	Details	Where deposited	Reference or source
Argentina				
Provincia de Buenos Aires				
-- -- 1862	Mouth of Río de la Plata	Mounted 162cm skin, male (168cm over curve). Cranium and mandible lost? Type Specimen.	MACN 27-2 (skin)	Burmeister, 1865 Praderi, 1971
-- -- --	Unknown	Small skull.	MLP 1481	This paper
05 Apr. 1984*	Río San Clemente Bahía Sanborombón	126cm, 22kg male stranded, would not eat, died 13 April.	Mundo Marino Aquarium	Beade *et al.*, 1988 Loureiro, 1986
-- -- --	Claromecó	Partial skeleton.	AAL	A.A. Lichter, pers. comm.
Provincia del Chubut				
18 Jun. 1903	'Patagonian coast'	Cranium only. Collected by S. Boudinoy.	MACN 3-32	Praderi, 1971
Early Sep. 1974*	Fondeadero Pueyrredón Golfo San José 42°25'S, 64°05'W	167cm stranded, sex ? Measurements published. Estimate 70-75kg.	JFM	Würsig *et al.*, 1977
Before 1975	Golfo San José, Whale Camp	One cranium CBL 318mm and parts of others, collected by M. Würsig.	CNP	G. Harris
27 Jun. 1986*	Golfo San José, near Whale Camp	181cm female, teeth worn, old animal; recently gave birth.	MCNO GH 860627	G. Harris
-- -- --	Puerto Rawson	No data, collected by A. Purgue.	MCNO	E. Crespo, pers. comm.
-- Feb. 1990	Punta Quiroga	Nearly complete specimen, skeletal length 167.7. CBL 284mm. Collected by E. Crespo.	CNP	S. Pedraza, pers. comm.
Tierra del Fuego				
-- -- --	Ushuaia	Skull and mandibles.	MACN	H.P. Castello pers. comm.
13 Jan. 1974*	Canal Beagle near Ushuaia	Taken in *centolla* net. Head preserved in fluid. Collected by Pedro Medina. Fish in throat.	MACN	Castello, 1974; Würsig *et al.*, 1977
02 Dec. 1975*	Canal Beagle, Isla Redonda	134cm female, 38.5kg without viscera. Caught in crab net. Complete skeleton.	RNP 110	Goodall, 1978
04 Dec. 1975*	Canal Beagle Isla Redonda	151cm male, 585kg Caught in crab net. Complete skeleton.	RNP 111	Goodall, 1978
24 Dec. 1975*	Canal Beagle,	185cm female, complete.	RNP 167	Goodall, 1978

Stranding* or collection date	Locality	Details	Where deposited	Reference or source
27 Dec. 1975	W. of Punta Segunda	Skeleton. Subadult.		
28 Jan. 1976	Bahía San Sebastián 7-8km	Incomplete cranium.	RNP 219	Goodall, 1978
21 Nov. 1976	Bahía San Sebastián 9km	Partial postcranial skeleton.	RNP 375	Goodall, 1978
03 Mar. 1977	Punta María 2km N	Cranium, young animal. Probably caught in robalo nets.	RNP 451	Goodall, 1978
01 Jun. 1977	Río Cullen N	Vertebrae.	RNP 551	Goodall, 1978
08 Dec. 1980	Estancia Las Violetas N	Partial cranium, very young animal.	RNP 859	This paper.
07 Feb. 1984	Península Mitre, Caleta Falsa	Vertebrae, physically mature.	RNP 1127	This paper.
05 May 1984	Península Páramo Ocean side near base	Nearly complete skeleton. Subadult.	RNP 1144	This paper.
21 Feb. 1986	Estancia Fueguina	Complete skeleton, physically mature; deformed jaw.	RNP 1207	This paper.
24 Mar. 1988	Estancia Las Violetas 8km N	±170cm. Complete skeleton, physically mature; deformed snout.	RNP 1354	This paper.
10 Dec. 1990	Río Ladrillero N	±120cm, nearly complete animal, young.	RNP 1540	This paper.
SOUTHEASTERN SOUTH PACIFIC				
Peru				
This list does not include the numerous specimens collected from 1983 to present from incidental captures, examination of animals in ports, strandings and specimens in village dumps, summarised by Reyes and Van Waerebeek 1990 and 1995 (this volume).				
Piura				
-- -- 1872	Bahía de Paita 05°S	±160cm female, second one known. Collected by Louis Agassiz, Hassler Expedition.	MCZ 1158	Allen, 1925: 251 Praderi, 1971
-- -- --	Paita	Cranium buried in sand. CBL 264mm. KSN 68-40SA. Another 267mm cranium, KSN 68-40SA.	Instituto del Mar, Paita	This paper. Reyes and Van Waerebeek, 1995
Ancash				
12 Jun. 1960	Chimbote 09°04'S, 78°34'W	Examined in fish market, Where sold. Collected?		Clarke, 1962 Praderi, 1971
05 Sep. 1968*	Chimbote	153cm female on boat dock; head, appendages, fluid specimens preserved.	- KSN 68-38 SA	This paper.

Stranding* or collection date	Locality	Details	Where deposited	Reference or source
Summer 1983	Mejillones, 23°06'S	37cm male foetus, preserved in formalin.	UA-AMM 13	Guerra *et al.*, 1987
-- Jan. 1985	Michilla, 22°44'S	Cranium.	UA-AMM9	Guerra *et al.*, 1987
		Cranium.	UA-AMM10	
		Skull.	UA-AMM11	
		Skull.	UA-AMM12	
28 Jun. 1986	Chipana, 21°24'S	Skull.	UA-AMM20	Guerra *et al.* 1987
		Skull.	UA-AMM21	
-- Aug. 1986*	Caleta Coloso, 23°43'S	Live stranding, collected cranium. Hurt by collision with vessel?	UA-AMM22	Guerra *et al.*, 1987
V Región				
-- -- --	Valparaíso	140cm animal; description of external characters; type of *Phocaena Philippi* Pérez Canto.	MHN-V	Phillipi, 1893, 1896
		Specimen not found in museum.	Praderi, 1971	
		Skull only, measured by Norris = KSN 68-62 SA.	MHN-V 108	This paper.
-- -- 1895	Cartagena 33°30'S	Mounted skin. 140cm. Collected by Dr. A. Medina. KSN 68-25 SA.	MNHN-S 11	Praderi, 1971
-- -- 1895	Cartagena	Skull. Measured by Norris KSN 68-16 SA. Collected by Dr. A. Medina. CBL±229mm.	MNHN-S	This paper.
-- -- 1940	Playa Ritoque, Viña del Mar. 33°S	Cranium. Collected by J. Carpeneto.	MHN-V 108	Praderi, 1971
VIII Región				
-- Mar. 1894	Bahía de Concepción, Talcahuano	162cm poorly mounted skin. Collected by G. Rudolphi, KSN 68-1 SA and by RNP & ISC, Oct. 1978. In exhibition in main hall.	MNHN-S 12 now MNHN-S 599	Philippi, 1893, 1894, 1896 Praderi, 1971
-- Mar. 1894	Talcahuano	Skull with abberant jaw *Acanthodelphis (Phocaena) Philippi* CBL±247mm, KSN 68-9 S	MNHN-S 938 now MNHN-S 588	Illustrated in 1896; Allen, 1925
10 Oct. 1968	Tubuil, Golfo de Arauco	Skull only, collected by K.S. Norris KSN 68-58 SA.	USNM 395,626	USNM Database

Stranding* or collection date	Locality	Details	Where deposited	Reference or source
13 Oct. 1968	Arauco, Golfo de Arauco	Three skulls found, one discarded. Partial skull, KSN 68-60 SA. Partial skull, KSN 68-60 SA.	 USNM 395,627 USNM 395,628	USNM Database
-- Jan. 1967	Río Carampague, Arauco	Cranium earbones collected by Y. Chapiro. Det. by R. Donoso as *D. Delphis*.	UCMZ 4148	I.S. Cameron 27/10/78
-- -- --	Concepción	Beach worn cranium. Det. as *D. delphis*.	UCMZ 4149	I.S. Cameron 27/10/78
IX Región				
06 Oct. 1968	Queule North of Valdivia	Collected by K.S. Norris: cranium incomplete skeleton. KSN 68-57 SA.	USNM 395,384	USNM Database
X Región				
18 Oct. 1968	Mehuín, north of Valdivia	Skull and skeleton without flippers and scapulae. Captured by P. Castro to KSN via Dr. Hugo Campos. KSN 68-61 SA.	USNM 395,376	USNM Database
-- -- --	-	Uncleaned skull at Mehuín laboratory.	IZUA-MM7	I.S. Cameron examined 25/10/78
-- -- --	-	Uncleaned skull at Mehuín.	IZUA-MM8	I.S. Cameron examined 25/10/78
02 Jan. 1976*	Mehuín	180cm female captured at depth of 15m. Stomach cont.	IZUA-MM.. JAO 02.1.76	J.A. Oporto
08 Jan. 1976*	Bahía de Maiquillahue	143cm male. Caught in net.	IZUA-MM.. JAO 8.1.76	J.A. Oporto
21 Jan. 1976	-	175mm male, measurements.	IZUA-MM.. JAO 21.1.76	J.A. Oporto
21 Jan. 1976	Mehuín	155cm female, measurements. JAO 21.1.76	IZUA-MM..	J.A. Oporto
-- Oct. 1978	Valdivia?	81.3cm foetus preserved in formalin. Mother caught in net.	IZUA-MM14	I.S. Cameron 28/02/79
-- -- 1979	Bahía Maiquillahue, Mehuín	172cm male taken in net at 15m depth.	IZUA-MM.. JAO 1979	J.A. Oporto
03 Nov. 1978	Mehuín	86cm foetus of female captured in nets. Collected by P. Castro.	IZUA-MM15	J.A. Oporto
-- -- --	Mehuín 39°26'S, 73°14'W	'Adult male'; capture. Skeleton collected.	IZUA	Crovetto & Lemaitre, 1988

Stranding* or collection date	Locality	Details	Where deposited	Reference or source
Lima				
-- -- 1900	Chancay 11°38'S	Young animal, capture. Collected by P.O. Simmons.	BMNH 1900.5.7.29	Noble & Fraser, 1971 Praderi, 1971
19 Jul. 1969	Chilca 7km SSE	Partial cranium. Collected by C. Pearson no. 14.	MVZ 137763	USNM Database
-- -- 1950	Off Callao	Skull and skeleton. Collected by R.O. Smith.	USNM 299.994	USNM Database
05 Sep. 1968*	Callao	143cm female captured. Measurements, stomach content. KSN 68-48 SA.	Instituto del Mar. Callao	This paper.
-- -- 1987	Pucusana 12'30'S	Estimated number of captures: 1985 = 47, 1986 = 24, 1987 = 83.	-	Van Waerebeek & Reyes, 1988
Ica				
13 Sep. 1969	Lagunillas, 5 miles SW of Paracas	Collected by C.B, Koford:		
		-	MVZ 145,780	USNM Database
		-	MVZ 145,781	
		Skull and earbones.	MVZ 139,502	
		Partial skull.	MVZ 139,500	
		Partial skull and earbones.	MVZ 139,501	
24 Mar. 1972	Paracas Peninsula	Immature skull, beach pick-up.	CAS 16179	J. Schoenwald pers. comm.
01 Feb. 1976	San Andrés	Bulla and periotic, partial skeleton, no skull. Incidental catch. Collected by J.G. Mead (JGM 161).	USNM 504,335	USNM Database
Note: R. Jones and L. Hobson-Jones collected 6 specimens in Peru (locality not known) in 1974. They are in the Paleontology Museum at UC Berkeley and at CAS.				
Chile				
This list does not cover the extensive work that has been carried out in Chile since 1989 by J.A. Oporto and others (see text).				
I. Región				
06 Aug. 1968*	5 miles S of Iquique	Caught at 05.00hrs, fresh: 152.7cm female, collected skull and skeleton, KSN 68-23 SA	USNM 395,379	USNM Database, This paper.
		152.7cm male, collected skull and skeleton KSN 68-24 SA.	USNM 395,380	

Stranding* or collection date	Locality	Details	Where deposited	Reference or source
-- -- --	Tarapaca, 15kms of beach beach between Arica and Peruvian border	Collection of W. Lester and J.V. Olst:		USNM Database
-- Jul. 1969		Cranium, partial postcranial.	USNM 395,729	
		Skull, partial postcranial.	USNM 395,730	
		Partial skull.	USNM 395,731	
		Skull.	USNM 395,732	
		Skull.	USNM 395,735	
		Skull.	USNM 395,736	
		Skull.	USNM 395,737	
		Skull.	USNM 395,738	
		Skull.	USNM 395,739	
		Skull.	USNM 395,740	
		Partial skull.	USNM 395,741	
		Partial skull.	USNM 395,742	
		Partial skull.	USNM 395,743	
		Partial skull.	USNM 395,744	
		Partial skull.	USNM 395,745	
		Skull and skeleton.	USNM 395,746	
		Partial skeleton, no skull.	USNM 395,747	
		Partial skull.	USNM 395,748	
		Cranium, partial skeleton.	USNM 395,749	
		Partial skull.	USNM 395,750	
		Skull and skeleton.	USNM 395,751	
		Skull and skeleton.	USNM 395,752	
		Skull.	USNM 395,753	
		Skull and partial skeleton.	USNM 395,754	
II Región				
11 Aug. 1968*	Antofagasta	146.8cm male, capture. KSN 69-29 SA.	Univ. de Antofagasta	This paper.
16 Aug. 1968*	Bahía Mejillones north of Antofagasta	Collected by K.S. Norris: KSN 68-31 SA.		
		164.5cm female, capture.	USNM 395,377	USNM Database
		131cm male. In net with the above. KSN 68-3 SA.	USNM 395,383	USNM Database

Castello (HPC) studied material of this species in Buenos Aires museums and along the east coast of the continent as well as two specimens sent to him from Tierra del Fuego, deposited in MACN (Castello, 1974).

Early specimens referred to in the literature (e.g. Burmeister, 1865; Pérez Canto in Philippi, 1893; 1896) were located and remeasured by KSN in 1968, by RNP and ISC in 1978 and by Praderi (1971). Further details on museum specimens were provided by colleagues, especially J.G. Mead, who obtained information from the USNM database for several US museums.

Fresh animals were measured using standard methods (Norris, 1961), dissected, the organs weighed and stomach and organ samples collected. Certain biological materials (stomach contents, parasites) were sent to outside experts. A preliminary study of the teeth of four specimens for examination of growth layer groups (GLGs – Perrin and Myrick, 1980) was performed by A.C.M. Schiavini by polishing with sandpaper to a thickness of ±100–200μ and reading with a microscope. Physical maturity classes were determined by examining skeletons along their complete length for vertebral fusion of both anterior and posterior epiphyses, following the methods of Perrin (1975) and Goodall *et al.* (1988a): Class 0, foetus or neonate, not all neural arches fused to vertebrae; Class 1, juvenile, neural arches fused but no epiphyses fused; Class 2, subadult, some but not all epiphyses fused; Class 3, adult, all epiphyses fused to their vertebrae.

PREVIOUS WORK

Burmeister's porpoise was described by G. Burmeister (1865; 1869; 1879) on the basis of a specimen caught much earlier near the mouth of the Río de la Plata. Further specimens, named *Phocaena philippi* and *Acanthodelphis philippi* were described by Pérez Canto in Philippi (1893) and by Philippi (1894; 1896). Allen (1925) reported a specimen collected in 1872 by Louis Agassiz at 'Payta', Peru, the fourth one known, giving skull measurements and comparing part of the vertebral column with that of *P. phocoena*. Clarke (1962) examined the fifth specimen in the fish market at Chimbote, Peru and raised the first warning of the exploitation of the species there.

Almost all specimens from off Uruguay (Praderi, 1971; Pilleri and Gihr, 1972; 1974; Brownell and Praderi, 1982; 1984) were taken singly in nets set for sharks. Observations of live animals and a stranded specimen were presented by Würsig *et al.* (1977). Goodall (1978; 1989) mentioned at least nine specimens from Tierra del Fuego, but gave no details on their biology.

The synonymy for this species is given by Allen (1925), Hershkovitz (1966) and Praderi (1971). General reviews were given by Praderi (1971) and Brownell and Praderi (1982; 1984).

Recent studies

Studies of the Burmeister's porpoise have expanded greatly in recent years, largely in response to high levels of direct and indirect exploitation, especially in Peruvian waters (Gaskin and Read, 1987; Van Waerebeek and Reyes, 1988; 1989; Van Waerebeek *et al.*, 1988; Reyes and Van Waerebeek, 1990; 1995).

Studies have also begun in Chilean waters. Guerra *et al.* (1987) present several sightings for northern Chile and information on seven specimens held at the Universidad de Antofagasta. Work is also taking place in south-central Chile, although as yet most of the information has been presented only at conferences (Brieva and Oporto, 1990; Oporto and Brieva, 1994; also see below). New networks have presented sightings or strandings (Brito and Reyes, 1990; Ruiz *et al.*, 1990).

A number of recent papers present the results of work off the coast of the Province of Buenos Aires, Argentina (Crespo *et al.*, 1990; 1994; Corcuera, 1991; Bastida *et al.*, 1992; Corcuera and Monzón, 1992a; b; and Corcuera *et al.*, 1995).

New reviews for *P. spinipinnis* are presented by Reyes and Van Waerebeek (1995), Van Waerebeek and Reyes (1990), Goodall *et al.* (1990b), Corcuera (1991) and IWC (1991).

DISTRIBUTION

Allen (1925), on the basis of the four specimens then known, believed that Burmeister's porpoise was probably limited to 'the cooler waters off the South American coast from the La Plata region, around Cape Horn, and northward in the Humboldt Current to northern Peru....'. For many years, its range was given as from Paita, Peru(05°S) to Valdivia (39°50'S) on the west coast and Punta del Diablo, Uruguay (34°22'S) to Península Valdés, Argentina (42°23'S) on the east, with a comment that some specimens had been reported for Tierra del Fuego (e.g. Brownell and Praderi, 1982; 1984; Leatherwood and Reeves, 1983).

New studies have amplified the range (Table 1, Fig. 1). The northernmost record on the east coast of South America is 28°48'S at Río Urucanga, Brazil (Simöes-Lopes and Ximenez, 1988; 1989); another specimen was found at Rio Grande do Sul, Brazil (Pinedo, 1989; Simöes-Lopes and Ximenez, 1993). These records extend the distribution on the east side of the continent by some 6° (360 n.miles) northward. At least five specimens are known from 'Patagonia' or Chubut, Argentina (Praderi, 1971; Würsig *et al.*, 1977; GH; E. Crespo, pers. comm.) and eleven for eastern Tierra del Fuego (Castello, 1974; Goodall, 1978; 1989). According to Cárdenas *et al.* (1987) this porpoise is found southward to near Cape Horn (56°S). On the west coast of South America, the northernmost record is still at Paita, Peru (Reyes and Van Waerebeek, 1995).

The 'gaps' that remain in the distribution of the species are along the coasts of Santa Cruz, Argentina, and the Patagonia channels of Chile. These are areas with long coastlines, few or no resident researchers and where few shore surveys have been carried out. It is likely that, with more research, Burmeister's porpoise will be found to occur more or less continuously from Brazil around the tip of the continent to Peru.

Guiler *et al.* (1987) reported a cranium of *Phocaena [sic] spinipinnis* from Heard Island, at 53°S, 73°30'E in the southern Indian Ocean. This specimen was misidentified and pertains to the spectacled porpoise, *Australophocaena dioptrica* (Brownell *et al.*, 1989). There are thus no records of Burmeister's porpoise from outside South American waters.

HABITAT AND ABUNDANCE

Burmeister's porpoise was at first assumed to be an inshore, coastal species (Brownell and Praderi, 1982; 1984) since it has most often been seen in inshore waters (Goodall *et al.*, 1990a). More recently, it has been found up to 25 n.miles (50km) from the coast of north-central Argentina, at a depth of 60m (Corcuera, 1991) and at least 20km from the coast of Valdivia, Chile, especially in winter when sardines move offshore (Oporto and Brieva, 1994). They have also been seen in the mouths of rivers and estuaries (Aguayo, 1975), 18kms up the Río Valdivia in Chile and appear to be fairly common in bays off the intricate channels of Tierra del Fuego in the southernmost part of the range (Goodall *et al.*, 1990a; 1995).

In the northern part of the range the porpoises inhabit warm to temperate waters off Peru, Chile, southern Brazil and Uruguay; their distribution appears to be related to the cool northward flowing currents on each side of the continent, the Humboldt (Peru)

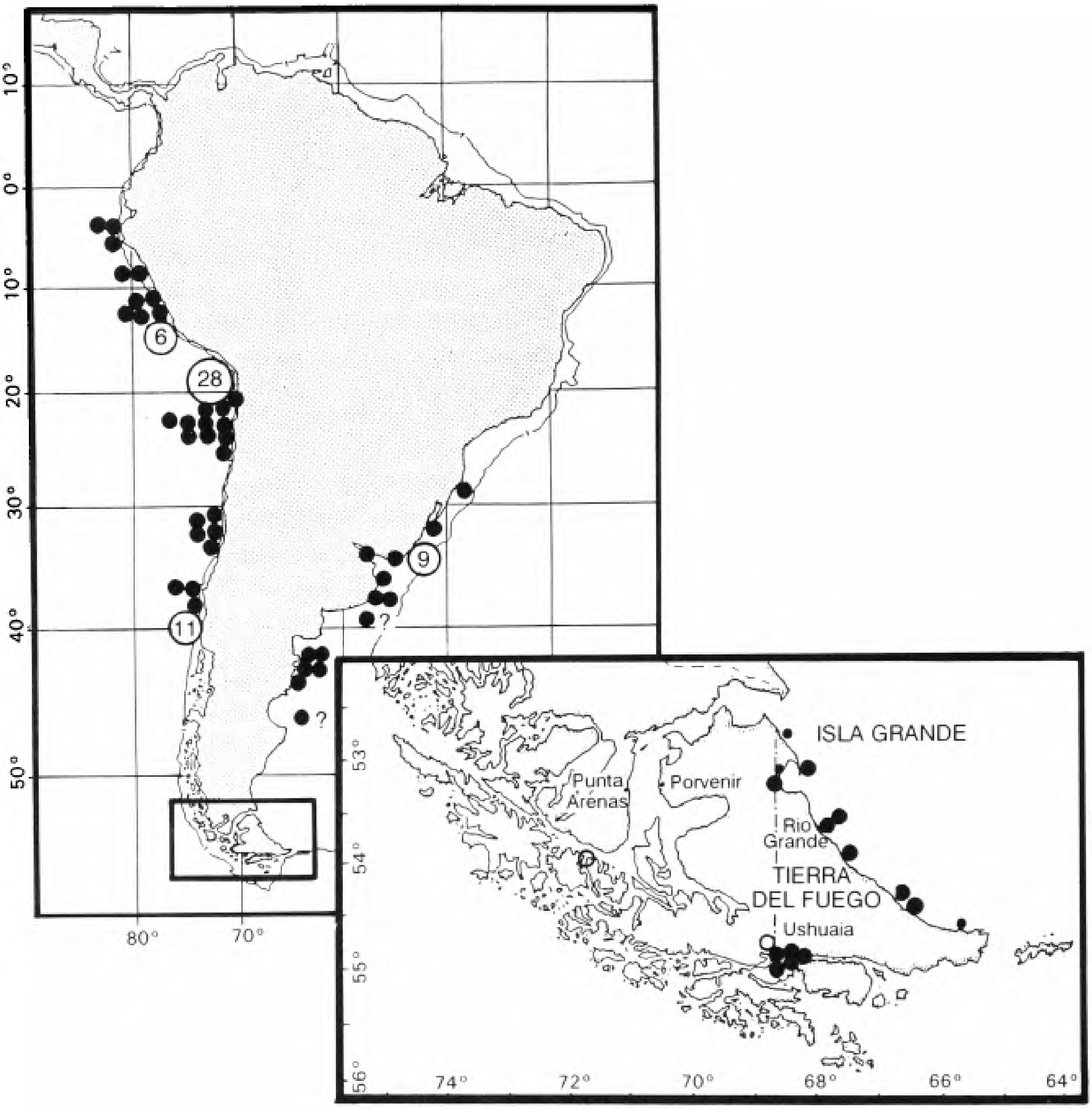

Fig. 1. Map of South America showing the location of specimens (strandings and captures) of the Burmeister's porpoise, *Phocoena spinipinnis*, not including the most recent studies in Peru, Chile and Argentina. Solid circles represent cranial or complete specimens; small circles indicate postcranial specimens; a small open circle, specimen observed but not collected; question mark, locality uncertain. Areas with greatest incidental capture can be deduced from location of specimens.

Current on the west coast and the Falkland (Malvinas) Current on the east. The sub-Antarctic waters in the southern part of its range, Tierra del Fuego to near Cape Horn, average from 4°C (winter) to 9°C (summer).

Brownell and Praderi (1982), on the basis of the little known at the time, felt that this could be the 'most abundant coastal small cetacean in southern South American waters', and that the Pacific stocks might be more numerous than the Atlantic because of more competition on the east coast with other small cetaceans. Recent investigations and research in progress seem to indicate that other species, such as the franciscana (*Pontoporia blainvilli*) are more numerous than *P. spinipinnis* off the coast of Buenos Aires, whilst the dusky dolphin (*Lagenorhynchus obscurus*) is more numerous off Chubut

(Würsig *et al.*, 1977; Würsig, 1992) and Peru. Dusky dolphins, beaked common dolphins (*Delphinus capensis*) and Burmeister's porpoises are the species most often exploited off Peru (Van Waerebeek and Reyes, 1988; 1989; 1994). However, there are no reliable estimates of population size for any small cetacean species off South America.

Specimens of *P. spinipinnis*, based on strandings and incidental captures, account for only 1.3% of the specimens of 22 species of small cetaceans collected in Tierra del Fuego from 1976–1989. By contrast Commerson's dolphin accounted for 37% and the spectacled porpoise for 19.7% (Goodall, 1989).

Sightings of Burmeister's porpoise are rare and sporadic throughout its range, partly due to the difficulty in sighting the low dorsal fin in rough waters and also lack of effort in the area (Goodall *et al.*, 1990a; 1995). Nothing is known of population size, stocks or abundance (Klinowska, 1991; Reeves and Leatherwood, 1994).

EXTERNAL FORM

Size

In collating all published (excluding the most recent work) and new data on external form, we have found measurements (at least total length) for eleven females, fourteen males and eleven animals of unknown sex. These are plotted by countries in Table 2; external measurements for unpublished specimens (countries combined) are given in Table 3.

Females

For the unpublished specimens, nine females ranged from 134 to 185cm in length (Table 2). One female was sexually mature at 164.5cm and simultaneously pregnant and lactating. A 181cm, 67kg female stranded at Golfo San José (GH 860627) had just calved. This animal was thought to be old because of tooth wear. In recent studies off Peru (Reyes and Van Waerebeek, 1995), the largest female measured 183cm (n=167) and sexually mature females averaged 165.5cm (n=56). Off Chile, 10 females (not included in our study) also ranged to 183cm, with the smallest at sexual maturity being 164cm (Brieva and Oporto, 1990).

The 164.5cm female was physically mature, although a larger animal of 185cm from Tierra del Fuego was still subadult; 185cm is thus probably not the maximum size for *P. spinipinnis* females in the southern part of the range. The largest of four females captured off northern Argentina was 196cm in length; it was both sexually and physically mature (Corcuera *et al.*, 1995).

Males

Length in nine males in our sample ranged from an estimate of 80cm for a young calf to 175cm. None of these were physically mature. In the studies off Peru, males reached 182cm (n=235) with a mean length at sexual maturity of 170.3cm (n=63); males were larger than females overall (Reyes and Van Waerebeek, 1995). Off Chile, the largest of 16 males was 182.5cm and the smallest at sexual maturity was 162cm (Brieva and Oporto, 1990). Animals from Peru and Chile were not examined for physical maturity.

Brownell and Praderi (1984) reported 'adults' of unstated sex of '180–200cm.' Corcuera *et al.* (1995) found sexually but not physically mature males of 169 and 179cm.

(*Text continued on page 332*)

Table 2

Summary of specimens of Burmeister's porpoises from Table 1 with measurable data. TLs are rounded to nearest cm.

Month	Location	Sex	TL (cm)	Weight (kg)	Sexual maturity	Phsyical maturity	How obtained	Age GLGs	Specimen No.	Reference
Peru										
Sep.	Callao	F	143	-	-	-	Capture	-	KSN68-48SA	KSN
Sep.	Chimbote	F	153	±30	-	-	Capture	-	KSN68-38SA	KSN
-	Paita	F	±160.0	-	-	2	Capture?	-	MCZ 1158	Allen, 1925
Chile										
	Región									
Aug.	I, Iquique	F	153	-	-	2	Capture	-	KSN68-23SA	KSN
Jan.	X, Mehuín	F	155	-	-	-	Capture	-	JAO 21.1.76	JAO
Aug.	II, Antofagasta	F	165	-	Lactating; with foetus.	3	Capture	-	KSN68-31SA	KSN
Jan.	X, Mehuín	F	180	-	-	-	Capture	-	JAO 02.1.76	JAO
Summ.	II, Mejillones	M	37	-	Fetus.	0	Capture	-	UA-AMM13	Guerra *et al.*, 1987
Aug.	II, Antofagasta	M	131	-	Still nursing 165cm F above?	1	Capture	-	KSN68-30SA	KSN
Jan.	X, Mehuín	M	143	±60	-	-	Capture	-	JAO 8.1.76	JAO
Aug.	II, Antofagasta	M	147	-	-	-	Capture	-	KSN68-29SA	KSN
Aug.	I, Iquique	M	153	-	-	-	Capture	-	KSN68-24SA	KSN
-	X. Mehuín	M	172	±80	-	-	Capture	-	JAO ±1979	JAO
Jan.	X, sin loc.	M	175	-	-	-	Capture	-	JAO 21.1.76	JAO
Oct.	X, Valdivia?	-	81	-	Fetus.	0	Capture	-	IZUA-MM14	I.S. Cameron
Nov.	X. Mehuín	-	86	7.7	Near term foetus.	0	Capture	-	IZUA-MM15	JAO
-	V, Cartagena	-	140	-	Mounted skin.	-	Capture	-	MNHN-S11	Praderi, 1971
-	V, Valparaíso	-	140	-	Specimen lost.	-	Capture	-	MHN-V	Philippi, 1893
Mar.	VIII, Talcahuano	-	±162.0	-	Fresh, later mounted skin.	-	Capture	-	MNHN-S599	Philippi, 1896
Jan. 1990	XII, T. del Fuego	F	-	-	Mother with dark calf.	-	Observation	-	Alive	Goodall *et al.*,
Brazil										
Oct.	Santa Catarina	-	180	-	-	-	Stranding	-	-	Simöes-Lopez & Ximenez, 1988

Month	Location	Sex	TL (cm)	Weight (kg)	Sexual maturity	Phsyical maturity	How obtained	Age GLGs	Specimen No.	Reference
Uruguay										
Feb.	Dept. Rocha	F	183+	-	Contained a 44cm M foetus.	-	Capture	-	RLB901	Brownell & Praderi, 1982
Feb.	Dept. Rocha	M	44	-	Fetus of 183cm F (RLB901).	0	Capture	-	RLB901f	Brownell & Praderi, 1982
Feb.	Dept. Rocha	M	179	-	-	-	Capture	-	RP301	Brownell & Praderi, 1976
Feb.	Dept. Rocha	M	180	-	Sexually mature.	-	Capture	-	AO 1974-23	Brownell & Praderi, 1976
Feb.	Dept. Rocha	-	180	-	-	-	Capture	-	-	Brownell & Praderi, 1976
-	Dept. Rocha	-	190	-	-	-	Capture	-	RLB	Mitchell, 1975b
-	Dept. Rocha	-	200	-	'Adults 180-200cm'.	-	Capture	-	-	Brownell & Praderi, 1984
Argentina										
Dec.	Tierra del Fuego	F	134		38.5kg without viscera.	2	Capture	1	RNP110	Goodall, 1978
Jun.	Chubut	F	181	67	Milk, recently calved.	-	Stranding	9	GH860627	GH
Dec.	Tierra del Fuego	F	185	80 est.	-	2	Capture	4	RNP167	Goodall, 1978
Apr.	Tierra del Fuego	M	±80	40 est.	Calf.	-	Cap. & rel.	-	Alive	Goodall *et al.*, 1990
Apr.	Buenos Aires	M	126	22	Emaciated calf.	-	Stranding	-	Mundo Marino	Loueiro, 1986
-	Buenos Aires	M	±162	-	Mounted skin.	-	Capture	-	MACN-BA27-2	Burmeister, 1869
Dec.	Tierra del Fuego	M	151	58.5	-	2	Capture	2	RNP111	Goodall, 1978
Dec.	Tierra del Fuego	-	120	-	Juvenile.	1	Capture?	-	RNP1540	RNP
Sep.	Chubut	-	167	70 est.	-	-	Stranding	-	JFM-	Würsig *et al.*, 1977
Mar.	Tierra del Fuego	-	170+	-	Physically adult.	3	Capture?	4	RNP1354	RNP

Table 3.
Formerly unpublished measurements (in cm) of unpublished specimens of *Phocoena spinipinnis* from Peru and Chile, and from Chubut and Tierra del Fuego, Argentina

	Juveniles, both sexes					Females					Males				
	n	min.	max.	mean	SD	*n*	min.	max.	mean	SD	*n*	min.	max.	mean	SD
Snout to															
fluke notch	5	131.1	146.8	139.6	6.7	7	152.7	185.0	167.3	14.4	4	151.0	175.0	162.7	12.6
post margin of blowhole	5	13.0	18.4	15.1	2.0	5	13.8	20.0	16.3	2.5	3	15.2	19.5	17.8	2.3
angle of mouth	5	6.0	11.0	9.2	2.1	6	6.4	12.0	9.7	1.9	4	10.4	12.0	11.2	0.8
centre of eye	5	11.8	17.5	14.6	2.5	6	9.2	20.0	14.9	3.7	3	9.2	18.5	14.8	4.9
centre of ear	2	16.0	22.7	19.4	4.7	4	21.0	24.0	22.2	1.4	2	22.4	26.0	24.2	2.5
ant. insert. of flipper	5	25.6	29.0	26.8	1.4	6	28.0	35.0	30.9	2.6	3	27.8	33.0	29.9	2.7
ant. insert. dorsal fin	-	-	-	-	-	1	86.0	86.0	86.0	-	-	-	-	-	-
post. tip dorsal fin	5	76.0	110.0	94.9	12.5	6	104.5	129.0	116.0	9.2	3	109.0	135.0	118.4	14.4
umbilicus	4	61.6	69.4	65.3	3.6	4	70.4	77.5	73.1	3.1	2	70.6	80.0	75.3	6.6
centre of genital slit	4	76.5	91.0	82.9	6.0	4	98.4	111.2	103.9	5.6	3	87.5	100.0	92.2	6.8
centre of anus	4	90.0	98.1	94.8	3.6	5	101.1	129.0	113.3	11.2	4	103.0	123.0	111.8	9.4
Centre of eye to:															
angle of mouth	5	5.0	7.5	6.2	1.1	4	6.5	7.5	6.9	0.5	4	6.3	7.5	7.0	0.6
ear	2	4.5	5.3	4.9	0.6	4	5.7	6.0	5.9	0.1	3	5.4	6.5	5.8	0.6
blowhole edge	2	9.0	11.0	10.0	1.4	1	13.2	13.2	13.2	-	2	11.5	13.2	12.4	1.2
Flipper															
ant. length	5	21.3	27.0	23.9	2.1	6	25.0	32.0	28.9	2.5	4	24.5	31.0	28.6	2.9
post. length	5	12.0	19.5	17.0	2.9	6	20.0	24.1	21.9	1.5	4	17.5	23.5	21.5	2.7
max. width	5	7.5	10.0	8.8	0.9	6	9.5	11.5	10.3	0.8	4	9.7	11.0	10.5	0.7
Dorsal fin															
height	4	7.0	8.5	7.9	0.6	6	7.4	11.5	9.2	1.6	4	9.0	18.0	11.5	4.3
length at base	3	24.5	29.0	26.7	2.3	5	20.0	41.0	32.3	9.2	4	21.5	41.0	33.0	9.1
Flukes															
width, tip to tip	4	30.0	40.0	34.2	4.6	6	36.1	45.0	40.6	3.3	3	33.0	41.4	37.5	4.2
ant. margin to fluke notch	3	9.5	13.0	10.9	1.8	5	10.7	14.5	12.3	1.8	3	10.9	12.0	11.6	0.6
depth of notch	4	1.0	1.8	1.3	0.4	6	1.7	3.0	2.3	0.5	4	1.5	3.0	2.1	0.6
Girth															
at axilla	5	33.0	80.0	66.3	19.3	5	77.6	101.0	87.0	8.8	3	76.0	97.0	88.4	11.0
max. (ant. dorsal fin)	3	80.5	89.0	84.0	4.4	4	85.0	104.0	93.5	7.9	4	86.0	103.5	97.4	7.8
at anus	3	50.3	50.8	50.5	0.3	4	54.0	58.6	56.0	2.0	4	55.8	64.0	60.0	4.1
midway anus to fluke notch	1	91.4	91.4	91.4	-	-	-	-	-	-	1	28.8	28.8	28.8	-
Height, same place	1	38.1	38.1	38.1	-	-	-	-	-	-	1	14.5	14.5	14.5	-
Thickness, same place	1	17.8	17.8	17.8	-	-	-	-	-	-	1	4.2	4.2	4.2	-
Aperture length, eye	3	1.1	1.5	1.4	0.2	4	1.2	1.5	1.4	0.2	4	1.6	2.0	1.7	0.2
blowhole	2	0.2	0.8	0.5	0.4	4	0.7	2.0	1.2	0.6	3	0.7	1.0	0.9	0.2
blowhole width	3	2.3	2.7	2.5	0.2	4	1.0	2.8	2.3	0.9	4	2.2	3.0	2.8	0.4
genital slit	3	7.8	9.0	8.2	0.7	5	2.8	13.0	9.8	4.0	3	7.0	8.5	7.8	0.8
Mammary slits															
max. length	1	0.9	0.9	0.9	-	4	0.5	1.5	1.1	0.5	-	-	-	-	-
Projection of lower jaw	3	0.0	0.6	0.3	0.3	4	0.0	0.5	0.2	0.3	3	0.0	0.2	0.1	0.1

From the limited data available, Corcuera and Monzón (1992a) and Corcuera *et al.* (1995) suggested that the Burmeister's porpoises from the South Atlantic coast are larger than those from the South Pacific. Although the sample size off Peru is large (n=402), nearly all were taken in nets. The method of capture may have an influence on the size of animals taken. In Commerson's dolphins (*Cephalorhynchus commersonii*) off Tierra del Fuego, the largest animals taken incidentally in nets during 20 years were 138cm for males and 145.5cm for females (n=215). In only 12 animals live-captured from the prow of a boat, maximum lengths were a 149cm male and a 152cm female (Goodall *et al.*, 1988a). There are too few data for *P. spinipinnis* outside Peru reach conclusions on maximum lengths.

Weight

Direct weights are available for only four animals in our data, a 7.7kg foetus, a 38.5kg subadult female (without viscera), a 58.5kg subadult male and a 67kg recently calved female; the other weights are estimates (Table 2). The greatest weights off Peru were 72kg for males and 79kg for females (Reyes and Van Waerebeek, 1995). Off northern Argentina, three females weighed 98–105kg, males 78kg (Corcuera *et al.*, 1995).

Body proportions

Descriptions of body shape are given by Burmeister (1865) and Brownell and Praderi (1982; 1984). External measurements of unpublished specimens are given in Table 3. The sexes are similar in shape. Maximum girth is 55–66% of TL (mean 60%, $n=13$), showing specimens of *P. spinipinnis* to be more heavily bodied than those of the spectacled porpoise (50–58%, mean 56% of TL; Goodall, 1990; Goodall and Schiavini, 1995).

The head is blunt with no beak, the forehead dropping rather abruptly to the rostrum tip. The lower jaw projects very slightly (less than 0.5cm). The gape is short and the eye is situated forward of the blowhole.

The dorsal fin is placed far back and is bluntly pointed. The largest in our specimens measured 18cm in height. We found no sexual dimorphism in dorsal fin size or shape, but

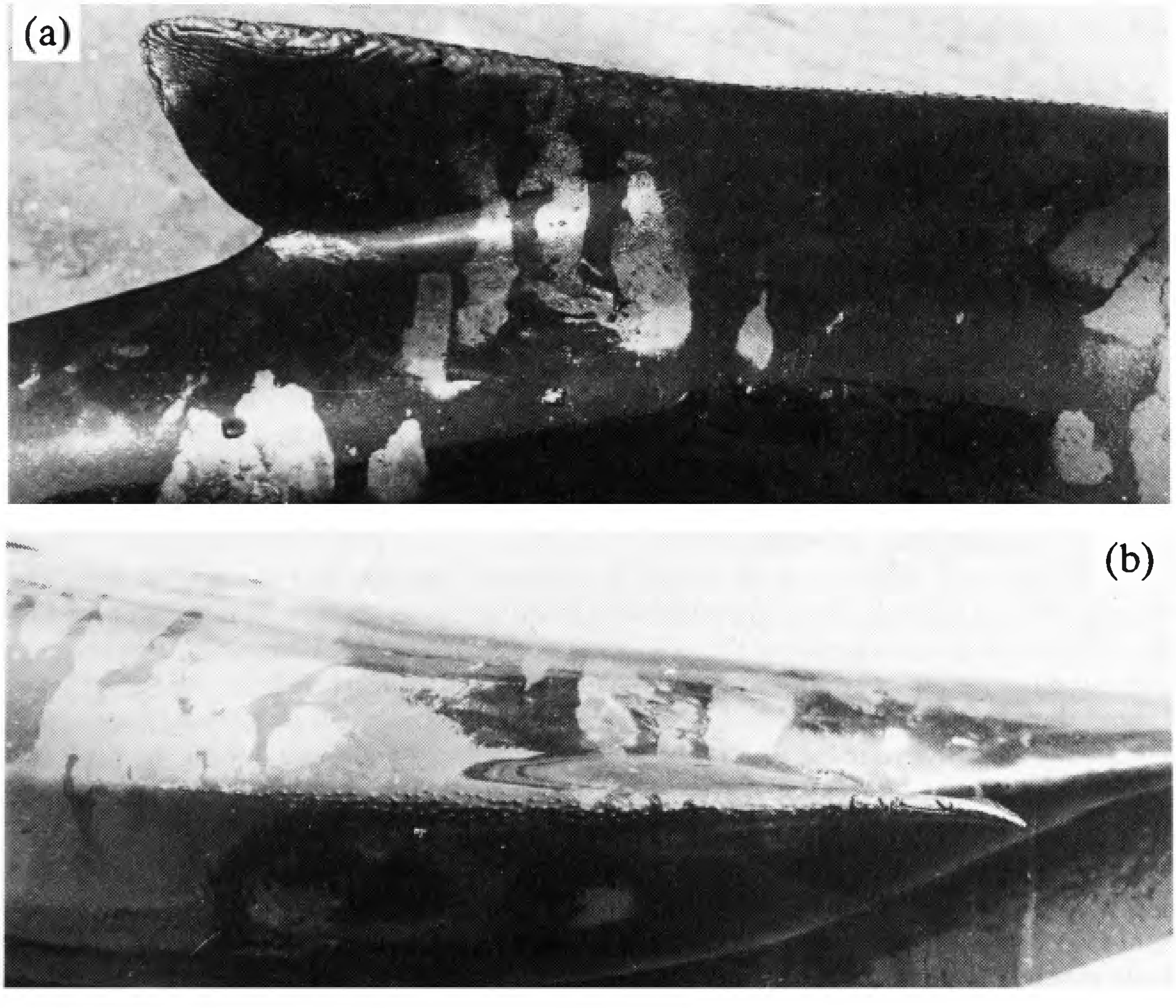

Fig. 2. The dorsal fin of the Burmeister's porpoise showing general shape (a) and the row of tubercles along the upper edge (b).

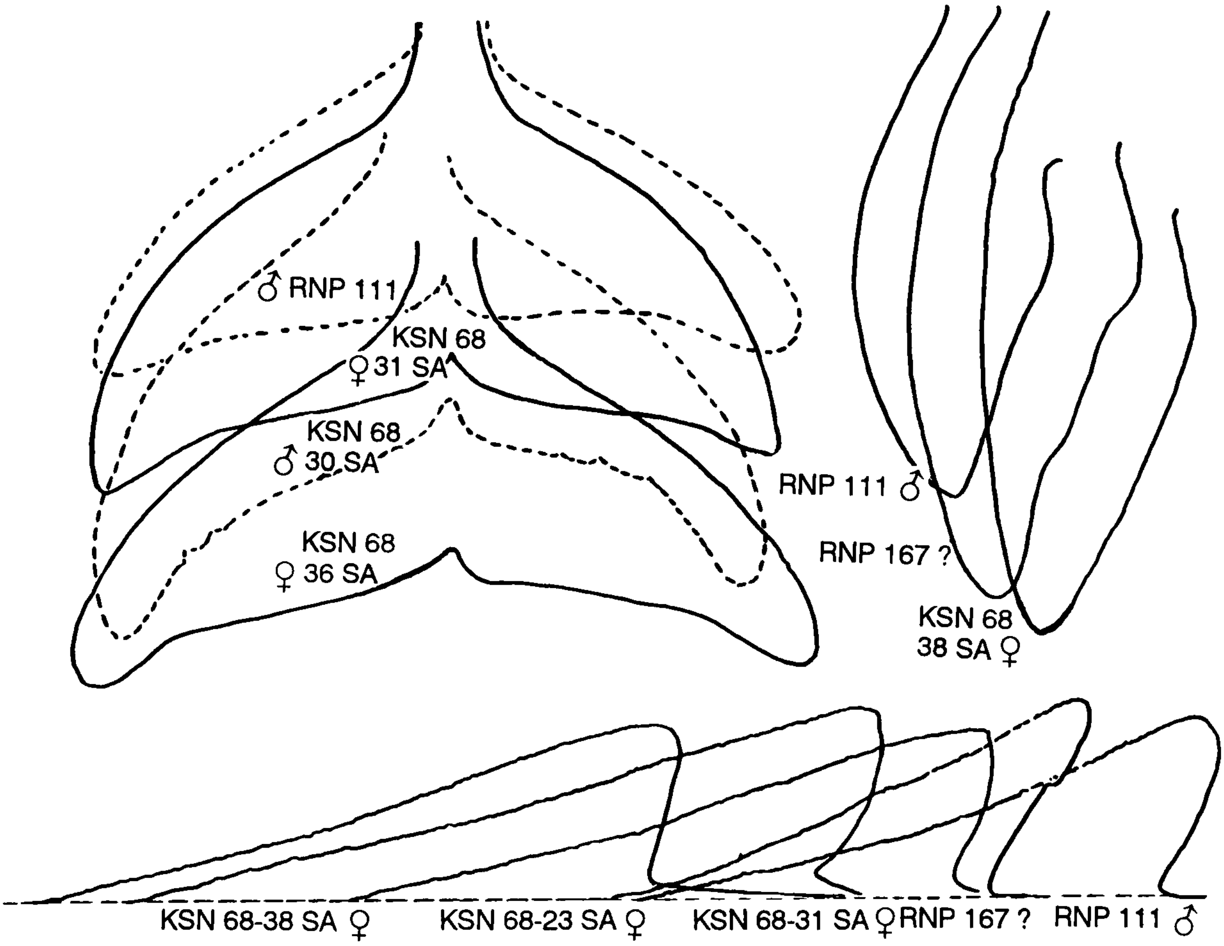

Fig. 3. Tracings taken to scale of flukes, flippers and dorsal fins of specimens of Burmeister's porpoise.

in a large number of animals off Peru males were found to have a larger fin (Reyes and Van Waerebeek, 1995). Two to four rows of small blunt tubercles run the length of the upper ridge of the fin, from the anterior insertion to the upper tip (Fig. 2). At least 184 tubercles were present on one animal in 1979 (JAO). In some animals these are pronounced and can be seen even at sea (Aguayo, 1975), but in others they are less marked (KSN obs.). They were present in a very young calf (A.P. Sobral, pers. comm.) but not in a foetus. Variation in dorsal fin shape is shown in Figs 2 and 3 and the shape is compared with other southern species in Goodall *et al.* (1988b).

The flippers are larger than those of *A. dioptrica* and are fairly straight along the posterior margin (Fig. 3). Some flippers had a slightly rugose surface on the upper leading edge. Flipper shape and bones of this species were illustrated and compared with those of *A. dioptrica, C. commersonii* and *C. eutropia* (Goodall *et al.*, 1988b).

The flukes are medium sized with blunt tips and a fairly straight posterior border (Fig. 3). They are larger than those of *A. dioptrica* (Goodall and Schiavini, 1995). At least two animals examined by Norris had a prominent hump on the lower tail stock posterior to the anus.

Teeth

Number of visible teeth is usually reported as ranging from 13–18 in each upper jaw and 15–20 in each lower (Brownell and Praderi, 1984) or 14–16/17–19 (Leatherwood and Reeves, 1983). Original references and our own specimens result in the ranges UL 11–16 (n=12), UR 10–16 (n=10), LL 16–19 (n=12), LR 16–19 (n=9) (Table 4). A 126cm calf

Table 4

Number of visible teeth present in specimens of Burmeister's porpoise.

Reference	Specimen	UL	UR	LL	LR
Burmeister, 1865	MACN-BA27-2	16	16	17	17
Allen, 1925	MCZ1158	16	16	17	18
Noble & Fraser, 1971	BMNH 1900.5.7.29	16	-	16	-
Pilleri & Gihr, 1972	T474	14	5	17	-
	-	18	14	19	17
Pilleri & Gihr, 1974	T532	16?	14(15)	18(19)	17(18)
Loureiro, 1986	(not all erupted)	9+	9+	8+	8+
This paper:	JAO ± 1979	13	12	17	17
	JAO 8.i.76	15	14	17	17
	RNP110	13	15	16	19
	RNP111	14	13	18	18
	RNP 167	11	11	19	19
	MACN s/n	14	-	17+	-
	GH 820627	13	10	17	16

had 9–9/8–8 erupted teeth (Loureiro, 1986). As stated by other authors (see Reyes and Van Waerebeek, 1995), teeth are often unerupted at the front and back of the row and may easily be lost in cleaning.

In a preliminary test, four teeth were examined for growth layer groups (GLGs – see Perrin and Myrick, 1980) by A.C.M. Schiavini. A 134cm female specimen with some fused epiphyses had one GLG, a 151cm male had two; a 170+cm physically mature animal of unknown sex and a 185cm subadult female both had four GLGS. The maximum age reported for the species is 12+GLGs (Corcuera *et al.*, 1995). The oldest animal in a study of 22 porpoises off Peru was 8 years (GLGs) for a 174cm female (Reyes and Van Waerebeek, 1995). The three specimens from Chubut (GH and A.P. Purgue) were aged between 4 and 9 years (Crespo *et al.*, 1994).

PIGMENTATION

Adults

The pigmentation of Burmeister's porpoise has only recently been well documented (Reyes and Van Waerebeek, 1995). Early specimens were all described as dark, black or even 'glistening' black. Brownell and Praderi (1984) describe a fresh specimen as being lead gray shading to light gray on the lateral surfaces with a gray to white abdominal field to the anal region. They describe the dark gray flipper stripe but not the eye or lip patches. At sea the animals appear light brown to dark gray, brown or black, depending on the colour of the water and reflections (Goodall *et al.*, 1990a; 1995).

The light pigmentation darkens very quickly upon death (GH, pers. obs.) and descriptions will be inaccurate even soon after an animal dies. Three fresh specimens examined by RNP which had been frozen (out of doors) for several days were shiny black on all surfaces, with no trace of eye patches, lip patches or flipper stripes. Another specimen (JAO 2.i.76) was dark slate gray with only a white spot around the anus.

The Norris team examined several fresh specimens in 1968. The upper surface is usually dark, from brownish to slate-gray to black. The head may be a lighter gray with a dark

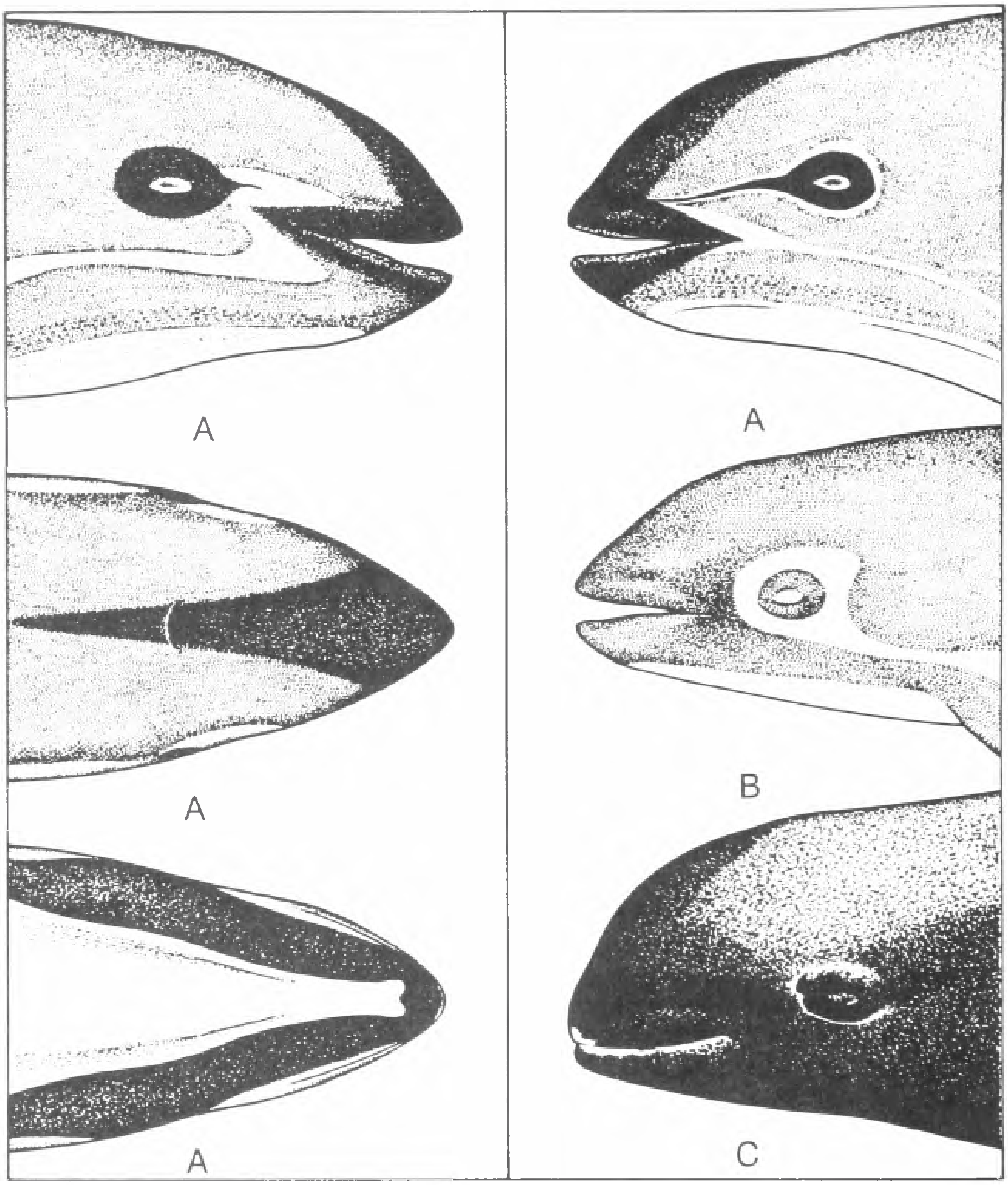

Fig. 4. Schematic representations of the pigmentation of the head in Burmeister's porpoise. A, lateral, dorsal and ventral views of a head preserved in formalin in MACN; B, foetus IZUA-MM 14; C, specimen KSN 68–31 SA.

streak running forward from behind the blowhole to the beak forming a dark triangle over the forward part of the head, which may join the lip patch (Fig. 4). The lips are surrounded with black, as in *A. dioptrica*, but the lower half of the face is not white as in that species (Lahille, 1912; Goodall, 1990; Goodall and Schiavini, 1995). The dark lips may have white or whitish outer margins. There is a dark patch around the eye, which may be outlined with a white or light gray line or band. This is best illustrated in a fluid-preserved head at MACN (Fig. 4). A narrow light (white or gray) line runs from the angle of mouth or outer

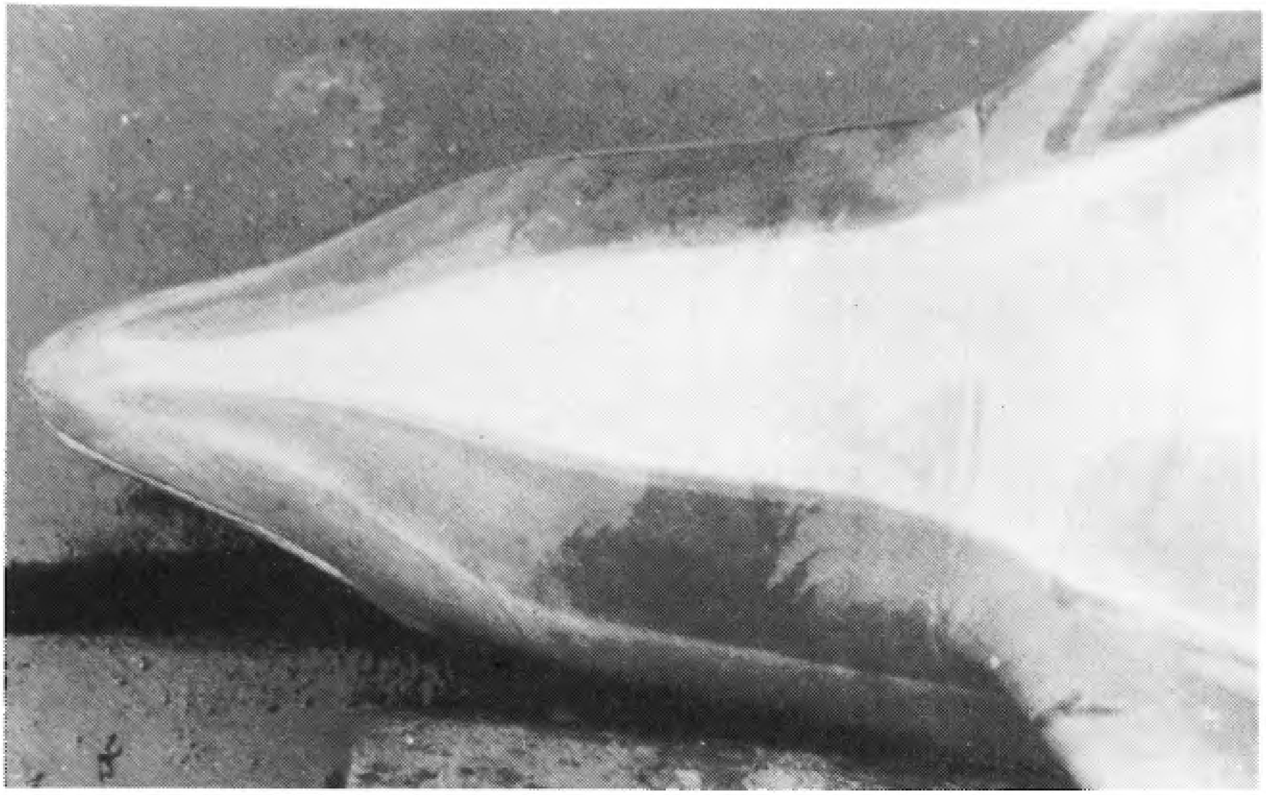

Fig. 5. Ventral pigmentation in the throat region in a specimen of Burmeister's porpoise (KSN68–315A).

eye patch to the centre or posterior insertion of the flipper. A wide medium-gray stripe runs from the lower lip (lower tip of jaw to almost the gape) backwards to the entire anterior insertion of the flipper. In specimen GH 860627 these stripes were light gray. There may be a lighter, ill-defined flipper patch. Reyes and Van Waerebeek (1995) note that the flipper stripe is asymmetrical, higher on the left side of the face and lower on the right. On re-examining the photographs, we found this to be true for KSN animals.

The lateral surfaces are dark, while the ventral surface is light gray to white. In the throat region this light area is narrow and ends with two forward-pointing lobes. It widens posteriorly with the widest part of the 'cross' behind the flippers (Fig. 5); the white then narrows toward the genital region. The ventral white area stops just behind the anus in a wide arc in females, more narrowly in males (Fig. 6). There may be gray striping or streaks on either side of the throat and genital region, which end at the mammary slits in the female, as described by Reyes and Van Waerebeek (1995). In some animals the ventral surface is light gray with a white patch (KSN 68–31 SA) in the genital area, or elongated lozenge from in front of the genital slit to behind the anus and another white spot around the umbilicus (JAO 8.1.76).

The flukes, flippers and dorsal fin are dark on all surfaces, although the tubercles on the anterior ridge of the dorsal fin may be a slightly lighter gray and more opaque (RNP 111).

Young

Young animals taken off Peru had the same pigmentation as the adults (Reyes and Van Waerebeek, 1995). Observers in other areas described calves at sea as darker than adults (Goodall *et al.*, 1990a; 1995). An 80cm live calf in the Canal Beagle had a uniformly opaque, very dark gray-black pigmentation, without any lighter areas on the ventral surface. The small dorsal fin sported the tubercles present in the adult (Goodall *et al.*, 1990a). An 86cm foetus examined by JAO (IZUA-MM15) was uniformly dark gray, with

Fig. 6. Ventral view and pigmentation of the genital region of a specimen of Burmeister's porpoise (KSN68–38SA).

a white line between the angle of mouth and anterior border of the flipper. The chest was lighter. An 81cm foetus examined by I.S. Cameron (IZUA-MM14) had a dark head and darker eye patch surrounded by white which continued backward just above the flipper (Fig. 4). The throat was a streaked or mottled white and there was a dirty white flipper patch. The flipper was dark with lighter posterior edges.

INTERNAL ANATOMY

Limited information is available for the species. Organ weights for a 58.5kg 151cm male (RNP 111) were: heart 520g; each lung 767g, liver *ca* 2,500g; spleen 48g; left kidney 266g, right kidney 259g; left testes 13.2g; right testes 13.5g. The intestine length for this specimen was 19m.

Blubber thickness was taken for six females and three males (Table 5). A young male (KSN 68–30SA), thought to be still suckling but also feeding on its own, had the highest blubber thickness. Females tended to have slightly thicker blubber in the austral summer.

KSN found that in 1968 there was a fishery for oil in the Golfo de Arauco, Chile, in which porpoises were caught, and that *Phocoena spinipinnis* produced markedly less oil than *Cephalorhynchus eutropia*. The fatty acids of this species are under study in Chile (Morales *et al.*, 1990).

The digestive system and liver of a 145cm female from Chile were studied by Pairoa and Garrido (1992). The skeleton is under study by Crovetto and Lemaitre (1991) and Menezes *et al.* (1994).

Table 5

Blubber thickness in specimens of Burmeister's porpoise, all taken incidentally in nets.

				Blubber thickness		
Specimen	Sex	TL	Month	Dorsal	Lateral	Ventral
RNP110	F	134.0	Dec.	2.2	2.5	2.7
KSN68-48SA	F	143.0	Sep.	1.5	-	-
KSN68-23SA	F	152.7	Aug.	2.0	1.8	1.9
KSN68-38SA	F	153.0	Sep.	1.6	-	-
KSN68-31SA	F	164.5	Aug.	2.0	1.8	2.0
RNP167	F	185.0	Dec.	-	2.3	-
KSN68-30SA	M	131.1	Aug.	3.7	3.0	3.0
RNP111	M	151.0	Dec.	2.0	2.0	1.8
KSN68-24SA	M	152.7	Aug.	-	2.3	2.0
JAO1979	-	172.0	-	-	2.3	-

Parasites

The only parasites reported in earlier literature were nematodes in the stomachs of one specimen (Brownell and Praderi, 1982; 1984). Detailed parasite examinations are given by Reyes and Van Waerebeek (1995) and by Corcuera *et al.* (1995). In animals taken off Chile, a variety of parasites were found (Torres *et al.*, 1990).

At least five of our specimens had parasites. RNP 111, a 151cm male, had parasites in the stomachs, lungs, liver, muscle and intestines. Specimen KSN 68–31 SA had the lungs filled with nematodes and had cysts in the ovaries. The stomachs of the 181cm GH female, which seemed to be an old animal, contained a large ball of nematodes. KSN 68–38 SA, a 153cm female, also had stomach parasites. A young 131cm male had no parasites. These parasites have not yet been studied.

Pathology

The GH female had gastric ulcers of 1.5cm in diameter on the walls of the forestomach and haemorrhages in the submucosa of the pyloric stomach. A small (126cm, 22kg) male that stranded alive near Mundo Marino Aquarium, south of Buenos Aires, was very thin and had sunken skin in the neck region. It did not recuperate during the eight days it lived; the necropsy revealed chronic lung lesions and bronchial pneumonia (Loureiro, 1986). Other pathological conditions in this species were reported by Reyes and Van Waerebeek (1995), and Van Bressem and Van Waerebeek (1994a; b). A description of poxvirus in this species is given by Van Bressem *et al.* (1993).

A number of diseased, deformed or rehealed bones have been found, including a mandible in MNHN-S (Philippi, 1896), and a mandible and snout in the Tierra del Fuego collection (RNP 1207, 1354).

AGE, REPRODUCTION AND GROWTH

Although a 44cm foetus taken in February off Uruguay was called 'full-term' (Brownell and Praderi, 1984), we concur with Reyes and Van Waerebeek (1995) that it probably was not near birth. These authors, on the basis of 33 foetuses and four neonates, determined birth size at about 86cm and occurrence in February and March.

We report two near-term foetuses of 81cm (IZUA MM14) and 86cm (IZUA MM15) collected in October and November off Valdivia, Chile; these animals would have been born in late spring. The latter animal was near birth and had meconium in the gut.

A small calf of approximately 80cm was caught live in a net in April in Tierra del Fuego (autumn birth), while a 126cm animal with few erupted teeth stranded in April far to the north, near Buenos Aires; it may have been born in summer (Loureiro, 1986).

The female studied by GH stranded in eastern Patagonia in late June (winter) and had recently given birth, as evidenced by the presence of milk, an enlarged uterus and a large corpora lutea in the ovary. The milk analysis (Table 6) was interesting in that it was mainly colostrum; it is the first milk analysis for this species. Corcuera *et al.* (1995) found a post-partum female in December off Buenos Aires.

Table 6

Analysis of milk (colostrum) of a 181cm Burmeister's porpoise which had recently given birth (GH 860627). Proteins (Kjeldhal method) 12.8% of weight. Fats (Geber method) 17.0% of weight.

Fatty acids (Chromatography F.6):			
Lauric acid	0.3%	Oleic acid	33.9%
Miristic acid	3.8%	Linoleic acid	0.9%
Miristoleic acid	0.2%	Linolenic acid	0.3%
Pnetadecanoic acid	0.6%	Arachidonic acid	3.4%
Pentadecenoic acid	0.3%	Gradoleic acid	0.3%
Plamitic acid	26.6%	Ecoisdodedoic acid	2.0%
Plamitoleic acid	10.2%	Uneicosenoic acid	0.7%
Heptadecanoic acid	1.2%	Behenic acid	1.8%
Stearic acd	9.2%	Tricosanoic acid	3.4%

Off Antofagasta, a simultaneously pregnant and lactating 165cm female was taken in August. It was caught in the same net with a 131cm male, assumed to be her offspring. Thirty four percent of the pregnant females off Peru were also lactating (Reyes and Van Waerebeek, 1995).

In our small study, females of 164.5, 181 and 183+cm were sexually mature.

Two males, the type specimen from Buenos Aires (Burmeister, 1869) and KSN-68-30SA from Chile, had false mammary slits.

BEHAVIOUR

Swimming pattern

The best series of observations on live animals was in Golfo San José, Península Valdés, Argentina (Würsig *et al.*, 1977; Würsig, 1992). Incidental sightings and other observations of behaviour have been compiled by Goodall et al. (1990a; 1995). This porpoise normally swims unobtrusively, with little disturbance of the water and showing little of the dorsal surface. It may swim fast and change direction erratically under water, staying down for two to four minutes, then taking a series of 7–8 breaths with an audible puffing noise. It is difficult to spot in windy weather.

A stranded calf held in an aquarium had a heart rate of 109 pulses per minute and took about seven breaths per minute (Loureiro, 1986).

Food habits

Detailed studies of stomach contents have been reported by Brownell and Praderi (1982; 1984) for one animal from Uruguay, 123 from Peru (Reyes and Van Waerebeek, 1995) and 35 from Chile (Escare and Oporto, 1992). Nine species of fish and one of squid were found, but the most common food was anchovy and hake (*merluza*). The Chilean animals sometimes picked up small snails, crustaceans and mollusc egg capsules. The diet in all cases was principally fish. Goodall and Galeazzi (1985) reported sparse amounts of fish, mysid shrimp and euphausiids in three specimens from Tierra del Fuego.

Food items were found in eight of the specimens in the present work but have not yet been studied. A 180cm female off Chile (JAO 2.i.76) had stomachs half full of fish vertebrae, probably *Trachurus* or *Thyrsites*. Three animals from the Canal Beagle had as yet unidentified stomach contents; that of a 151cm male weighed 134g. Four KSN specimens had stomach contents. A 131cm male caught near Antofagasta, Chile, had a little 'fish mash' in its stomachs, while a 165cm female, assumed to be its mother, had the first stomach filled with fish mash of what seemed to be anchovies. Another animal, off Chimbote, Peru, had 'some food', while a fourth, from Callao, Peru, contained 348g of food, including 15 vertebral columns of anchovies.

The head of a specimen caught near Ushuaia in 1974 was cut off and sent to MACN, where it is spirit-preserved. When received, the oesophagus contained half of a tailed hake (*merluza de cola, Macruronus magellanicus*), cut along with the head (HPC). A summary of prey species known to date is given in Table 7.

Table 7

Summary of prey species found in stomach contents of Burmeister's porpoises to date.

Area	Prey species	Common names	Reference
Peru			
Pucusana &	*Eugraulis ringens*	Anchovy	Reyes and Van Waerebeek,
other ports	*Merluccius gayi*	Hake, Merluza común	1995
n=123	*Sciaena deliciosa*	Drum	(includes McKinnon, 1988)
	Trachurus murphyi	Jack mackerel	
	Odontesthes regia	Silverside	
	Sardinops sagax	Sardine	
	Cynoscion analis	Weakfish	
	Seriolella violacea	Blackruff	
	Loligo gahi	Patagonian squid	
Callao n = 1	*Engraulis* sp.	Anchovy	KSN, this paper
Chile			
Antofagasta n = 2	*Engraulis* sp.?	Anchovy?	KSN, this paper
Quele	*Merluccius gayi*		Escare and Oporto, 1992
n = 35	*Engraulis ringens*	Anchovita	
	Trachurus murphyi	Jurel	
	Sardinops sagax	Sardina española	
	Clupea bentincki	Sardina común	
	Genypterus chilensis	Congrio colorado	
	Eleginops maclovinus	Róbalo	
	Odontestes regia	Cauque	
	Loligo gahi	Squid (one occasion only)	
	--	Small snails	
	--	Small crustaceans	
	--	Mollusc egg capsules	

Continued

Table 7 cont.

Area	Prey species	Common names	Reference
Argentina			
Tierra del	--	Unidentified fish	Goodall & Galeazzi, 1985
Fuego	--	Mysid shrimp	
n = 3	--	Euphausiids	
n = 1	*Macruronus magellanicus*	Tailed hake, merluza de cola	HPC, this paper
Sighting of 6-7 animals feeding	*Sprattus fuegensis*	Fuegian sardine	A.C.M. Schiavini, this paper
Necochea	*Engraulis anchoita*	Anchovy, anchoita	Corcuera, 1991
n = 1	*Loligo sanpaulensis*	Calamarete (one beak)	
	Unidentified shrimp	Camarón (one individual)	
Uruguay			
n = 1	*Merluccius hubbsi*	Patagonian hake	Brownell & Praderi, 1982
	Pagrus sedecim	Porgy	
	Unidentified ephalopod	Squid (one individual)	
Brazil			
Río Grande	*Cynoscion striatus*	Pescadilla	Pinedo, 1989
do Sul	*Mactra* sp.	Molluscs	
n = 1	*Pelecytallas*	--	

EXPLOITATION

Bones and part of a skull identifiable as *P. spinipinnis* were found in Canal Beagle aboriginal kitchen middens carbon-dated at 6,500 years and 2,400 years ago, indicating early exploitation of this species as a food resource (Piana *et al.*, 1985).

The heavy recent exploitation of this species has been dealt with in several recent papers. Off Peru, Burmeister's porpoises are taken principally in nets and may be used as bait or food (Clarke, 1962; Grimwood, 1969; Gaskin and Read, 1987; Van Waerebeek and Reyes, 1988; 1989; Reyes and Van Waerebeek, 1995). Off northern and central Chile they are also taken in nets (Aguayo, 1975; Mitchell, 1975; Goodall and Cameron, 1980; Guerra *et al.*, 1987). Near Queule in south-central Chile they are taken in nets set for ratfish and sciaenids from 2–12 n.miles offshore. From 1988–90, 159 Burmeister's porpoises were taken in this fishery (Oporto and Brieva, 1994; Reyes and Oporto, 1994). In southern Chile these porpoises may be harpooned for bait for crab traps (Anon., 1987; Cárdenas *et al.*, 1987; Lescrauwaet and Gibbons, 1994).

Off Uruguay these porpoises die incidentally in nets set for sharks (Pilleri and Gihr, 1972; 1974; Brownell and Praderi, 1982; 1984). Off the province of Buenos Aires, Argentina, they die in gillnets set in waters up to 25 n.miles from the coast (Corcuera *et al.*, 1994; 1995).

In southern Tierra del Fuego, Argentina, one animal died in 1974 and four were caught in 1976 in bottom nets set for southern king crab (*centolla*); this fishery no longer exists. Specimens found along the northeast coast of Tierra del Fuego (Fig. 1) were probably taken incidentally in shore-based gillnets set for fish (Goodall, 1978; 1989; Goodall and Cameron, 1980; Goodall *et al.*, 1994).

Although the method of beaching of many worn skulls is unknown (Table 1), we found that most specimens in this study came from captures of one sort or another; only three specimens could be traced directly to strandings (Table 2). Only one small stranded animal has been kept in captivity; it died after eight days (Loureiro, 1986).

The Burmeister's porpoise is on CITES Appendix II and is labelled 'insufficiently known'. Because of the high level of take, 'estimates of abundance .... basic information on range, stock identity, biology and behaviour' are needed in planning for conservation and management of the species (IWC, 1991; Klinowska, 1991; Reeves and Leatherwood, 1994).

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Aspects of the Biology of Burmeister's Porpoise from Peru

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ABSTRACT

Burmeister's porpoise (*Phocoena spinipinnis*), one of the most common small cetaceans in Peruvian waters, suffers the second highest fishing mortality. Biological data obtained from porpoises caught in gillnets off Peru from 1983 to 1989 are presented. The largest specimens are a 183cm female and a 182cm male (n=402), although on average, mature males are significantly (p<0.0001) larger than females: 170.3cm (n=63) versus 165.5cm (n=56). The relationship between standard length (X) and body mass (Y) is best described by the equation $\log Y = -0.714 + 2.48 \log X$ (r=0.97; n=123; p<0.0001). Sexual dimorphism is statistically significant (p<0.05 and p<0.005) in eight cranial measurements and one meristic, but not in the condylobasal length. The correlation between condylobasal length and body length is relatively low (r=0.72). Sexual dimorphism in the colour pattern of the ventral field is described. A characteristic of this species is the bilateral asymmetry in the shape and extent of the flipper stripe. Minimum and average length (50%) at sexual maturity are respectively 153cm and 154.8cm in females (n=56) and 158cm and 159.9cm in males (n=63). The pregnancy rate is estimated at 0.60. Of the pregnant females, 34% were lactating. No evidence for a male seasonal reproductive cycle was found but the sample size was small (n=37). Periodicity in occurrence and size of foetuses and neonates suggests a gestation period of 11–12 months, with a peak of conceptions in summer. The sex ratio of foetuses and small neonates did not deviate significantly from 1:1 (chi^2, p >0.50). Length at birth is estimated as approximately 86cm. The Burmeister's porpoise mainly feeds on fish, including *Engraulis ringens*, *Sciaena deliciosa*, *Anchoa* sp. and *Merluccius gayi*. Endoparasites found include the trematodes *Nasitrema globicephalae*, *Synthesium tursionis*, *Pholeter gastrophylus* and *Braunina cordiformis*, as well as the nematodes *Anisakis typica*, *Stenurus* sp., *Halocercus* sp. and *Pseudalius inflexus*. Ectoparasites recorded are *Isocyamus* sp. and *Xenobalanus globicipitis*. Paita Bay (05°S) is confirmed as the northern distribution limit of the species on the Pacific coast of South America.

KEYWORDS: BURMEISTER'S PORPOISE; SOUTH PACIFIC; INCIDENTAL CAPTURE; MORPHOLOGY/ANATOMY; GROWTH/LENGTH DISTRIBUTIONS; BIOLOGICAL PARAMETERS; REPRODUCTION; SEXUAL MATURITY; FEEDING; FISH; PARASITES; DISTRIBUTION

INTRODUCTION

Burmeister's porpoise, *Phocoena spinipinnis*, was described by Burmeister (1865) from a specimen caught in the mouth of the La Plata River in Argentina. The Louis Agassiz expedition collected a second specimen in Paita Bay, northern Peru, in 1872 (Allen, 1925). Pérez Canto (1895) described his *Acanthodelphis philippii* from a porpoise collected at Valparaiso, central Chile. These, and an additional specimen from Chile (Philippi, 1896), are the only known records of the species in the 19th century.

This century, several authors have contributed to our knowledge of the general biology of this porpoise, including Gallardo (1917), Allen (1925), Praderi (1971), Pilleri and Gihr (1972; 1974), Würsig *et al.* (1977) and Brownell and Praderi (1984). However, as most reports were based on a single or a few specimens, the amount of information available has

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been limited. Other authors have discussed incidental mortality of this species in fishing operations (Clarke, 1962; Grimwood, 1969; Aguayo, 1975; Mitchell, 1975; Clarke *et al.*, 1978; Brownell and Praderi, 1982).

In recent years a systematic study of the status and biology of small cetaceans in Peru, greatly accelerated by the UNEP/IUCN Burmeister's Porpoise Project, has yielded a large amount of new data (Gaskin *et al.*, 1987; Reyes and Van Waerebeek, 1990). Burmeister's porpoise is one of the most common small cetaceans in Peruvian waters, and the species which suffers the second largest fishing mortality (Read *et al.*, 1988; Van Waerebeek and Reyes, 1990; 1994).

Here we present a preliminary analysis of biological parameters of the Burmeister's porpoise from Peru based on a large sample obtained during the UNEP/IUCN project and subsequent studies. Goodall *et al.* (1995) review the available information for this species for southern South American waters.

MATERIALS AND METHODS

Almost all of the porpoises examined had been caught in gillnets set by artisanal fishermen and were obtained fresh. A few stranded animals were, however, included in the material. Most of the specimens were collected at Pucusana (12°30′S), Cerro Azul (13°00′S), Huacho (11°07′S), San Andrés (13°45′S), Ancón (11°47′S) and Pacasmayo (7°24′S). For most specimens, standard length and sex were recorded. However, due to the nature of the fishery and fishery terminal activities, sampling for studies of reproduction, feeding, colour pattern, morphometrics, parasites and osteology was opportunistic. Consequently, sample sizes for each parameter considered vary widely. External morphometrics were recorded as modified from Norris (1961). Colour transparencies were taken in both lateral and ventral aspects supported by notes on the colouration whenever necessary.

Gonads were weighed (testis with epididymis), measured and examined macroscopically before wholly or partially being preserved in 10% formalin. Sexual maturity in females was determined by the presence of ovarian corpora or from evidence of lactation. Males were considered sexually mature if seminal fluid was clearly visible upon cutting the fresh epididymis ('functional maturity' *sensu* Sergeant, 1962). Size at birth was estimated through interpolation of sizes from the largest foetuses and the smallest neonates. Standard length at 50% sexual maturity was derived from a plot of percent mature versus standard length. In calculating the 0.50 maturity estimator it was assumed that a linear relationship exists between bordering experimental values. Confidence intervals have not been developed for this type of estimator (DeMaster, 1984).

Five teeth were removed from the middle of the left lower jaw, fixed in formalin and preserved in 70% ethanol for later examination. The stomach chambers were examined separately. Otoliths found were preserved dry. Squid beaks were preserved in 5% formalin. The skin and internal organs were inspected for the presence of parasites which were collected and preserved according to standard techniques (Dailey, 1978; Pritchard and Kruse, 1982). Osteological material was collected from fresh specimens at fishmarkets and through surveys of beaches and refuse dumps near fishing towns.

A total of 32 skull measurements, taken with vernier callipers to the nearest mm, and four meristics were recorded following Perrin (1975) and Schnell *et al.* (1982). Two-tailed t-tests were applied to examine for sexual dimorphism in the skull morphology. Because no skull character was found to determine unequivocally physical maturity, only skulls of sexually mature animals (20 males, 12 females) were used in the analysis.

RESULTS AND DISCUSSIONS

Of a total of 402 Burmeister's porpoises of known length and sex (235 males, 167 females) the largest female measured 183cm and the largest male 182cm standard length. The mean length of sexually mature males was 170.3cm (SD=5.36; n=63), which was significantly larger (two-tailed t-test, this and all subsequent; t=4.20, df=117, $p<0.0001$) than the 165.5cm (SD=7.06; n=56) mean length of mature females, a characteristic that distinguishes this species from the harbour porpoise, *Phocoena phocoena* and probably from the vaquita *Phocoena sinus* (Gaskin *et al.*, 1984; Brownell *et al.*, 1987; Vidal, 1994).

The greatest body weights recorded were for males (n=70), 72kg for a 170cm specimen and females (n=60), 79kg for a 173cm animal. A standard length-body mass relationship was derived from a dataset of 123 (postnatal) porpoises. A linear regression was applied after a log-log transformation of the variables (Fig. 1): with Y = body mass (in grams); X = standard length (in cm); $\log Y = -0.714 + 2.48 \log X$ (r=0.97; $p<0.0001$). Weights for some organs of both sexes are shown in Table 1.

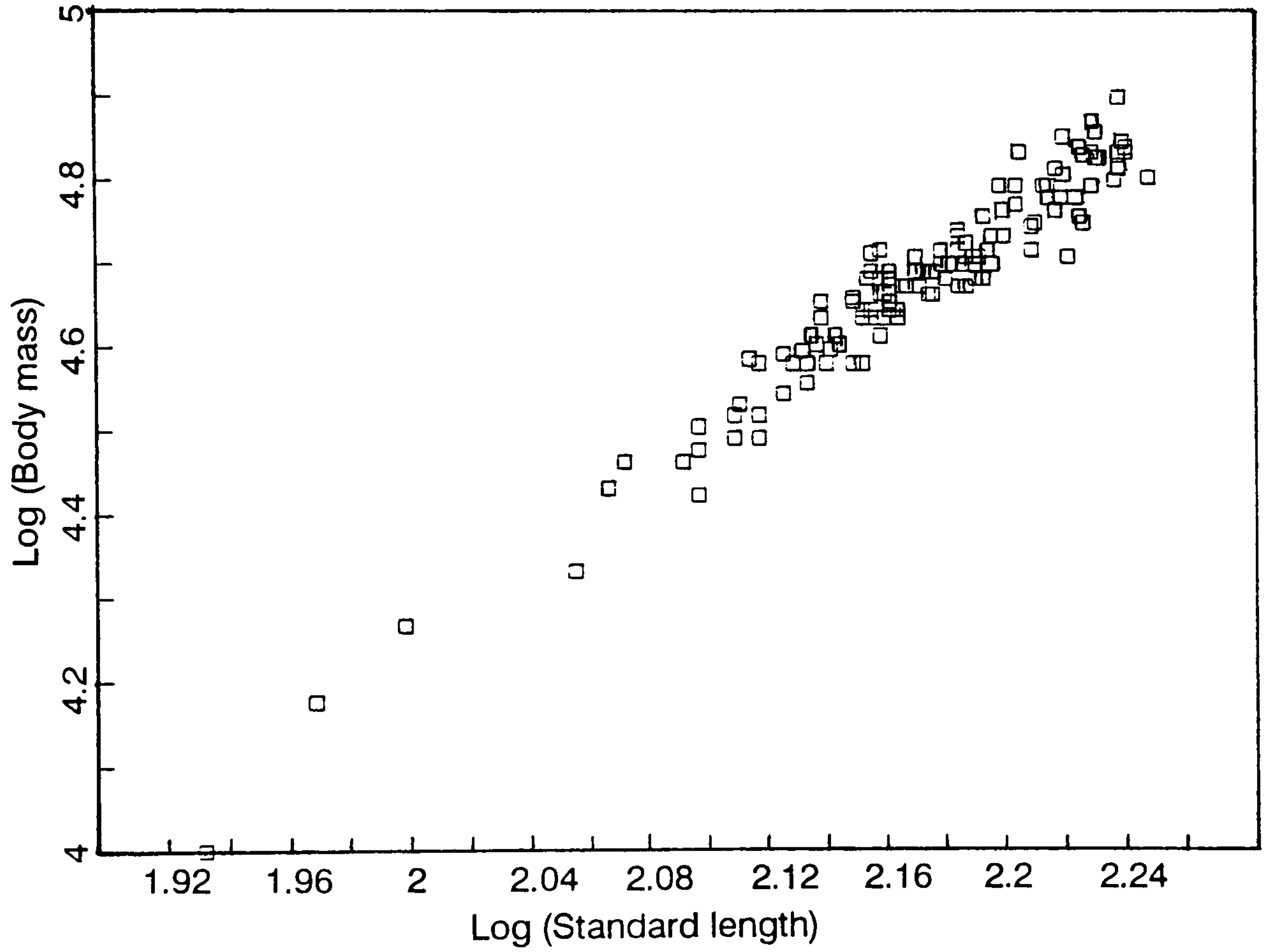

Fig. 1. Standard length-body mass relationship for 123 postnatal Burmeister's porpoises from Peru. The regression is described by: $\log Y = -0.714 + 2.48 \log X$ (r=0.97, $p<0.0001$), where Y = body mass (in grams) and X = standard length (in cm).

Cranial morphology

Summary statistics for cranial measurements and meristics of sexually mature Burmeister's porpoises are listed in Table 2. No significant difference in skull size (condylobasal length, CBL) was found between sexes (t-test, $p>0.05$), but the sample

Table 1

Weights of selected organs, in grams, of adult *P. spinipinnis* from Peru.

No.	Sl(cm)	Total wt(kg)	Left gonad	Right gonad	Left kidney	Right kidney	Liver	Pancreas	Spleen	Heart	Left lung	Right lung
Females												
JCR273	153	55	11	1	150	181		90	21			
JSM003	159	58			214	248		93	22			
KVW928	160	59	26	8	210	225		130	26			
KVW754	164	62	17	2	270	270		160				
KVW199	164	62	7	2	200	210		84	25			
JCR1150	164	60	12	8	305	270		165	24			
JCR256	165	65	26	1	278	291		190	14			
JCR975	166	71	17	2	290	300	2450	160	30	400	1130	1150
JCR500	169	68	12	1	228	224		132	20			
JCR657	173	63	7	1	300	325		100	52			
JCR1485	173	79	14	1	280	275		150	21			
Males												
KVW383	160	62	240	240	180	185		110				
JSM001	162	56	183	182	204	186			52			
KVW954	162	52	100	85	215	215		150				
JSM005	163	56	256	240	197	210		95	16			
JSM002	169	56	228	216	205	223			31			
JSM226	170	62	300	300	170	190	1600	80	10	290	860	740
KVW366	170	72	360	320	280	280			60			
JCR702	171	67	296	247	160	170		154				
JCR1275	174	69	290	270	285	270		160	54			

sizes were small. Sexual dimorphism was statistically highly significant ($p<0.005$) in zygomatic width, parietal width, height of braincase and maximum length of tympanic bulla, and significant ($p<0.05$) in rostrum length from base, postorbital width, upper tooth row length, number of teeth upper right and greatest width of tympanic bulla (Table 2).

A linear regression of CBL against standard length, with sexes pooled ($n=54$) gave a line of best fit of $Y = -1190.63 + 9.90X$ ($r=0.72, p<0.0001$), where Y = standard length in mm and X = CBL in mm (Fig. 2). In general, the size of the skull was found to be a poor index of maturity because small animals may have relatively large skulls and vice versa. Estimation of standard length and cranial maturity based on the CBL is not to be recommended.

Teeth

The number of erupted teeth in fresh animals ranged from 10 to 23 ($n=148$) in each upper row and from 14 to 23 ($n=147$) in each lower row. There is great variation in the number of visible upper teeth, in particular due to the presence on both sides of a series of 3–5 small teeth which are not anchored in alveoli and only slightly protrude from the gums. Young porpoises tend to have higher tooth counts than older animals, suggesting that these non-alveolar teeth are lost with age, as the latter can easily be removed by simple pulling. Non-alveolar teeth are often lost during preparation of the skull. In addition one to three pairs of very small teeth are embedded in the gum at the tip of both upper and lower toothrows and are rarely seen in the fresh animal. Both factors together explain why tooth counts in skulls and in fresh heads are not directly comparable.

Table 2

Cranial measurements (in mm) and meristics of sexually adult Burmeister's porpoises from Peruvian waters. Student t-values are given where significant differences (two sided, $p<0.05$) exist between sexes. NS = not significant. Condylobasal length (CBL), length rostrum from base (LRBA), length rostrum from pterygoid (LRPT), width rostrum at base (WRBA), width rostrum at 1/4 length (WR1/4), width rostrum at 1/2 length (WR1/2), width premaxillaries at 1/2 length (WP1/2), width rostrum at 3/4 length (WR3/4), preorbital width (PROW), postorbital width (POOW), zygomatic width (ZYW), parietal width (PARW), height braincase (HBR), length braincase (LBR), maximum width of premaxillaries (MWPR), width external nares (WEN), temporal fossa length (TFL), temporal fossa width (TFW), orbital length (ORL), length of antorbital processus (LAP), separation pterygoids (SEPT), width of internal nares (WIN), length upper toothrow (UTRL), number of teeth upper left (NUUL), number of teeth upper right (NUUR), number of teeth lower left (NULL), number of teeth lower right (NULR), length lower toothrow (LTRL), height of mandibular ramus (HRA), length of mandibular ramus (LRA), width of foramen magnum (WFM), maximum width of nasals (WINA), maximum width of palatines (WIPA), length of tympanic bulla (LTY), width of tympanic bulla (WTY), and length of periotic (LPE).

	Females				Males					
Variable	n	Range	Mean	SD	n	Range	Mean	SD	t	p
CBL	14	279-292	284.64	3.95	22	270-297	283.68	7.61		NS
LRBA	14	121-131	127.07	2.79	22	116-132	124.64	3.74	2.09	<0.05
LRPT	13	149-165	155.46	4.88	20	141-162	153.45	5.18		NS
WRBA	13	78- 87	83.08	2.29	19	77- 87	83.00	3.04		NS
WR1/4	14	58- 66	61.93	2.62	20	55- 64	60.85	2.30		NS
WR1/2	14	48- 54	51.71	2.13	21	48- 56	51.38	2.50		NS
WP1/2	14	25- 29	26.93	1.44	22	23- 29	26.68	1.49		NS
WR3/4	14	36- 41	39.00	1.75	21	35- 43	38.95	2.38		NS
PROW	14	124-139	131.07	4.34	21	127-140	133.38	3.47		NS
POOW	14	147-156	152.21	2.69	21	150-162	154.81	2.82	2.72	<0.02
ZYW	14	150-160	156.00	2.88	21	155-166	159.10	2.90	3.11	<0.005
PARW	14	128-137	132.21	3.19	22	127-144	135.27	4.07	3.76	<0.001
HBR	14	79- 90	87.07	2.70	22	86- 95	90.05	2.61	3.29	<0.005
LBR	14	109-119	113.00	3.37	22	110-121	114.64	3.36		NS
HWPR	14	32- 43	39.36	2.98	22	36- 45	40.14	2.32		NS
WEN	14	27- 34	30.36	2.06	22	27- 35	30.73	2.21		NS
TFL	13	55- 63	59.85	2.15	21	53- 65	59.76	3.74		NS
TFW	13	45- 54	47.62	3.31	21	40- 55	48.48	3.84		NS
ORL	13	45- 55	49.23	2.83	20	46- 59	50.75	3.31		NS
LAP	14	24- 30	26.86	1.70	21	19- 32	28.10	2.72		NS
SEPT	14	22- 27	23.57	1.40	21	18- 27	22.19	2.11		NS
WIN	14	44- 51	47.71	2.02	22	43- 52	47.68	2.28		NS
UTRL	14	72-103	84.86	10.6	22	69- 99	77.86	6.86	2.41	<0.05
NUUL	12	13- 21	17.50	2.20	17	14- 22	16.82	1.74		NS
NUUR	12	16- 20	17.42	1.24	20	14- 19	16.40	1.35	2.12	<0.05
NULL	12	17- 22	20.00	1.28	22	18- 21	19.23	1.02		NS
LULR	12	18- 25	19.42	1.93	22	18- 23	19.59	1.33		NS
LTRL	14	86- 97	90.50	2.77	22	82- 98	89.77	4.00		NS
HRA	14	53- 59	57.14	1.92	22	53- 60	56.68	2.23		NS
LRA	14	211-229	219.57	4.36	22	209-225	218.14	4.69		NS
WFM	14	28- 34	31.29	1.73	21	28- 34	31.00	1.64		NS
WINA	14	25- 31	28.07	2.09	22	24- 33	29.10	2.69		NS
WIPA	14	47- 54	49.86	1.96	21	47- 54	51.14	1.98		NS
LTV	14	29- 32	30.36	0.74	19	30- 33	31.47	0.70	4.40	<0.0005
WTY	14	18- 20	19.50	0.65	19	18- 21	20.05	0.78	2.15	<0.05
LPE	14	27- 30	28.86	1.03	20	26- 31	29.10	1.29		NS

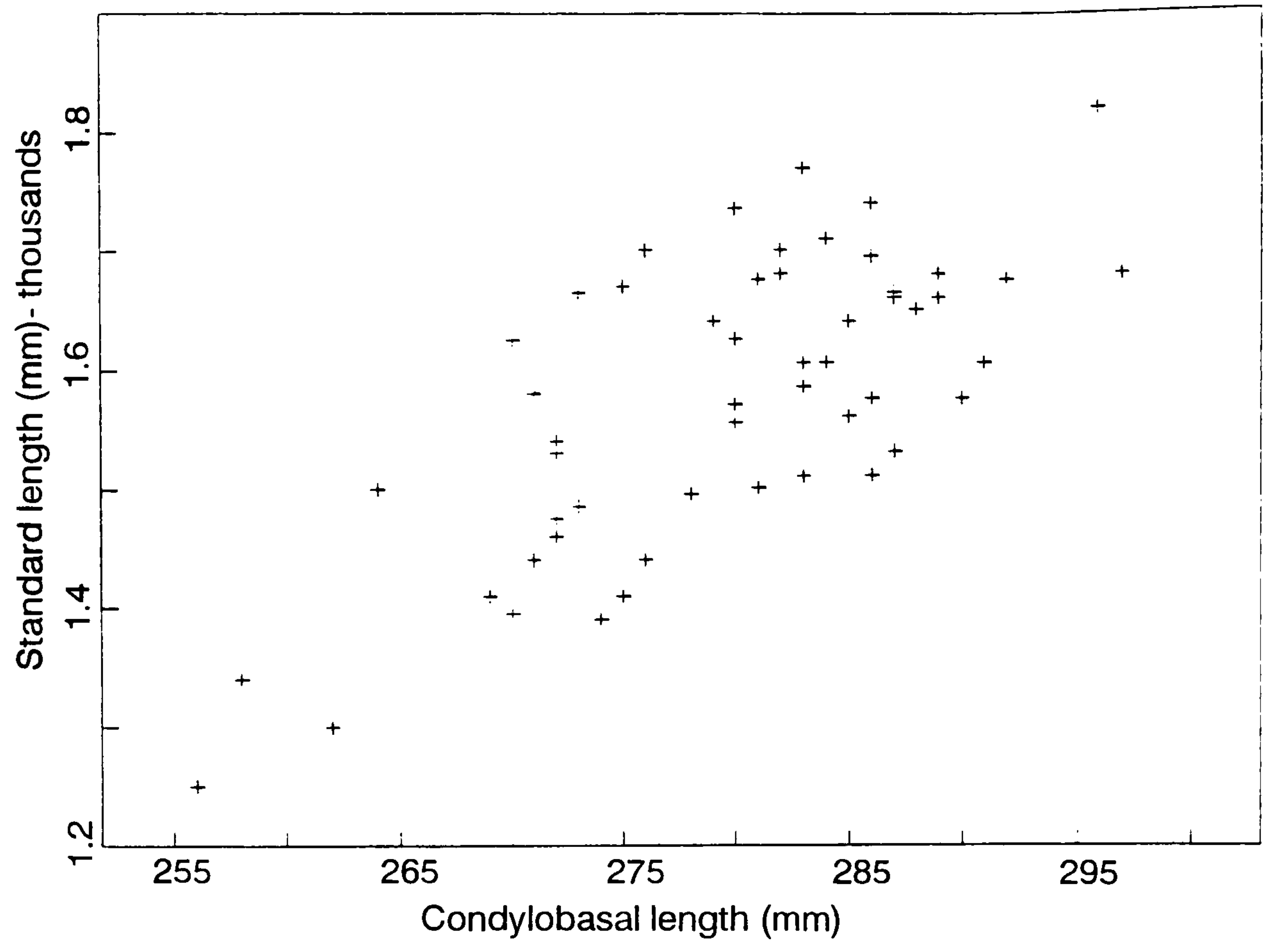

Fig. 2. Relationship between standard length and condylobasal length for 54 Burmeister's porpoises from Peru. The regression line was fitted from the equation: $Y = -1190.63 + 9.89X$ ($r=0.72$, $p<0.0001$), where Y=standard length (in mm) and X=condylobasal length (in mm).

Colouration

Several authors (Burmeister, 1869; Pérez-Canto, 1895; Philippi, 1896; Würsig *et al.*, 1977; Brownell and Praderi, 1984) have given, sometimes conflicting, descriptions of colouration of Burmeister's porpoise. Fresh porpoise carcasses of both sexes and all age classes examined in this study (n=87) were dark gray (less often lead gray) dorsally and laterally, with a light gray abdominal field. The gray sometimes had a brownish hue although this was not widespread in the sample. The few animals landed alive did not differ from this pattern. The porpoise has a well-defined eye patch surrounded by a light gray halo, a distinctive feature it shares with the vaquita and the spectacled porpoise (*Australophocaena dioptrica*). An anterior projection of the eye patch ('tear' after Brownell *et al.*, 1987) is observed in some specimens. A wide apex to the blowhole stripe (*sensu* Mitchell, 1970) which joins the lip patch is also present. The flipper stripe is dark gray and sharply defined and extends from the mandible to the insertion of the flipper. Unique among phocoenids is the asymmetry in the shape and width of the flipper stripe. On the left side the width of the stripe is nearly uniform, and at its anterior end fuses with the lip patch beneath the mouth angle. However, on the right side the flipper stripe becomes narrower with curving borders, and descends towards its anterior end where it joins the lip patch near (or often in) the chin patch (Fig. 3). A thin, light gray line runs parallel to, and below, the flipper stripe.

A pair of stripes is also present on the abdominal field. These project from the middle of the lower flanks, extending posteriorly towards the genital area where they bifurcate,

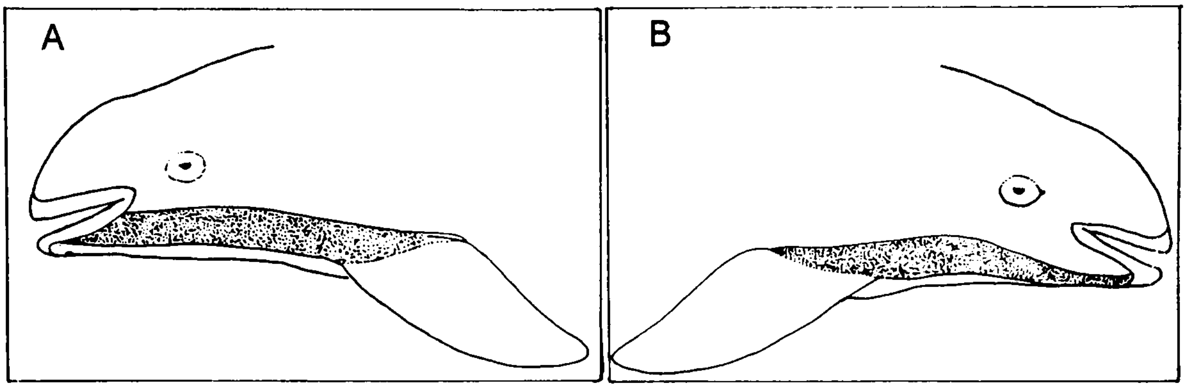

Fig. 3. Schematic representation of the asymmetry in the flipper stripe in Burmeister's porpoise: A. left side; B. right side.

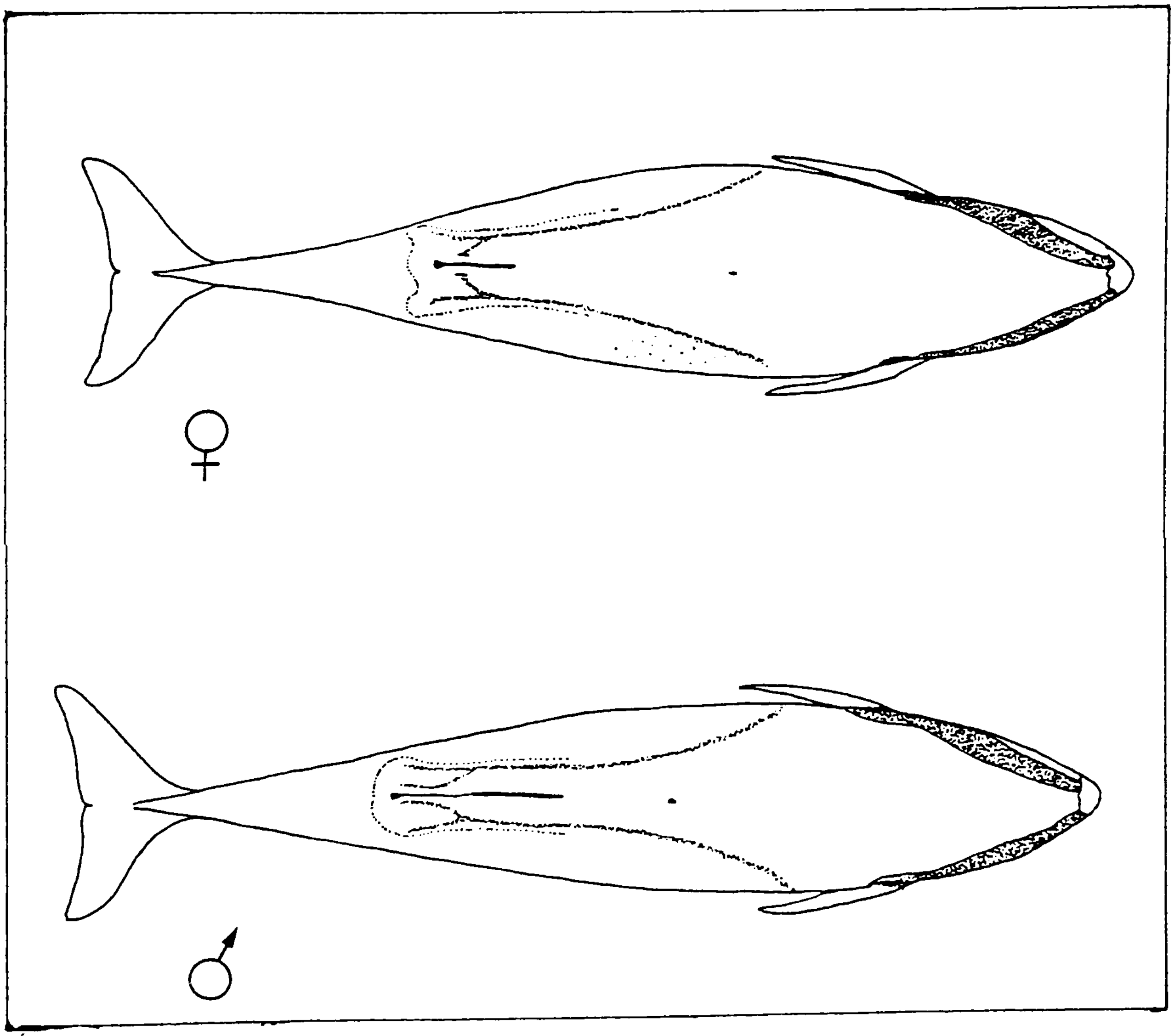

Fig. 4. Sexual dimorphism in the ventral colour pattern of the Burmeister's porpoise.

producing accessory stripes. In females, the accessory stripes end in the mammary slits, while in males they converge immediately behind the genital slit to flank the perineal groove (Fig. 4).

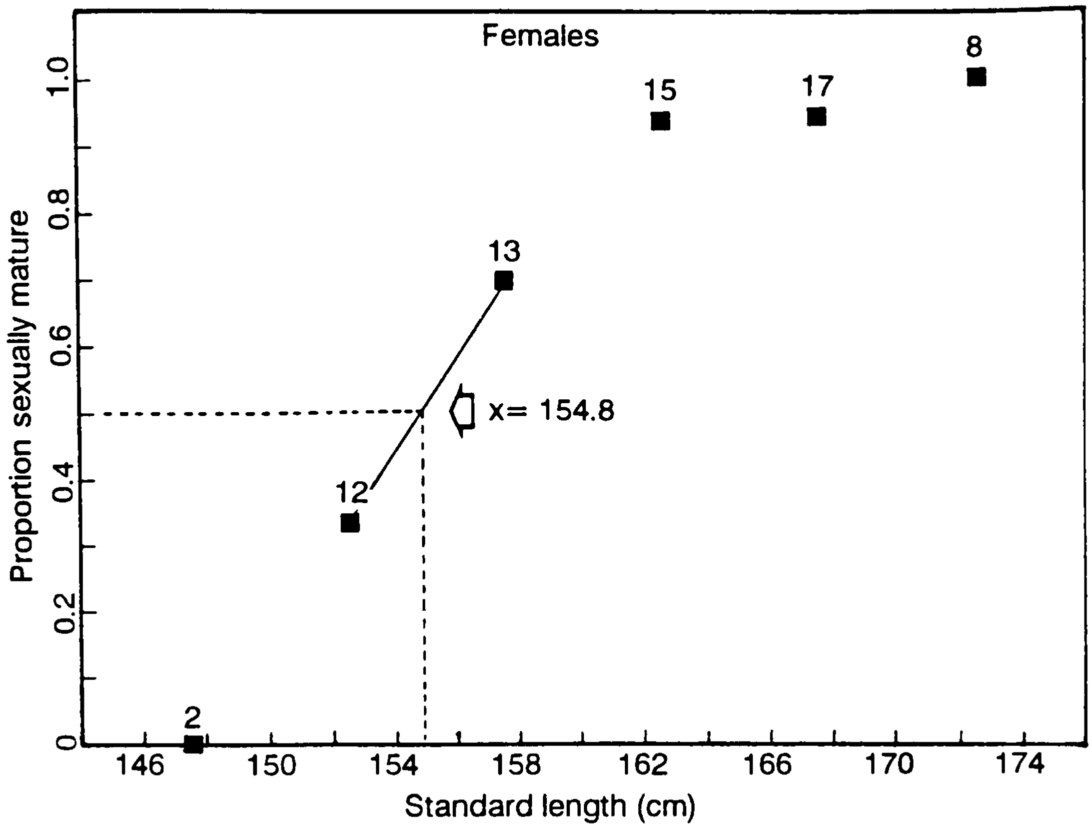

Fig. 5. Plot of standard length class midpoints versus proportion mature female *P. spinipinnis* of Peruvian waters. Figures above plot marks indicate class frequencies. Length at $P(0.50)$ is estimated through linear interpolation between bordering class midpoints: $Y = -10.62 + 0.072X$. Variance estimates have not been developed.

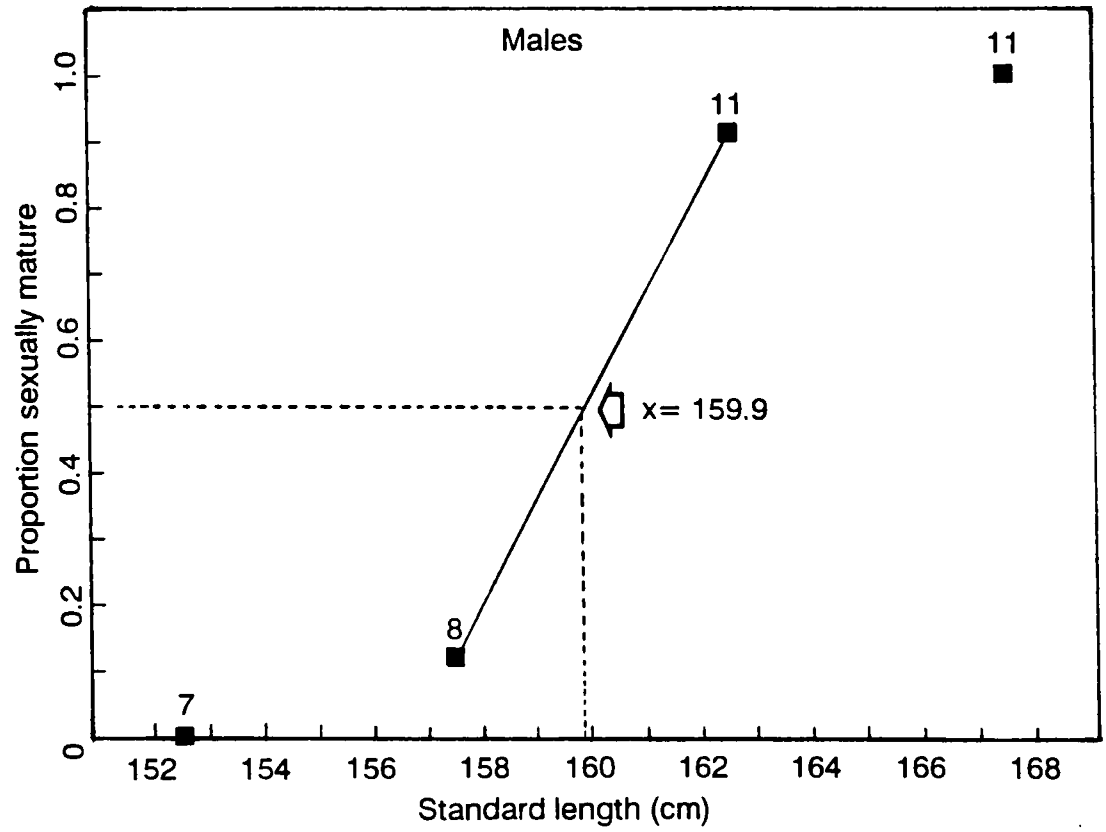

Fig. 6. Plot of standard length class midpoints versus proportion mature male *P. spinipinnis* of Peruvian waters. Length at $P(0.50)$ is estimated through linear interpolation between bordering class midpoints: $Y = -24.57 + 0.157X$.

Reproduction

In our sample, 50% of females (n=148) had attained sexual maturity at an estimated length of 154.8cm (Fig. 5), which is about 5cm smaller than for males (see below). The largest sexually immature female (n=92) was 166cm long while the smallest mature female (n=56) measured 153cm. Of the 53 adult females examined, 60% (32) were pregnant. The actual pregnancy rate however may be somewhat higher, since only females with a foetus large enough to be noted by gross examination were included. Eleven (34%) of the pregnant females were simultaneously lactating, indicating that annual reproduction can occur, assuming that lactation is less than one year as in *Phocoena phocoena* (Gaskin *et al.*, 1984).

On a combined sample (n=31) of foetuses above 50mm (below which they cannot be sexed reliably, see Kasuya and Marsh, 1984) and small neonates, 54.8% are female. The observed deviation from a 1:1 sex ratio is not significant (chi^2=0.29; p>0.50).

Length at 50% sexual maturity in males is estimated at 159.9cm (Fig. 6). The smallest sexually mature male (n=63) was 158cm with a mean testis length and weight of 129mm and 300g respectively. The minimum weight for a mature testis (with epididymis) was 85g. The mean single testis weight of adult porpoises plotted by month did not suggest seasonality in the male reproductive cycle (Fig. 7). However, the sample size was small and further work is required to confirm or deny this.

Brownell and Praderi (1982) reported on a 44cm long foetus of Burmeister's porpoise which they referred to as 'near term'. Gaskin *et al.* (1984) discussed size at birth in phocoenids and stated that 'probably no phocoenid is less than about 60cm long at birth'. The data for *P. spinipinnis* from Peruvian waters are in agreement with the latter statement. The largest recorded foetuses were 85.5cm and 87cm in length (n=33). The smallest neonate seen measured 85.5cm (n=4). Therefore length at birth in this species is approximately 86cm.

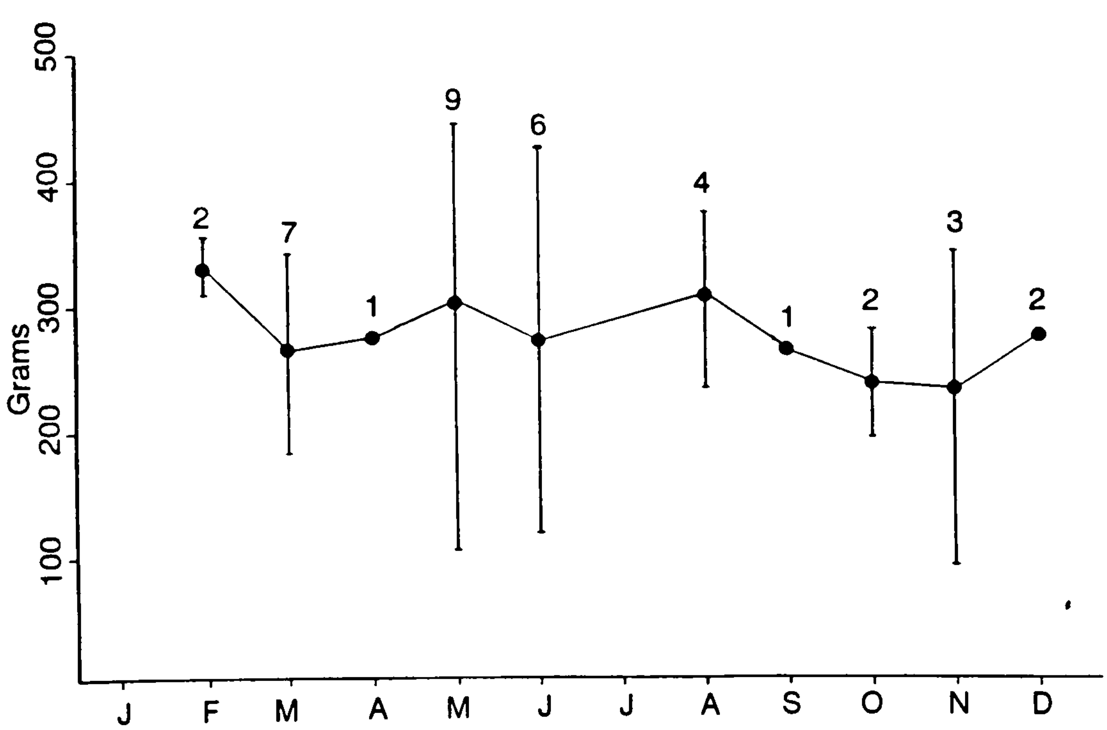

Fig. 7. Mean single testis weight and range bars for sexually mature *P. spinipinnis* from Peru plotted by month. Sample sizes are shown.

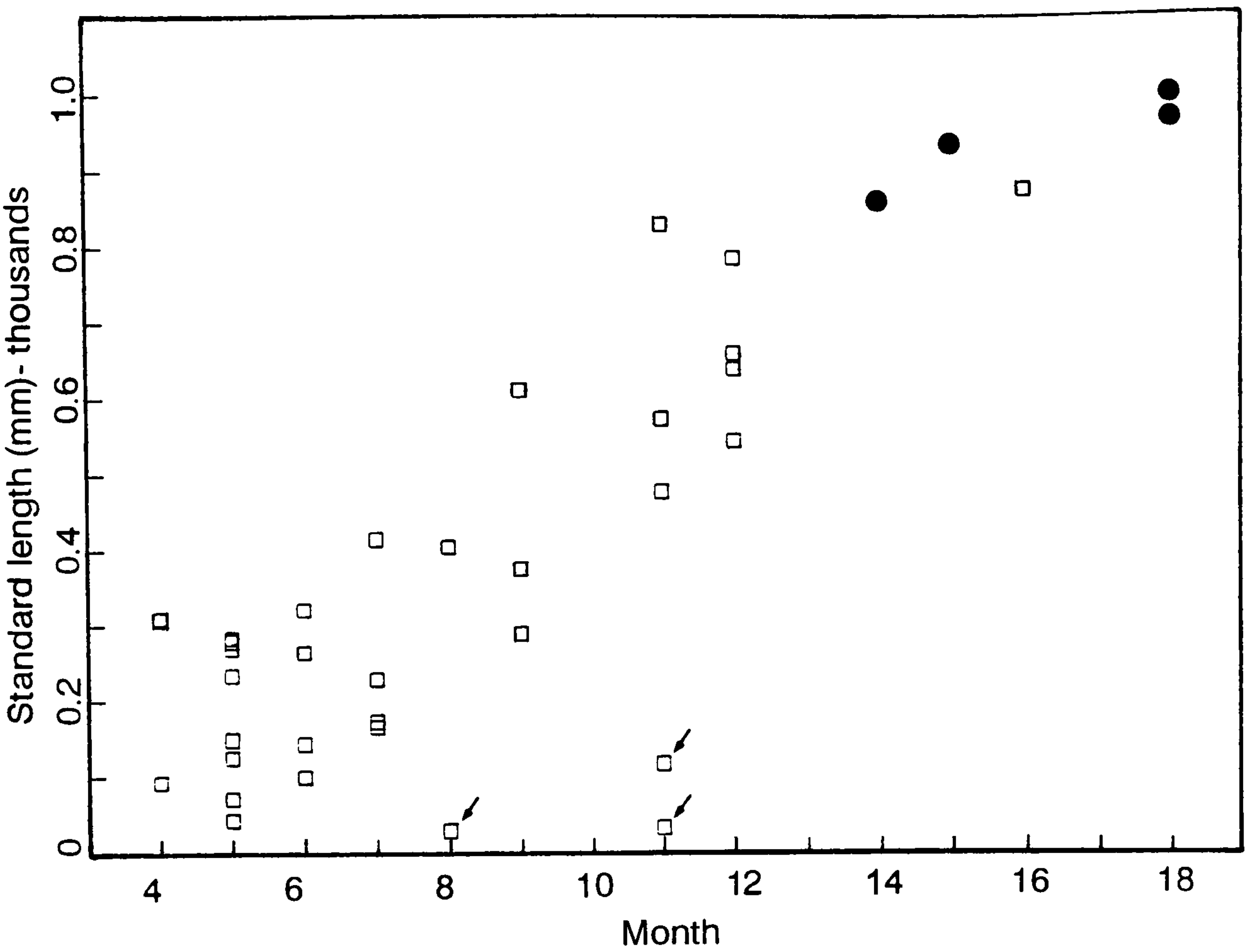

Fig. 8. Size of foetuses (boxes) and small neonates (circles) of *P. spinipinnis* from Peru by month of occurrence. Data are adjusted to a 14 month period (e.g. April=4 and 16) so as to permit small neonates to be plotted in linear sequence and fitted by regression: $Y = -152.3 + 66.09X$ ($r=0.93$; $p<0.0001$). Three outliers, indicated by an arrow, were eliminated from the regression dataset.

The correlation between time of the year and size of foetuses and small neonates ($n=34$) is shown in Fig. 8. Although data on foetuses smaller than 29mm, representing the earliest phase of the growth curve, are not available, it indicates that the peak of the mating season occurs during summer, possibly in February-March. This, and the fact that the smallest neonates were seen in February (85.5cm) and in March (93cm) suggests a gestation period of 11–12 months. A few small foetuses found in November and August (outliers in Fig. 8) indicate that at least some successful mating occurs out of the main season.

Feeding habits

McKinnon (1988) examined stomachs from 62 incidentally-caught Burmeister's porpoises from Peru. In the present study, stomachs from an additional 61 porpoises were examined to compare for possible temporal or spatial shifts in food composition. The results of stomach content analysis for porpoises landed at Pucusana and Cerro Azul during the period 1987–9 are shown in Table 3.

Anchovy was by far the most common food (52 of 54 stomachs (96%) with contents examined) similar to findings of McKinnon (1988) in the period 1985–6. Hake was another important prey species with the second highest incidence (13%). Surprisingly, no anchoa otoliths were found in the period 1987–9.

Table 3

Prey composition from stomach content analysis of Burmeister's porpoises (n=61) from Peruvian waters.

Species	Scientific name	% Total count of prey items	% Incidence of items	% Incidence in McKinnon (1988)*
Anchovy	*Engraulis ringens*	91.0	96.3	94.2
Hake	*Merluccius gayi*	0.6	13.0	3.8
Drum	*Sciaena deliciosa*	0.5	7.4	17.3
Jack mackerel	*Trachurus murphyi*	0.4	7.4	-
Silverside	*Odontesthes regia*	5.9	5.5	-
Sardine	*Sardinops sagax*	0.1	3.7	5.8
Patagonian squid	*Loligo gahi*	1.1	3.7	9.6
Unidentified/traces		0.3	5.5	

* Also weakfish (*Cynoscion analis*) 9.6% and blackruff (*Seriolella violacea*) 1.9%.

Stomach contents analysis and ecological data on prey species found (Sánchez, 1977) suggest that Burmeister's porpoises may feed at varying distances from the coast. Supposedly, demersal species such as drum and weakfish as well as the pelagic Patagonian squid are preyed upon close to shore. Hake and possibly blackruff are thought to be pursued further offshore. Anchovy and sardine may be captured either inshore or offshore.

McKinnon (1988) suggested that Burmeister's porpoises were less affected than dusky dolphins (*Lagenorhynchus obscurus*) by the reduction of food availability resulting from the *El Niño* phenomenon that occurs regularly in the area. However during the summer of the *El Niño* year 1983, several emaciated porpoises were landed at the port of Chorrillos (12°15′S) and several specimens were found stranded on beaches south of Lima. It is not known whether or not these incidences were induced by the *El Niño*. With oceanographic conditions returning to normal, these events have not happened again.

On the other hand, no strandings of dusky dolphins were recorded in central Peru during the 1983 *El Niño* event. Arntz (1986) reported a reduction in 'porpoise' sightings (supposedly delphinids, including dusky dolphins) off Lima and Pisco in summer 1983 and an abundance of these animals off southern Peru during the autumn of 1983. It may be that Burmeister's porpoises do not undertake long-range movements such as dusky dolphins are known to do (Cockcroft *et al.*, 1991), possibly in search of prey.

It is believed that changes in the composition of the fish fauna during a severe *El Niño* event, such as in 1983 (Arntz, 1986), may have a significant effect on *P. spinipinnis* off the Peruvian coast.

Parasites

The only previous report of parasites in Burmeister's porpoise was that of Brownell and Praderi (1984) who reported unidentified nematodes in the stomach of one specimen from Uruguay. In the present study, 158 porpoises (83 males, 75 females) were investigated for parasites. The organs most regularly examined were stomachs, intestine, pancreas, kidneys, cranial sinuses and lungs. Liver and blubber were checked in a more opportunistic way.

Eight species of helminths were collected, including four trematodes and four nematodes (Table 4). A single adult acanthocephalan encountered in the forestomach of one porpoise was thought to have been secondarily introduced as a parasite of an ingested

Table 4

Helminth parasites of Burmeister's porpoises (*Phocoena spinipinnis*) from Peruvian waters. Ne = number examined; Ni = number infected.

Parasites	Infection site	Ne	Ni	Incidence %
A. Trematoda				
Synthesium tursionis	Pyloric stomach, middle ear	114	85	74.6
Pholeter gastrophylus	Pyloric stomach, small intestine	59	8	13.5
Nasitrema globicephalae	Air sinuses, middle ear	54	5	9.3
Braunina cordiformis	Pyloric stomach	56	1	1.8
B. Nematoda				
Stenurus sp.	Air sinuses, middle ear	76	71	93.4
Pseudalius inflexus	Lungs	32	27	84.4
Anisakis typica	Stomachs	128	36	28.1
Halocercus sp.	Lungs	18	3	16.7

fish. Adult and larval cestodes such as *Tetrabothrius forsteri, Phyllobothrium delphini* and *Monorygma grimaldi* commonly reported in Peruvian bottlenose dolphins (Reyes, 1989; Van Waerebeek *et al.*, 1990) were not recorded.

All porpoises infested with the trematode *Nasitrema globicephalae* were adults. This fluke was always found in mixed infestation with the nematode *Stenurus* sp., by far the most common parasite found in Burmeister's porpoises (93.4% incidence, n=76). In severe cases, *Stenurus* sp. was found tightly packed in the cranial sinuses and middle-ear. Delyamure (1968) reported haemorrhages and tissue reaction to the presence of *Stenurus* in harbour porpoises from the Black and Azov Seas. However, gross inspection did not reveal damage to the internal mucosa of Burmeister's porpoises. Animals less than 125cm in length (n=7) were not infested, suggesting that ingestion of solid food may be a necessary condition for infestation. Evident pathology with formation of cysts was only visibly associated with the presence of the lungworm *Halocercus* sp. and the fluke *Pholeter gastrophylus*. In some cases calcified remains of these parasites were found inside the cysts, but it is unknown if this had a significant effect on the health of the porpoises infested. Crater-like ulcers were often visible in the forestomach. These ulcers were the point of attachment of some specimens of the nematode *Anisakis typica*.

Ectoparasites, specifically cyamids of the genus *Isocyamus* were seen on seven out of 116 porpoises (6%) examined. These crustaceans were found on fresh wounds and in areas such as the angle of the mouth, the genital slit, the axillae and the posterior base of the dorsal fin. The specific identity of the cyamids is currently under study.

Huaman and Reyes (1986) reported on the presence of *Xenobalanus globicipitis* attached to the fins of Burmeister's porpoises captured in Peruvian waters. These aberrant sessile barnacles (Clarke, 1966) were present in 10 out of 42 porpoises (23.8% incidence). The largest number of barnacles collected was 40 from a young porpoise landed in the summer of 1983.

Pathology

One specimen showed extensive necrosis and infection of soft tissues on the left side of the head. Underlying bones, in particular maxillary, the premaxillary, the nasal and the pterygoid were characterised by a severe osteolysis on both upper and lower surfaces.

Degeneration of the pterygoid bone has been associated with nematodes of the genus *Crassicauda* (Dailey and Perrin, 1973; Raga *et al.*, 1982). Reviewing other authors, Dailey and Perrin (1973) suggested *Stenurus* may be another cause for such osseous lesions. Although this porpoise was heavily infested with *Stenurus*, we doubt that this nematode was directly involved, because with a population infestation rate of over 90% (see above) such a pathological condition would be much more common.

Strandings

Only a few stranded Burmeister's porpoises have become available for examination. The cause for the strandings generally could not be determined, although one porpoise was found on the shore after a storm. A few specimens have been recovered from the Bahía de Paracas which is suspected to act as a natural trap. Since in Peru small cetaceans are used for food, stranded animals will quickly be taken away by locals, reducing the chances for scientists to study the probable cause of strandings.

In a recent survey (February-April 1990) of the northern Peruvian coast, S. Zambrano (pers. comm.) found several porpoises on the beaches of Bahía de Sechura (05°40'S), which had been discarded after being caught in nets. The area is one of the few in Peru where small cetaceans are only rarely consumed. A general disinterest for dolphin meat is also known for neighbouring Ecuador (Van Waerebeek and B. Haase, unpub. data).

Distribution

The known range of Burmeister's porpoise on the Atlantic coast of South America has recently been extended north to Santa Catarina (28°48'S, 49°12'W), southern Brazil (Pinedo, 1989; Simoes-Lopes and Ximenez, 1989) and as far south as Tierra del Fuego (Goodall, 1978). On the Pacific coast, Burmeister's porpoise has been recorded from Valdivia (39°50'S), Chile, north to Bahía de Paita (05°05'S) (Allen, 1925; Aguayo, 1975). Despite systematic surveys, no specimens have been encountered north of Paita (Van Waerebeek *et al.*, 1988; B. Haase, pers. comm.). It must be noted that at this locality the cold Humboldt Current veers off west away from the coast (Schweigger, 1964). The southernmost confirmed record in Peru is from San Juan de Marcona at 15°22'S (Gaskin *et al.*, 1987; Van Waerebeek *et al.*, 1988). However there is no reason to doubt that the distribution is continuous into Chile (Guerra *et al.*, 1987).

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Life History Data, Organochlorine Pollutants and Parasites from Eight Burmeister's Porpoises, *Phocoena spinipinnis*, Caught in Northern Argentine Waters

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ABSTRACT

Eight fresh specimens of Burmeister's porpoise caught in gillnets in the Necochea area (Buenos Aires Province) were studied for external morphometrics, age, basic reproductive data, organochlorine pollutant levels and parasites. Data from this work and from previous information about the species support the idea that the asymptotic body size of Burmeister's porpoises from the Uruguayan and northern Argentine waters is larger than that observed in individuals from the Peruvian and Chilean coasts. This provides some support for the hypothesis that at least two stocks of Burmeister's porpoises exist, one in the Pacific Ocean and another in the temperate South Atlantic. Organochlorine pollution levels in the examined animals were low and appear not to represent a threat to the population. High tDDT/PCB and low DDE/tDDT ratios indicated a preponderance of agricultural pollutants in relation to those of industrial origin. PCB congeners composition was consistent with the high trophic level occupied by the species. The diversity of parasites seems less than that in the Peruvian porpoises. The abundance of *Pseudalius inflexus* in lungs and *Stenurus minor* in cranial sinuses is similar to the Peruvian specimens. The presence of *Polymorphus* (*Polymorphus*) *cetaceum* in some stomachs and intestines suggests that the franciscanas *Pontoporia blainvillei* and Burmeister's porpoises of this area probably feed on the same intermediate host.

KEYWORDS: BURMEISTER'S PORPOISE; INCIDENTAL CAPTURE; SOUTH-ATLANTIC; REPRODUCTION; AGEING; MATURITY; POLLUTION-ORGANOCHLORINES; PARASITES; STOCK IDENTITY

INTRODUCTION

Although the known distribution of the Burmeister's porpoise (*Phocoena spinipinnis*) extends from Perú to southern Brazil, it is unclear whether the species is present continuously throughout this range (Klinowska, 1991; Goodall *et al.*, 1995). Brownell and Praderi (1984) have suggested that porpoises from the Peruvian and Chilean Pacific and those of the Uruguayan Atlantic comprise two separate populations.

During 1988–90, a study of interactions between marine mammals and fishing activities was conducted in Necochea-Quequén and Claromecó, two fishing harbours located on the northern Argentine coast (Corcuera *et al.*, 1994). The survey showed that a small number of Burmeister's porpoises (maximum estimated at 21–25 individuals) are caught annually in gillnets set in waters 30–60m deep and within 25 n.miles of the coast.

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As there is almost no published information on the life history, pollutant levels and parasite burden, we present here the life history data obtained from eight fresh specimens incidentally caught off the northern Argentine coast and compare these with data from other areas.

MATERIALS AND METHODS

Fieldwork

Seven individuals incidentally caught in gillnets were obtained from fishermen in Necochea (38°37'S, 58°50'W) and one from Claromecó (38°52'S, 60°05'W) during 1989–90. Data recorded in the field included standard body length, sex, body weight and reproductive condition (pregnancy, lactation, presence of ovulation corpora in females, presence of sperm in epididymis in males). Teeth, the complete vertebral column, a sample of dorsal blubber and all the parasites found in the different organs were collected.

Age determination

Mandibular teeth were removed from the midpoint of the jaw, cleaned and preserved in a 5% buffered formalin solution. At the laboratory, at least two teeth from each porpoise were decalcified with 5% formic acid for 16–72 hours. Two series of sections of 18–25µm thick, one parallel to the mandible and another parallel to the bucco-lingual plane, were obtained using a *Reichert-Jung* cryostat. Sections were stained with Hematoxylin for 20–60 minutes and mounted in glycerine for examination. Growth layer groups (GLGs) were analysed only in sections made through the central axis of the pulp cavity and the crown. GLGs were counted in dentine with transmitted light using a stereoscopic microscope (30x-120x). Cementum layers were counted under a compound microscope (100x-400x). Two preliminary estimates were obtained for each porpoise's age by having two authors (J.C. and F.M.) independently examine sections from each tooth; the final estimate was obtained following recommendations from Bjørge *et al.* (1995). Agreement between the readers was reached at the first (blind) count in three of the eight specimens examined; the maximum difference between the readers was 2 GLGs. This occurred in porpoises with 3–6 GLGs and in the oldest (12+ GLGs) specimen. These differences were resolved by taking into account cemental layer readings and if necessary, biological data. Partial GLGs were not counted due to a lack of appropriate data to determine the timing of births for the Burmeister's porpoises in the region.

Physical maturity

Physical maturity was determined by examining the degree of epiphyseal fusion in the vertebrae. The vertebral column was boiled, cleaned, dried and examined macroscopically. Vertebrae from the caudal region were frozen, X-rayed and then processed as the rest of the column. Four degrees of epiphyseal fusion to the vertebral centrum were recorded according to the following classification: 0% = totally unfused (both epiphyses free); 50% = partially fused (at least one epiphysis broke when trying to separate it from the centrum); 80% = almost totally fused (both epiphyses were impossible to separate from the centrum but at least one showed a distinct fusion line); 100% = totally fused (both epiphyses were impossible to separate from the centrum and no distinct fusion line could be observed). Physical maturity for each specimen was calculated as the mean percentage of vertebral fusion along the whole column.

Organochlorine pollution

Full depth, skin to muscle blubber samples, each weighing at least 10g, were excised from the dorsal region posterior to the dorsal fin of the porpoise, wrapped in aluminum foil and kept deep frozen prior to the analysis. At the laboratory, tissue samples were prepared, extracted and purified following the procedures described by Aguilar and Borrell (1991). The chromatographic analyses were performed in a *Hewlett Packard* 5890 gas chromatograph equipped with an electron capture detector of 63Ni. For all the analyses a fused-silica capillary column of 0.25mm internal diameter and 60m length and a stationary phase SPB-1 with a film thickness of 0.25μm were used. Temperatures and analytical conditions of the chromatographic runs were identical to those detailed by Aguilar and Borrell (1991). Concentrations here reported are expressed in parts per million (ppm) calculated on the basis of the extractable lipids.

Parasites

During the necropsy, the specimen was examined to search for external parasites and crustacean ectocommensals. The blubber, muscles, kidneys, heart, lungs, liver, stomach chambers, intestine, mesenteries and cranial sinuses were also examined. All the detected parasites were washed in a saline solution and then fixed and preserved in 70% ethanol. In order to examine the internal structures they were cleared with lactophenol and in some cases were dyed with aluminous carmine.

RESULTS AND DISCUSSION

Age

The standard body length, body weight, sex, age and collection data of the studied porpoises are detailed in Table 1. The mean number of cemental GLGs detected per dentinal GLG was 1.85 (SD = 0.37). According to the cemental counts and the biological data for each porpoise, dentine counts of bucco-lingual sections were more reliable in three specimens and less reliable in one; in the remaining four cases the results were identical. Teeth of the older females (N90–13, length 196cm, 12+ GLGs; N89–06, 191cm, 6+ GLGs) showed the crown eroded in a plane parallel to the tongue. Erosion did not, however, prevent detection of the neonatal layer. The oldest male (N90–03, 179cm) had 5+ GLGs.

Table 1

Body length, weight, sex, age and collection data for *Phocoena spinipinnis* from northern Argentine waters.

Specimen no.	Date	Locality	Std. length (cm)	Weight (kg)	Age (GLG)	Sex
N89-05	18-11-89	Necochea	119.0	32.5	0+	F
N89-11	12-12-89	"	182.0	98.0	5+	F
N89-06	21-11-89	"	191.0	105.0	6+	F
N90-13	15-10-90	"	196.0	> 96.9 *	12+	F
N90-27	04-12-90	Claromecó	135.0	39.5	1+	M
N90-28	05-12-90	Necochea	152.0	54.0	2+	M
N89-04	16-11-89	"	169.0	78.0	3+	M
N90-03	13-11-90	"	179.0	78.0	5+	M

\+ = Next GLG incomplete.

* Blood not included.

Morphology and life history data

Table 2 shows the degree of physical maturity and reproductive status of the specimens; external morphometrics of sexually mature individuals are presented in Table 3. The vertebral formula of the studied specimens was Cv 7/ Tx 14/ L 15/Cd 32–35. The previously

Table 2

Physical maturity and reproductive status of the sampled animals.

Specimen no.	Std. length (cm)	Sex	% of fused vertebrae	Reproductive status
N89-05	119.0	F	0	Immature
N89-11	182.0	F	59	Mature [1], Lactating
N89-06	191.0	F	80	Mature, Pregnant [2], Lact.
N90-13	196.0	F	98	Mature, Lact.
N90-27	135.0	M	5	Immature
N90-28	152.0	M	5	Immature? [3], inactive
N89-04	169.0	M	45	Mature, active
N90-03	179.0	M	42	Mature, active

[1] Relatively recent post partum or abortion; [2] Foetus size 28.7cm; [3] Lack of testis histological examination.

Table 3

External morphometrics (cm) of sexually mature Burmeister's porpoises from northern Argentine waters. % of BS = % of body size

	Females					Males				
Measurements	N	Range	Mean	SD	% of BS[1]	N	Range	Mean	SD	% of BS[1]
Body size	3	182.0-196.0	189.7	7.1		2	169.0-179.0	174.0	7.1	
Snout to end of mouth	3	9.0- 12.0	11.0	1.7	5.8	2	8.4- 9.5	9.0	0.8	5.1
Snout to blowhole	3	14.0- 15.5	14.5	0.8	7.6	1		15.0		8.4
Snout to eye	3	16.0- 19.0	17.4	1.5	68.0	2	14.5- 16.0	15.3	1.1	8.8
Snout to slipper insertion	3	30.0- 34.6	31.9	2.4	16.8	2		29.0	0.0	16.7
Snout to umbilicus	1		85.0		44.5	1		79.0		46.7
Snout to mid-genital slit	2	126.0-132.0	129.0	4.2	68.0	2	99.8-102.6	101.2	2.0	58.2
Snout to anus	2		132.0	0.0	69.6	2	120.0-123.2	121.6	2.3	69.9
Snout to dorsal fin tip	3	130.0-141.0	135.3	5.5	71.3	2	131.5-133.3	132.4	1.3	76.1
Girth at genital slit	3	76.0- 86.0	80.7	5.0	42.5	2	90.0- 96.5	93.3	4.6	53.6
Girth at axillae	3	96.0-103.0	99.7	3.5	52.6	2	91.0- 91.1	91.1	0.1	52.3
Maximum girth	3	115.0-118.0	116.3	1.5	61.3	2	106.6-110.5	108.6	2.8	62.4
Dorsal fin: base length	2	27.0- 28.0	27.5	0.7	14.5	1		27.6		16.3
Dorsal fin: height	3	8.3- 11.5	9.4	1.8	5.0	2		12.0	0.0	6.9
Maximum width of flipper	3	11.3- 12.0	11.5	0.4	6.1	2	10.9- 12.0	11.5	0.8	6.6
Flipper: anterior length	3	29.5- 31.6	30.7	1.1	16.2	2	28.5- 30.7	29.6	1.6	17.0
Flipper: posterior length	3	22.0- 25.0	23.0	1.7	12.1	2	22.0- 22.5	22.3	0.4	12.8
Depth of fluke	2		2.5	0.0	1.3	1		2.8		1.7
Fluke span	3	44.3- 46.0	45.3	0.9	23.9	2	42.0- 44.2	43.1	1.6	24.8
No. of left upper teeth	2	13 - 14				1	10			
No. of right upper teeth	2	13				1	11			
No. of left lower teeth	2	13 - 17				1	16			
No. of right lower teeth	2	17 - 18				1	17			

[1] When N=1, percentage of body size is calculated in relation to the correspondent specimen's body size.

reported vertebral formula (Brownell and Praderi, 1982) appears to have neglected the smaller caudal vertebrae which are evident only under X- ray analysis. The largest (196cm) non-pregnant female had a body weight of at least 96.9kg (excluding blood) and is the largest known sex animal recorded for the species. The maximum body weight recorded in our sample was 105kg for a 191cm pregnant female (N89–06).

The mean body length of the adults in the sample was 174.0cm for males and 189.7cm for females. Examination of the vertebral ephiphyses suggests that the larger males were still growing as they had only 42–45% of vertebrae fusion. Larger females were almost fully physically mature (80–98% fusion), suggesting that they reach their maximum body length at around 200cm. Despite the very small sample size this suggests that the asymptotic body size in northern Argentine waters is greater than that for the Pacific coast of South America. From 402 individuals caught in Peruvian waters, the maximum length recorded was 183cm and the maximum weight was 79kg (Reyes and Van Waerebeek, 1995). According to Brieva and Oporto (1990), Burmeister's porpoises caught in Chile (n=28) had the same maximum body length as those from Perú. Goodall *et al.* (1995) reported that specimens caught at the southern tip of the continent (Tierra del Fuego) showed a maximum body size of 185cm for females (n=11) and 180cm for males (n=14).

Because the largest reported Burmeister's porpoises (unknown sex, length 200cm, n = 'some individuals') were from Uruguayan waters (Brownell and Praderi, 1984), these authors proposed that the porpoises from Perú, apparently smaller, belonged to a different population. Our results support the distinction between a Pacific and at least a temperate South Atlantic population and suggest that the catches from Uruguay and Buenos Aires province may belong to the same stock. The southern boundary of this population remains unknown, but it is assumed that it extends at least to 38–39°S. Sightings and one stranding recorded by Würsig *et al.* (1977) show that the Burmeister's porpoise also inhabits the more southerly located waters of northern Patagonia. Whether or not the Patagonian and Tierra del Fuego specimens belong to a single 'temperate South Atlantic population' remains unclear. The apparent continuum in length increase from Peruvian to Uruguayan waters may reflect differences in their respective environments and/or their history of isolation from a centre of dispersion.

The sample size was obviously too small to calculate reproductive parameters. Two sexually active males caught during October-November were 169 and 179cm long with 3+ to 5+ GLGs. Mature females were 182–196cm with 5+ to 12+ GLGs. A 28.7cm foetus found in November was considered to be mid-term and, therefore, if calving is seasonal, would have been born some months later, probably by March-June. However, Brownell and Praderi (1982; 1984) reported a 44cm foetus in February in Uruguay and we observed an apparently post-partum female (N89–11) in December. This suggests that reproduction is either not highly seasonal or that more than one calving peak occurs during the year.

Organochlorine levels

Organochlorine concentrations detected in the blubber are detailed in Table 4. Males showed higher levels overall than females, no doubt due to the discharge of organochlorines by females during gestation and lactation. Although comparison with individuals from other regions is impossible because of the lack of published data for the species, the residue levels found in these specimens are overall very low for a small, top predator, marine mammal. The observed concentrations are of the same order of magnitude as those previously reported for franciscanas (*Pontoporia blainvillei*) from the same region (O'Shea *et al.*, 1980; Borrell *et al.*, 1990) and reflect the low levels of organochlorine pollution in northern Argentine waters. Given the low concentrations detected, organochlorines are not considered to represent a threat to the population.

The tDDT/PCB ratio observed (mean = 1.04, SD = 0.5) is relatively high in comparison to that usually found in small cetaceans from other geographical locations (Wagemann and Muir, 1984; Aguilar and Borrell, 1995). This indicates a greater contribution by agriculture to organochlorine pollution in the region in comparison to industrial activities. In addition, the input of DDT into the ecosystem appears to have ocurred relatively recently according to the low percentage of *pp*'DDE/tDDT detected in the samples (mean = 49.5%, SD = 8.9). The *pp*'DDE is the main product of the metabolization of commercial DDT and, in areas where the use of this pesticide has been discontinued, its relative abundance in the tissues of top predator marine mammals is much higher, usually ranging from 55–70% of the total DDT load (Aguilar, 1984; Addison *et al.*, 1984).

Table 4

Concentration of organochlorine compounds (ppm lipid basis) detected in the blubber of Burmeister's porpoises.

Sex	Females				Males			
Field no.	N89-05	N89-06	N89-11	N90-13	N89-04	N90-03	N90-27	N90-28
% of extraction	84.33	89.95	79.41	60.50	75.67	60.91	67.64	83.63
p,p DDE	2.377	0.111	1.549	0.147	5.641	4.572	0.587	2.321
p,p TDE	0.502	0.027	0.267	0.037	0.464	0.522	0.160	0.417
o,p DDT	0.533	0.029	0.434	0.060	0.643	0.844	0.171	0.559
p,p DDT	1.220	0.081	1.316	0.136	1.530	2.605	0.398	1.114
tDDT	4.632	0.248	3.566	0.380	8.278	8.543	1.316	4.411
Total PCB	3.806	0.562	3.874	0.899	5.574	5.238	1.941	2.840
IUPAC #95	0.053	0.003	0.022	0.005	0.044	0.039	0.016	0.041
IUPAC #101	0.046	0.009	0.031	0.016	0.026	0.024	0.023	0.021
IUPAC #110	0.016	0.003	0.009	0.001	0.010	0.023	0.001	0.006
IUPAC #128+182	0.028	0.005	0.043	0.008	0.054	0.049	0.015	0.025
IUPAC #136	0.015		0.009		0.017	0.015	0.003	0.013
IUPAC #138	0.255	0.026	0.193	0.038	0.361	0.352	0.104	0.204
IUPAC #141	0.015	0.004	0.014	0.006	0.015	0.017	0.010	0.011
IUPAC #149	0.309	0.023	0.177	0.043	0.258	0.271	0.113	0.231
IUPAC #151	0.039	0.002	0.023	0.008	0.045	0.040	0.015	0.035
IUPAC #153	0.382	0.039	0.285	0.059	0.526	0.494	0.154	0.333
IUPAC #170	0.073	0.017	0.147	0.025	0.179	0.190	0.048	0.054
IUPAC #174	0.046	0.004	0.039	0.007	0.059	0.055	0.017	0.028
IUPAC #177	0.024	0.004	0.031	0.007	0.045	0.040	0.011	0.018
IUPAC #180	0.188	0.030	0.209	0.045	0.243	0.248	0.072	0.084
IUPAC #187	0.074	0.015	0.110	0.022	0.141	0.130	0.039	0.062
IUPAC #201	0.019	0.008	0.046	0.009	0.041	0.045	0.008	0.008
IUPAC #202+171	0.013	0.002	0.018	0.003	0.023	0.023	0.008	0.010
IUPAC #203+196	0.024	0.012	0.081	0.013	0.072	0.092	0.021	0.013

The PCB profile is mostly composed of congeners with a high chlorine content, especially *o,o*'-substituted hexachlorobiphenyls (IUPAC numbers 138, 149, 153) and heptachlorobiphenyls (IUPAC numbers 170 and 180). This preponderance of the highly chlorinated non-planar PCB forms, which are relatively resistant to degradation and are highly bioaccumulative (Safe, 1989) is also consistent with the high position occupied by Burmeister's porpoises in the marine trophic web.

Parasites

Although the specimens were fresh and carefully examined, no external parasites or ectocommensals were found. The most abundant internal parasites were Metastrogyloidean nematodes. A large number of males and females of *Pseudalius inflexus* Rudolphi, 1808 were present in the lungs of adult porpoises. Abundant individuals of both sexes of *Stenurus minor* Kuhn, 1829 were found in the aerial sinuses of the cranium, particularly around the tympanic bullae. No pathology was detected in relation to the presence of these two species, which are also the most abundant parasites of the species in Peruvian waters (Reyes and Van Waerebeek, 1995).

Larvae of the nematode Ascaridoidea (genus *Anisakis*) were found free in the stomach without producing lesions. The pyloric stomach of one individual showed cysts containing abundant specimens of the Digenean *Pholeter gastrophilus* Kossack, 1910. Males and females of the Acanthocephalan *Polymorphus (Polymorphus) cetaceum* Johnston and Best, 1942 were found in all the stomach chambers and the intestines of two porpoises.

A comparison with the internal parasites from Peruvian animals (Reyes and Van Waerebeek, 1995) reveals a lower diversity in our sample, although this may merely reflect the small sample size. No Nasitrematidae or Campulidae were found in the Burmeister's porpoises of this area. The absence of the former family might be related to a Pacific endemic character. The presence of *P. (Polymorphus) cetaceum* is the first reference to an Acanthocephalan parasiting Burmeister's porpoise. This helminth is the most abundant parasite in the franciscana from the same area and it may use cephalopods as an intermediate host.

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Finless Porpoise

Finless porpoise, *Neophocaena phocaenoides*

REMARKS

There are no finless porpoise papers in this book, reflecting the general lack of knowledge of this species. In its first examination of the species in 1990, the only information presented to the Scientific Committee was that small numbers (4 in 1989) were taken incidentally in Japanese waters (IWC, 1991b). Martin (1990) refers to a directed, apparently small, fishery for finless porpoises in Pakistan.

In Japan, the species is found in the southwestern Sea of Japan (M. Shirakihara *et al.*, 1992), in bays and channels around Kyushu and along the Pacific coasts south of about 36°N (R. Shirakihara *et al.*, 1992). In these areas it appears to be confined to shallow waters of less than 50m. Perrin and Brownell (1994, p. 395) summarise what is known of the distribution and stock identity. Based on a morphological examination of 218 specimens, Gao (1991) proposed 5–6 populations: (1) South Asia; (2) South China Sea; (3) Yellow Sea; (4) Yangtze River; and (5–6?) Japan (possibly two populations).

Information presented to the Workshop on Mortality of Cetaceans in Passive Fishing Nets and Traps (IWC, 1994b) provided limited information on incidental catches occurring in India (no estimates of numbers – Lal Mohan, 1994) and China (over 110 between 1974 and 1990 – Zhou and Wang, 1994). However, despite the lack of direct evidence, extensive coastal fisheries are known to occur within the range of the finless porpoise and incidental takes are likely to occur. Such takes may well be significant for this coastal species and research should be undertaken as a matter of some urgency.

Concerns for the status of finless porpoise in Thailand were reported to the Committee in 1993. Preliminary research indicated that the porpoises apparently had deserted large parts of their previous range of distribution in Thailand where this species used to inhabit shallow inshore marine and estuarine waters. Concerns were expressed about the increasing habitat degradation due to pollution and fisheries. The Committee recommended that research should be augmented and that the research should include habitat use and habitat requirements, and that information on small cetacean habitat requirements should be incorporated in coastal zone planning and in any plans for habitat protection in Thailand's coastal waters (IWC, 1994a).

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Dall's Porpoise

Dall's porpoise, *Phocoenoides dalli*

INTRODUCTORY REMARKS

In 1983, abundance estimates for the entire offshore North Pacific first became available to the Scientific Committee and ranged between 790,000 and 2,300,000. No estimate was available for Japanese coastal waters. There were indices for more than one population and the two colour morphs were recognised as the *dalli*-type and the *truei*-type. The Dall's porpoise was being incidentally taken in Japanese driftnet fisheries for salmon across the North Pacific, with catches in the low thousands for the years 1980–1982. An undocumented incidental catch of Dall's porpoises in Washington State was also reported (IWC, 1984).

The reported take in the Japanese coastal harpoon fishery was 12,833 in 1982, an increase of approximately 25% since the previous year. The Committee expressed concern at the high number of incidental kills and the increase in the harpoon fishery (IWC, 1984). It was recommended that studies on population identity be conducted, that Japan should institute a system for collecting effort data (in the harpoon fishery) and that Japan should carry out sighting surveys to estimate abundance. It was also recommended that the Soviet Union should analyse and make available sightings data from the Kurile Islands area of the Sea of Okhotsk (the porpoises that are exploited off Japan migrate there during the summer). The following year the Committee reiterated its concern over the take of about 13,000 Dall's porpoises from the localised population of the *truei*-type (IWC, 1985).

In 1987, estimates of abundance for the two colour types of Dall's porpoise in waters around Japan were presented to the Committee. The number of *dalli*-type porpoises in the Sea of Japan/Okhotsk Sea area was estimated at 32,000 (CV=0.225) and the total abundance of the *truei*-type was estimated at between 56,000 and 90,000. The Committee recommended that the harvest be sampled to determine the proportion of the colour types in the catches (IWC, 1988).

A dramatic increase in the Japanese catch of Dall's porpoise was reported to the Committee in 1989 (IWC, 1990). The total catch in 1988 was 41,455, mainly due to an increase in the harpoon fishery. In addition, undocumented incidental takes of the *truei*-type were known to occur in the Taiwanese and Korean squid gillnet fisheries in the western North Pacific. The Committee was extremely concerned about this development and stated that the total catches were clearly not sustainable and should be reduced. Further it recommended that catch statistics be collected and reported on a stock by stock basis. The Republic of Korea was requested to report bycatches in its squid fishery. However, as summarised in Donovan (1994), pelagic driftnet fishing had effectively ceased in the Pacific by 1 January 1993. A considerable effort to reduce bycatch levels in the Japanese salmon driftnet fishery had been carried out by Japan and the USA in the context of the International North Pacific Fisheries Commission.

In 1990, the Committee conducted a major review of the Dall's porpoise (IWC, 1991). It concluded that there was evidence for six stocks of the *dalli*-type and one stock of the *truei*-type. It was pleased to note that catch statistics had been reported on a stock by stock basis and that the level of catches for 1989 had been reduced to 29,000. However, the Committee believed that the catches were still above sustainable levels and recommended their further reduction. It also recommended that a new abundance estimate be carried out.

New abundance estimates were presented for review in 1991, based on surveys carried out in 1990 (IWC, 1992). The abundances of the three stocks in waters adjacent to Japan were estimated to be 111,000 (CV=0.29) *dalli*-type in the northern Okhotsk Sea, 226,000 (CV=0.15) *dalli*-type in the southern Okhotsk Sea stock and 217,000 (CV=0.23) *truei*-type in the central Okhotsk Sea stock. The new abundance estimates and the further reduction of catches (21,800 in 1990) showed that the hunt was now of the order of 4.2–6.3% of the exploited stocks. The Committee encouraged further reduction in catch levels to ensure that the harvest was sustainable.

At the 1992 meeting, the Committee was pleased to note that catches had steadily been reduced, from 40,367 in 1988 to 17,634 in 1991 (IWC, 1993). Since then catches have been 11,403 (1992), 14,318 (1993) and 15,947 (1994).

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Population Abundance of Dall's Porpoise (*Phocoenoides dalli*) in the Western North Pacific Ocean

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ABSTRACT

Dall's porpoise in the western North Pacific Ocean suffered incidental mortality from the gillnets of the Japanese high seas salmon fishery until 1987 and mortality from the high seas squid gillnet fishery until 1992. Their abundance is estimated from line transect data gathered during 1979/89. Correction factors are estimated for the bias in abundance estimates because of the attraction of animals to the survey vessel and the failure to detect all animals close to the trackline. Data from experimental surveys carried out in 1983 and 1984, using a helicopter to detect schools ahead of the ship before responsive movement occurs, are analysed. The multiplicative correction factor for the 1983 survey is 0.314 (SE 0.131) and for the 1984 survey, 0.130 (SE 0.050). Animals were sighted at shorter distances in the 1984 survey than in the 1983 survey. A linear combination of these correction factors is proposed which adjusts for the observed distribution of perpendicular distances. After applying the resulting corrections, a conservative estimate of population abundance for the western North Pacific Ocean of 141,800 animals is obtained, with 95% CI (83,100; 241,700). Possible biases in this estimate are discussed.

KEYWORDS: DALL'S PORPOISE; ABUNDANCE; NORTH PACIFIC; SURVEY-VESSEL; BEHAVIOUR

INTRODUCTION

Dall's porpoises (*Phocoenoides dalli*) were incidentally taken in gillnets used in the Japanese high seas salmon mothership fishery, which operated in the North Pacific Ocean from 1952 to 1987. The high seas squid gillnet fishery with vessels from Japan, Korea and Taiwan also caught marine mammals including Dall's porpoise and operated from the 1970s to the end of 1992. Sighting surveys for marine mammals were conducted by US observers aboard Japanese salmon research vessels and US vessels from 1978 to 1989 to obtain data to estimate the population abundance and to assess the impact of incidental mortality.

The purpose of this paper is to present estimates of abundance of Dall's porpoise in the western North Pacific Ocean specifically in the area affected by the fishery. There are two main problems with using line transect methods for Dall's porpoise: (1) the animals react to vessels (most are attracted); and (2) some animals near the transect line are missed ($g(0)<1$). The first problem causes overestimation of abundance; the second causes underestimation.

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Many attempts to estimate *g*(0) in sightings surveys of whales are summarised by Hiby and Hammond (1989). Several field studies to measure movement of marine mammals in response to survey vessels have been conducted (Au and Perryman, 1982; Leatherwood *et al.*, 1982; Bouchet *et al.*, 1983; 1984; Hewitt, 1985; Withrow *et al.*, 1985; Barlow, 1988). Most concluded that little responsive movement occurred before detection of the animals, or that movement was random and consequently bias in abundance estimates was negligible. Leatherwood *et al.* (1982) tested the angle of direction of travel of minke whales and concluded that movement was random. However, in studies of Dall's porpoise (Bouchet *et al.*, 1983; 1984; Withrow *et al.*, 1985), there was a significant responsive movement of animals before detection by shipboard observers.

The problem of bias due to responsive movement has been investigated by Burnham *et al.* (1980), Laake (1978), Smith (1979) and Turnock and Quinn (1991). Turnock and Quinn utilised the positions of animals near the observer after movement occurred to correct population estimates. Repeat positions of animals were recorded for only one of the two surveys analysed here, so that a different approach from that of Turnock and Quinn (1991) is required. Here, we use the method of Buckland and Turnock (1992). The resulting corrections, which also allow for missing animals on the trackline, are applied to population estimates. Other biases result from non-random distribution of effort, which will only partially be accounted for here and from errors in measurement of distances and angles to sightings, which is not addressed.

DEFINITION OF AREA

Jones *et al.* (1986) and Kasuya and Yoshioka (1988) argue for the existence of separate stocks of Dall's porpoise in the North Pacific Ocean, with a dividing line somewhere near 170°W to 180°W. In this paper the boundary is arbitrarily drawn at 172°W. The stock in the western North Pacific Ocean is impacted by the Japanese salmon mothership fishery (Fig. 1). Within the western North Pacific Ocean area is the 'fishing zone'. This area is defined by boundaries established under the 1978 International Convention for North Pacific High Seas Fisheries. We define the western North Pacific Ocean as the area west of 172°W, south of the Aleutian Islands and north of 40°N. The southern boundary is approximately the average 15°C isotherm, which is generally considered the upper limit of the temperature range for Dall's porpoise. The western boundary excludes areas where a separate stock of Dall's porpoise (the *truei*-colour type) is found.

METHODS

The Japanese salmon research vessels followed systematic cruise tracks designed for sampling salmon distribution. The same cruise track was followed each year by the same vessel, although US observers were not always present on the same vessels from year to year, nor were they placed on all vessels, so that effort was not uniform through the area. In the fishing zone, sighting surveys were conducted by US observers on the Japanese salmon catcher boats. These vessels travelled back and forth from the positions where nets were set, to the motherships, resulting in effort that was neither systematic nor random. During periods when sea and weather conditions were favourable, a single observer searched the area from beam to beam ahead of the vessel by eye and with the aid of binoculars.

Since the catcher boats operated within the fishing zone, a relatively large proportion of sighting effort was concentrated there (Figs 1 and 2). This area was therefore analysed separately from the rest of the North Pacific area, for which data are from research vessels.

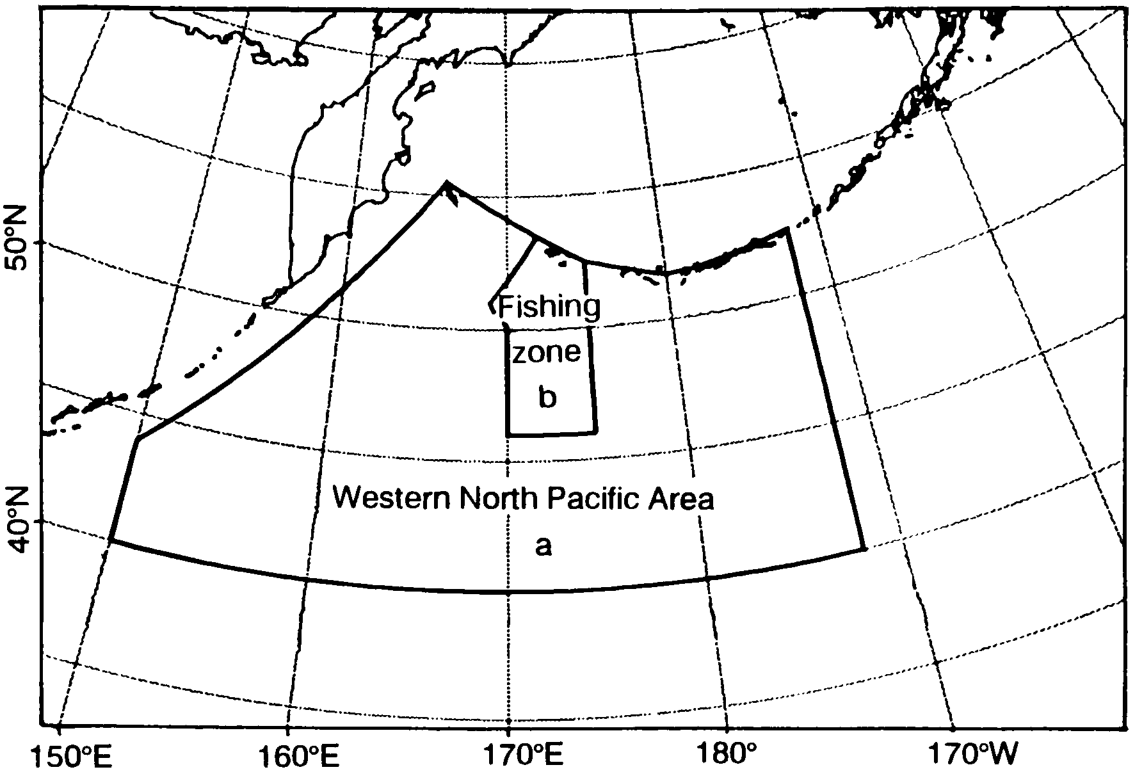

Fig. 1. Subareas used for population estimation.

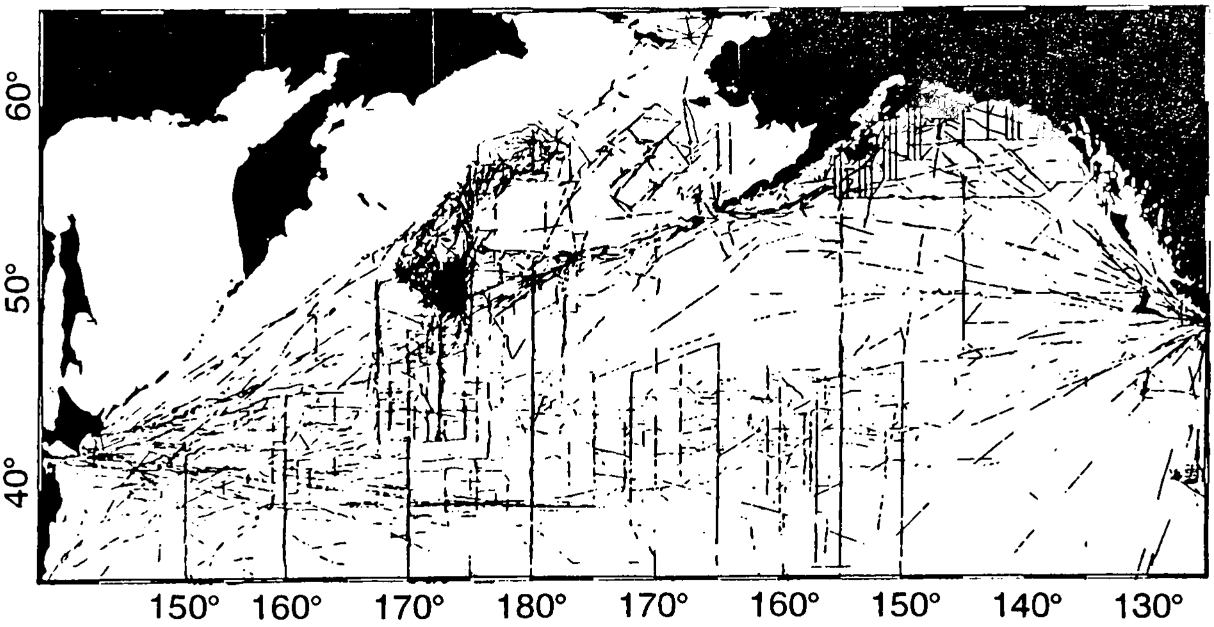

Fig. 2. Survey effort in the North Pacific Ocean, 1979/89.

Outside the western area of the North Pacific, there are insufficient effort and sightings for reliable analysis, so no population estimates were calculated.

A general problem in line transect surveys for marine mammals is that animals near the trackline might be missed. The probability of observing a group or an individual that is close to the line is usually assumed to be unity, but for Dall's porpoise, this is unlikely to be true, except perhaps in good sighting conditions. Weather and sea state were recorded by observers and a visibility code (from 1 to 6) determined for each leg of effort (Table 1).

Table 1

Definition of visibility codes (Boucher and Boaz, 1989).

Code	Definition
1	Excellent: surface of water calm, a high overcast cloud solid enough to prevent sun glare. Marine mammals will appear black against a uniform gray background.
2	Very good: may be a light ripple on the surface or slightly uneven lighting, but still relatively easy to distinguish animals at a distance.
3	Good: may be light chop, some sun glare or dark shadows in part of the survey track. Animals up close (400m or less) can still be detected and fairly readily identified.
4	Fair: choppy waves with some slight whitecapping, sun glare or dark shadows in 50% or less of the survey track. Animals further away than 400m are likely to be missed.
5	Poor: wind in excess of 15 knots, waves over 2' with whitecaps, sun glare may occur in over 50% of the survey track. Animals may be missed unless within 100m of the survey trackline. Identification difficult except with the larger species.
6	Unacceptable: wind in excess of 25 knots, waves over 3' with pronounced whitecapping. Sun glare may or may not be present. Detection of any marine mammal unlikely unless the observer is looking directly at the place where it surfaces. Identification very difficult due to improbability of seeing animals more than once.

Apparent densities at different visibility codes up to code 5 were estimated and compared. In addition, the effects on estimation of stratifying by behaviour code were assessed. Dall's porpoise commonly show two types of sighting cue, 'slow rolling' and 'rooster-tailing', of which rooster-tailing is more easily detected.

Within each area stratum, abundance was estimated using line transect methods. The perpendicular distance from the trackline (which may be calculated from the sighting distance and sighting angle relative to the trackline) of each detected animal group is recorded and a detection curve $g(x)$, which is the probability of detecting an animal group that is at perpendicular distance x, is estimated (Buckland *et al.*, 1993). The hazard-rate model (Buckland, 1985) was used for this purpose. Data were pooled for years 1979 to 1989, to reduce the effects of small samples when stratifying by visibility code and area. (No visibility code was recorded in 1978 and those data are not analysed here.) To reduce the effect of rounding errors in distance and angle measurements, the perpendicular distance data were grouped by 100m intervals and truncated at w=500m. The effective search half-width ($1/f(0)$) of the transect is estimated as

$$1/\hat{f}(0) = \int_0^w \hat{g}(x)\,dx,$$

where $\hat{g}(x)$ is the fitted detection function. The density of animals was estimated as

$$\hat{D} = \frac{\mathrm{n}\cdot\bar{s}\cdot\hat{f}(0)}{2L},$$

where n is the number of groups observed, $\bar{s}$ is the average group size and L is the transect length.

The variance of n was estimated empirically by (Buckland *et al.*, 1993),

$$\widehat{var}(n) = \frac{L\sum_{i=1}^{R} l_i\left[\frac{n_i}{\mathrm{l_i}} - \frac{n}{L},\right]^2}{(R-1)},$$

where n_i is the number of groups observed on transect leg i, l_i is the length of leg i and R is the number of legs.

The variance of $\bar{s}$, $\widehat{var}(\bar{s})$, was estimated by the sample variance of observed group sizes divided by n and the variance of $\hat{f}(0)$, $\widehat{var}\{\hat{f}(0)\}$, was obtained from the information matrix. The variance of $\hat{D}$ was estimated by the delta method (Seber, 1982):

$$\widehat{var}(\hat{D}) = \hat{D}^2 \left[\frac{\widehat{var}(n)}{n^2} + \frac{\widehat{var}(\bar{s})}{\bar{s}^2} + \frac{\widehat{var}\{\hat{f}(0)\}}{\{\hat{f}(0)\}^2} \right].$$

To convert the density estimate into an abundance estimate, it is multiplied by the size A of the area to which the density estimate applies. Thus,

$$\hat{N} = A \cdot \hat{D}, \text{ with } \widehat{var}(N) = A^2 \cdot \widehat{var}(\hat{D}).$$

Abundance estimates corresponding to different visibility codes were combined using a weighted average, with weights equal to respective effort L carried out in each visibility code. Abundance estimates were combined across the two areas by addition, to give an estimate for the whole western North Pacific area.

Attraction of Dall's porpoises to vessels causes overestimation of abundance and if animals near the trackline are missed, underestimation occurs. Corrections, $\hat{c}$, for these biases were estimated as described below and abundance estimates were adjusted using

$$\hat{N}_c = \hat{c} \cdot \hat{N}$$

$$\text{with } \widehat{var}(\hat{N}_c) = \hat{N}_c^2 \cdot \left[\frac{\widehat{var}(\hat{c})}{\hat{c}^2} + \frac{\widehat{var}(\hat{N})}{\hat{N}^2} \right].$$

If the coefficient of variation of an abundance estimate is large, a CI calculated assuming asymptotic normality can be very poor. Here, we assume $\hat{N}$ is log-normal and estimate a 95% CI by the method of Burnham *et al.* (1987):

$$(\hat{N}/k, \hat{N} \cdot k),$$

where

$$k = exp\,[1.96 \cdot \surd\{\widehat{var}(log_e\hat{N})\}]$$

and

$$\widehat{var}(log_e\hat{N}) = log_e \left[1 + \frac{\widehat{var}(\hat{N})}{\hat{N}^2} \right].$$

To estimate the correction $\hat{c}$, three experimental surveys were conducted with a helicopter flying in front of a ship to detect movement of Dall's porpoise before detection by shipboard observers. In 1982 a pilot study determined the feasibility of using a helicopter (Bouchet *et al.*, 1983). However, information collected was not sufficient for analysis of the effect of movement. In 1983 the survey was repeated; animals were tracked by a Bell 206 B3 ('Jet Ranger') helicopter and the animals seen by both the helicopter and the ship determined (Bouchet *et al.*, 1984). The *M/V Norpac I*, a 26m vessel which cruises at 10kts, was used in 1983. In 1984, a larger, noisier helicopter (a military UH1H) was used. At close range, porpoise responded to the helicopter, so no attempt was made to follow animals, although it was still possible to identify which animals were resighted from the ship. The NOAA ship *Surveyor*, which is 88.5m long and cruises at 10kts, was used in 1984. In 1983 and 1984, there was one observer who sat in front in the helicopter next to the pilot and one data recorder who sat in the back. On the ship in 1983, one observer was located 10m above the water level, searching with the unaided eye and confirming sightings with 8X binoculars. In 1984, two observers were located on the ship, together with one data recorder. The search method was the same as in 1983, except that 25X binoculars were used as well as 8X binoculars to confirm sightings.

In both 1983 and 1984, the helicopter flew approximately 1.5 to 2.5km in front of the ship and from side to side out to about 1.5 to 3km from the trackline in a pattern approximately as shown in Fig. 3. Observers on the ship conducted line transect surveys, independent of the helicopter. An independent observer (on the ship) was in radio contact with both the helicopter and the line transect observers in order to determine resighted animals. The independent observer tracked animals sighted by the helicopter until they were sighted by the shipboard observers or until they could no longer be seen. Initial positions of animals when detected by the helicopter were estimated by radar measurements from the ship to the helicopter, while the helicopter was as close as possible to the animals. The distances at which observers searched for Dall's porpoise were much less than the distance between the helicopter and the front of the ship. Observers on the ship were instructed to ignore the helicopter and conduct line transect surveys in the usual manner; however, at times it was possible for the observers on the ship to see and hear the

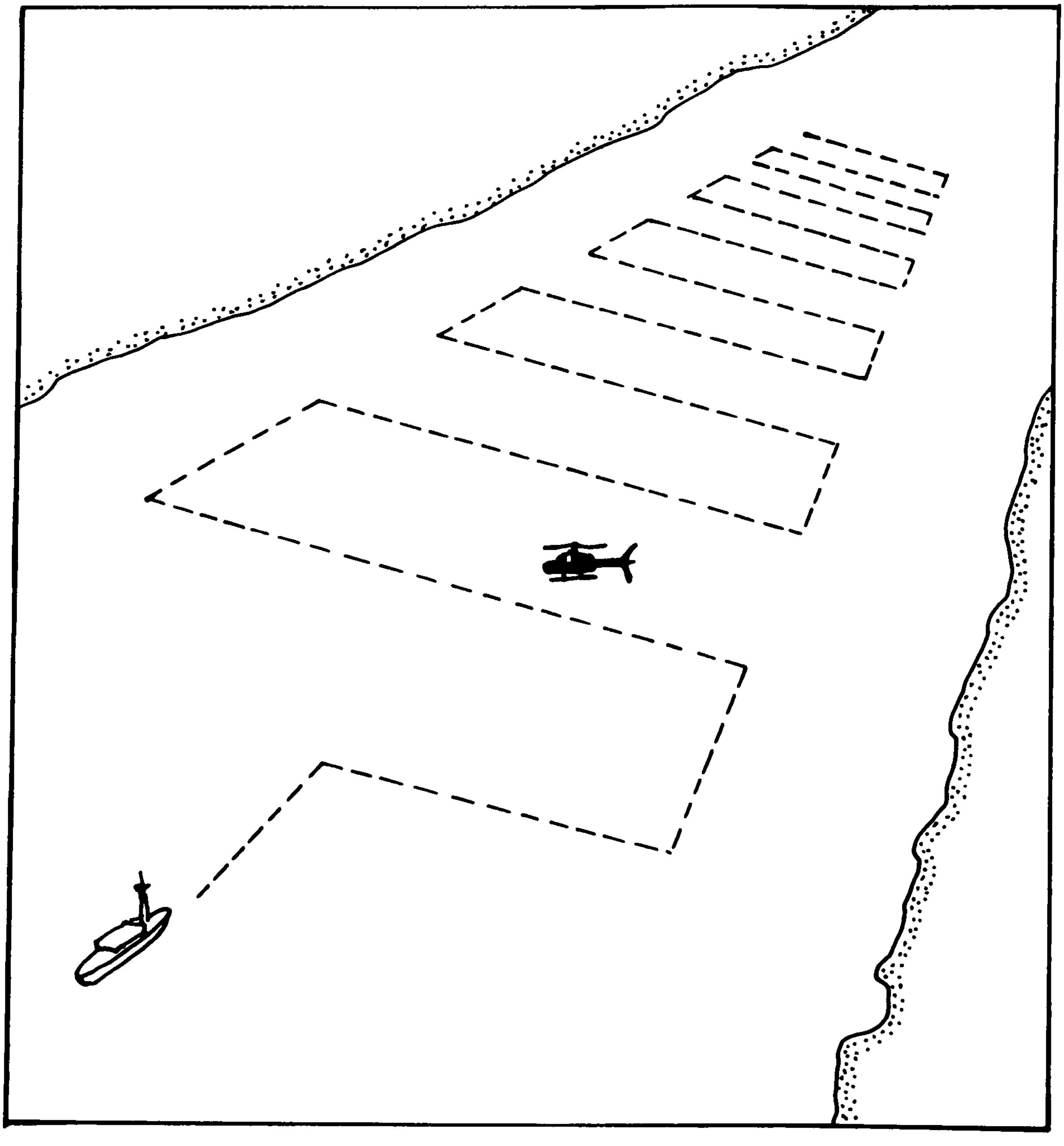

Fig. 3. Approximate helicopter flight path for surveys of responsive movements. The maximum distance of the helicopter from the trackline varied between 1.5 and 3km.

helicopter. The observers on the ship searched with naked eye; it would be difficult to observe Dall's porpoise at the distance of the helicopter unless the observers were searching with binoculars and sighting conditions were good. The independent observer was informed by the helicopter of the movements of the animals and also used binoculars to track them. Only those animals that the independent observer was sure were duplicates were counted as duplicate sightings; thus some animals that in reality were duplicates might have been omitted. Some animals sighted by the helicopter dived and were lost by the independent observer. Some of these may have surfaced near the ship and been sighted by the shipboard observers and, therefore, not counted as duplicate sightings. However, the helicopter and the independent observer were able to track most of the animals sighted by the helicopter.

In 1983 the survey was in Prince William Sound and in 1984, the survey took place in both Prince William Sound and in offshore waters between there and Seattle. The data were analysed separately for the two areas, as well as pooled over both areas. The visibility codes of Table 1 were assigned to each transect depending on Beaufort state, visibility conditions and weather.

The sightings data from the ship were analysed independently of the data from the helicopter, using the methods described above for the salmon research vessel and catcher boat data, to yield a conventional line transect density estimate $\hat{D}_s$ of animal groups per unit area, calculated assuming no movement and $g(0)=1$. For the subset of duplicate detections (i.e. animal groups detected from both platforms), the position of the animals prior to any response to the ship is known. A detection curve may therefore be fitted to the perpendicular distances of duplicate detections from the ship trackline, recorded at the time of detection by the helicopter. Similarly, a detection curve, relative to the trackline of the ship, is fitted to all helicopter detections. A density estimate $\hat{D}_u$, allowing for animal movement and for failure to detect all animal groups on the trackline, is calculated as follows (Buckland and Turnock, 1992).

Let

$g_s(y)$ = probability that a group detected from the helicopter at perpendicular distance y from the trackline of the ship is subsequently detected from the ship,
w = truncation distance for perpendicular distances y,
$f_s(y)$ = $g_s(y)/\mu$, with $\mu = \int_0^w g(y)\,dy$,
n_h = number of helicopter detections,
n_s = number of ship detections,
n_{hs} = number of detections made from both platforms (duplicate detections),
$f_h(y)$ = probability density of helicopter detection distances,
$f_{hs}(y)$ = probability density of duplicate detection distances as recorded from the helicopter,
$f(x)$ = probability density of perpendicular distances recorded from the ship,
L = length of transect line.

Then the conventional estimate of density of animal groups, assuming no movement and $g(0)=1$, is

$$\hat{D}_s = \frac{n_s \cdot \hat{f}(0)}{2L}.$$

An estimate free of bias from movement or imperfect detection on the trackline is given by

$$\hat{D}_u = \frac{n_s \cdot \hat{f}_s(0)}{2L \cdot \hat{g}(0)}.$$

where $$\hat{f}_s(0) = \frac{\hat{g}_s(0)}{\int_0^w \hat{g}_s(y)dy}$$

and $$\hat{g}_s(y) = \frac{n_{hs} \cdot \hat{f}_{hs}(y)}{n_h \cdot \hat{f}_h(y)},$$

where $f_{hs}(y)$ and $f_h(y)$ are estimated by standard line transect methods, with a common truncation distance of w. The correction factor for abundance estimates of Dall's porpoise is then estimated by

$$\hat{c} = \hat{D}_u \,/\, \hat{D}_s.$$

The densities $f(y)$, $f_h(y)$ and $f_{hs}(y)$ were estimated using the hazard-rate model (Buckland, 1985). The variance of $\hat{c}$ was estimated by bootstrapping on the legs of effort and applying the whole estimation procedure to each of 199 bootstrap data sets.

In the absence of responsive movement to the ship, random movement between the time of detection by the helicopter and the time of passing the ship would cause some animals which were beyond the ship's detectable range when detected from the helicopter, to be detected from the ship and some initially within detectable range of the trackline would move further away. This does not invalidate the above correction, but does imply that the estimate $\hat{g}_s(0)$ cannot be used as a correction factor in its own right. It is an estimate of the probability that an animal group on the ship's trackline at the time of detection by the helicopter (1.5–2.5km ahead of the ship) will subsequently be detected by the ship, which would be a negatively biased estimate of $g(0)$ if there was random movement.

The above method can be used to estimate a correction factor from each of the 1983 and 1984 surveys. Observers sighted animals farther from the ship in 1983 than in 1984, so that bias arising from responsive movement should be greater in 1984. To obtain a correction factor that is a function of observer efficiency, the following approach was adopted:

Define

$\bar{x}_j$ = mean of untruncated perpendicular distances recorded by the ship in experimental survey in year j, $j = 83, 84$;
$\bar{x}$ = mean of untruncated perpendicular distances from main surveys for which an estimate of absolute abundance is required;
$\hat{c}_j$ = correction estimated from equation (1) for year j, $j = 83, 84$;
$\hat{c}$ = estimated correction for abundance estimate from analyses of data from the main surveys.

Then $$\hat{c} = \frac{(\bar{x} - \bar{x}_{84}) \cdot \hat{c}_{83} - (\bar{x} - \bar{x}_{83}) \cdot \hat{c}_{84}}{\bar{x}_{83} - \bar{x}_{84}}. \tag{2}$$

Note that if $\bar{x} = \bar{x}_{83}$, the correction factor $\hat{c}$ is simply equal to $\hat{c}_{83}$ and similarly if $\bar{x} = \bar{x}_{84}$, $\hat{c} = \hat{c}_{84}$. Since variances in mean perpendicular distances are small relative to those for the correction factors, the variance of $\hat{c}$ may be approximated by

$$\widehat{var}(\hat{c}) = \frac{(\bar{x} - \bar{x}_{84})^2 \cdot \widehat{var}(\hat{c}_{83}) + (\bar{x} - \bar{x}_{83})^2 \cdot \widehat{var}(\hat{c}_{84})}{(\bar{x}_{83} - \bar{x}_{84})^2}$$

Mean visibility code $\bar{v}$ provides an alternative to mean perpendicular distance $\bar{x}$ when calculating the final correction, $\hat{c}$. The linear combination of estimates in equation (2) can be regarded as a regression of correction $\hat{c}$ on $\bar{x}$ (or $\bar{v}$); as there are just two observations, the regression line passes through both points. This was judged to be more robust than simply averaging the two estimates.

Table 2

Estimated effective search half-width ($1/\hat{f}(0)$), encounter rate (n/L, where n is the number of groups detected within 500m of the trackline) and mean group size ($\bar{s}$) by area and visibility code. (Standard errors in parentheses.) Estimates in the same column with different superscript letters differ significantly ($p < 0.05$).

Visibility code	Fishing zone			Western N. Pacific excluding fishing zone		
	$1/\hat{f}(0)$ (km)	n/L(groups/km)	$\bar{s}$	$1/\hat{f}(0)$ (km)	n/L (groups/km)	$\bar{s}$
1	0.188^{a}	0.0671^{a}	3.65^{a}	0.222^{a}	0.0575^{a}	$3.90^{a,b}$
	(0.016)	(0.0097)	(0.16)	(0.027)	(0.0102)	(0.25)
2	0.196^{a}	0.0222^{b}	3.53^{a}	0.186^{a}	0.0261^{b}	3.68^{b}
	(0.012)	(0.0016)	(0.14)	(0.022)	(0.0021)	(0.13)
3	$0.164^{a,b}$	0.0132^{c}	3.52^{a}	0.219^{a}	0.0161^{c}	4.26^{a}
	(0.012)	(0.0008)	(0.12)	(0.016)	(0.0013)	(0.17)
4	0.119^{b}	0.0105^{d}	3.74^{a}	0.199^{a}	0.0173^{c}	$4.07^{a,b}$
	(0.022)	(0.0008)	(0.22)	(0.015)	(0.0015)	(0.16)
5	0.146^{b}	0.0082^{d}	3.46^{a}	0.168^{a}	0.0124^{d}	$3.94^{a,b}$
	(0.013)	(0.0012)	(0.31)	(0.022)	(0.0012)	(0.25)

RESULTS

Table 2 shows that encounter rate is a strong function of visibility code. Encounter rate is estimated to be over three times higher at visibility code 1 than at code 2 in the fishing zone and over twice as high outside the fishing zone. However, effective search width shows no evidence of declining with visibility code outside the fishing zone and within the fishing zone, there is only evidence of a decline beyond code 3. Group size shows no evidence of a trend with visibility code and is slightly larger on average outside the fishing zone than inside. The abundance estimates obtained from the estimates of Table 2 are given in Table 3. They show a similar pattern to the encounter rates; abundance is estimated to be lower from data collected in worse visibility, although there is little difference between estimates calculated from data recorded during visibility codes 3, 4 and 5. In Table 4, abundance estimates have been averaged across visibility codes, weighting by effort. The overall abundance estimate using data from visibility code 1 alone is 2.7 times higher than that obtained by using data from all codes from 1 to 5.

Table 3

Sample size n (groups within 500m of the trackline), transect length L and abundance estimate $\hat{N}$ (thousands) by area and visibility code. Abundance estimates in the same column with different superscript letters differ significantly ($p < 0.05$).

Visibility code	Fishing zone				Western North Pacific excluding fishing zone			
	n	L(km)	$\hat{N}$	$SE(\hat{N})$	n	L(km)	$\hat{N}$	$SE(\hat{N})$
1	238	3,547	204^{a}	35	104	1,814	$1{,}794^{a}$	404
2	478	21,558	63^{b}	6	317	12,153	918^{b}	134
3	445	33,596	45^{c}	4	308	19,146	557^{c}	65
4	207	19,694	$52^{b,c}$	11	258	14,911	$630^{b,c}$	76
5	67	8,132	31^{c}	6	123	9,933	516^{c}	91

Table 4

Uncorrected abundance estimates $\hat{N}$ (thousands) averaged across visibility code categories, weighted by effort.

Visibility code	Fishing zone		WNP excluding FZ		Western North Pacific		
	$\hat{N}$	$SE(\hat{N})$	$\hat{N}$	$SE(\hat{N})$	$\hat{N}$	$SE(\hat{N})$	95% CI
1	204	35	1,794	404	1,998	405	(1,348, 2,962)
1-2	83	7	1,032	128	1,115	128	(890, 1,395)
1-3	61	4	757	66	818	66	(699, 958)
1-4	59	4	718	51	776	51	(682, 884)
1-5	56	4	683	45	739	45	(656, 833)

Table 5

Estimated effective search half-width ($1/\hat{f}(0)$), encounter rate (n/L, where n is the number of groups detected within 500m of the trackline) and mean group size ($\bar{s}$) by behaviour code and visibility code, western North Pacific area excluding the fishing zone. (Standard errors in parentheses.) Estimates in the same column with different superscript letters differ significantly ($p<0.05$).

Visibility code	Unobtrusive behaviour			Obvious behaviour		
	$1/\hat{f}(0)$ (km)	n/L(groups/km)	$\bar{s}$	$1/\hat{f}(0)$ (km)	n/L (groups/km)	$\bar{s}$
1	$0.234^{a,b}$	0.0254^{a}	3.36^{a}	0.200^{a}	0.0331^{a}	$4.27^{a,b}$
	(0.037)	(0.0069)	(0.30)	(0.046)	(0.0086)	(0.37)
2	$0.240^{a,b}$	0.0094^{b}	3.33^{a}	0.162^{a}	$0.0172^{a,b}$	3.86^{b}
	(0.029)	(0.0012)	(0.20)	(0.028)	(0.0017)	(0.17)
3	0.259^{a}	0.0038^{c}	3.74^{a}	0.202^{a}	$0.0126^{c,d}$	4.43^{a}
	(0.025)	(0.0006)	(0.27)	(0.021)	(0.0011)	(0.20)
4	0.140^{b}	0.0020^{d}	3.67^{a}	0.205^{a}	$0.0159^{b,c}$	$4.15^{a,b}$
	(0.042)	(0.0004)	(0.49)	(0.015)	(0.0014)	(0.17)
5	-	0.0011^{d}	3.09^{a}	0.174^{a}	0.0114^{d}	$3.93^{a,b}$
		(0.0004)	(0.65)	(0.024)	(0.0012)	(0.24)

The behaviour code corresponding to slow rolling was recorded predominantly during visibility codes 1 and 2. Only 20% occurred during visibility code 3 or higher. By contrast, 68% of records of rooster-tailing occurred during visibility code 3 or greater. Of records for which no specific behaviour was noted, only 33% were during code 3 or greater. These were combined with records of slow rolling animals to yield the 'unobtrusive behaviour' estimates of Tables 5 and 6, and other behaviour codes, which either showed a similar distribution to records of rooster-tailing or were very rare, were combined with rooster-tailing records to yield the 'obvious behaviour' estimates of Tables 5 and 6.

Estimates from the helicopter experiments are summarised in Table 7. Weather during the 1983 survey was good, with most effort at visibility codes 1 and 2, whereas during the 1984 survey, most effort was during visibility codes 2 and 3, with no effort at visibility code 1. Despite very small sample sizes, 1984 correction factor estimates for Prince William Sound ('near shore') and for offshore are very similar (Table 7), and we pool the data to increase sample size. Figs 4 and 5 illustrate the analyses for 1983 and 1984 respectively.

No stratification of data by visibility code was made, due to small sample sizes. Otherwise, analyses of the ship sightings data were as comparable as possible with analyses of data collected from 1979 to 1989 from the western North Pacific, so that the

Table 6

Estimated effective search half-width ($1/\hat{f}(0)$), encounter rate (n/L, where n is the number of groups detected within 500m of the trackline) and mean group size ($\bar{s}$) by behaviour code and visibility code, fishing zone. (Standard errors in parentheses.) Estimates in the same column with different superscript letters differ significantly ($p<0.05$).

Visibility code	Unobtrusive behaviour			Obvious behaviour		
	$1/\hat{f}(0)$ (km)	n/L(groups/km)	$\bar{s}$	$1/\hat{f}(0)$ (km)	n/L (groups/km)	$\bar{s}$
1	0.205^{a}	0.0490^{a}	3.44^{a}	0.120^{a}	0.0184^{a}	4.20^{a}
	(0.018)	(0.0089)	(0.17)	(0.054)	(0.0028)	(0.34)
2	0.273^{b}	0.0092^{b}	$3.03^{a,b}$	0.155^{a}	$0.0135^{a,b}$	3.85^{a}
	(0.024)	(0.0010)	(0.24)	(0.016)	(0.0012)	(0.16)
3	0.197^{a}	0.0024^{c}	$2.91^{a,b}$	0.156^{a}	$0.0110^{b,c}$	3.65^{a}
	(0.028)	(0.0003)	(0.23)	(0.014)	(0.0007)	(0.14)
4	-	0.0008^{d}	$3.33^{a,b}$	0.125^{a}	$0.0099^{c,d}$	3.76^{a}
		(0.0002)	(0.81)	(0.022)	(0.0008)	(0.23)
5	-	0.0006^{d}	2.20^{b}	0.148^{a}	0.0076^{d}	3.56^{a}
		(0.0005)	(0.37)	(0.014)	(0.0010)	(0.33)

Table 7

Components from which a correction for movement and for animals missed on the trackline is calculated. Truncation distance w refers to distances of animal groups from the ship trackline when detected by the helicopter; distances for ship detections were truncated at 500m.

	1983	1984		
		Near shore	Offshore	Pooled
Length of transect, L(km)	457	177	829	1006
Truncation distance, w(km)	2.5	4.0	4.0	4.0
Number of helicopter detections, n_h	54	20	37	57
Number of ship detections, n_s	90	24	53	77
Number of ship detections after truncation at 500m	69	23	51	74
Number of duplicate detections, n_{hs}	21	10	12	22
Eff. search half-width of helicopter, $1/\hat{f}_h(0)$ (km)	1.528	2.389	2.639	2.597
Eff. search half-width for duplicates, $1/\hat{f}_{hs}(0)$ (km)	1.383	2.222	1.333	1.696
Apparent eff. search half-width of ship, $1/\hat{f}(0)$ (km)	0.206	0.143	0.138	0.140
Apparent density estimate, $\hat{D}_s$(groups/km^2)	0.366	0.454	0.223	0.263
Corrected density estimate, $\hat{D}_u$(groups/km^2)	0.1149	0.0537	0.0344	0.0342
Ship detection probability 'near' trackline, $\hat{g}_s(0)$	0.430	0.544	0.666	0.597
Correction factor, $\hat{c}$	0.314	0.118	0.154	0.130
Standard error, $SE(c)$	0.131	0.163	0.051	0.050
Mean perpendicular distance to ship detections, $\bar{x}$(km)	0.3672	0.0730	0.0917	0.0880
Mean visibility code, $\bar{v}$	2.177	2.883	2.776	2.803

correction factor may be applied to the abundance estimate derived from our analyses of salmon research vessel and catcher boat data. Thus data were truncated at 500m perpendicular distance and grouped into five equal distance intervals. The resultant fits of the hazard-rate model are shown in Figs 6 and 7. Note the marked difference between the two years.

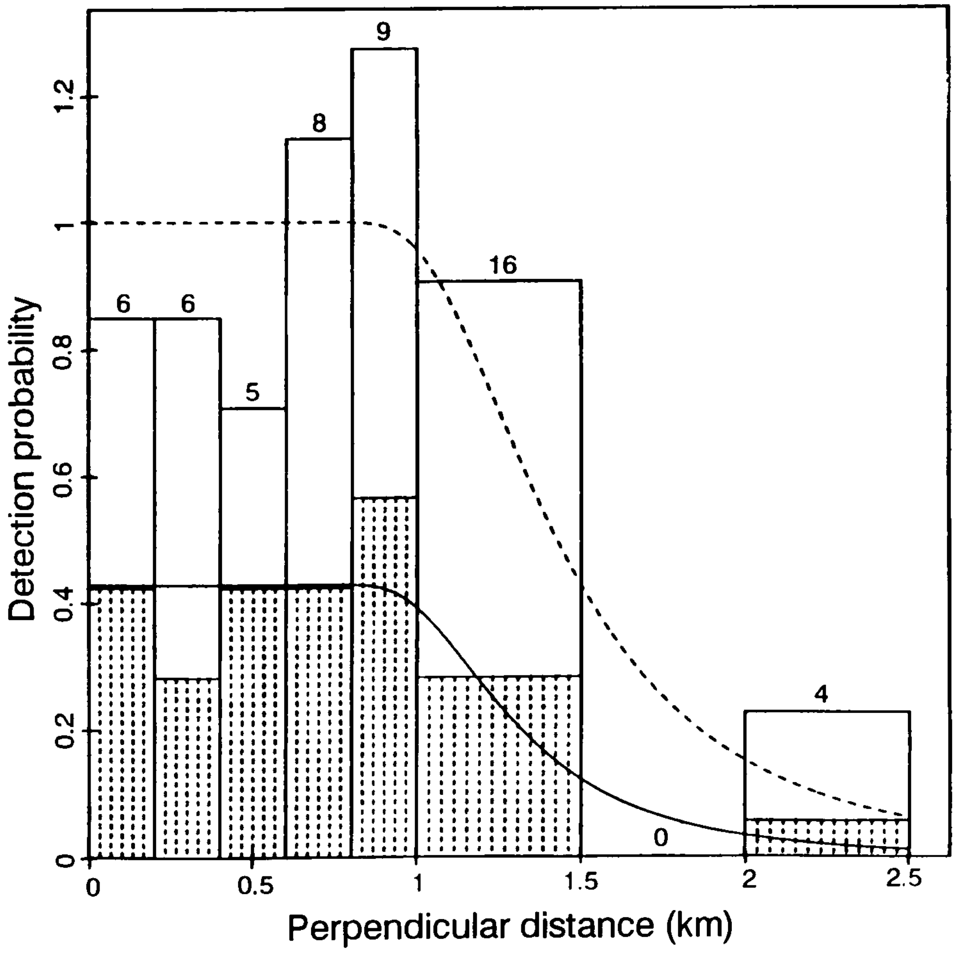

Fig. 4. Fitted densities to all helicopter sightings (upper curve) and to duplicate sightings (lower curve), 1983. The hatching indicates the number of duplicate detections in each perpendicular distance interval (from the ship's trackline, as recorded by the helicopter), and the open bars correspond to detections made by the helicopter alone.

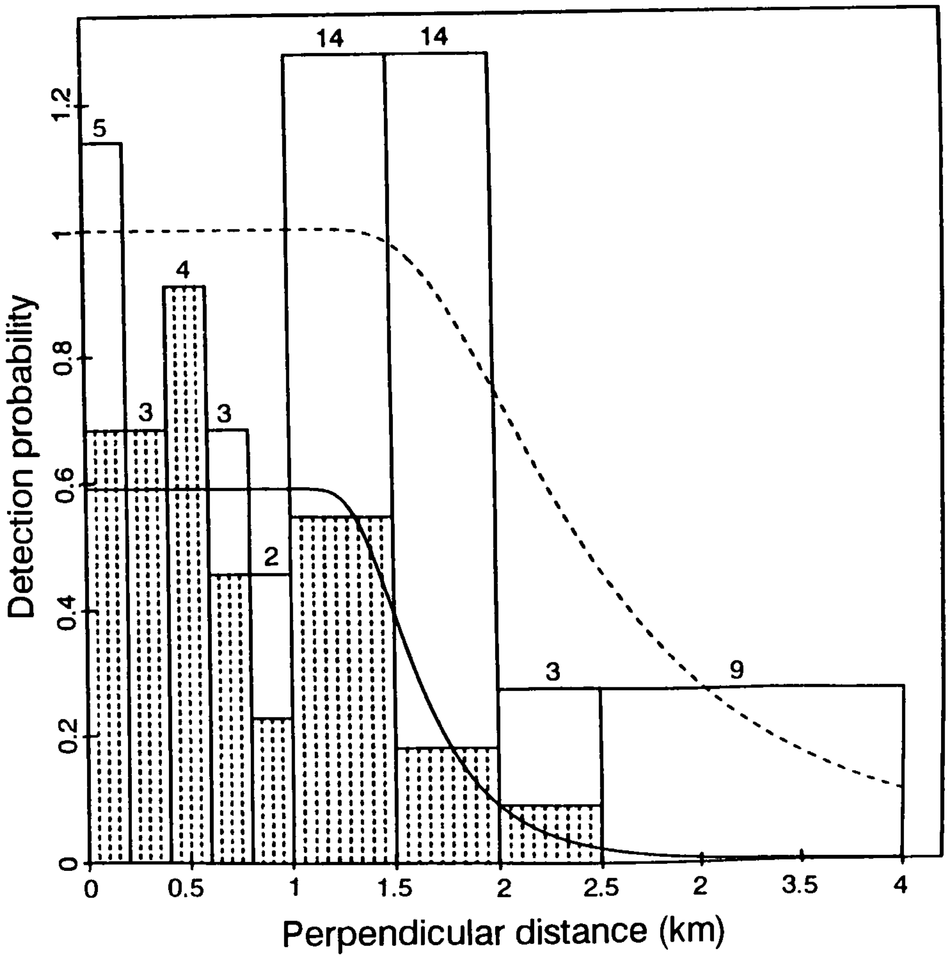

Fig. 5. Fitted densities to all helicopter sightings (upper curve) and to duplicate sightings (lower curve), pooled data, 1984. The hatching indicates the number of duplicate detections in each perpendicular distance interval (from the ship's trackline, as recorded by the helicopter), and the open bars correspond to detections made by the helicopter alone.

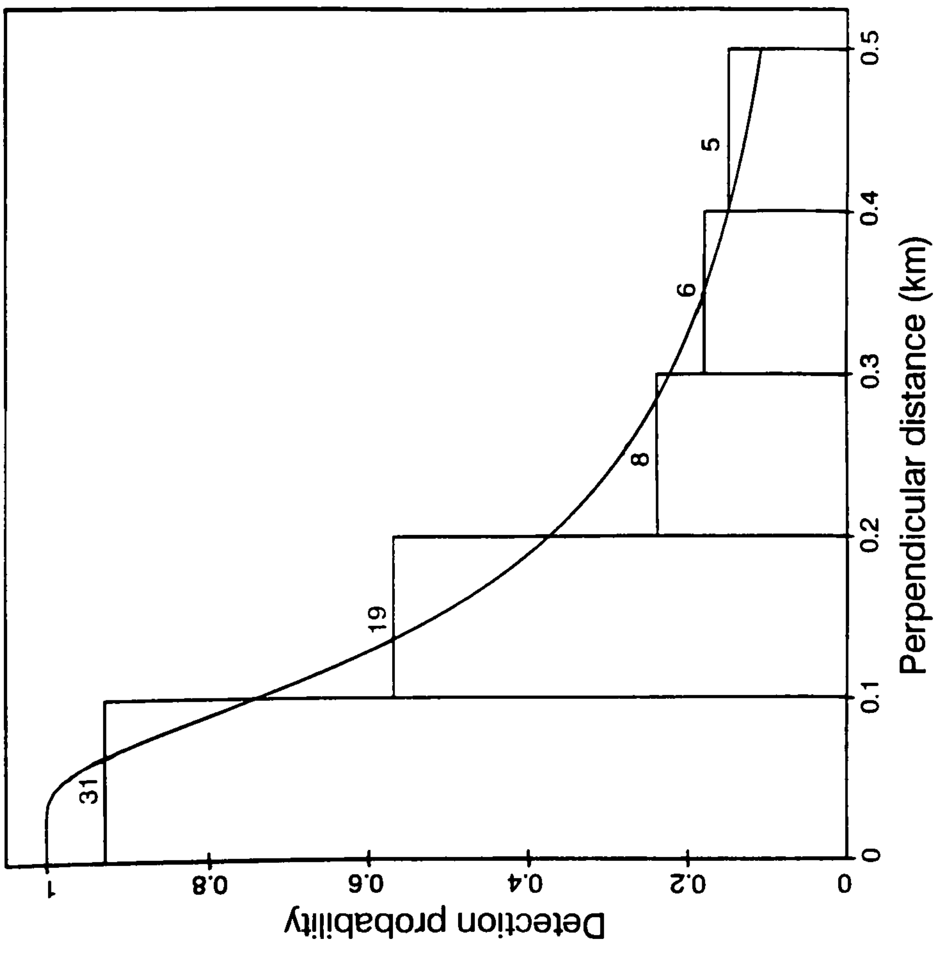

Fig. 6. Fit of the hazard-rate model to the shipboard perpendicular distance data, 1983.

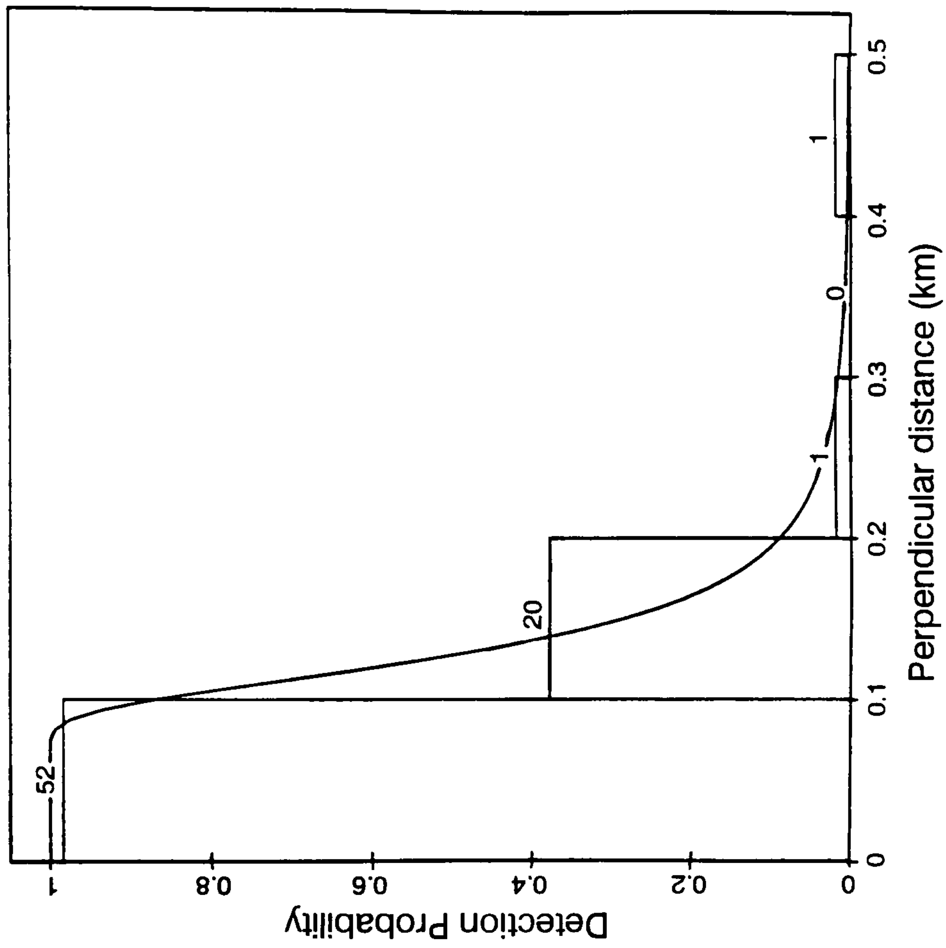

Fig. 7. Fit of the hazard-rate model to the shipboard perpendicular distance data, 1984.

Table 8

Mean perpendicular distance ($\bar{x}$) and correction factor for movement ($\hat{c}$) by area.

Visibility code	Fishing zone			Western N. Pacific excluding fishing zone		
	$\bar{x}$(m)	$\hat{c}$	$SE(\hat{c})$	$\bar{x}$(m)	$\hat{c}$	$SE(\hat{c})$
1	150.7	0.1713	0.0487	259.0	0.2427	0.0825
1-2	166.7	0.1819	0.0515	200.9	0.2044	0.0608
1-3	149.3	0.1704	0.0485	202.8	0.2057	0.0614
1-4	145.7	0.1680	0.0480	190.3	0.1974	0.0575
1-5	143.0	0.1662	0.0477	185.0	0.1939	0.0560

Table 9

Corrected abundance estimates $\hat{N}_c$ (thousands) averaged across visibility code categories, weighted by effort.

Visibility code	Fishing zone (FZ)		WNP excluding FZ		Western North Pacific (WNP)		
	$\hat{N}_c$	$SE(\hat{N}_c)$	$\hat{N}_c$	$SE(\hat{N}_c)$	$\hat{N}_c$	$SE(\hat{N}_c)$	95% CI
1	35.0	11.6	435.3	177.5	470.3	177.9	(229.6, 963.1)
1-2	15.1	4.5	210.9	67.9	226.0	68.1	(126.8, 402.7)
1-3	10.4	3.0	155.7	48.1	166.1	48.2	(95.1, 290.2)
1-4	9.9	2.9	141.7	42.3	151.5	42.4	(88.4, 259.6)
1-5	9.3	2.7	132.4	39.2	141.8	39.3	(83.1, 241.7)

A multiplicative correction of 0.314, with standard error 0.131 and 95% percentile CI (0.077, 0.566), was obtained from the 1983 experiment. The comparable estimates for 1984 were 0.130, with standard error 0.050 and 95% CI (0.075, 0.262). Note that, although the 1983 estimate lies well above the upper confidence limit for 1984, its precision is poor and the lower confidence limit is almost the same for each year.

Corrections to adjust the estimates of Table 4 for movement and for failure to detect all animals near the trackline, calculated from equation (2), are shown in Table 8 and the corrected abundance estimates are in Table 9.

DISCUSSION

The magnitude of the corrections for movement is large, indicating that abundance would have been overestimated by five- or six-fold (Table 8) in the absence of correction. The difference in the correction factor between the two experimental surveys (Table 7) may be due to a number of factors. On average, animals were sighted much farther from the ship in 1983. Factors that might have contributed to this include poor visibility conditions in the 1984 cruise, different searching efficiency by observers (possibly due in part to different locations of the observation platform) and the use of a much larger vessel in 1984, which may have resulted in stronger vessel attraction. The correction for movement and for animals missed on the trackline may be inappropriate for data from surveys on other ships and in other areas. Sighting probabilities may vary geographically or between observers and the reaction of the porpoise to the ship might vary geographically or between ships;

different vessels produce different sounds underwater to which the porpoises may react in different ways. Data from which the correction is calculated should ideally be collected during normal survey mode, but this is logistically difficult for several reasons: (i) the use of a helicopter in areas far from land (as is most of the area of interest) is not practical due to weather and sea conditions in the North Pacific; (ii) data are collected from several vessel types; (iii) many of the sightings data are collected from fishery vessels, from which it would be problematic to operate a helicopter. Application of equation (2) should lessen the bias arising from the above factors and therefore give an indication of the magnitude of the effect of movement on abundance estimates.

The corrections estimated here suggest that there was strong vessel attraction. A relatively high proportion (39%) of sightings made by the helicopter was subsequently recorded from the ship and the shipboard distances from the trackline were far smaller on average than those recorded at the time of detection by the helicopter. In the absence of vessel attraction, a much smaller proportion of duplicates would be recorded, as most animals detected by the helicopter would pass beyond the detection range of observers searching from the vessel with naked eye. Tracking data showed that not all animals moved toward the trackline; some animals sighted by the helicopter moved toward the ship and some moved away. However, the predominant pattern was movement toward the trackline.

Our analyses of salmon research vessel and catcher boat data are not straightforward to interpret. The strong dependence between visibility code and encounter rate suggests that probability of detection is far higher at visibility code 1 than in sighting conditions that are not excellent. However, effective search width seems only weakly dependent on visibility code, with no evidence of differences between codes 1, 2 and 3, the range over which encounter rate changes most. There are two possible explanations. Either many animals close to the trackline are missed, at least during visibility codes 2–5, or animal density is actually higher when conditions are good. The first explanation requires that probability of detection is lower during poor visibility, by an amount that is more or less independent of distance from the vessel. This might occur if unobtrusive, slow rolling animals close to the boat are more likely to be detected as visibility improves, thus increasing 'near' detections, while detections of more obvious rooster-tailing animals increase at larger distances. Tables 4 and 5 show that this particular explanation is false (although the possibility that encounter rate decreases for some other reason while effective search width remains constant as visibility deteriorates cannot be ruled out). Effective search width for unobtrusive animals during visibility codes 1–3 is actually wider than for rooster-tailing animals, perhaps because rooster-tailing is a response to the proximity of the vessel. The encounter rate for animals showing either behaviour falls as visibility worsens, although it falls faster for slow rolling animals, either because behaviour is correlated with sighting conditions or because many slow rolling animals are missed in poor conditions, or both.

The second explanation, that animals are more numerous when sighting conditions are good, is plausible if conditions tend to vary geographically. For example, if perfectly calm conditions usually occur in the vicinity of up-wellings, or in relatively sheltered regions and porpoise density is also high in such areas, the results obtained here would be expected. An analysis of weather conditions might help reveal whether this explanation is possible.

Whichever interpretation is correct, the adjusted abundance estimates should be valid, since our corrections adjust for both movement and failure to detect all animals near the trackline. Since those corrections were obtained by combining data from visibility codes 1–5, they should be applied to abundance estimates calculated by combining data from all five codes. In the 1983 experiment reported above (but not in the 1984 experiment), average visibility code was appreciably better than for these data. However, if data collected during codes 4 and 5 are deleted, the abundance estimate is not affected greatly (Table 9). In any case, the adjustment of the correction factor for observed mean perpendicular distance should, to some extent, compensate for such variation.

If true density is not greater in good sighting conditions, there is still some inconsistency in the estimates, which might be resolved if animals show much stronger vessel attraction in calm conditions, which would invalidate our corrections if they were applied to data from good sighting conditions only. Thus arguably the most appropriate abundance estimate for the western North Pacific area is also the most conservative of Table 9: 141,800 animals, with 95% CI (83,100 – 241,700). Since data were pooled over an eleven year period, this should be interpreted as an estimate of average abundance.

Response of animals to the ship may vary by area, season, between sexes and in different sighting conditions. Kasuya and Jones (1984) analysed the bow riding behaviour of Dall's porpoise sighted on a cruise in the Western North Pacific Ocean and reported differences by area, time of day and water temperature. However, it is difficult to interpret their results because when animals were sighted, they were chased to try to get them to ride the bow wave so that they could be harpooned. All animals that they were able to get to ride the bow wave by chasing were counted as bow riders. Kasuya and Jones' analysis of the bow riding behaviour therefore is arguably not directly applicable to sighting surveys. Bow riding behaviour is an indication of attraction, but does not indicate the level of bias due to attraction for line transect sampling because there is no information about where the animals were before they reacted to the ship. Further, in our analyses, animals that are attracted to within 100m of the ship will contribute the same level of bias whether or not they bow ride, given that we group distances recorded by shipboard observers into 100m intervals.

The population estimates presented here may be biased by inaccuracies in measurement of angle and distance. These biases might cause overestimation of density due to the tendency of observers to underestimate distances by eye. However, if many animals near the trackline were missed and search efficiency of the observers taking part in the 1983 and 1984 experiments was appreciably greater than for observers operating in the Pacific, underestimation of abundance could be substantial.

Non-random distribution of effort by area and year may bias the population estimates from the pooled data in an unknown direction. Even though research vessels followed systematic cruise tracks, their effort may be more concentrated in certain parts of the area of interest, since they are concerned with sampling squid and salmon distribution. More effort is needed in a single year to estimate abundance and eliminate any biases due to pooling data over many years. To reduce any bias due to non-random effort and spatial variability in density, stratification of the data into smaller areas would be desirable. Again, more effort in a single year would be needed. This bias would be reduced if search effort was more systematic.

Even if the assumptions behind our method of estimating abundance hold, the variance of the corrected estimate is large. Use of trends in a relative abundance index (Turnock and Buckland, 1995) may be more appropriate for assessing the status of the population, although here too, estimates are not easily interpreted; if biases in the index change over time, then the trend may give a misleading indication of changes in abundance.

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Trends in Abundance of Dall's Porpoise in the Western North Pacific, 1979 to 1989

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ABSTRACT

Two density indices of Dall's porpoise abundance were estimated for the western North Pacific from 1979 to 1989. One index is the density of animals (number of animals per n.mile^2) estimated using line transect methods and the other is the encounter rate (number of Dall's porpoise sighted per n.mile). The encounter rate increased significantly between 1979 and 1984 ($p<0.05$), then fell between 1984 and 1986 ($p<0.01$). The estimated density of animals showed no significant trend between 1979 and 1984. There was evidence of a fall in density between 1984 and 1986 ($p<0.05$).

KEYWORDS: DALL'S PORPOISE; NORTH PACIFIC; TRENDS; SURVEY-VESSEL

INTRODUCTION

The Japanese high seas salmon fishery has operated in the North Pacific Ocean since 1952. Incidental kills of Dall's porpoise (*Phocoenoides dalli*) in the gillnets number several thousand annually. Since 1978, US observers have been placed on board US and Japanese research vessels and Japanese catcher boats to record data on marine mammal sightings for analysis by line transect methods. The catcher boats travel between the mothership and where the nets are set, so that transects radiate out from the mothership position within the fishing zone. Resulting estimates of abundance of Dall's porpoise are biased both by the attraction of the animals to the survey vessel and by missing the animals near the transect line (Turnock and Quinn, 1991; Turnock *et al.*, 1995). An estimate of animal density without correction for these biases is a valid index for estimating trends in abundance provided biases are consistent over time. This paper presents estimates of two indices of Dall's porpoise density between 1979 and 1989. The western North Pacific Ocean area defined by fig. 1 of Turnock *et al.* (1995) is assumed to be the range of a single stock of Dall's porpoise.

METHODS

Data from visibility codes 2 and 3 only (very good and good; see table 1 of Turnock *et al.*, 1995 for definitions) were analysed. Weather and sea state conditions have a large effect

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on the probability of sighting Dall's porpoise (Turnock *et al.*, 1995); by restricting analyses to codes 2 and 3, any bias in the abundance indices across time is more likely to be consistent. Two indices were estimated, density (animals per n.miles^2) and encounter rate (animals sighted per n.mile of transect). Following Burnham *et al.* (1980), the first density index was estimated by

$$\hat{D}_1 = \frac{\mathrm{n} \cdot \bar{s} \cdot \hat{f}(0)}{2L}$$

where

n is the number of groups of animals observed;
$\bar{s}$ is the average group size;
L is the transect length;
and $\hat{f}(0)$ is the inverse of the effective half-width of the transect.

The variance of the index is estimated by

$$\widehat{var}(\hat{D}_1) = \hat{D}_1^2 \left[\frac{\widehat{var}(n)}{n^2} + \frac{\widehat{var}\{\hat{f}(0)\}}{\{\hat{f}(0)\}^2}\right] + \frac{\widehat{var}(\bar{s})}{\bar{s}^2}.$$

The variance of n, the number of groups sighted, is estimated from the variance of sample size by transect leg, weighted by leg length (Burnham *et al.*, 1980):

$$\widehat{var}(n) = \frac{L \sum_{i=1}^{R} l_i \left[\frac{n_i}{l_i} - \frac{n}{L}\right]^2}{(R - 1)},$$

where

R is the number of transects;
n_i is the number of observed groups in transect i, so that $\sum_{i=1}^{R} n_i = n$;
l_i is the length of transect i;
and $L = \sum_{i=1}^{R} l_i$.

Variance of mean group size was estimated by the sample variance of size of detected groups divided by the number of groups detected. The hazard-rate model (Buckland, 1985) was used to estimate $f(0)$ and $var\{\hat{f}(0)\}$. All perpendicular distance data were grouped into intervals and truncated at 500m for estimation of $f(0)$.

The number of Dall's porpoise sighted per n.mile was estimated by

$$\hat{D}_2 = \frac{n.\bar{s}}{L},$$

with estimated variance

$$\widehat{var}(\hat{D}_2) = \hat{D}_2^2 \left[\frac{\widehat{var}(n)}{n^2} + \frac{\widehat{var}(\bar{s})}{\bar{s}^2}\right].$$

Data were stratified by area to reduce bias due to non-random effort. Thus both density indices were estimated separately within and outside the salmon fishery area (the 'fishing zone'; see fig. 1, Turnock *et al.*, 1995), since a high proportion of sighting effort from the catcher boats was in the relatively small area of the fishing zone. An average density index was estimated, weighting by the respective areas:

$$\hat{D} = \frac{A_f.\hat{D}_f + A_n.\hat{D}_n}{A_f + A_n},$$

where

A_f is the size of the fishing zone within the western North Pacific area (91,740 n.miles^2);
A_n is the size of the western North Pacific excluding the fishing zone (1,036,354 n.miles^2);
$\hat{D}_f$ is the density index of Dall's porpoise in the fishing zone;
$\hat{D}_n$ is the density index in the western North Pacific area excluding the fishing zone; and $\hat{D}$ is the density index for the entire western North Pacific area.

RESULTS

Tables 1 and 2 show sample size, search effort and estimates of mean group size and $f(0)$ by area and year. Table 3 shows the weighted average density indices for the western North Pacific Ocean area. The number of Dall's porpoise sighted per n.mile (D_2) increased from

Table 1

Sample size n, search effort L, mean group size s and estimates of $f(0)$ by year, western North Pacific Ocean area excluding the fishing zone, visibility codes 2 and 3 only. CV denotes coefficient of variation (standard error/estimate).

Year	n	CV(n)	L(nm)	$\bar{s}$	CV($\bar{s}$)	$\hat{f}(0)$	CV{$\hat{f}(0)$}
1979	56	0.199	1922	3.952	0.076	9.715	0.195
1980	58	0.190	1737	4.148	0.081	10.320	0.149
1981	105	0.145	2490	4.368	0.068	7.012	0.108
1982	112	0.122	2215	3,478	0.053	13.989	0.136
1983	59	0.192	1350	3.613	0.092	10.000	0.163
1984	99	0.133	1537	3.776	0.053	8.795	0.268
1985	4	0.474	342	3.500	0.247	-	-
1986	22	0.250	1561	5.478	0.172	8.313	0.268
1987	52	0.195	1337	3.136	0.066	7.816	0.183
1988	41	0.163	1555	5.400	0.096	5.127	0.105
1989	9	0.392	635	4.667	0.176	-	-

Table 2

Sample size n, search effort L, mean group size s and estimates of $f(0)$ by year, fishing zone, visibility codes 2 and 3 only. CV denotes coefficient of variation (standard error/estimate).

Year	n	CV(n)	L(nm)	$\bar{s}$	CV($\bar{s}$)	$\hat{f}(0)$	CV{$\hat{f}(0)$}
1979	5	0.621	248	5.600	0.377	-	-
1980	44	0.163	922	4.386	0.103	35.753	0.160
1981	120	0.111	4410	3.758	0.058	10.074	0.093
1982	107	0.105	5564	2.860	0.059	13.285	0.181
1983	140	0.096	3727	3.542	0.054	9.136	0.093
1984	76	0.181	2099	3.099	0.081	6.246	0.135
1985	66	0.123	2691	3.147	0.061	20.540	0.745
1986	137	0.156	2626	3.359	0.059	11.256	0.095
1987	159	0.113	4360	3.284	0.046	7.235	0.088
1988	0	-	0	0	-	-	-
1989	0	-	0	0	-	-	-

Table 3

Weighted average density $\hat{D}_1$ and number of animals observed per nautical mile $\hat{D}_2$ for the western North Pacific Ocean area.

Year	$\hat{D}_1$	$CV(\hat{D}_1)$	$\hat{D}_2$	$CV(\hat{D}_2)$	Year	$\hat{D}_1$	$CV(\hat{D}_1)$	$\hat{D}_2$	$CV(\hat{D}_2)$
1979[1]	0.559	0.289	0.115	0.213	1985[2]	-	-	-	-
1980	0.898	0.234	0.144	0.190	1986	0.375	0.321	0.085	0.280
1981	0.635	0.178	0.177	0.148	1987	0.473	0.253	0.121	0.189
1982	1.159	0.175	0.166	0.122	1988[1]	0.365	0.217	0.142	0.190
1983	0.774	0.247	0.155	0.196	1989[1]	-	-	0.066	0.430
1984	1.011	0.280	0.232	0.133					

[1] Estimated from the area outside the fishing zone only.

[2] Insufficient effort outside the fishing zone to allow reliable estimation.

1979 to 1984, was lower in 1986, then increased from 1986 to 1988 before falling again in 1989 (Table 3 and Fig. 1). The highest rate (0.232 animals/n.mile) occurred in 1984 and the lowest rate (0.085 animals/n.mile) in 1986. The difference between these estimates is significant ($p<0.01$). A regression over the period 1979/84, weighted by the inverse of the CV^2 indicates a significant increase in the encounter rate ($p<0.05$), although the linear trend over the entire period (1979/88) is not significantly different from zero.

The estimated density ($\hat{D}_1$) shows an increasing but non-significant trend over 1979 to 1984, but the estimates for 1986/88 are all lower than the lowest pre-1984 estimate (Table 3 and Fig. 2). The 1986 estimate, which is significantly lower than the 1984 estimate ($p<0.05$), is based on a very small sample size; the density estimate for the western North

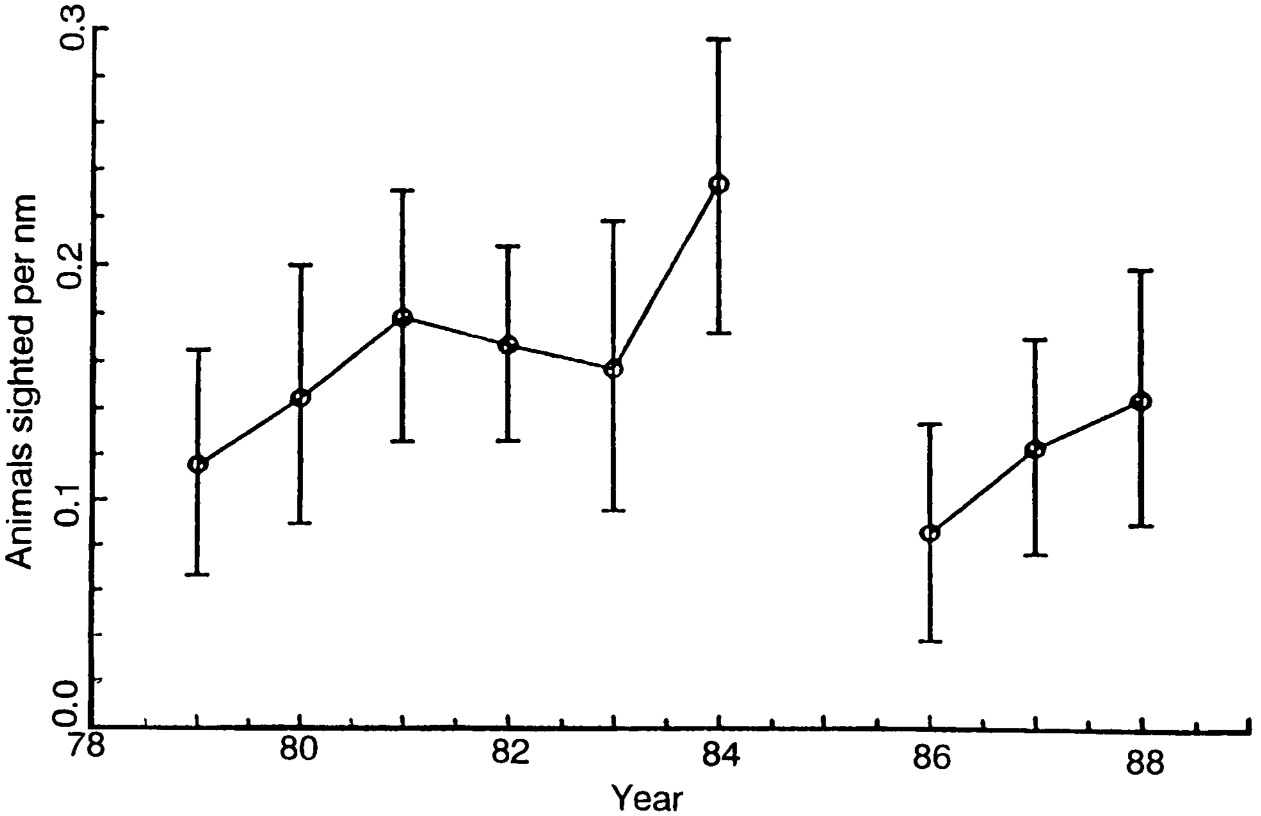

Fig. 1. Weighted average number of Dall's porpoise sighted per n.mile for the western North Pacific Ocean area, visibility codes 2 and 3. The vertical bars represent ±two standard errors.

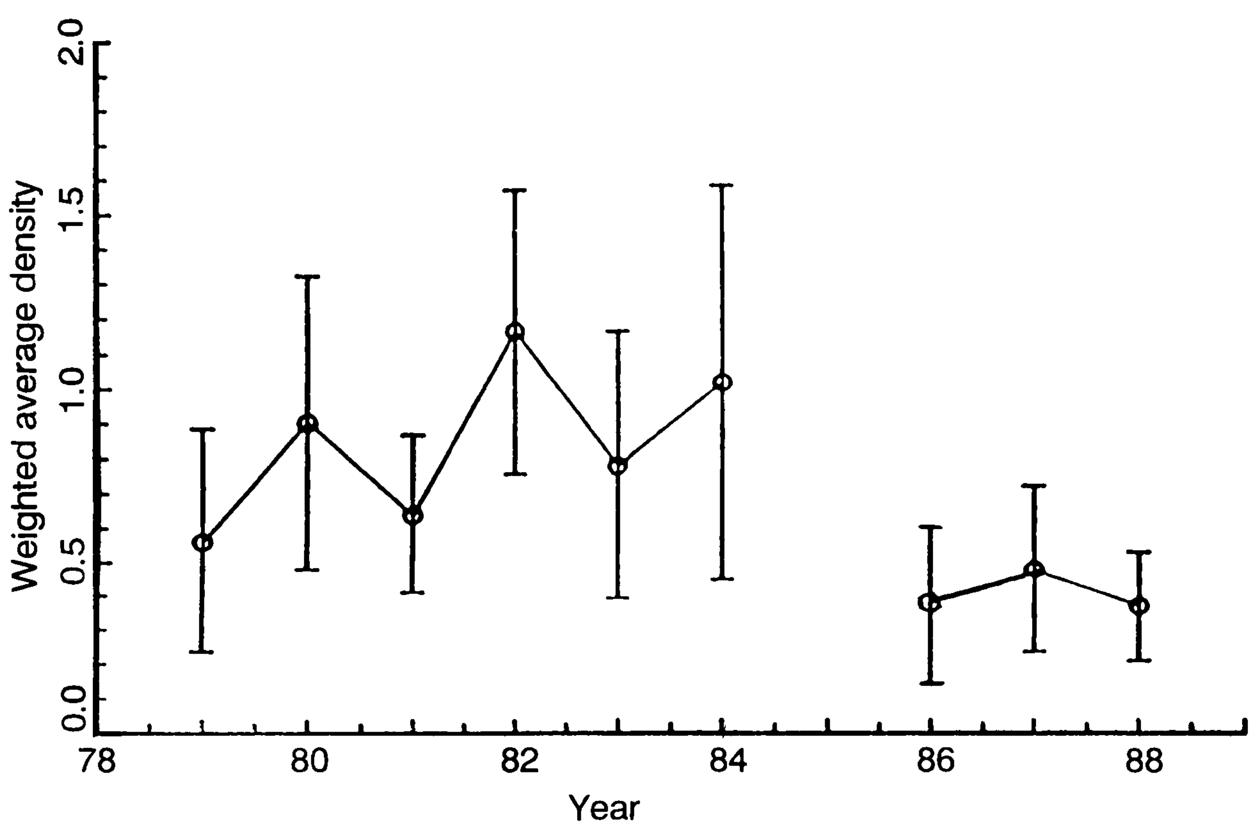

Fig. 2. Weighted average density (animals/n.mile^2) for the western North Pacific areas, visibility codes 2 and 3. The vertical bars represent ±two standard errors.

Pacific area outside the fishing zone dominates the weighted average calculated from Equation (1) and $f(0)$ was estimated from just 22 sightings (Table 1). However, the estimates for 1987 and 1988 appear to confirm that density was lower than in the early 1980s. The linear component of trend over the entire time period is not significantly different from zero.

DISCUSSION

Only 8% of the western North Pacific Ocean area is within the fishing zone. Thus abundance indices calculated using Equation (1) are dominated by the data from the area outside the fishing zone, for which the level of effort is low. The distance covered ranged from 1,300 to 2,500 n.miles per year (less in 1985), for an area exceeding 1,000,000 n.miles^2. Such sparse coverage might generate substantial variation in the annual estimates due to spatial variability in density of animals. An increase in effort would allow stratification by smaller areas to reduce bias arising from this variability.

Binoculars with reticles or gauges (plexiglass strips held a measured distance from the eye, working on the same principle as reticles) were used by some observers in 1987 to estimate distances to sightings. In 1988, most observers used reticles. If there is a tendency to underestimate distances by eye, this would lead to larger estimated distances on average in 1987 and 1988, and hence lower density indices. A χ^2 test on the distribution of perpendicular distances to detections for observers using a reticle, a gauge or neither was not significant ($\chi^2_6 = 4.05$; $p>0.1$), and the mean log perpendicular distance recorded by observers with access to neither a reticle nor a gauge did not differ significantly from either the mean for those using a reticle ($t_{146} = 0.89$; $p>0.1$) or the mean for those using a gauge

Table 4

Estimated density $\hat{D}_1$ and number of animals observed per nautical mile $\hat{D}_2$ for the western North Pacific Ocean area, research vessel data only, unstratified by geographic area.

Year	$\hat{D}_1$	CV($\hat{D}_1$)	$\hat{D}_2$	CV($\hat{D}_2$)	Year	$\hat{D}_1$	CV($\hat{D}_1$)	$\hat{D}_2$	CV($\hat{D}_2$)
1979	0.545	0.266	0.114	0.193	1985[1]	-	-	0.146	0.400
1980	1.148	0.267	0.168	0.157	1986	0.285	0.522	0.069	0.339
1981	0.596	0.164	0.172	0.135	1987	0.475	0.131	0.128	0.103
1982	1.177	0.200	0.178	0.156	1988	0.346	0.221	0.135	0.194
1983	0.739	0.257	0.157	0.210	1989[1]	-	-	0.066	0.430
1984	1.078	0.250	0.234	0.178					

[1] Insufficient data for estimation of D_1.

(t_{106} = 1.74; $0.1 > p > 0.05$). The respective untransformed mean distances were 204.5m (eye), 236.3m (reticle) and 236.3m (gauge). Thus any bias from this source is unlikely to be sufficiently large to invalidate the interpretation of the trend estimates.

It is unclear whether density or encounter rate provides the better index for assessing trend. Density is more valid if the effective width of search of the observers varies over time, for example if observers search more efficiently as they gain experience or if training improved with time, enabling observers to identify Dall's porpoises at greater distances. Further, if effective search width is highly dependent on conditions, then density should be the preferred index, since the estimate of $f(0)$ for a year should in some sense reflect 'average' conditions in that year. Since analyses were constrained to visibility codes 2 and 3, the encounter rate index is less susceptible to this bias than if data from more heterogeneous environmental conditions were analysed. Since an additional parameter ($f(0)$) must be estimated for each year to obtain the density index, it has a larger CV than the encounter rate index (Table 3). Table 2 shows that variation in estimates of $f(0)$ is large. If density was estimated by pooling data across both years and areas prior to estimating $f(0)$, exactly the same trend estimates would be obtained as for the encounter rate index. Thus the significant increasing trend from 1979 to 1984 detected by the encounter rate index but not by the density index might reflect increasing efficiency of search over that period, or might indicate that the greater imprecision in the density index has prevented it from detecting a real increase in density. Both indices suggest a reduction in density between 1984 and 1986.

The proportion of effort carried out on board catcher boats was very variable. If data from research vessels alone are analysed, less biased trend estimates might be obtained. For research vessel effort, there are insufficient data from the fishing zone to stratify analyses by geographic area. However, since effort is more uniform than for the catcher boats, geographic stratification is of little benefit. In Table 4, both abundance indices are shown, calculated from unstratified research vessel effort alone. Trend estimates are closely comparable with those of Table 3, so that conclusions are largely unaffected by whether catcher boat effort is included.

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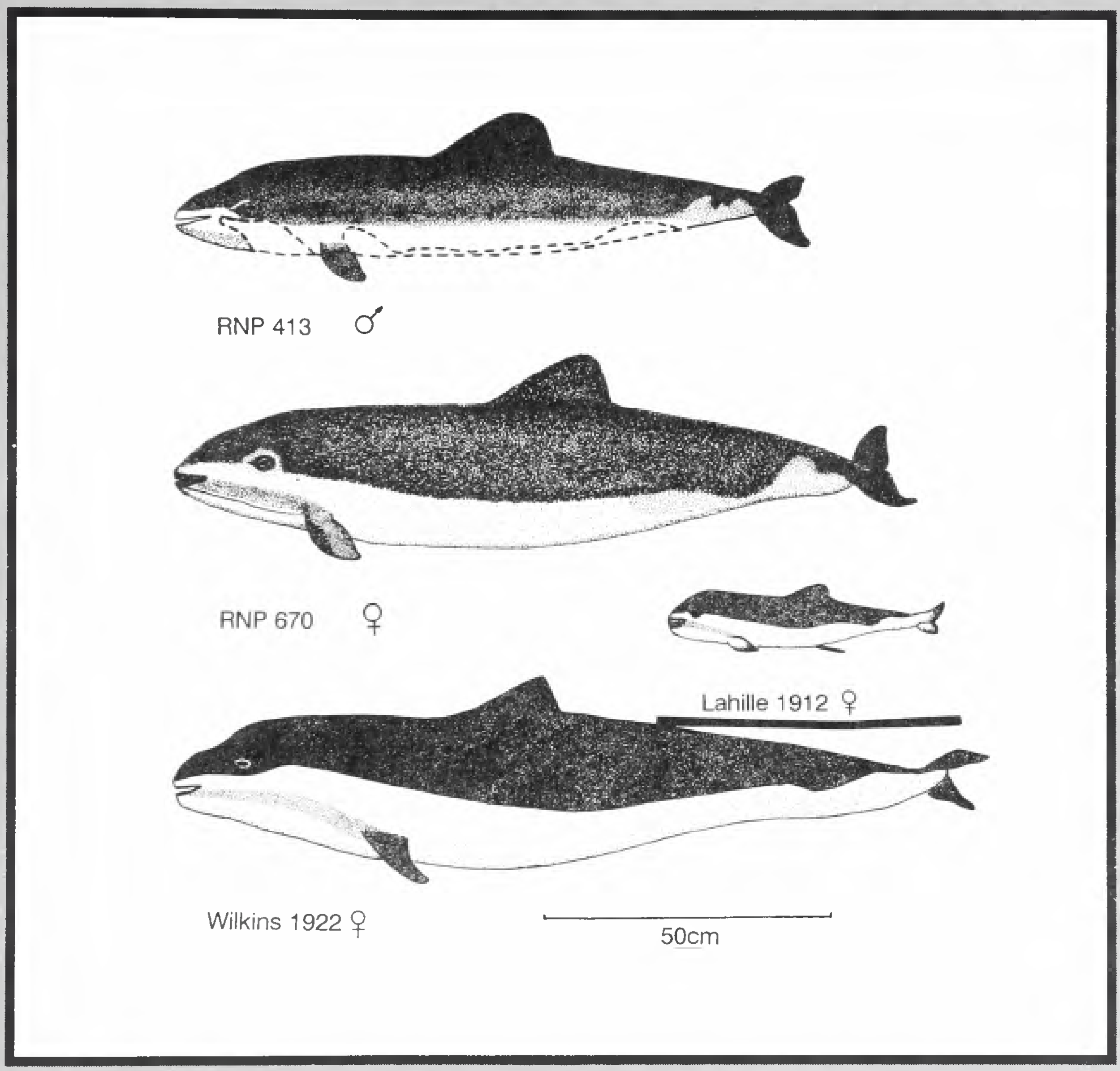
Spectacled Porpoise



Pigmentation of the foetus and calves of spectacled porpoises, drawn to scale. *Illustration courtesy of R.N.P. Goodall.*

Spectacled porpoise, *Australophocaena dioptrica*

INTRODUCTORY REMARKS

At its 1987 meeting, the Committee first received information that the spectacled porpoise was probably taken incidentally by fishing operations in Argentina. No information on the extent of this take was available and there was no information from other areas (IWC, 1988).

The only other information provided to the Committee around that time was that a total of 11 spectacled porpoises was observed during the 1978/79–1987/88 Southern Hemisphere Minke Whale Assessment Cruises. All sightings were made between 54°S and 59°S and most of them were distant from shore (IWC, 1991). This supported the hypothesis of an offshore as well as a coastal distribution for the species.

Some additional information on incidental catches was presented to the Workshop on Mortality of Cetaceans in Passive Fishing Nets and Traps (IWC, 1994). Goodall *et al.* (1994) reported that at least 34 animals were taken incidentally off Tierra del Fuego between 1975 and 1990. Crespo *et al.* (1994) stated that some spectacled porpoises were probably taken off the coast of Chubut in Argentina.

The information provided in this section thus represents a welcome addition to the sparse literature on this poorly known species.

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On the Biology of the Spectacled Porpoise, *Australophocaena dioptrica*

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ABSTRACT

Published descriptions of the biology of the spectacled porpoise, *Australophocaena dioptrica*, are reviewed and compared to new material collected in Tierra del Fuego and Chubut, Argentina. Although over 173 cranial and about 120 additional postcranial specimens have been found, minimal external measurements are available for only 28 individuals; 7 females, 11 males, 9 animals of unknown sex and 1 foetus. Males ranged in length from 109 to 224cm, females from 124.6 to 203.5cm. The smallest neonate (of unknown sex) measured 94cm, a foetus 48.4cm. Two females of 183 and 186cm were sexually mature; a female of 203.5cm was physically mature, a male of 224cm had just reached maturity. This probably does not represent the maximum size for the species. The maximum age to date (n=27) was an animal of unknown sex with 8 GLGs. Two physically adult males had 4 and 5 GLGs, and one female had 6. Young animals (n=4) are dark grey dorsally and light grey ventrally with darker grey or brownish streaks, including a well-defined mouth to flipper stripe. This pigmentation changes in the adult to black on the dorsal surface, sharply separated from the pure white ventral region. The flipper stripe seems to lighten or disappear with growth. Both young and adults have variably shaped dark eye patches outlined in white and dark lips. Most animals had a dark upper tail stock and dark flukes and flippers, which are lighter below. A live stranding of a calf is described. The stranding distribution ranges from southern Brazil (32°S) to Tierra del Fuego (55°S) in the southwestern South Atlantic and to offshore islands of the Southern Ocean: South Georgia, Auckland, Macquarie and Heard. Spectacled porpoises have been sighted both inshore and far from the coast, off eastern South America, Kerguelen, south of Tasmania and south and southeast of New Zealand; the southernmost sighting was at 58°05′S in the Drake Passage. Two specimens and several sightings were near or south of the Antarctic Convergence. The porpoises may enter rivers and channels. Food habits are unknown, but one stomach contained meagre amounts of anchovy and stomatopods. In the southwestern South Atlantic, neonates and young calves stranded in February, March and May; birth is probably in late spring or summer (November to February). These porpoises are taken incidentally in nets; the amount of exploitation is unknown, but is probably higher than formerly thought. Nothing is known of the abundance, habitat preference, seasonal movements or behaviour of this species.

KEYWORDS: SPECTACLED PORPOISE; SOUTH ATLANTIC; SOUTH PACIFIC; REVIEW; AGEING; GROWTH/LENGTH DISTRIBUTIONS; MORPHOLOGY/ ANATOMY; DISTRIBUTION; REPRODUCTION; FEEDING

INTRODUCTION

Less than twenty years ago, the spectacled porpoise, then known as *Phocoena dioptrica*, was considered one of the rarest of the world's mammals. Although the first four specimens were fresh animals with good descriptions of pigmentation, external morphology and the skeleton (Lahille, 1912; Bruch, 1916; Hamilton, 1941; Fraser, 1968), by 1976 the species was known from only 10 occurrences (9 specimens) and had never been seen alive except by whalers or fishermen (Fraser, 1968; Praderi, 1971; Brownell, 1974; 1975; Mitchell, 1975). All records were from southeasternmost South America.

The surge of interest in cetacean studies in the last 20 years has resulted in greater research and collecting effort throughout the world. Numerous remains of spectacled porpoises have been found on beaches at the southern tip of South America, and isolated crania have been recovered from offshore islands on opposite sides of the Southern Ocean, bringing the total to at least 22 specimens outside the Tierra del Fuego (TF) area, where 149 cranial and over 117 other postcranial specimens have been collected. Despite the still limited biological data, the new information obtained warrants this review of the species.

The taxonomy of the species remains controversial. In his review of the family Phocoenidae, Barnes (1985) decided that *P. dioptrica* could not justifiably be retained in the genus *Phocoena* and described the new genus *Australophocaena* for this species, placed in the subfamily Phocoenoidinae along with *Phocoenoides dalli*. However, more recent genetic analyses cast some doubt on this classification (Rosel *et al.*, 1993).

MUSEUM CODE ABBREVIATIONS

The following abbreviations are used throughout this paper. *Argentina*: CHD, Centro Histórico Documental, Río Grande, TF; CNP, Centro Nacional Patagónico, Puerto Madryn, Chubut; MLP, Museo de la Plata, La Plata; MACN, Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires; RNP, the Goodall collection, Ushuaia, TF; UBA, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires. *Australia*: NMV, National Museum of Victoria, Melbourne; TM, Tasmanian Museum, Hobart. *Brazil*: MORG, Museo Oceanográfico do Río Grande do Sul. *Chile*: IPPA, Instituto de la Patagonia, Punta Arenas; MNHN-S, Museo Nacional de Historia Natural, Santiago. *New Zealand*: NMNZ, National Museum of New Zealand (now The Museum of New Zealand Te Papa Tongarewa). *United Kingdom*: BMNH, British Museum (Natural History). *Uruguay*: ZVC, Facultad de Humanidades y Ciencias, Montevideo.

METHODS AND MATERIALS

In addition to an extensive review of the available literature, information was sought from colleagues throughout the Southern Hemisphere. Our own research largely concerns information collected from beaches in Tierra del Fuego, Argentina, which have been repeatedly surveyed for strandings since 1974. Because of the rarity of the species and the number of deformed or diseased bones found, isolated postcranial material was collected as well as skulls. Some results for this area have been presented earlier (Goodall, 1978; 1985; 1989; 1990a; b; 1991; Goodall and Cameron, 1979; Lichter and Goodall, 1988; 1989).

The fresher specimens were photographed and measured using standardised methods (Norris, 1961). Since the dorsal fin has no 'tip', measurements were taken to the uppermost point. Some published measurements were recalculated to put them in modern form. For example, the dorsal fin measurements of Lahille (1912) and Bruch (1916) were drawn on paper and the height calculated. One fresh calf was preserved whole in formalin.

The state of decomposition precluded dissection of most animals; no gonads were obtained. Badly dried, partial or decomposed specimens were measured for skeletal length when complete. Complete skeletons were collected, cleaned and are preserved in the Goodall collection in Ushuaia (RNP) or CHD.

Physical maturity was determined by the degree of fusion of the vertebral epiphyses, recorded after the skeleton had been cleaned by maceration, reassembled and checked along the entire length. Specimens in MACN, MLP and BMNH were also examined for physical maturity. Maturity classes were assigned following Perrin (1975) and Goodall *et al.* (1988a): class 0, foetus or neonate, no epiphyses fused and some neural arches unfused; class 1, juvenile, neural arches fused but no epiphyses fused; class 2, subadult, some epiphyses fused to the centra; class 3, adult, all epiphyses fused.

A preliminary study of age was carried out on 27 specimens from Tierra del Fuego and one from Chubut by decalcification, cutting and staining with Mayer's hematoxylin (Schiavini and Goodall, 1991; Crespo *et al.*, 1994c). Not all of these were for animals for which total lengths were available.

PREVIOUS WORK

Specimens

Although the first likely recorded sightings (porpoises with rounded dorsal fins) were reported during the second expedition of Capt. James Cook between 52°S and 54°S off South America (Forster, 1777, quoted in Racovitza, 1902), a specimen was not obtained until 1912, when a live pregnant female came ashore just south of Buenos Aires; photographs, measurements and a careful description were given by Lahille (1912). The adult skeleton has disappeared (Praderi, 1971; Brownell, 1975), but the foetus (not the entire adult, as stated by Hershkovitz, 1966) is still preserved in alcohol as MACN 12–14 (Table 1).

The second and third specimens, another pregnant female and the first male, were also examined while fresh and reported by Bruch (1916). The foetus was not kept, but well-made painted casts of the whole animals and their mounted skeletons are exhibited side by side at MLP (MLP 1201 and 1202).

The next recorded animal was a female calf which came ashore alive on South Georgia and was collected by H. Wilkins in May 1922[1] (BMNH 1922.11.3.1). J.E. Hamilton (1941) described it and a skeleton from the Falkland (Malvinas) Islands (BMNH 1939.9.30.1). His were the first description and photographs of the skull and skeleton. More detail on the Wilkins specimen was given by Fraser (1968), who also summarised the external measurements reported to that date.

A cranium found on Tierra del Fuego described as *Phocoena storni* (Marelli, 1922a; b) was later shown to be *P. dioptrica* (Norris and McFarland, 1958; Cabrera, 1961; Praderi, 1971). Carcelles (1948) reported that a plaster model of the head of this porpoise was in the Museo de Puerto Quequén but there is no information on the specimen. An additional report of a stranded animal which was not collected was given by Hamilton (1952).

Philippi (1893) described an animal from the coast of Chile, with a strange pigmentation pattern consisting of a black dorsal surface separated from the ventral white by a deeply undulating line, as *Phocoena obtusata*. Although some authors (e.g. Allen, 1925; Donoso-Barros, 1975) concluded that *P. obtusata* must be an individual of the species *P. dioptrica*, in which case the name *obtusata* would have precedence, the view of others (True, 1903; Brownell, 1975) was that it might be a specimen of *Cephalorhynchus*. This has since been confirmed by studies of the Philippi specimen in Santiago (MNHN-S 604) (Venegas and Sielfeld, 1978; Goodall *et al.*, 1988d). In fact, the first Chilean specimens were not discovered until the late 1970s (see below).

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[1] Hamilton (1941) says that Sir Hubert Wilkins collected this specimen at South Georgia in 1923 during the Quest expedition. Fraser (1968) reproduced Wilkin's notes, which are labelled Shackleton-Rowett Expedition, May 2nd 1922.

(*Text continues on p. 417*)

Table 1

Specimen, stranding and capture records of the spectacled porpoise, *A. dioptrica*. Note: under 'Date' actual stranding date is followed by an asterisk (*); most entries are date of collection: 'Skull' means both cranium and mandibles, as opposed to 'cranium' only; 'Cranial specimens' may have partial or complete skeletons, but 'postcranial specimens' were found without the head. Most RNP specimens are listed in Table 2.

Date	Locality	Details	Deposition	Reference
New Zealand				
-- Jan. 1975	Sandy Bay, Enderby Island Auckland Islands. 50°40'S, 166°10'E	Cranium only. First specimen from sub-Antarctic Pacific Ocean.	NMNZ Ma 1670	Baker, 1977
Australia				
24 July 1957	Aerial Cove, Cataline Point, Macquarie Is. 54°30'S, 159°00'E	Incomplete skull, unknown sex. Collected by S. Csordas. Subadult?	NMV C10323	Fordyce *et al.*, 1984
Oct.-Nov. 1985	Heard Island 53°S, 73°30'E	Cranium without teeth or mandibles. Second specimen south of Antarctic Convergence. Originally determined as *Phocoena spinipinnis*.	TM A1411	Guiler *et al.*, 1987
Brazil				
-- -- --	Río Grande do Sul approx. 32°S, 52'W	Adult male. Skull collected.	MORG	M.C. Pinedo, pers. comm.
Uruguay				
28 Oct. 1945	Balneario Lagomar, 10km mouth Arroyo Carrasco Río de la Plata 34°51'S, 56°01'W	200cm male, advanced decomposition. Pigmentation and large dorsal fin visible. Collected by E. Palerm and L. Lecour.	ZVC M850 (skull)	Praderi & Palerm, 1971 Praderi, 1971
1970's	Oceanic coast of Uruguay: Cabo Polonia, Coronilla, Punta del Diablo, La Paloma	Occasionally captured by fishermen, who easily recognise its pigmentation.	-	Praderi, 1971
Argentina, SW South Atlantic				
Provincia de Buenos Aires				
30 Dec. 1899	'Costa Atlántica, Argentina'	Incomplete cranium. Collected by M. Eugía.	MACN 292	Praderi, 1971
01 Sept. 1907	'Costa Atlántica, Argentina'	Incomplete cranium. Collected by M. Albieri.	MACN 7-45	Praderi, 1971

Date	Locality	Details	Deposition	Reference
28 Jul. 1911*	Punta Colares, near Quilmes, R. de la Plata 34°43'S, 58°15'W	186cm female with 48.4cm female foetus, came ashore alive (191cm to posterior edge of fluke). Holotype, *Phocoena dioptrica*, Lahille, 1912	Adult lost foetus, MACN 12-14	Lahille, 1912
14 Aug. 1912*	Río Santiago, La Plata 34°30'S, 57°55'W	186cm female with female foetus captured by fishermen? Collected by F. Damiani.	MLP 1202 Skel. and cast	Bruch, 1916
-- Sept. 1913*	Río Santiago? 34°30'S, 57°55'W	204cm male, evidently taken by fishermen. Collected by F. Damiani (209cm to posterior edge of flukes).	MLP 1201 Skel. and cast	Bruch, 1916
-- Dec. 1925?	Mar del Plata	3 photographs of animal and 3 of skull taken by Martín Jurado and sent to Museo Público de Buenos Aires. Envelope stamped 31 Dec. 1925. Female on basis of dorsal fin. No other data.	Photographs in MACN	H.P. Castello, pers. comm. Photo published in Capozzo and Junín, 1991
Before 1948	-	Plaster cast of head Was there a specimen?	Museo de Puerto Quequén	Carcelles, 1948
Provincia del Chubut				
Before 1975	Golfo San José. Camp 39 Península Valdés	Cranium, beach pick-up. Collected by M. Wursig. CBL 290mm	G. Harris	G. Harris, pers. comm.
26 Jun. 1985*	Near Puerto Madryn 42°45'S, 65°05'W	202cm, 6yr-old male, weight 115kg. Probably captured at sea.	CNP 116 (APP 850802)	Pagnoni and Saba, 1989 A. Purgue, pers. comm.
-- Nov. 1986	Puerto Rawson	Incomplete skeleton.	APP collection	A. Purgue, pers. comm.
Provincia de Santa Cruz				
12 Nov. 1983	Punta Loyola S	Caudal vertebrae.	RNP 1077	Goodall & Galeazzi, 1987
13 Nov. 1983	Cañadón Palos	Vertebrae.	RNP 1084	
04 Apr. 1986	Punta Desengaño S	Incomplete cranium.	RNP 1234	
06 Apr. 1986	Río Coyle N	Complete skeleton, teeth, L. flipper.	RNP 1245	
Tierra del Fuego				
6,000 yrs BP	Túnel, Canal Beagle	A few bones found in 6,000 year-old layer in shell midden.	CADIC	Piana *et al.*, 1985
ca 1,400 BP	Bahía Crossley, Isla de los Estados, TF	Several vertebrae from an undated, eroded shell midden.	RNP 1270a	RNP col.
-- -- 1921	'Tierra del Fuego'	Cranium only, holotype of *Phocoena storni* Marelli, 1922. Collected by Primera Exped. Tierra del Fuego	MACN 16407 (formerly UBA-M-116)	Marelli, 1992 Norris & McFarland, 1958

Date	Locality	Details	Deposition	Reference
-- -- 1974	1km north of Río Grande	Cranium collected by M. Canevari (H.P. Castello No. 4)	MACN	H.P. Castello pers. comm.
1974-1977	NE coast of Tierra del Fuego	46 specimens	RNP numbers	Goodall, 1977
1974-1978	Especially B. San Sebastián	Total: 87 cranial, 25 postcranial,		Goodall, 1978
1984-1987		6 more collected.		Lichter & Goodall, 1988
1987-1988		5 more collected.		Lichter & Goodall, 1989
1974-1990		Total: 136 cranial, 103 postcranial,		Goodall, 1990
1974-May 1995		Total: 155 cranial, 117 postcranial[1]		This paper.
25 Mar. 1978*	Puerto Harberton, Canal Beagle	125cm, 24kg female calf came ashore alive. Lived for several hours; swimming observations. Preserved in formalin.	RNP 670	Goodall, 1978 This paper.
03 Feb. 1989*	North side mouth of Río Chico, N. Cabo Domingo	134cm male calf found on beach by Luis Benegas. Probably taken in net.	CHD 890203 RNP 1446	This paper
Falkland (Malvinas) Islands				
-- -- 1939	West Falkland	185.5cm skeleton found on beach by G. Butler	BMNH 1939.9.30.1	Hamilton, 1941 Hamilton, 1952
-- -- --	-	Stranding record, no specimen kept described to Hamilton	-	Hamilton, 1952
South Georgia				
02 May 1922*	Leith Harbour	135.9cm female calf,[2] came ashore alive. Illustration by G.H, Wilkins, Shackleton-Rowett Expedition. Skeleton, drawings, measurements. 1st record south of Antarctic convergence.	BMNH 1922.11.3.1	Hamilton, 1941
1920's	'Off South Georgia'	Taken by whalers.	-	Fraser, 1968
Chile				
XII Región, Magallanes; Bahía Lomas, TF				
28 May 1978	8km E Cuarto Chorrillo	Cranium and 24 vertebra (RNP 703).	IPPA CE-35	Goodall & Cameron, 1979; Siefeld 1980
28 May 1978	7.5km E Cuarto Chorrillo	Incomplete cranium (RNP 704).	(IPPA CE-36)	
28 May 1978	7.5km E Cuarto Chorrillo	Incomplete cranium (RNP 705).	(IPPA CE-37)	
28 May 1978	Mouth of Cuarto Chorrillo	Incomplete cranium (RNP 710).	IPPA CE-38	

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[1] Of the Goodall collections, four specimens from Santa Cruz, four from Chile and two fresh animals are listed here; the others are in Table 2.

[2] Wilkins called his animal a female; the specimen in BMNH is labelled male.

Praderi and Palerm (1971) reported the first specimen from Uruguay (ZVC M850); detailed descriptions of this and two old crania (MACN 292 and 7–45 labelled 'Atlantic coast, Argentina', collected in 1899 and 1907), as well as a review of measurements, were given by Praderi (1971). The Uruguayan specimen was a 200cm 'adult' male from the Río de la Plata coast. Thus at the beginning of the 1970s all known records were from the southwestern South Atlantic.

However, in January 1975, a cranium of *P. dioptrica* was found on Enderby Island in the Auckland Islands (Cawthorn, 1975; Baker, 1977; IWC, 1978). A second cranium from the sub-Antarctic southwestern Pacific was collected on Macquarie Island at 54°30'S in 1957 (Fordyce *et al.*, 1984) (Fig. 1).

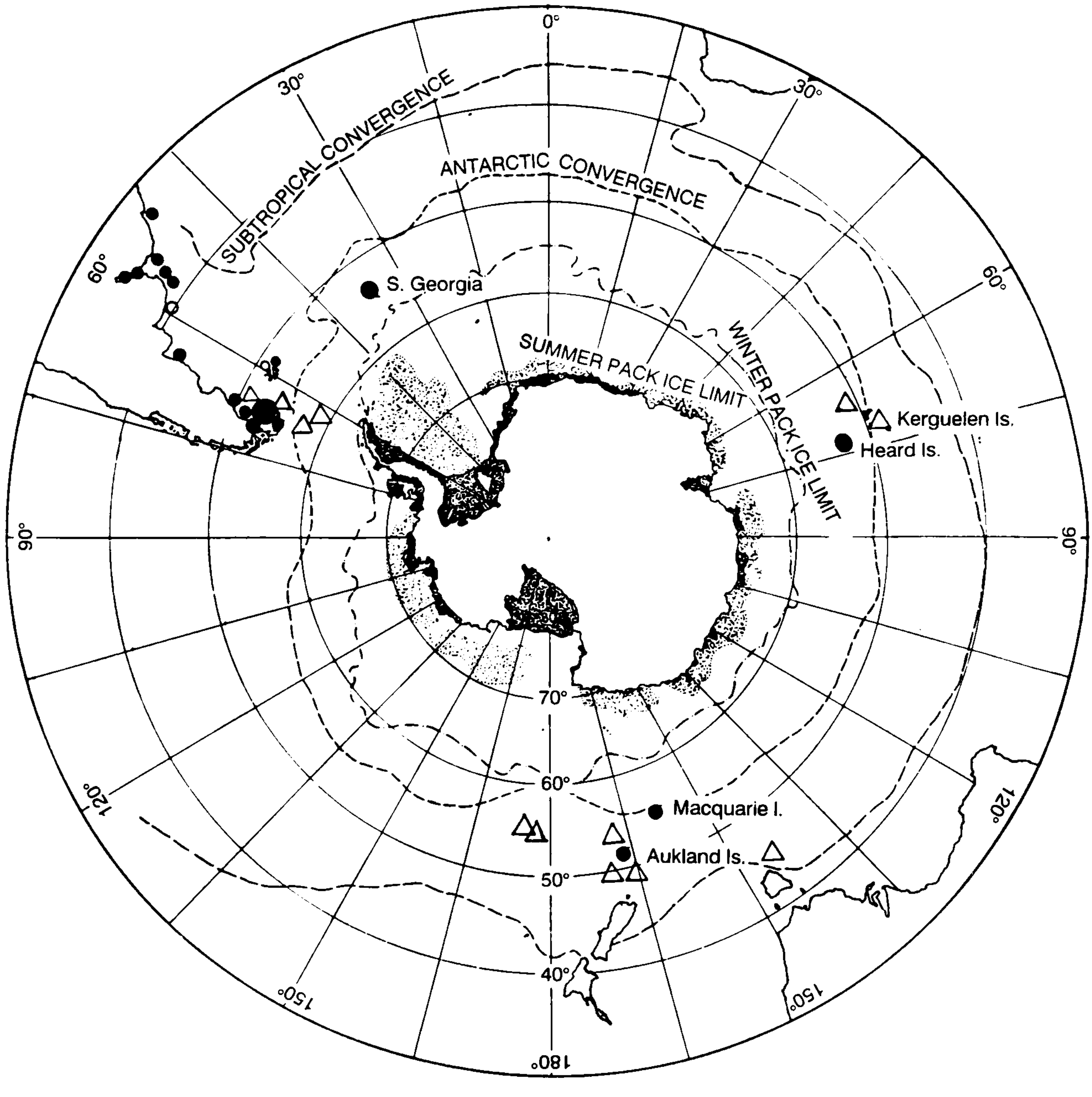

Fig. 1. Map showing the world distribution of the spectacled porpoise. Small dark circles indicate single specimens, the medium one four specimens and the large one over 260 specimens. Open circles indicate stranding observations (no specimen collected); open triangles are sightings.

During the mid-late 1970s, due to increased effort relatively large numbers were discovered on Tierra del Fuego and Goodall (1977; 1978) reported that this was the species most often found in her preliminary beach surveys.

The first Chilean specimens ($n=4$) were reported from the eastern Strait of Magellan (not from the Pacific coast) by Venegas and Sielfeld (1978), Goodall and Cameron (1979) and Sielfeld (1980).

By the late 1980s specimens from the remaining areas of the Patagonian coast had been reported: for Santa Cruz by Goodall and Galeazzi (1987); and for Chubut by Pagnoni and Saba (1989) who reported a large, fresh male. A further skeleton and a beach-worn cranium were also found in Chubut (G. Harris and A.P. Purgue, pers. comms.).

Given the absence of land in the high southern latitudes of the Indian Ocean, it is perhaps not surprising that the first specimen was not found there until 1985 when a cranium was found on Heard Island (Guiler *et al.*, 1987). Although the authors had identified the skull as *P. spinipinnis*, it is clearly a specimen of *A. dioptrica* (Brownell *et al.*, 1989).

Specimens continued to be obtained from Tierra del Fuego (Lichter and Goodall, 1988; 1989; Goodall, 1989; 1990b). In this paper we report on a recently dead male calf found on the beach north of Río Grande in February 1989 (L.G. Benegas, pers. comm.) and other new skeletons, bringing the world total to about 173 cranial specimens, 151 of them from Argentine Tierra del Fuego (Table 2, Figs 2 and 3). Many of these are beach worn and in poor condition. There are an additional 117 postcranial specimens. The most recent record (July 1994) is the cranium of an adult male from Brazil (about 32°S), the northernmost specimen known (M.C. Pinedo, pers. comm.).

DISTRIBUTION AND ABUNDANCE

There are few documented sightings of this species and these are summarised in Table 3 and Figs 1 and 2. Our present understanding of the distribution of *A. dioptrica* is that it is circumpolar and found in cool temperate, sub- and low-Antarctic waters, at least near the offshore islands of the West Wind Drift: Tierra del Fuego, the Falklands (Malvinas) and South Georgia in the southwest South Atlantic; Auckland and Macquarie in the southwestern South Pacific; Heard and Kerguelen in the southern Indian Ocean (Fig. 1). At these latitudes there is practically no other land. It has also been reported in the Falkland (Malvinas) Current along the Argentine coast as far north as 32°S off southern Brazil.

The degree of contact among populations near the offshore islands in the different oceans or with the population off southeastern South America is unknown (Klinowska, 1991). Reeves and Leatherwood (1994) point out that since sightings have been made far offshore, 'some movement across expanses of open ocean may occur'.

Even for Tierra del Fuego, where most of the specimens were found, there is little or no information on abundance. In the early years of the work on Tierra del Fuego it was the most numerous species found on the beaches (Goodall, 1977; 1978), but once the beaches had been cleared, the most numerous species found was *Cephalorhynchus commersonii*. Of course strandings may not reflect the whole distribution or abundance of a species or the state of the population offshore.

In ten years of IWC/IDCR Minke Whale Cruises, *A. dioptrica* was sighted only five times (Kasamatsu *et al.*, 1990). There are no reports of sightings from the many research and tourist ships which visit the Antarctic. In view of the many years of research in the sub-Antarctic and Southern Ocean, this species can only be called rare at our present state of knowledge.

(*Text continues on p. 423*)

Table 2

Specimens collected in Tierra del Fuego, 1974-May 1995, by specimen type (A: complete. B: nearly complete, e.g. lacking flippers. Sk: cranium - a-c, good to poor condition. M: mandible. V: vertebrae). Note: ** under Sex = determined from dorsal fin size; TL = total length; PM = physical maturity (see text); * under date = exact date of death; Condition ranges from 1 (alive) to 6 (clean articulated skeleton) and 7 (clean disarticulated). BSS, Bahía San Sebastián; Ea, estancia, farm; C., cabo, cape; Pta, punta, point; R, río, river.

RNP no.	Sex	TL in cm	PM	Age	Date collected	Locality	Cond -ition	Specimen type	Notes
0412	F	183+	2	2	13 Feb. 77*	BSS 1km	4b	A	Net
0413	M	109+	0	0	13 Feb. 77	BSS 4km	4b	A	Net
0533	-	183+	2	5	30 May 77	BSS 2.5km	4b	A	
0536	-	180+	2	3	31 May 77	BSS 15km	4b	A	
0658	F	203.5	3	6	29 Jan. 78	BSS 5km	3b	A	
0670	F	124.6	1	-	25 Mar. 78*	Canal Beagle, Bahía Harberton	1	A	In formalin
1000	M?	-	2	3	14 Mar. 82	Cabo Espíritu Santo	5	A	CADIC
1196	-	185+	2	3	18 Oct. 85	Ea Sara, Puesto 17, 2km S	6	A	
1353	M	189+	3	4	24 Mar. 88	Ea Las Violetas 8km N	5b	A	Net? CADIC
1703	M	-	-	-	10 Apr. 93*	Los Chorrillos 5.4m W	2b	A	Collected 20 April
0082	-	-	2a	1	31 Jul. 75	C. Peñas S	6	B	
0298	M?	-	3	3	13 Feb. 76	BSS 12km	6	B	MACN 20493
0429	-	-	2	-	16 Feb. 77	C. Peñas 4km S	7	B	To GUAYMAS
0469	-	-	2	-	04 Mar. 77	Pta. María S	7	B	
0525	-	-	-	-	29 May 77	Los Chorrillos W	6	B	To MNHN-M
0625	-	-	1a	-	11 Dec. 77	BSS 13km	6	B	
0695	M	224+	3a	-	14 May 78	Pta. María 5.5km N	4b	B	Deformed
0750	-	-	3	4	29 Nov. 79	Pta. María N	6	B	
0770	-	-	1b	1	14 Jan. 80	BSS 16-17km	4b	B	
0870	-	-	2	2	23 Jan. 81	BSS 8km	6	B	
0896	-	-	2b	-	05 Jul. 81	Paso de las Cholgas S	6	B	
0906	-	-	2b	-	22 Aug. 81	Ea Viamonte, beach field	6	B	
0970	M	196	3	5	19 Jan. 82	BSS 9.5km	4a	B	To NMNZ
1014	-	94+	0	-	06 Apr. 82	Pta. María N	4a	B	
1030	F?	-	3	6	30 Nov. 82	C. Peñas 0.5km S	7	B	To USNM
1061	-	-	2	1	07 Mar. 83	BSS 25km	6	B	To USNM
1146	F	-	2	2	06 May 84	Ea Sara, Campo 15 Abajo	6	B	To LACM
1220	-	-	3	3	05 Mar. 86	Ea Sara, Puesto 17km N	4b	B	Net?
1313	M**	-	3	-	26 Oct. 87	C. Domingo S	3b	B	Net?
1348	F	174+	2	4	24 Mar. 88	Paso de las Cholgas	6	B	Net?
1465	-	198+	2	-	04 Dec. 89*	R. Chico near mouth	6	B	Net, 1 of 4 caught 23 Nov.
1559	-	185+	-	-	19 Dec. 90	BSS 5.5km	6	B	
1628	-	-	-	-	19 Feb. 92	BSS 6.5km	6	B	
1652	F**	-	2	-	11 Sep. 92	BSS, Ea San Martín N	6	B	Mother of 1653? Net?
1669	F?	203+	2	-	15 Nov. 92	BSS 13.5km	6	B	
1682	-	-	-	-	16 Nov. 92	Arroyo Gama S	4b	B	Deformed
1687	-	201+	3	-	17 Jan. 93	BSS 18km	4b	B	
1718	M**	200+	-	-	27 May 93*	Los Chorrillos E	3b	B	
1791	M	198+	2b	-	10 Apr. 94	Ea Viamonte, Auricosta N	3b	B	
1024	-	-	1	-	18 Nov. 82	BSS 12.1km	7	Sk	
1481	-	-	2	-	08 Dec. 89	Los Chorrillos W	6	Sk V	
1653	-	-	1	-	11 Sep. 92	BSS, Ea San Martín N	6	Sk V	Young of 1652? Net?
1615	-	-	-	-	25 Jun. 91	BSS 8.5km	7	Sk	
1705	-	-	2a	-	10 Apr. 93	Los Chorrillos 1.7mi E	6	Sk V	
0034	-	-	-	-	12 May 75	Ea San Martín N	7	Ska	Collected by Padre J. Tico

Continued

Table 2 continued

RNP no.	Sex	TL in cm	PM	Age	Date collected	Locality	Cond -ition	Specimen type	Notes
0599	-	-	-	-	28 Nov. 77	BSS 18km	7	Ska	To NMNZ
1333	-	-	-	2	13 Mar. 88	Pta. María S	6	Ska V	
0609	-	-	3	-	28 Nov. 77	BSS 17km	7	Ska M V	
0039	-	-	-	6	12 May 75	Ea San Martín N	7	Ska M D	Collected by Padre J. Tico
0299	-	-	2a	3	13 Feb. 76	BSS 10km	6	Ska V	Deformed
0033	-	-	-	-	12 May 75	Ea San Martín N	7	Skb	Collected by Padre J. Tico
0036	-	-	-	-	12 May 75	Ea San Martín N	7	Skb	Collected by J. Tico to USNM
0065	-	-	3	-	06 Jul. 74	Pta. María N	7	Skb V	To IZUA
0085	-	-	-	-	31 Jul. 75	C. Peñas S	7	Skb M	
0123	-	-	2	-	18 Dec. 75	R. Chico mouth N	7	Skb M V	
0297	-	-	-	-	13 Feb. 76	BSS 13km	7	Skb	
0319	-	-	-	-	13 Feb. 76	BSS 10.5km	7	Skb	SWFC 01222
0324	-	-	-	-	13 Feb. 76	BSS 12km	7	Skb	
0325	-	-	-	-	13 Feb. 76	BSS 12km	7	Skb	MACN 20491
0372	-	-	-	-	21 Nov. 76	BSS 9km	7	Skb	
0403	-	-	3	3	16 Jan. 77	C. Peñas S	7	Skb V	
0404	-	-	-	-	16 Jan. 77	C. Peñas S	7	Skb V	
0440	-	-	2	-	03 Mar. 77	C. Peñas 5km S	7	Skb V	
0443	-	-	2	-	03 Mar. 77	C. Peñas 6km S	7	Skb M V	
0455	-	-	-	-	03 Mar. 77	Pta. María 1-2km N	7	Skb	
0460	-	-	2	-	04 Mar. 77	Pta. María S	7	Skb V	
0464	-	-	-	-	04 Mar. 77	Pta. María S	7	Skb	
0505	-	-	-	-	08 Apr. 77	Los Chorrillos E	7	Skb	
0583	-	-	-	-	21 Nov. 77	BSS 20km	7	Skb	To LACM
0587	-	-	-	-	21 Nov. 77	BSS 22km	7	Skb	
0600	-	-	2	-	28 Nov. 77	BSS 18km	7	Skb V	
0628	-	-	-	-	11 Dec. 77	BSS 13km	7	Skb	
0657	-	-	-	-	29 Jan. 78	BSS 18km S	7	Skb	
0690	-	-	2	-	13 May 78	C. Peñas S	7	Skb V	
0694	-	-	-	-	14 May 78	Pta. María 5.5km N	7	Skb V	
0732	-	-	-	-	05 Jan. 79	BSS 11km	7	Skb	MACN 20492
0737	-	-	-	-	06 Jan. 79	BSS 44km	7	Skb	
0757	-	-	-	-	29 Nov. 79	BSS 19km S	7	Skb	To GUAYMAS
0776	-	-	-	-	18 Feb. 80	Ea Las Violetas N	7	Skb	
0969	-	-	-	-	19 Jan. 82	BSS 11km	7	Skb	
1008	-	-	3a	-	15 Mar. 82	BSS 22.5km	7	Skb V	
1013	-	-	-	-	06 Apr. 82	C. Peñas S	7	Skb	
1461	-	-	2	-	03 Dec. 89	C. Viamonte SE	7	Skb V	
1627	-	-	-	-	19 Feb. 92	BSS 9km	7	Skb	Young
0011	-	-	-	-	30 Sep. 75	Ea Viamonte, 1km S	7	Skc	Occipital region
0017	-	-	-	-	30 Sep. 75	R. Fuego N	7	Skc	Occipital region, poor
0035	-	-	-	-	12 May 75	Ea San Martín N	7	Skc	Collected by Padre J.Tico
0037	-	-	-	-	12 May 75	Ea San Martín N	7	Skc	Collected by J. Tico to LACM
0038	-	-	-	-	12 May 75	Ea San Martín N	7	Skc	Collected by Padre J. Tico
0048	-	-	-	-	12 Apr. 74	Ea Viamonte S	7	Skc	
0050	-	-	-	-	12 Apr. 74	Ea Viamonte S	7	Skc V	
0070	-	-	-	-	06 Jul. 74	Pta. María 4km N	7	Skc	Occipital region

Continued

Table 2 continued

RNP no.	Sex	TL in cm	PM	Age	Date collected	Locality	Cond -ition	Specimen type	Notes
0071	-	-	-	-	06 Jul. 74	Pta. María 4km N	7	Skc	
0117	-	-	-	-	18 Dec. 75	C. Peñas S	7	Skc	
0118	-	-	-	-	18 Dec. 75	C. Peñas S	7	Skc	
0141	-	-	-	-	20 Dec. 75	Cabo Espíritu Santo S	7	Skc	
0176	-	-	-	-	21 Dec. 75	BSS 28km	7	Skc	
0191	-	-	-	-	28 Jan. 76	BSS 6km	7	Skc	Crushed
0194	-	-	-	-	28 Jan. 76	BSS 6km	7	Skc M	Right mandible
0195	-	-	2	-	28 Jan. 76	BSS 6km	7	Skc V	
0198	-	-	-	-	28 Jan. 76	BSS 6km	7	Skc	
0204	-	-	2	-	28 Jan. 76	BSS 6.5km	7	Skc V	Worn
0206	-	-	-	-	28 Jan. 76	BSS 6.5km	7	Skc	
0216	-	-	-	-	28 Jan. 76	BSS 7-8km	7	Skc	Occipital region
0220	-	-	-	-	28 Jan. 76	BSS 7-8km	7	Skc	
0221	-	-	-	-	28 Jan. 76	BSS 7-8km	7	Skc	
0224	-	-	-	-	28 Jan. 76	BSS 7-8km	7	Skc	
0225	-	-	-	-	28 Jan. 76	BSS 7-8km	7	Skc	
0234	-	-	-	-	28 Jan. 76	BSS 5-6km	7	Skc	
0239	-	-	2	-	28 Jan. 76	BSS 5-6km	7	Skc V	
0251	-	-	3	-	28 Jan. 76	BSS 8km	7	Skc V	
0267	-	-	-	-	28 Jan. 76	BSS 0.5km	7	Skc	
0275	-	-	-	-	13 Feb. 76	BSS 20.5km	7	Skc	
0301	-	-	2b	-	13 Feb. 76	BSS 10.5km	7	Skc V	
0316	-	-	-	-	13 Feb. 76	BSS 10.5km	7	Skc	
0317	-	-	-	-	13 Feb. 76	BSS 10.5km	7	Skc	
0318	-	-	2a	-	13 Feb. 76	BSS 10.5km	7	Skc V	
0349	-	-	-	-	21 Nov. 76	BSS 8-9km	7	Skc	
0350	-	-	-	-	21 Nov. 76	BSS 8-9km	7	Skc	
0351	-	-	-	-	21 Nov. 76	BSS 8-9km	7	Skc	
0361	-	-	-	-	21 Nov. 76	BSS 8-9km	7	Skc	
0401	-	-	-	-	16 Jan. 77	C. Peñas S	7	Skc	
0411	-	-	-	-	13 Feb. 77	BSS 21km	7	Skc	
0441	-	-	-	-	03 Mar. 77	C. Peñas 5km S	7	Skc	
0445	-	-	2a	-	03 Mar. 77	C. Peñas 6km S	7	Skc V	
0449	-	-	-	-	03 Mar. 77	Pta. María 3-4km N	7	Skc V	
0459	-	-	2	-	04 Mar. 77	Pta. María S	7	Skc V	
0463	-	-	-	-	04 Mar. 77	Pta. María S	7	Skc V	
0465	-	-	-	5	04 Mar. 77	Pta. María S	7	Skc V	
0539	-	-	-	-	31 May 77	BSS 15km	7	Skc	
0546	-	-	0?	-	01 Jun. 77	R. Cullen S	7	Skc	Neonate
0586	-	-	-	-	21 Nov. 77	BSS 22km	7	Skc	
0589	-	-	-	-	21 Nov. 77	BSS 22km	7	Skc	
0592	-	-	-	-	21 Nov. 77	Pen. Páramo, tip E	7	Skc	
0639	-	-	-	-	01 Jan. 78	R. Ewan mouth N	7	Skc	
0697	-	-	-	-	14 May 78	Pta. María 10km N	7	Skc	
0855	-	-	-	-	21 Dec. 80	BSS 15km N	7	Skc	Young
0856	-	-	-	-	21 Dec. 80	BSS 15km	7	Skc	
1003	-	-	-	-	14 Mar. 82	Pen. Páramo, near tip	7	Skc	
1143	-	-	2a	-	25 Mar. 84	R. San Pablo S	7	Skc V	
1181	-	-	3	-	07 Jun. 85	Ea Sara, Campo 15 Abajo	7	Skc V	Deformed
1347	-	-	-	-	24 Mar. 88	Ea Sara, Puesto 17km S	7	Skc	Net?
1547	-	-	-	-	11 Dec. 90	San Pablo S, Arroyo Azara	7	Skc	
1832	-	-	-	-	30 Jan. 95	BSS, 17km N	7	Skc	
1026a	-	-	1?	-	18 Nov. 82	BSS 17.3km	7	Skc	

The collection also contains 115 postcranial elements, without skulls, 14 of them complete vertebral columns.

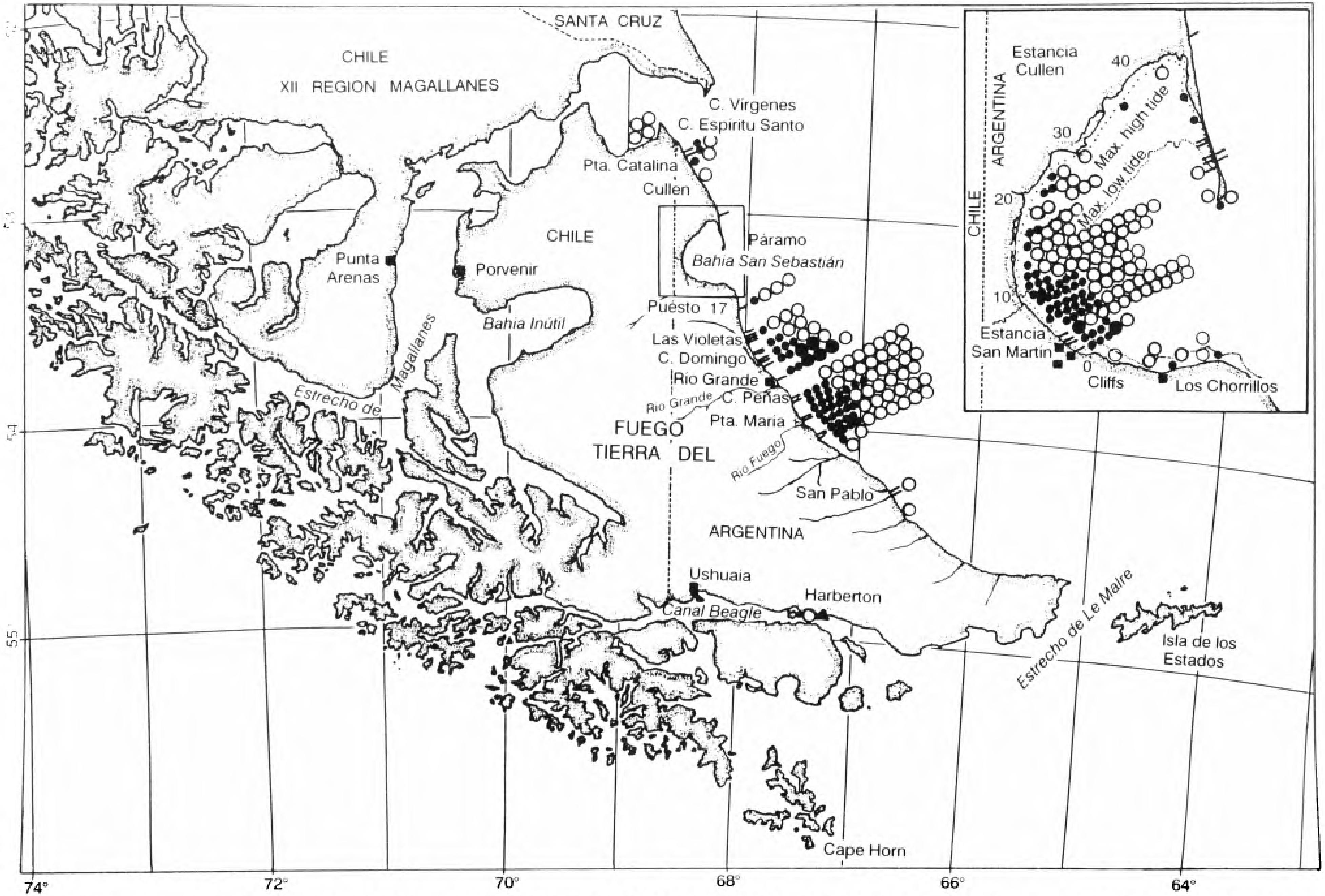

Fig. 2. Distribution of the specimens found in Tierra del Fuego (Table 2). The short lines indicate localities where gillnets are set in the tidal zone for fish. Open circles are cranial specimens (often including postcranial skeleton); closed circles indicate captures, small closed circles are postcranial specimens. The closed triangle indicates a sighting.

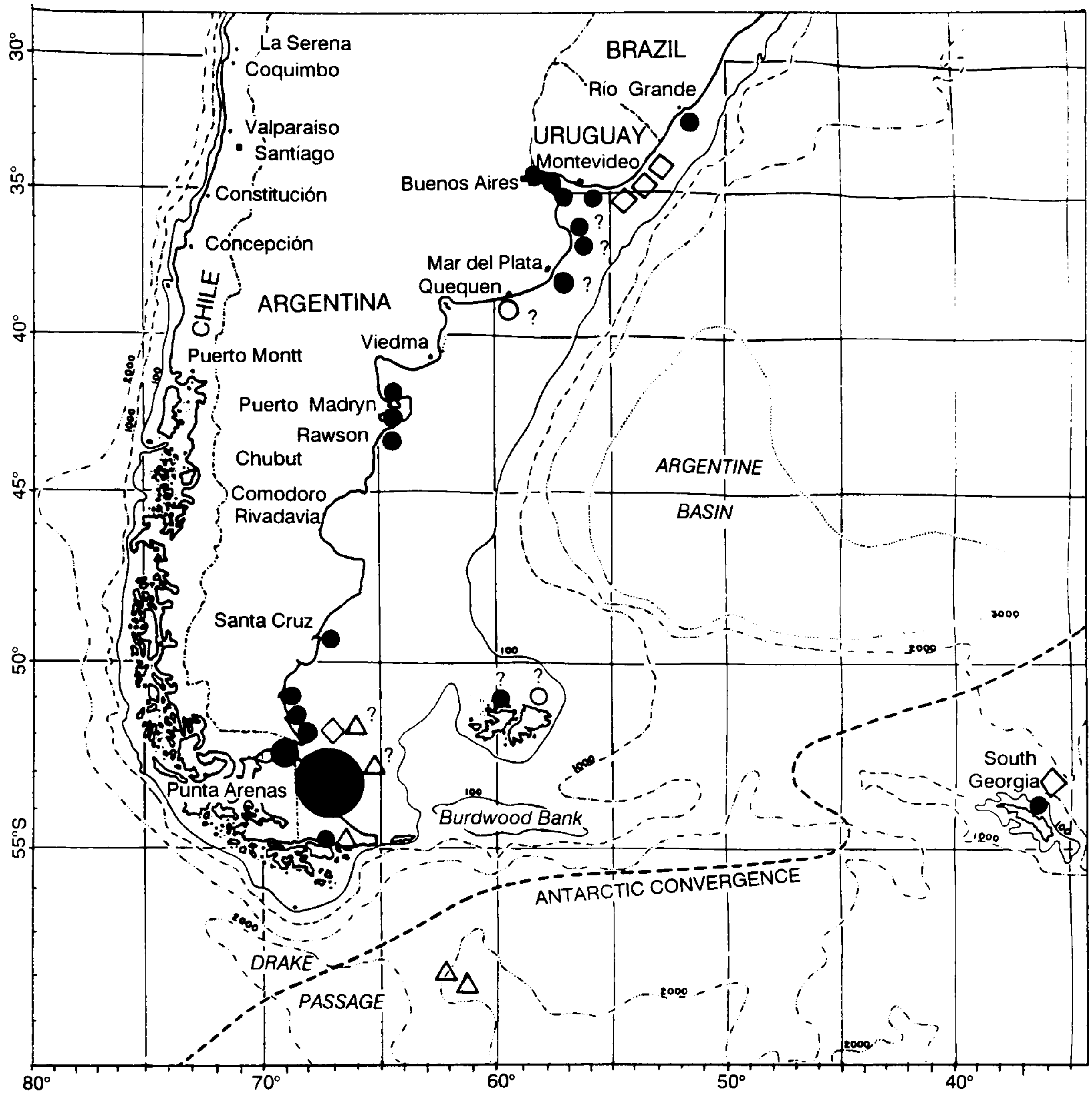

Fig. 3. South American distribution of the spectacled porpoise. Small dark circles are single specimens, middle sized indicates four specimens and the large circle over 260 specimens. Open circles are stranding observations, open triangles are sightings and diamonds indicate records of incidental exploitation. A question mark means the locality is uncertain.

EXTERNAL SIZE AND PROPORTIONS

Length

Up to 1976, only four of the specimens were fresh and total lengths were published for only five animals. Even for the many specimens found on Tierra del Fuego beaches, most were highly decomposed or only beach-worn bones and taking reliable external measurements was usually impossible. At present, some external measurements are available for 7 females (and a small foetus), 11 males and 9 animals of unknown sex (Tables 4 and 5), giving a total of 27 specimens. Skeletal lengths are available for several more animals.

The total lengths for seven females ranged from 124.6 to 203.5cm (Table 4, Fig. 4). The formerly known maximum length for females was 186cm (Lahille, 1912) which Brownell (1974) erroneously quoted as 191cm; this was in fact the length to the posterior border of the flukes.

Table 3

Sightings or observations believed to be of the spectacled porpoise, *Australophocaena dioptrica*.

Date	Location	Details	Ship	Ref./Observer
		Southwestern South Atlantic		
-- Jan. 1775	52°-54°S in the western South Atlantic	Two possible sightings of porpoises with rounded dorsal fins by Cook expedition.	*Resolution*	Forster, 1777 *in* Racovitza, 1902
1920s	South Georgia	Whaling captains often see it in schools about 16km offshore; they shoot them for food.	-	H. Wilkins *in* Fraser, 1968
1970s	Oceanic coast of Uruguay	Fishermen hunt this species occasionally, 'easily recognised by its peculiar colouration'.	-	Praderi, 1971
25 Mar. 1978	Puerto Harberton Canal Beagle	125cm live calf stranded at head of bay, attached to a line, swam in bay for over an hour.	Shore Rowboat	Goodall, 1978
09 Jul. 1978	Golfo San Jorge 45°45'S, 65°05'W	Five animals with dark upper body, white below, triangular fin. Jorge R. Davola, observer.	ARA *Comodoro Rivadavia*	Goodall & Polkinghorn1979
28 Dec. 1986	Drake Passage 58°02'S, 62°19'W	1901hrs. group of three with low dorsal fins. Sea temp. 5.5°C.	*Shonan Maru II*	Kasamatsu & Joyce 1990; IWC, 1991
28 Dec. 1986	Drake Passage 58°05'S, 62°09'W	1928hrs. Two animals with low dorsal fins. Sea temp. 5.5°C	*Shonan Maru II*	Kasamatsu & Joyce, 1990; IWC, 1991
-- Apr. 1988	Bahía Relegada, Canal Beagle	One animal, swimming near shore, going into the bay.	Shore	Christina Folger
		Southern Indian Ocean		
02 Apr. 1976	SW of Iles Kerguelen 49°29'S, 70°15'E	Possible sighting, animals with slow rolling motion, dark, no beak, triangular fin.	M.S. *Marion Dufresne*	Frost & Best, 1976
-- -- --	Golf du Morbihan Kerguelen island	Possible sighting, dark-backed animals with low, triangular dorsal fins.	-	Frost & Best, 1976
		Southwestern South Pacific Ocean		
-- Mar. 1977	NE of Auckland Islands	A pair sighted by M. Cawthom.	-	IWC, 1978
-- Mar. 1977	NW of Auckland Islands	A pair sighted by M. Cawthorn.	-	IWC, 1978
-- -- --	South of Tasmania	No details	-	Leatherwood & Reeves, 1985
22 Dec. 1985	54°54'S, 167°12'E	One animal seen. Sea temperature 6°C.	*Kyo Maru 27*	Kasamatsu & Joyce, 1990; IWC, 1991
19 Feb. 1986	56°12'S, 174°36'W Antipodes Is	Two adults with calf. Water temperature 8.4°C. Photographs.	*Kyo Maru 27*	Kasamatsu & Joyce, 1990; IWC, 1991
19 Feb. 1986	55°41'S, 175°14'W	Two animals. Water temperature 9.5°C.	*Kyo Maru 27*	Kasamatsu & Joyce, 1990; IWC, 1991

The Lahille foetus was 48.4cm in length. Calves of 124.6cm and 135.9cm had unerupted teeth; the latter, the Wilkins skeleton in BMNH, has no fused epiphyses.

The 203.5cm female was physically mature (Class 3), while specimens of 183cm+ (RNP 412) and 186cm (Bruch, 1916, in MLP) were subadults (Class 2). Two 186cm animals contained very small foetuses (Lahille, 1912; Bruch, 1916). RNP 412 (183cm) was netted with a neonate (RNP 413) which may have been its offspring.

The total lengths for nine males range from 109cm+, a neonate, to 224cm. The latter is 20cm greater than the previously published (204cm, Bruch, 1916) maximum length (Table 4, Fig. 4). Although Pagnoni and Saba (1989) reported a 202cm 'adult' male from Puerto Madryn, Purgue (1987 and pers. comm.) remeasured the same specimen and found a total

Table 4. External measurements (in cm) of specimens of spectacled porpoises, *Australophocoena dioptrica*.

	Foetus	Neonates and Juveniles					Females					Sex unknown					Males				
	n=1	*n*	min.	max.	mean	SD	*n*	min.	max.	mean	SD	*n*	min.	max.	mean	SD	*n*	min.	max.	mean	SD
Snout to																					
fluke notch	48.4	5	94.0	135.9	119.5	17.8	5	174.0	203.5	186.5	10.7	6	180.0	203.0	189.1	9.2	8	189.0	224.0	202.4	10.1
post margin of blowhole	7.1	4	11.0	15.2	13.1	2.0	2	17.2	21.0	19.1	2.7	-	-	-	-	-	1	16.0	16.0	16.0	-
angle of mouth	4.0	4	6.0	7.6	6.9	0.7	3	8.9	9.5	9.1	0.3	-	-	-	-	-	1	7.5	7.5	7.5	-
centre of eye	-	4	12.9	16.5	14.4	1.5	2	15.7	21.5	18.6	4.1	-	-	-	-	-	1	17.9	17.9	17.9	-
centre of ear	-	2	17.6	8.0	17.8	0.3	1	23.6	23.6	23.6	-	-	-	-	-	-	1	23.2	23.2	23.2	-
ant. insert. of flipper	11.3	4	22.1	25.4	23.6	1.4	3	33.3	35.0	34.4	1.0	-	-	-	-	-	1	32.5	32.5	32.5	-
ant. insert. dorsal fin	17.4	3	48.0	64.8	55.2	8.7	2	81.0	84.8	82.9	2.7	-	-	-	-	-	3	69.0	88.0	76.8	9.9
tip of dorsal fin	-	3	58.0	77.0	68.1	9.6	2	99.7	110.3	105.0	7.5	-	-	-	-	-	2	117.5	123.0	120.3	3.9
umbilicus	26.3	1	59.7	59.7	59.7	-	2	85.0	91.0	88.0	4.2	-	-	-	-	-	-	-	-	-	-
centre of genital slit	35.1	2	74.0	82.2	78.1	5.8	3	119.5	136.7	127.1	8.8	-	-	-	-	-	1	119.0	119.0	119.0	-
centre of anus	36.2	4	81.0	94.0	87.7	5.4	2	124.9	131.5	128.2	4.7	-	-	-	-	-	2	141.0	145.0	143.0	-
Centre of eye to:																					
angle of mouth	3.5	2	7.7	8.0	7.9	0.2	3	10.0	12.0	11.3	1.2	-	-	-	-	-	2	10.0	11.6	10.8	1.1
ear	2.6	2	4.5	4.6	4.6	0.1	2	5.0	6.2	5.6	0.8	-	-	-	-	-	1	5.7	5.7	5.7	-
blowhole edge	-	1	10.8	10.8	10.8	-	-	-	-	-	-	-	-	-	-	-	1	14.0	14.0	14.0	-
Flipper																					
ant. length	-	3	13.0	20.0	16.1	3.6	2	15.1	18.9	17.0	2.7	-	-	-	-	-	2	20.0	21.0	20.5	0.7
post. length	-	3	9.0	13.0	10.7	2.1	2	10.6	12.0	11.3	1.0	-	-	-	-	-	2	12.5	16.5	14.5	2.8
max. width	2.3	4	5.6	8.0	6.8	1.0	4	6.9	8.4	7.3	0.7	-	-	-	-	-	3	9.8	11.0	10.3	0.6
Dorsal fin																					
height	2.9	5	6.5	10.2	9.0	1.6	4	7.1	12.5	9.2	2.3	3	13.7	14.0	13.9	0.2	9	17.0	32.0	23.0	4.7
length at base	7.1	4	16.0	24.0	21.5	3.7	5	21.5	36.0	30.5	6.8	3	26.0	36.0	30.3	5.1	9	29.0	48.5	40.6	6.3
Flukes																					
width, tip to tip	8.7	4	22.8	33.0	29.2	4.6	1	32.0	32.0	32.0	-	5	25.7	40.0	32.5	4.8	5	33.5	51.0	42.6	6.8
ant. margin to fluke notch	4.9	2	7.7	12.9	10.3	3.7	4	12.0	16.0	14.0	1.6	4	12.0	15.0	13.1	1.2	5	11.8	21.5	15.7	3.6
depth of notch	-	3	1.1	2.0	1.5	0.5	1	2.8	2.8	2.8	-	2	1.5	1.8	1.7	0.2	3	1.8	2.5	2.1	0.4
Girth																					
at axilla	-	1	61.5	61.5	61.5	-	-	-	-	-	-	-	-	-	-	-	1	99.0	99.0	99.0	-
max. (ant. dorsal fin)	28.0	2	68.2	78.0	73.1	6.9	2	108.0	108.0	108.0	-	-	-	-	-	-	2	102.0	114.0	108.0	8.5
at anus	14.0	2	30.4	40.4	35.4	7.1	1	62.0	62.0	62.0	-	-	-	-	-	-	1	73.4	73.4	73.4	-
midway anus to fluke notch	-	2	18.2	23.8	21.0	4.0	1	28.8	28.8	28.8	-	-	-	-	-	-	1	34.5	34.5	34.5	-
Height, same place	-	2	8.5	10.4	9.5	1.3	1	13.0	13.0	13.0	-	-	-	-	-	-	-	-	-	-	-
Thickness, same place	-	2	3.0	4.0	3.5	0.7	1	4.0	4.0	4.0	-	-	-	-	-	-	-	-	-	-	-
Aperture length, eye	0.7	2	1.2	1.9	1.6	0.5	1	1.7	1.7	1.7	-	-	-	-	-	-	1	2.0	2.0	2.0	-
blowhole	-	1	0.7	0.7	0.7	-	-	-	-	-	-	-	-	-	-	-	1	1.0	1.0	1.0	-
blowhole width	1.5	2	2.2	5.1	3.7	2.1	2	4.2	4.2	4.2	-	-	-	-	-	-	2	3.3	3.5	3.4	0.1
genital slit	2.4	1	6.6	6.6	6.6	-	1	19.0	19.0	19.0	-	-	-	-	-	-	1	9.8	9.8	9.8	-
perineal length	-	1	9.0	9.0	9.0	-	-	-	-	-	-	-	-	-	-	-	1	12.7	12.7	12.7	-
mammary gland slits, max.	-	1	0.6	0.6	0.6	-	1	8.0	8.0	8.0	-	-	-	-	-	-	-	-	-	-	-
Projection of upper jaw	-	1	0.2	0.2	0.2	-	1	0.3	0.3	0.3	-	-	-	-	-	-	-	-	-	-	-

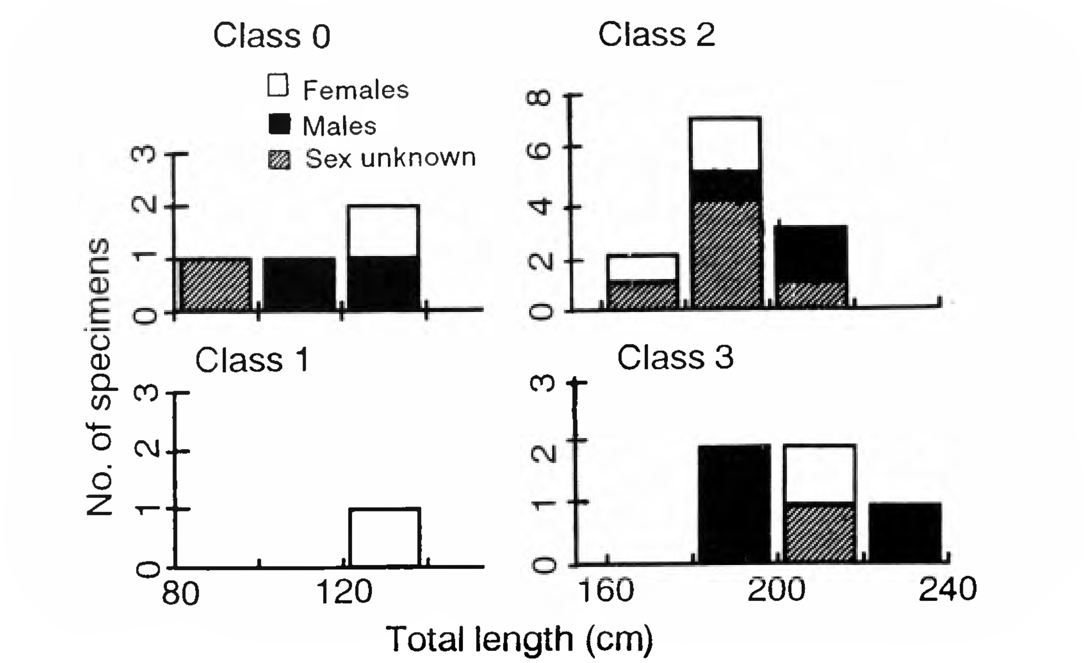

Fig. 4. Progression by length and vertebral fusion. Class 0, neonate; class 1, juvenile; class 2, subadult; class 3, physically adult.

length of 205cm, noting it to be sexually mature but physically immature. We have used Purgue's measurements in Table 4 because they were taken by standard methods.

Males of 189 and 196cm were physically mature, whereas the largest male of 224cm (RNP 695) had just reached physical maturity; the Bruch male of 204cm was subadult, as was the 205cm male from Puerto Madryn (see above). The 200cm male from Uruguay and the 204cm Bruch male were thought to be 'adult on the basis of size' (Praderi, 1971; Brownell, 1975). On this basis, Gaskin *et al.* (1984) called these animals physically mature, but the Bruch male in MLP has epiphyseal fusion only in the posterior caudal vertebrae.

A freshly stranded (or netted) male calf measured 134cm. Six animals of unknown sex ranged from a neonate of 94cm, the smallest animal known, to 198+cm (RNP 1465). Only the latter was physically mature.

The limited data suggest that females may reach sexual maturity at about 185cm and that both sexes may reach physical maturity at about 190–210cm. Although males seem larger, the sample size is too small to determine if there is sexual dimorphism in size. On the basis of the few physically adult animals found, the maximum length for this species is probably greater than the animals discovered to date. Length frequency distribution is shown in Fig. 4.

Weight

Only five animals have been weighed: the Lahille foetus at 1.6kg, an eviscerated 109cm calf at 14.8kg, a 124.6cm calf at 24.2kg, the Lahille subadult female at 85kg and the 205cm Chubut subadult male at 115kg. Despite this Mörzer Bruyns (1971) gave a weight of 54kg and Watson (1981) stated that weight averages 50kg with a possible maximum to 84kg; these are essentially fictitious but have unfortunately been repeated by several other authors in general cetacean guides.

Body proportions

Descriptions of body proportions were given by Lahille (1912), Fraser (1968) and Brownell (1975). It is a strongly built, streamlined animal with a maximum girth in front of the dorsal fin of about 50–60% of total length (mean 55.9%, n=6).

The head is cone-shaped, evenly rounded in front and without a beak. The upper jaw projects just slightly (0.2–0.3cm). The gape is extremely short; Lahille (1912) stated that the mouth was less than half as long as the flipper and used this as one of the characters to distinguish this species from the harbour porpoise (*Phocoena phocoena*).

The eye is small and the blowhole is well forward at about the level of the eye (in three cases slightly ahead, one at the same level and one behind). There is a slight depression in the area of the blowhole, giving the animal a small 'forehead'. The overall shape of the head of a juvenile spectacled porpoise was strikingly similar to that of an adult specimen of Commerson's dolphin (*Cephalorhynchus commersonii*), an animal which is considerably smaller (Goodall *et al.*, 1988d, p.271).

The flippers are relatively small (Fig. 5), with a mean anterior length of only 11% TL (range 8.3–14.9%, n=6) of body length, compared to a mean of 16.7% in the Burmeister's porpoise, *Phocoena spinipinnis* (Goodall *et al.*, 1988d). The flippers are situated well forward on the body, low down and fairly close together. Tracings of flippers were given by Fraser (1968) and Goodall *et al.* (1988d), the latter comparing shape and flipper bones with those of *P. spinipinnis, C. commersonii* and the Chilean dolphin, *C. eutropia.*

The dorsal fin (Fig. 6) is characteristic in shape, being broadly triangular, with leading and trailing edges somewhat convex and with a well-rounded tip, situated at about the middle of the back. The fin is highly sexually dimorphic, as described by Bruch (1916). In our sample the height and length of the dorsal fin was significantly larger in males than females (excluding juveniles) (Student's test: height, p=0.00009, n=4 females and 9 males; length, p=0.008, n=5 females and 9 males). The dorsal fin is resistant to decomposition and often remains attached to dried carcasses which have been almost skeletonised, allowing the determination of sex. Goodall *et al.* (1988d) compared the dorsal fins of this and other southern South American small cetaceans. The single row of tubercles on the anterior edge of the dorsal fin reported by Lahille (1912) for his female have not been seen on any of the animals we have examined.

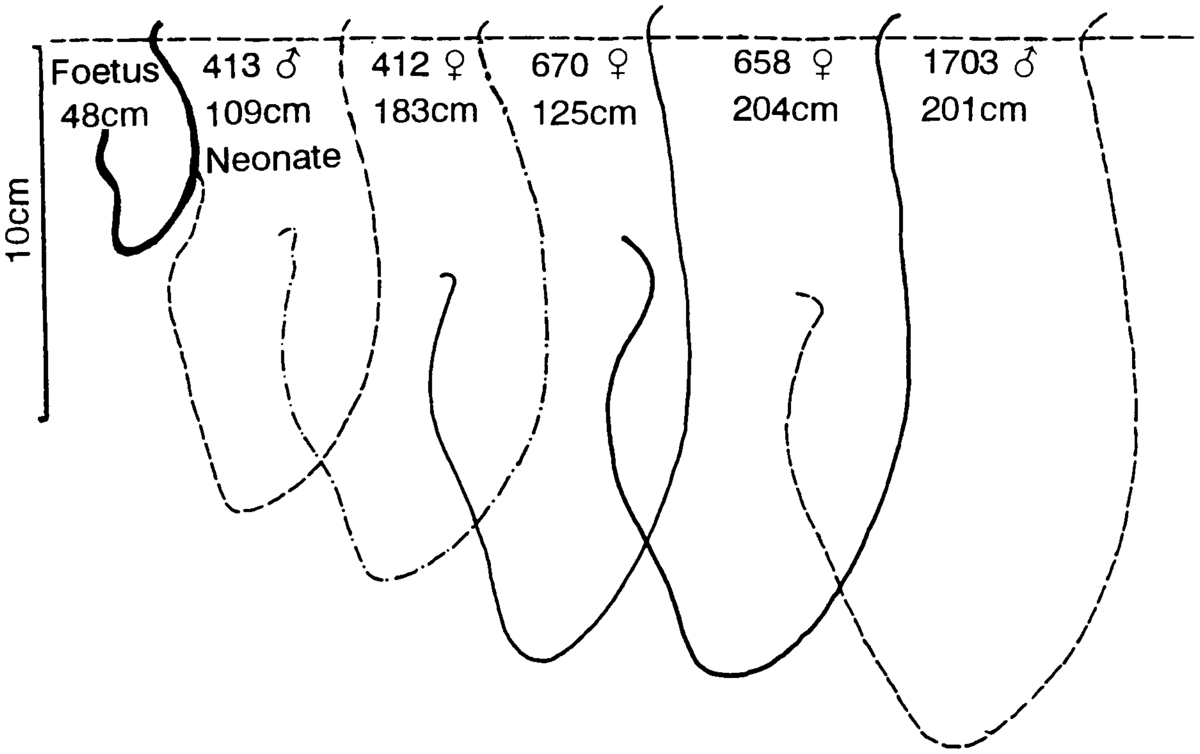

Fig. 5. Tracings of flippers of specimens of *A. dioptrica* drawn to scale. The scale is 10cm.

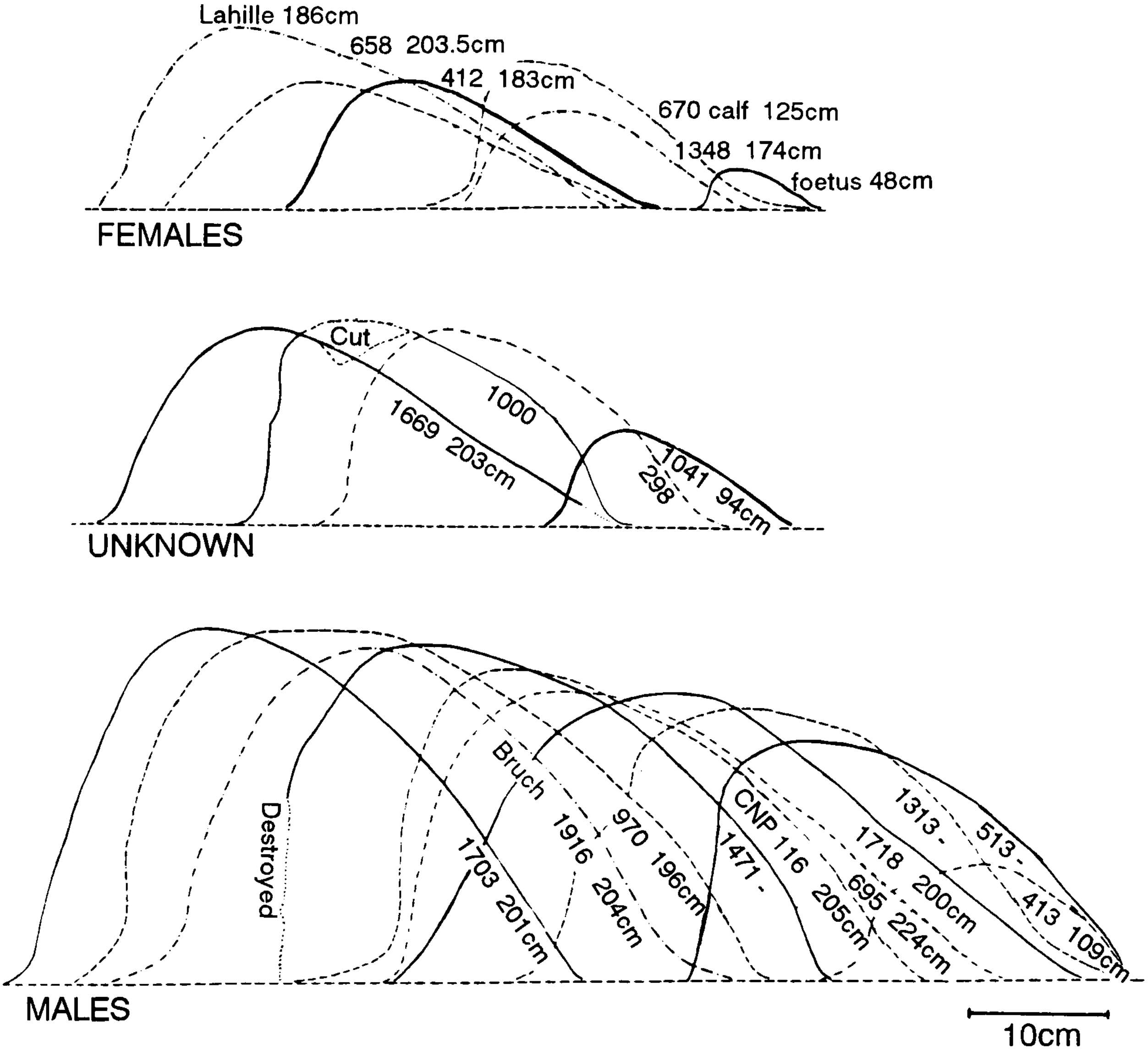

Fig. 6. Tracings showing variation in shape and size of dorsal fins of specimens of *A. dioptrica* drawn to scale: six females, above; four of unknown sex, centre; 10 males, lower. The scale in all cases is 10cm. Specimen numbers are RNP unless otherwise indicated. Lahille and Bruch specimens were calculated from measurements and enlarged photographs.

The flukes have well-rounded tips with a fairly straight posterior border and are relatively small for the size of the animal (Fig. 7 and Goodall *et al.*, 1988d).

Teeth

As in other phocoenids, the teeth are small and somewhat spade-shaped; the pulp cavity seems to fill rapidly, as found by Kasuya (1978) for the Dall's porpoise (*P. dalli*) and Gaskin *et al.* (1984) for other phocoenids. There is considerable variation in size and shape, some with rounded crowns, others with lobes or almost straight sides and no crown. Some teeth are heavily worn.

The number of visible teeth in fresh animals ranged from 13–22 (mean 18±3, n=11) in each maxillary row and 15–21 (mean 18±2, n=9) in each mandible. Even in large animals, up to six maxillary teeth per side may be hidden in the gums (Lahille, 1912), so that the total is probably 19–26 upper and 19–22 lower.

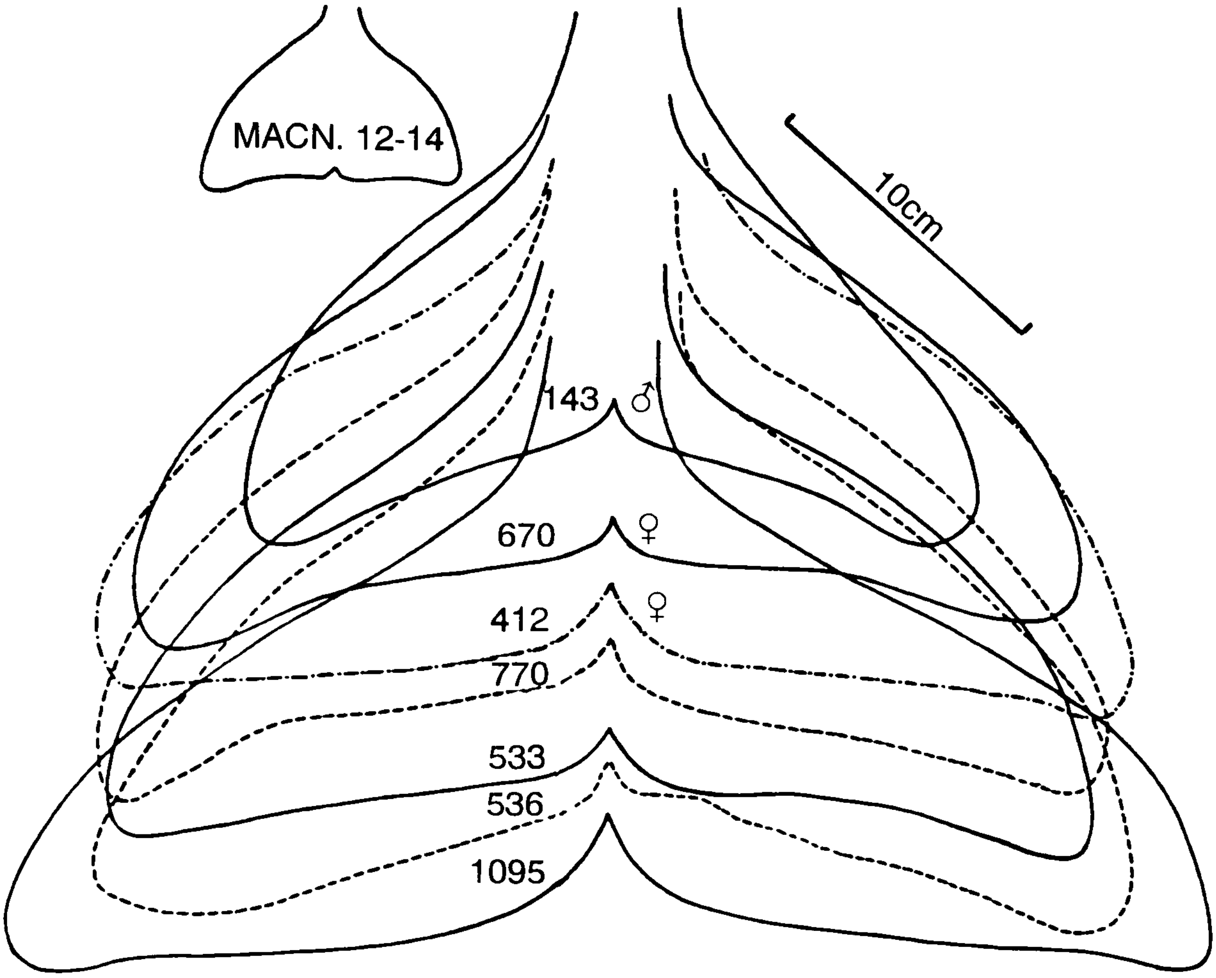

Fig. 7. To-scale tracings of flukes of RNP specimens of *A. dioptrica* and of the foetus from MACN.

In cleaned skulls, the posterior (often hidden) teeth are situated in a narrow groove without alveoli; as these lift off in beach specimens, it is almost impossible to determine the number of teeth from skeletal material. In cleaned skulls with teeth still in the dried gum, from 16–25 (mean 20±3, $n=11$) were found in each maxillary row and 17–23 (mean 20±2, $n=9$) in each mandible. Thus, the number of alveoli on clean skulls may not represent the total number of teeth, as noted by Brownell *et al.* (1989) for the Heard Island specimen.

PIGMENTATION

Photographs or drawings of the pigmentation pattern have been published for only three 'adult' animals (Lahille, 1912; Bruch, 1916; Capozzo and Junín, 1991[2]), a foetus (Lahille, 1912) and a calf (Fraser, 1968). This paper adds details for three more calves, two fresh animals and for incomplete animals found on the beach.

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[2] Capozzo and Junín (1991) published a lateral view of a spectacled porpoise from a photograph in MACN. It has since been discovered that it was a specimen found by the *Escuela Normal* No. 3 in Mar del Plata and that the photograph had been sent to Buenos Aires in an envelope dated December 1925; there is no other information on this specimen (H.P. Castello, pers. comm.). Since there are so few photographs of this species, it is a valuable record.

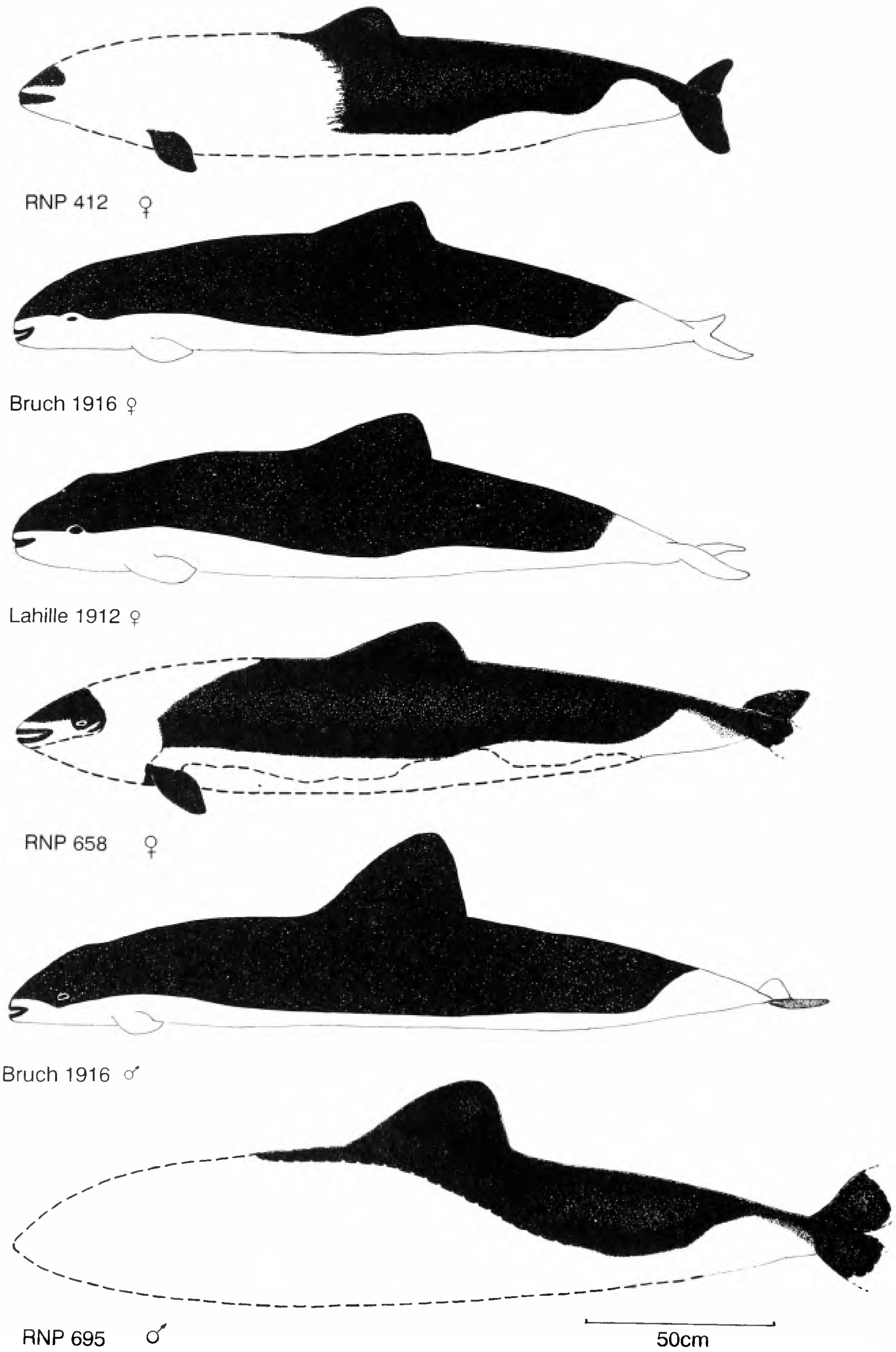


Fig. 8. Pigmentation of larger (sexually adult) specimens of *A. dioptrica*, drawn to scale.

Adults

The spectacled porpoise is a brightly pigmented animal which, in subadults and adults, is jet-black on the dorsal surface and half way down the sides and white below. The black is usually separated from the white on the sides by a sharply defined line, but in a few specimens there is some fading or feathering on the sides of the tail stock, where the black undulates upward before joining the flukes. The dorsal fin is black.

In the description of the first specimen, Lahille (1912) said that the black dorsal pigment stopped short of the tail, leaving a completely white tail stock, but that the upper surface of the flukes was black. His photograph seems to show a white keel and white flukes, but in his fig. 5 (comparing his *P. dioptrica* with other species of *Phocoena*), he gives a drawing of an animal with a narrow black ridge along the tail stock, joining with the black flukes.

Similarly, the photographs of the two Bruch (1916) animals seem to show white tail stocks and white flukes, but the models in the Museo de La Plata both show black pigment on the upper tail stock and upper surface of the flukes (photograph in Brownell, 1975). It is possible that the original photographs are deceptive and that the shiny pigment reflects light. In the specimens we have examined, the upper tail stock was black (Fig. 8).

Towards the front of the body, the division between black and white passes almost across the eye to the upper beak, where the black upper surface is joined by a small black triangle to the black lips (Lahille, 1912; Fig. 9).

Lahille's female had the faint remains of a mouth to flipper stripe which does not show well in the photograph. The photograph of the Mar del Plata specimen shows a faint lower-mouth to flipper stripe (Fig. 10). Specimen CNP 116 had a faint eye to flipper stripe.

Watson (1981) erroneously illustrated an adult with a solid black line running from the angle of the mouth to the flipper and down the forward edge to the tip; unfortunately this drawing has been copied by others.

The eye of the type specimen was surrounded by a black patch, in turn outlined in white, giving it a spectacled appearance and its common name. The pigmentation around the eye is variable, usually with a black patch and some degree of white streaking or circling. Some animals have a 'tear' mark running anteriorly (Figs 10 and 11).

The ventral surface in all adult animals was white.

Flippers

The colouration of the flippers shows some variation. Lahille (1912) reported that the dorsal surface of the flipper was white with a grey posterior border. It was white in the Bruch female and the Mar del Plata specimens and mottled grey to black in all others. In one of the TF adults, the flipper pigment ended in a straight line across the base of the flipper, as illustrated for the Wilkins animal (Fraser, 1968). In another specimen there was a grey border between the black flipper and white body whilst in yet others, the division was as abrupt as that on the sides of the animal (Figs 8 and 10).

The ventral surface of the flipper was either white (Lahille and Bruch females) or white with a dark posterior border (RNP 412 and 658). However, A. Purgue (pers. comm.) reported that the CNP animal had white flippers with radial grey lines (Fig. 9).

Flukes

As with the flipper stripe, eye patch and flippers, there is considerable variation in the pigmentation of the flukes. The dorsal surface was white in the photographs of the Lahille and Bruch females but dark in the Lahille description and the Bruch model. All other animals had dark or black upper flukes.

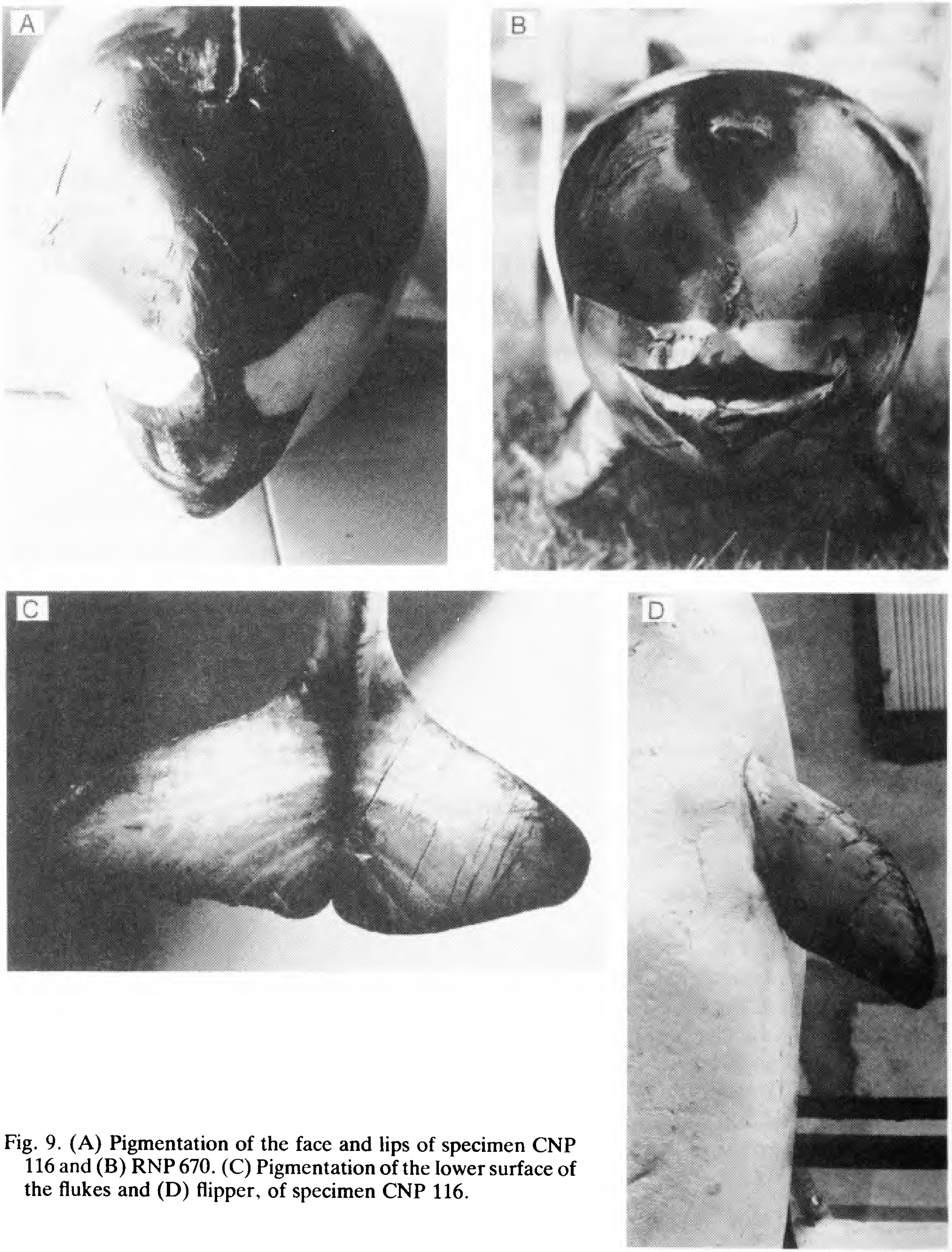


Fig. 9. (A) Pigmentation of the face and lips of specimen CNP 116 and (B) RNP 670. (C) Pigmentation of the lower surface of the flukes and (D) flipper, of specimen CNP 116.

The ventral surface is usually lighter. In three animals it was all white (including the Bruch female), white with a black posterior border (RNP 412), or mottled with lighter grey radiating lines. Several specimens were mottled grey on a white surface with white streaks outward from the midline (RNP 658, CNP 116). The outer edges were usually darker (Fig. 9) and the veination pattern usually visible.

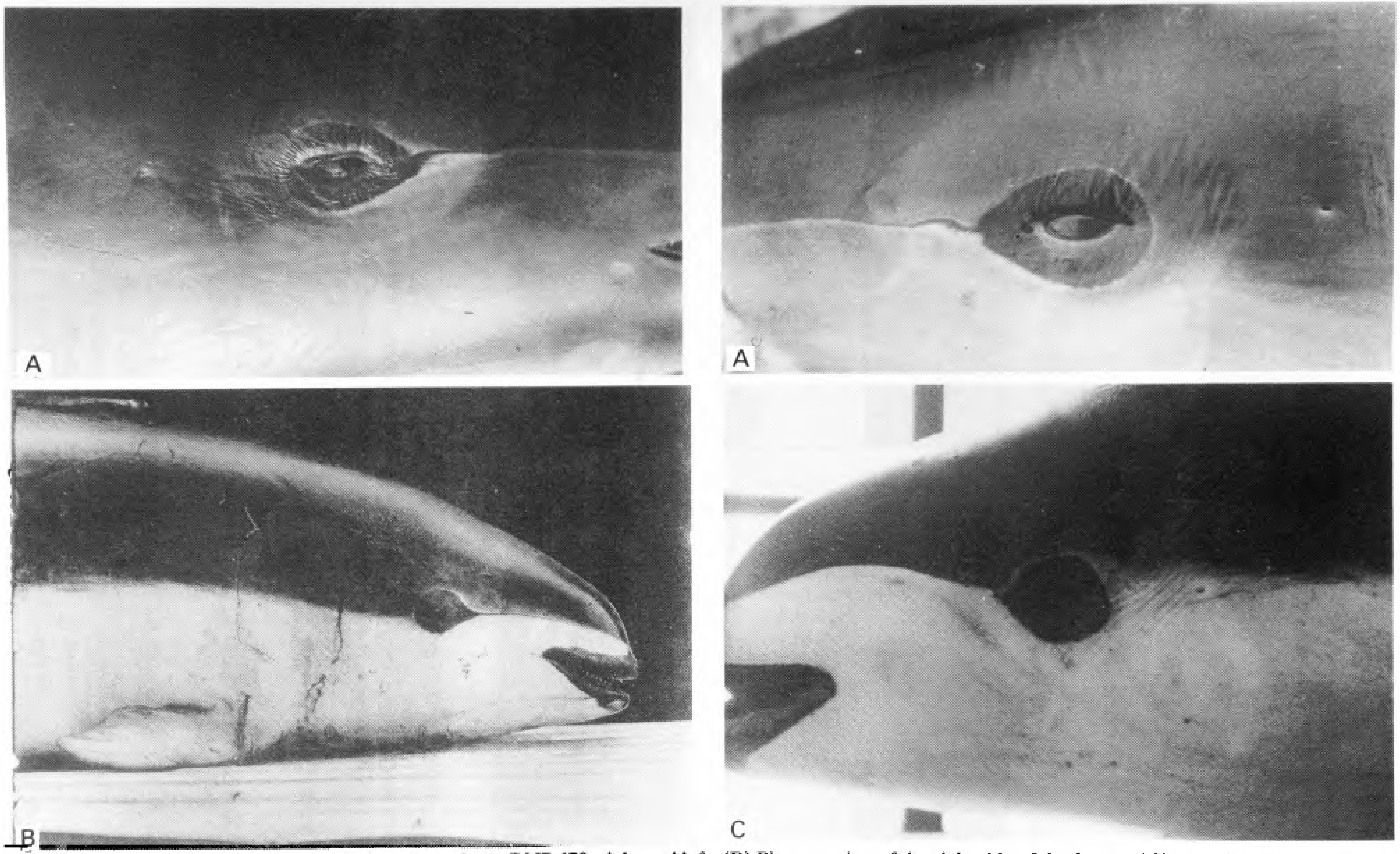
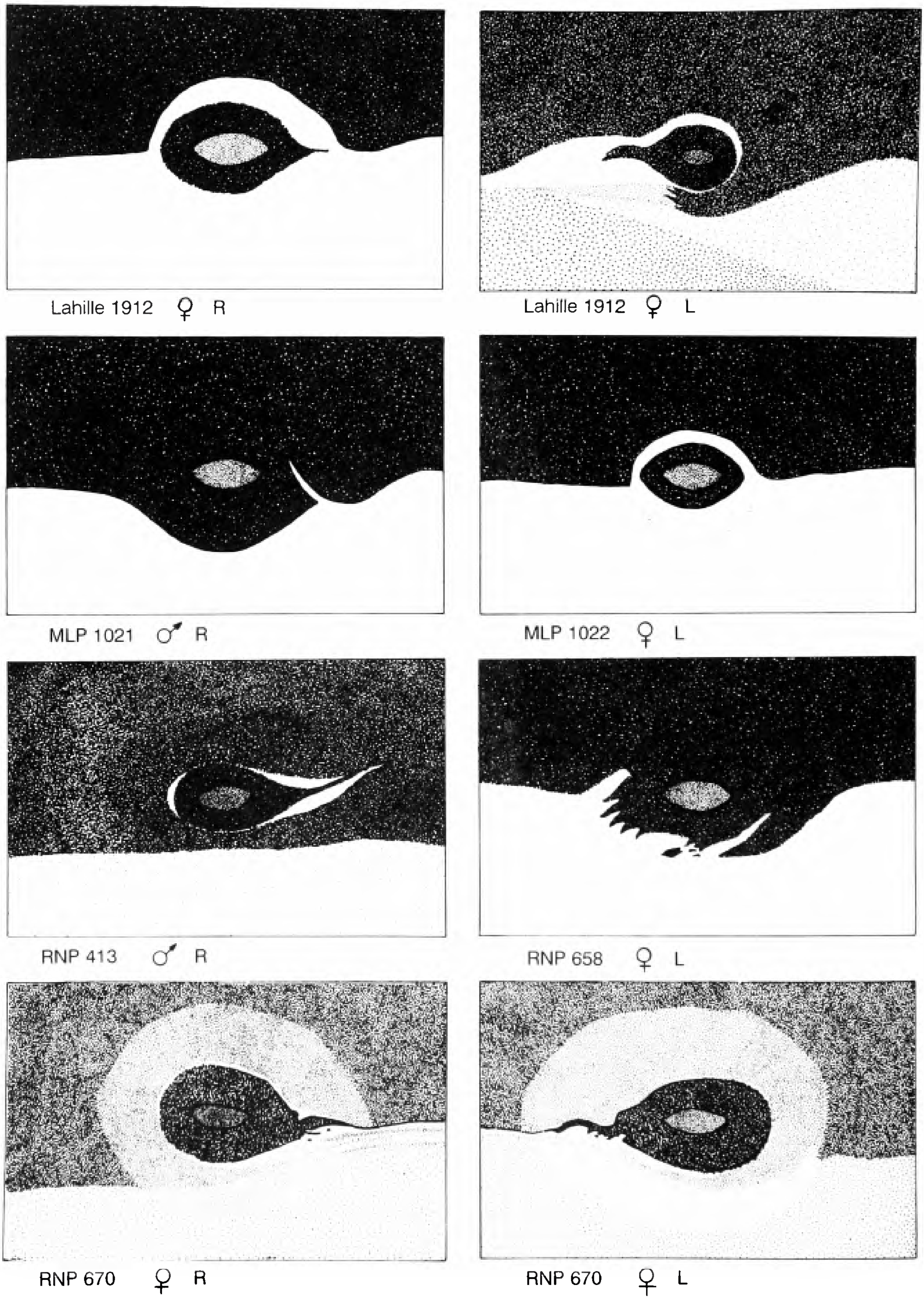


Fig. 10. (A) Pigmentation of the eye region of specimen RNP 670, right and left. (B) Pigmentation of the right side of the face and flipper of the Mar del Plata specimen; (C) pigmentation of the left side of the face of CNP 116.



Lahille 1912 ♀ R

Lahille 1912 ♀ L

MLP 1021 ♂ R

MLP 1022 ♀ L

RNP 413 ♂ R

RNP 658 ♀ L

RNP 670 ♀ R

RNP 670 ♀ L

Fig. 11. Variation in pigmentation around the eye in spectacled porpoises.

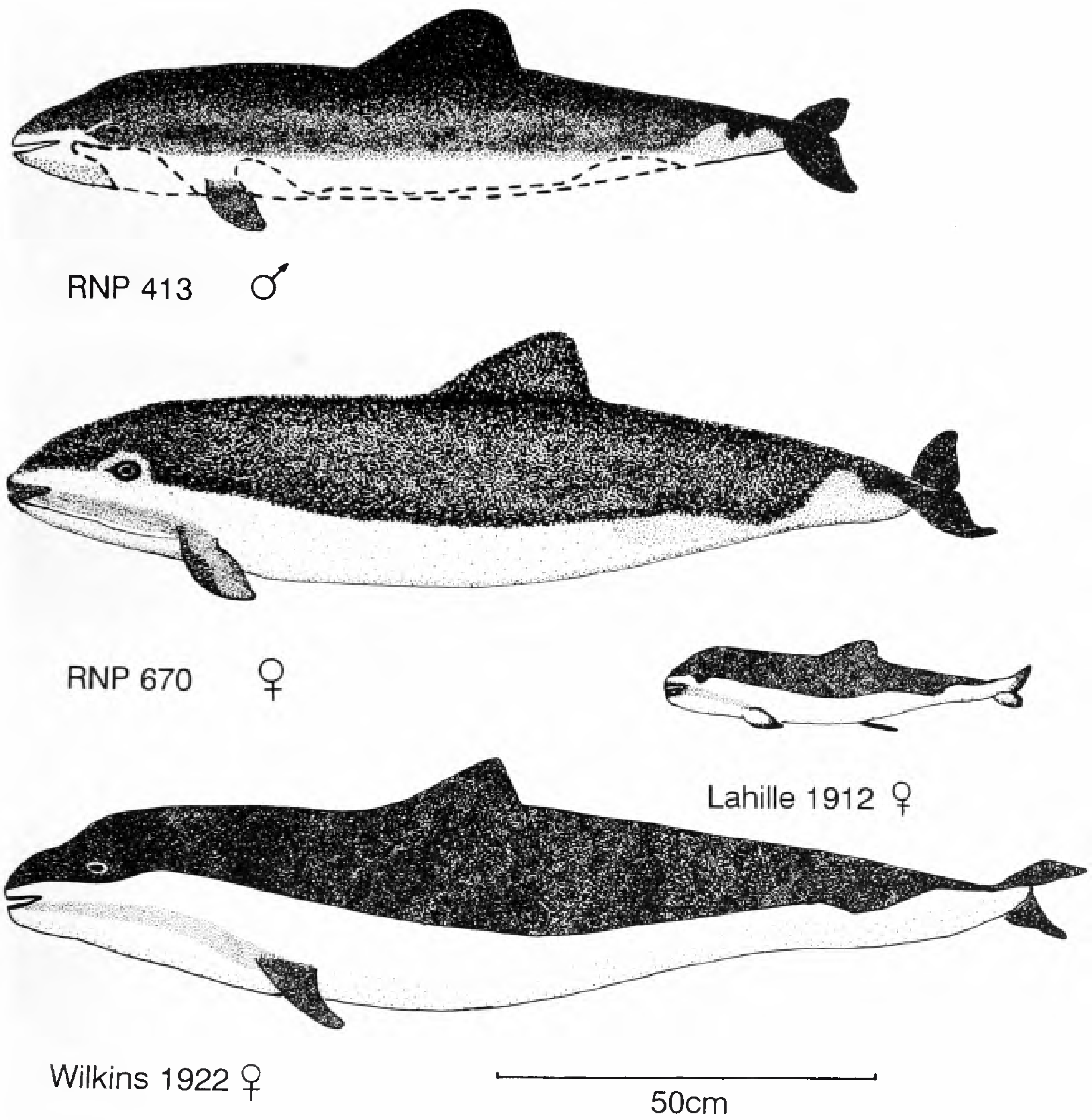


Fig. 12. Pigmentation of the foetus and calves of *A. dioptrica*, drawn to scale.

Young

The four calves (Hamilton, 1941 and three from Tierra del Fuego) and the foetus (Lahille, 1912) were not as brightly pigmented as the adults (Fig. 12). They were dorsally dark grey or blue-black and ventrally grey-white with a slight yellowish tinge; the demarcation between dark and light on the lateral surface was quite evident.

Specimen RNP 670 was alive when examined and photographed. The eye of this specimen had a grey halo around the dark eye patch and thin white line (Figs 10, 11 and 13).

The lips of these animals were as darkly outlined as in the adults. All had a noticeable wide mouth to flipper stripe, darkest in the foetus and a diffused medium grey in the others. In addition to the flipper stripe, RNP 670 had a narrow dark stripe below it on each side which ran from the mid-lower lip near the chin to the lower edge of the flipper insertion (Figs 13 and 15). This was not seen in the other animals.

(*Text continues on p. 441*)

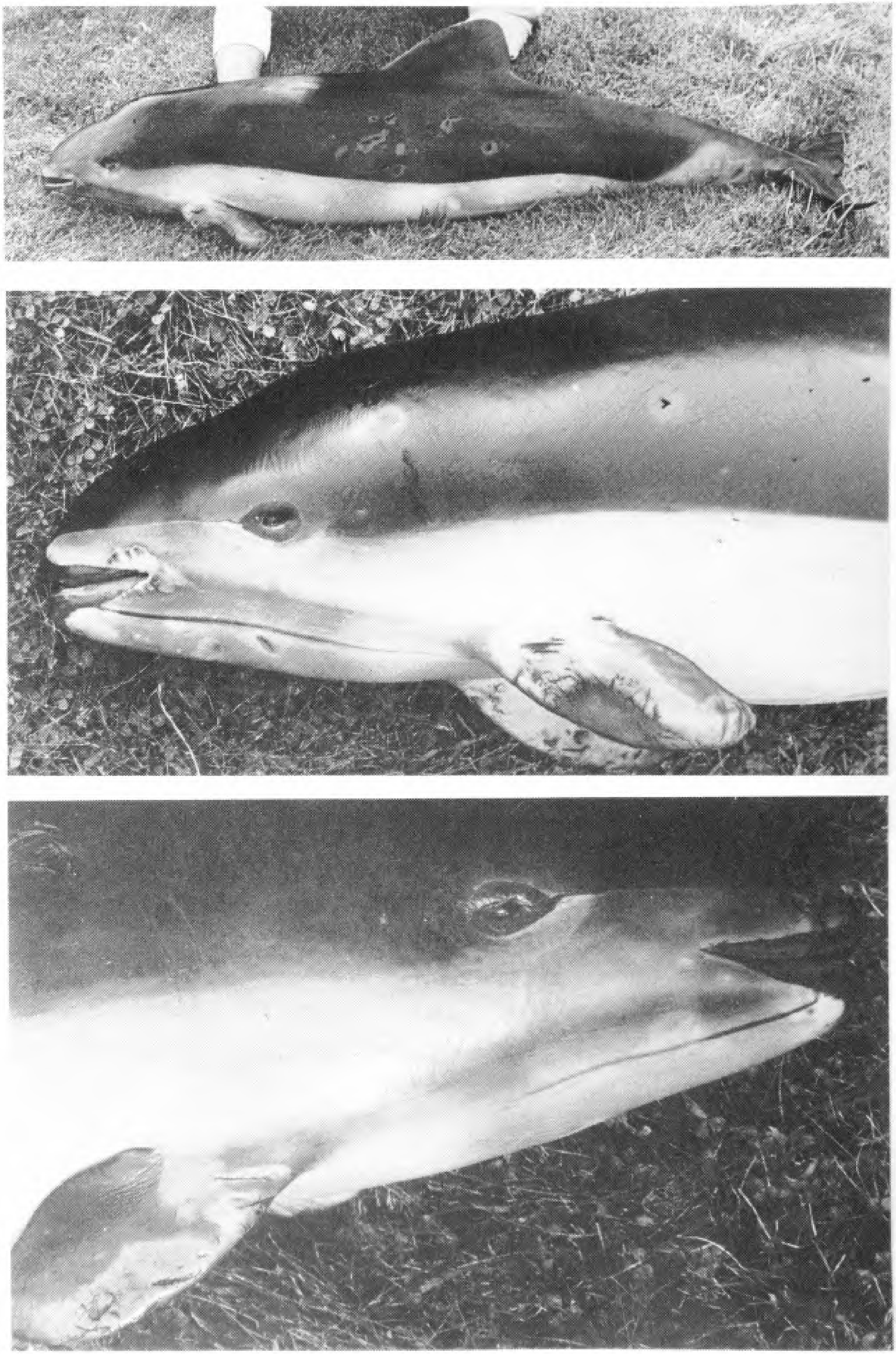


Fig. 13. Pigmentation of specimen RNP 670, a 125cm female calf which stranded live at Puerto Harberton on the north coast of the Canal Beagle, showing the lateral, dorsal and ventral surfaces.

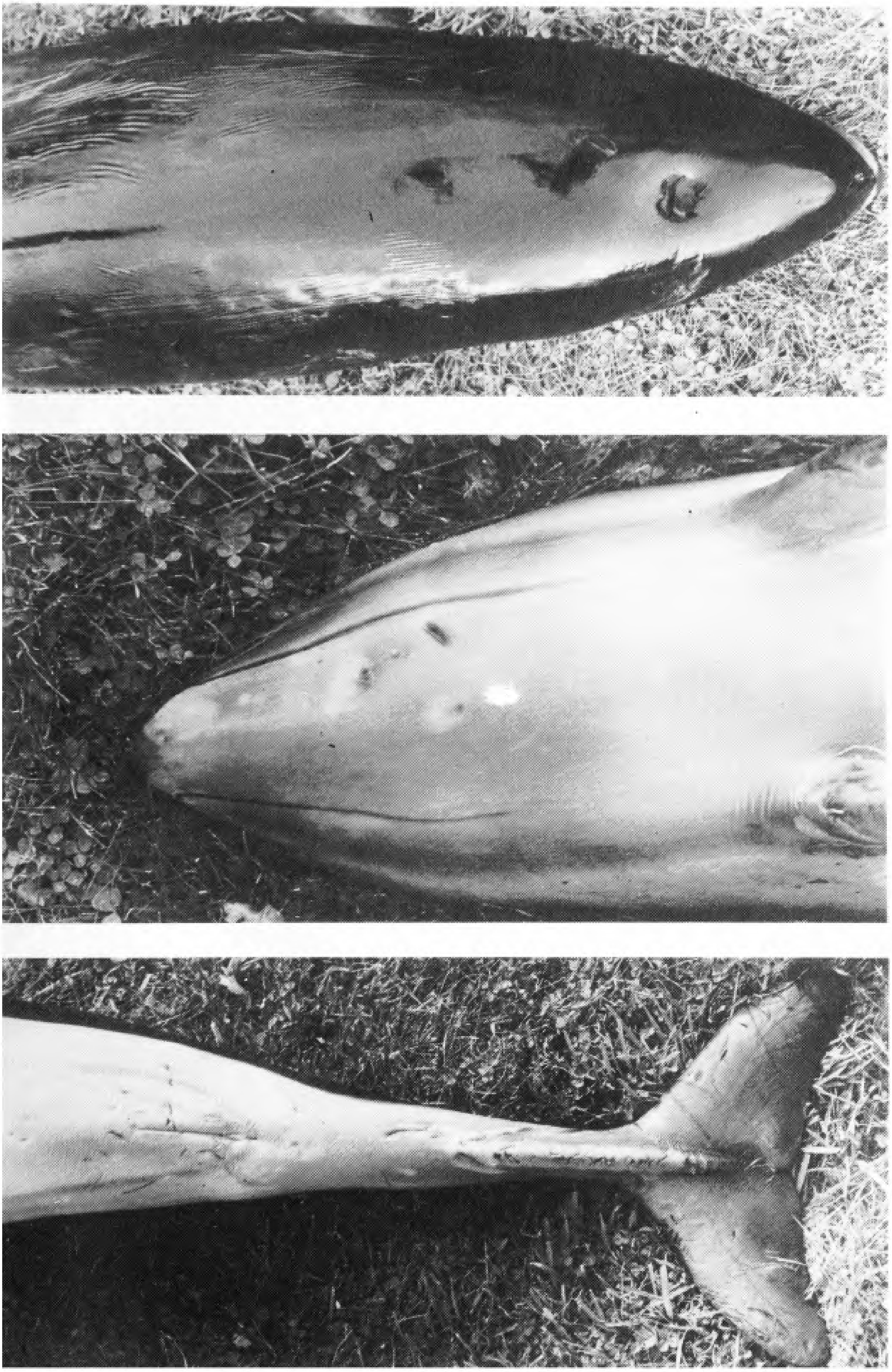


Fig. 13—*continued*.

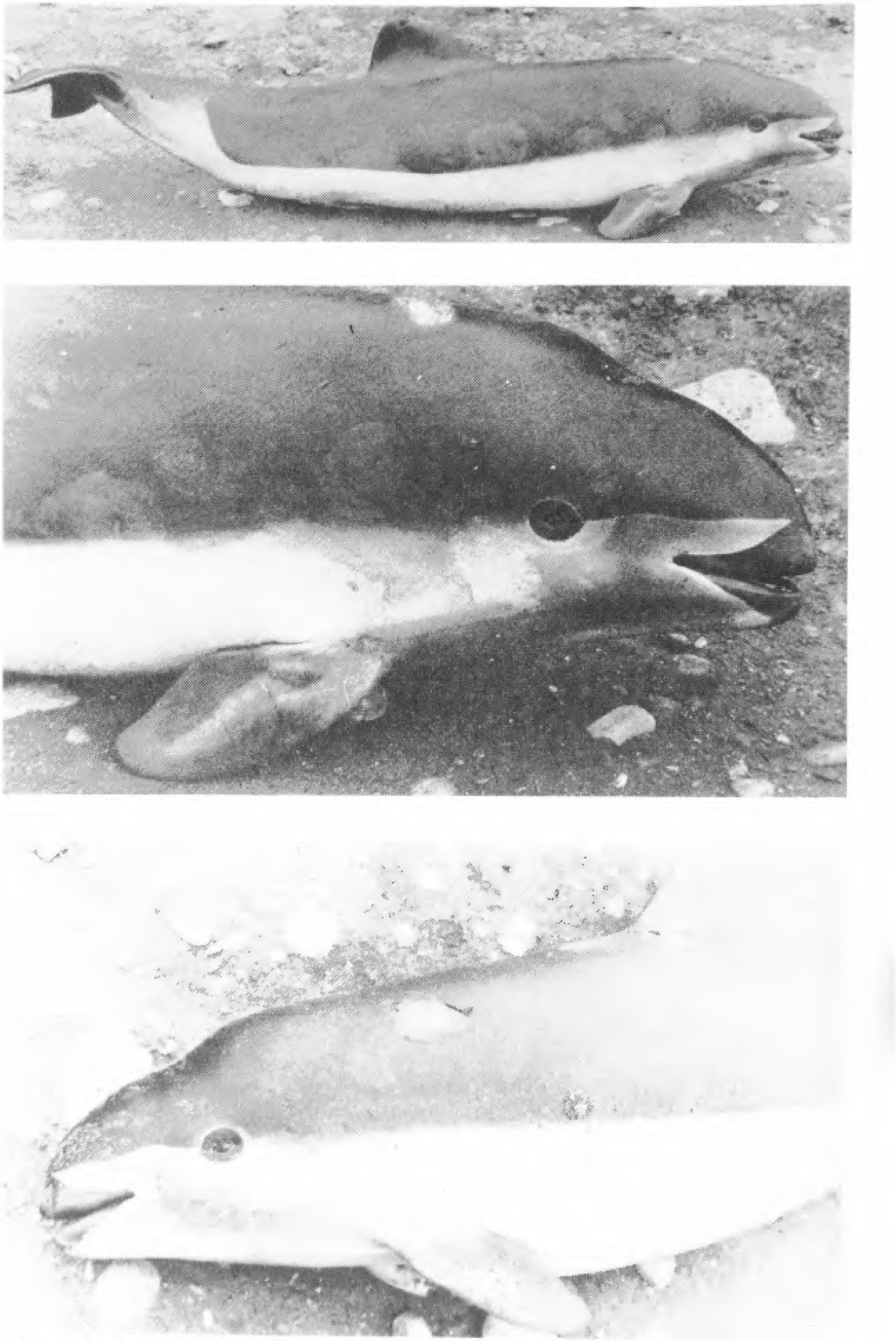


Fig. 14. Pigmentation of specimen CHL 890203, a 134cm male calf which was found at the mouth of the Río Chico, north of Río Grande, Tierra del Fuego, a favoured fishing spot.

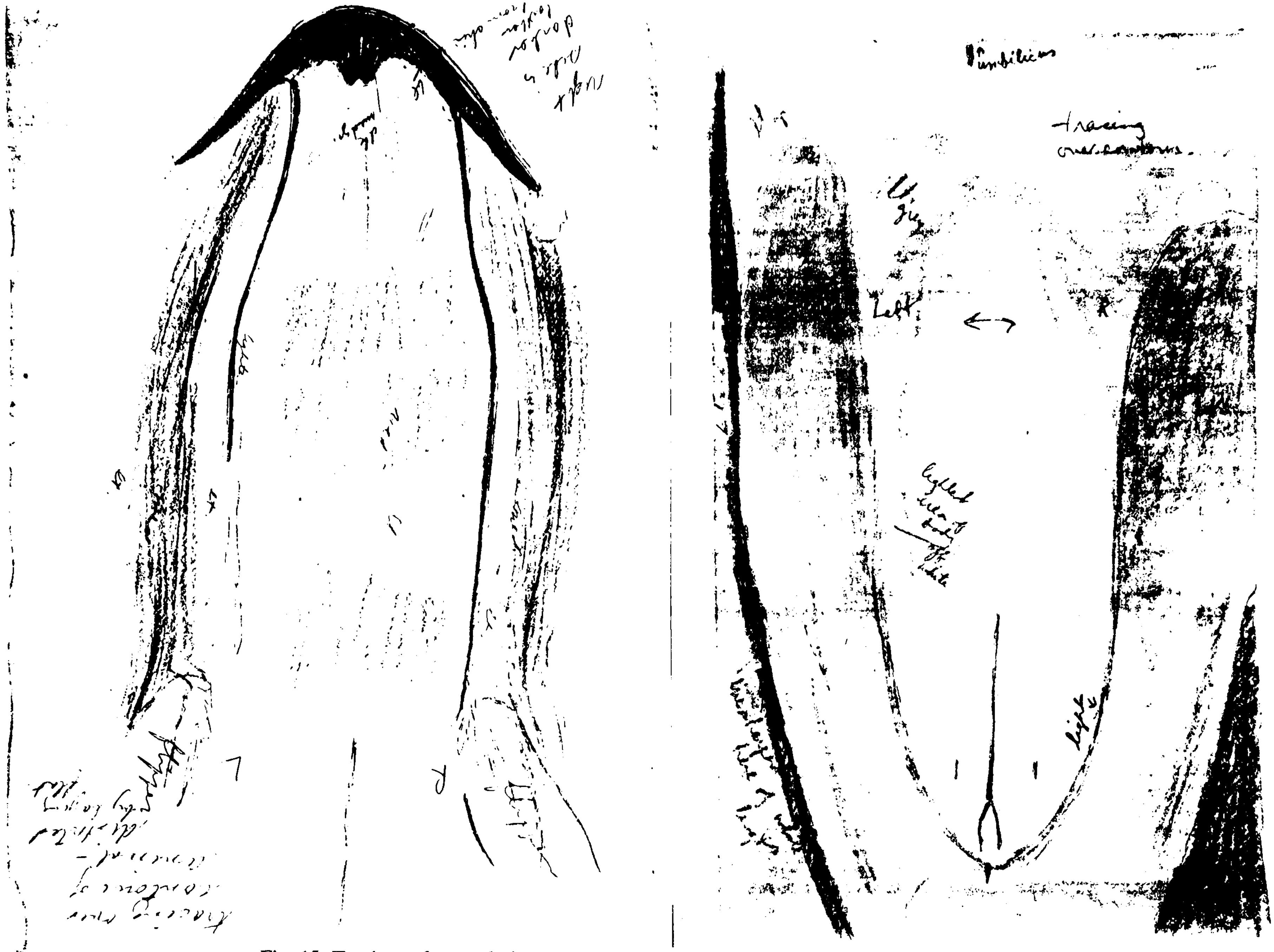


Fig. 15. Tracings of ventral pigmentation in calf RNP 670, taken over the curve of the animal.

Table 5

Comparison of pigmentation patterns. A dash means pigmentation could not be determined. Specimens 1-5 are young animals and the rest are older animals.

Specimen key: 1 = Lahille foetus (photo); 2 = RNP 413: 3 = RNP 670; 4 = CHD 890203; 5 = Wilkins; 6 = RNP 412; 7 = Lahille; 8 = Bruch*; 9 = Mar del Plata; 10= RNP 1703; 11 = RNP 658; 12 = Bruch* (model); 13 = CNP 116 (Purgue); 14 = RNP 695. TL= total length in cm. Stripes refer to mouth-flipper (M⇒Fl) and throat.

		TL	Stripes		Flipper		Dorsal keel in front of	Flukes	
No.	Sex	in cm	M⇒Fl	Throat	Upper	Lower	of flukes	Upper	Lower
1	F	48.4	Wide	No	Dark	-	Black	Black	Dark
2	M	109+	-	Yes	Black	Grey-white	Black; grey- lavender border	Black	Black
3	F	124.6	Yes	Yes	Both sides medium grey shading to dark grey on dist, post. edges		Dark grey	Black	Dark grey
4	M	134	Yes	Yes	Grey, lighter - in centre	Dark grey	Black	-	-
5	F	136	Yes	Yes	Dark	Lighter on ant. edges	Dark blue black	Dark	Dark
6	F	183	-	-	Black post. border	White, black	Black	Black	White with black posterior border
7	F	186	V. faint	No	White with grey border	White	White in description & photo, dark in Fig. 5	White in photo, black in description & Fig. 5	White with grey lines
8*	F	186	No	No	White	White	White in photo, black on model	White in photo, black on model with lighter trailing edge	White
9	F?	-	Faint	-	White	-	-	-	-
10	M	±200	-	-	Both yellow-white post. edge grey		Dark	White with dark centre, radiating white lines	
11	F	203.5	-	-	Black	White with dark post. border	Black; feathered in front of flukes	Black	Mottled grey on white with white streaks
12	M	204	No	No	Both black in front, white trailing		White in photo? Black on model	Black both with trailing edge lighter (streaked)	Black
13	M	205	Yes**	No	-	Grey, black on trailing edges	-	-	Grey with white lines
14	M	224	-	-	-	-	Black	Black	-

* The Bruch `models' are painted body cast of these two specimens in MLP. I cite this pigmentation, although painted, because of the careful, exquisite taxidermy done there at that time. ** Front of eye to flipper faint

Lahille's foetus had a white blaze from the beak to the blowhole which has been seen on no other specimens. All the young were black or dark grey on the dorsal surface of the tail stock and the flukes were dark grey on both surfaces. The flippers were light, medium or dark mottled grey on the upper surfaces shading to darker on the posterior edges (Figs 13 and 14). They were slightly lighter on the lower surface.

In the genital region of RNP 670, a curved line descended from the black lateral pigment at about the level of the mid-dorsal fin, to curve parabolically around the back of the genital slit (Figs 14 and 15). The area above this line was a light yellowish-grey (lateral and posterior tail stock), while the encircled genital area and the rest of the ventral surface was white. A similar area appears to occur in young *P. sinus* (Brownell *et al.*, 1987; Fig. 2B). On the basis of photographs of RNP 670, this line was shown in paintings of the adult in Leatherwood and Reeves (1983), although it has yet to be reported for adult animals. The painting in Minesian *et al.* (1984) is also that of a young animal.

That a slightly darker or grey pigmentation in calves should fade to white in adults is common in cetaceans, e.g. Commerson's dolphins (Goodall *et al.*, 1988a) and white whales (Fraser, 1968; Mitchell, 1970).

No vibrissae were recorded for the foetus or neonates, although they are present in *Phocoena phocoena* (Gaskin *et al.*, 1974).

Scars and marks

No tooth rakes or other marks have been reported for this species. However, the live calf (RNP 670) had many healed wounds, including one near the left side of the mouth and a long slash on the right latero-dorsal surface between flipper and blowhole (Fig. 13); their cause is unknown. The Río Grande calf (CHD 890203) had a series of circular patches on the upper sides which may have been fungal growths (Fig. 14).

INTERNAL ANATOMY

Skeleton

The skull of this species was first described, illustrated and compared with that of *Phocoena phocoena* by Hamilton (1941). Skull descriptions and comparisons are given by Praderi (1971) and Brownell (1975). Photographs of the skull and/or measurements for newer specimens can be found in Baker (1977), Goodall (1978), Goodall and Cameron (1979), Fordyce *et al.* (1984) and Guiler *et al.* (1987). The earbones are illustrated in Brownell (1975).

The postcranial skeleton was described by Hamilton (1941) and certain elements were illustrated. A photograph of one of the Bruch skeletons was presented by Brownell (1975) and a section of caudal vertebrae by Goodall and Cameron (1979). The number of fused cervical vertebrae has varied from 3–7 (mean 6±1, n=68) and the total number of vertebrae reported from 65 to 69, the most frequent numbers being 67 and 68 (mean 67±1, n=22).

There are usually 14 ribs, nine of them two-headed; the last may be short and without articulation with the vertebra. There are usually eight sternal ribs, but these and the last vertebral rib are easily lost in beach-cast specimens. Several specimens had one or two very small cervical ribs. Hamilton (1941) stated that the ribs of this species are 'markedly flattened in a manner reminiscent of *Neobalaena*' (*Caperea*) and this has been 'translated' in several popular guides as 'the ribs are flat like those of *Caperea*'. Although in some animals the posterior ribs are slightly flattened or spatulate-shaped in the lower half, it is not to the extent of those of *Caperea*.

Organ and internal systems

The blowhole, larynx and hyoids of the first specimen were studied by Gallardo (1913), and a detailed study of the facial complex of specimen CNP 116 has been prepared by Purgue (1987).

No other systems of this species have been studied. The young calf (RNP 670) has been preserved whole in formalin for future examination as have the organs of the Río Grande calf.

Stranded specimens are usually quickly devoured by predators and few organs have been weighed. The heart of a 109cm neonate weighed 410g and its kidneys 86 and 76g. The lungs of a 183cm female weighed 537 and 387g. These animals were partially destroyed, so total weights are not available.

Parasites

Although Lahille (1912) stated that the parasites of the type specimen would be the subject of a separate paper, no such paper appeared. Gallardo (1913) found some nematodes in the blowhole and prenasal sacs of this specimen. One nematode was found in each of the stomachs of three TF specimens (RNP 412, 658 and 1703). No parasites were found in the preserved organs of the CHD calf. Specimen RNP 1703 had many small worms in each ear sinus. The parasites are under study by A. Raga (University of Valencia). No ectoparasites were found, but few animals were in fresh condition.

AGE, REPRODUCTION AND GROWTH

Age determination

A preliminary study was carried out to examine teeth for GLGs (growth layer groups – see IWC, 1980) for this species in untreated, unstained longitudinal sections (n=11) and stained (n=27) sections (Schiavini and Goodall, 1991; Crespo *et al.*, 1994c). Prenatal dentine was slightly globular or homogeneous. The neonatal line was distinctive. Postnatal dentine comprised a thick stained and a narrow unstained band. As for other phocoenids, the GLGs were difficult to read because of the number of accessory layers. In the two above works, we reported that the maximum number of GLGs was 13 and a female found in a net with a neonate had 8 GLGs. However, on processing further teeth from these animals, we recalculated the maximum number of GLGs as 8 in an animal of unknown sex and only 2–3 GLGs in the female with the neonate. We therefore believe the value of 13 to be erroneous. Although no calibration studies have been carried out, by analogy with other phocoenids (Lockyer, 1995) it has been assumed that 1 GLG=1 year for the purposes of this paper.

Sexual maturity

Due to the state of decomposition of most of the specimens, little reproductive information is available. Gonads were examined for one male (CNP116) which at 205cm and 6 GLGs was sexually but not physically mature. Its gonads were sent away for histological analysis, but this has not provided further information (A. Purgue, pers. comm.)

No ovaries have been examined. Two females of 186cm were sexually mature and carried small foetuses (Lahille, 1912; Bruch, 1916). The latter was physically subadult but the Lahille female was lost and epiphyseal fusion was not recorded. Female teeth showed a change in layering after the second or third GLG, suggesting stress in the deposition of material at this stage and an early sexual maturation, as found in harbour porpoises (Gaskin *et al.*, 1984; Lockyer, 1995). A 183cm subadult female with 2–3 GLGs (RNP 412) was taken in a net with a 109cm calf. Another subadult animal of unknown sex was found with a calf (RNP 1652 and 1653). No other data are available.

Young

The foetus of the Lahille female, stranded on 28 July, measured 48.4cm. Lahille (1912), who had little cetacean experience stated that it was 'without doubt, almost at the termination of the pregnancy' but did not provide his reasoning. Succeeding authors described this foetus as 'near term' and assumed that young of this species might be born in late winter or early spring (Brownell, 1975; Goodall, 1978; Leatherwood and Reeves, 1983). However, Gaskin *et al.* (1984) advised that the consideration of this foetus 'as 'near term' should be treated with considerable caution'. The length of the Bruch foetus, which stranded on 14 August, was not recorded but was thought by Bruch to be near birth (Bruch, 1916).

We examined the Lahille foetus, preserved in alcohol in MACN, and concluded that, although fully formed except for the genital slit, it was not near birth. It measured only 26% of its mother's length and 2% of her weight. Near term foetuses or neonates of other small cetacean species we have examined have been 33–50% of the mother's length. Slijper (1976) stated that newborn cetaceans may reach 45% of maternal length and 15% of weight. The harbour porpoise length at parturition is between 43–52% of the mother's length (Gaskin *et al.*, 1984).

The smallest neonates examined measured 94 and 109cm. The latter was 59.6% of the length of the accompanying female trapped in a net in early February. Calves of 125, 134 and 136cm with unerupted teeth stranded on 25 March, 3 February and 2 May in Tierra del Fuego and South Georgia, respectively. The calf of 125cm had a healed umbilicus. The male of 134cm had most of the neural arches unfused, but they were fused in the 136cm female. A mid-sized calf, RNP 1653, was found on the beach in September. On the basis of these neonates and calves, it seems likely that young of the spectacled porpoise, a larger animal than *P. phocoena*, are probably born in late spring or summer (November to February) off Tierra del Fuego at about 90–100cm.

Physical maturity

The oldest female to date is also the largest, at 203.5cm, with 6 GLGs and physically mature. One female was physically immature with 4 GLGs. Two females with 2 GLGs were physically subadult.

The teeth of the largest (224cm) male were unreadable; the second largest male at 205cm had 6 GLGs (E. Crespo in Pagnoni and Saba, 1989) and was subadult. Two males, one *ca* 189cm with 4 GLGs and the other 196cm with 5 GLGs were physically mature. Therefore, females may become subadult (and perhaps sexually mature) by two years and at least some males are physically adult at four years. The length at age relationship, in spite of the small sample size, is plotted in Fig. 16.

Age at physical maturity is shown in Fig. 17. The maximum age obtained was 8 GLGs in an animal of unknown sex that was not quite physically mature. The youngest age at complete physical maturity was found in three animals of unknown sex with 3 GLGs. As sexual maturity is normally reached before physical maturity, these animals were probably also sexually mature. The limited data available suggests that animals may reach sexual maturity at 3 years or even younger. Further data are needed to confirm or refute this.

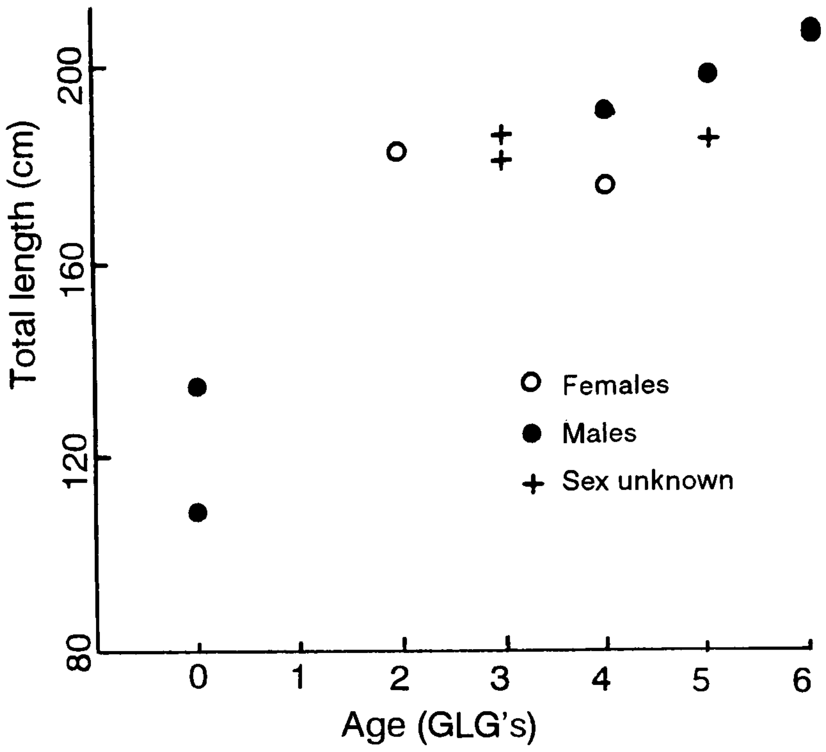


Fig. 16. Length at age distribution for specimens of *A. dioptrica*.

Of 130 specimens (mostly postcranial) for which physical maturity could be determined, 59% were physically subadult, 30.8% adults, 6.9% juveniles and 3.1% neonates (Fig. 18). Apart from the obvious potential biases in stranded samples, the small proportion of juveniles may in part be explained by the fact that physical maturity seems to be reached relatively early in the life of these animals; no animal older than two years old was less than subadult. There is little information on physical maturity in the literature for the other phocoenids.

TAPHONOMIC CONSIDERATIONS

Seven specimens of the spectacled porpoise were found fresh and entire. Nearly all the others were in an advanced state of decomposition or were bleached skulls and bones on the beach. In 20 years of taking taphonomic notes in TF, we have found that this species appears to be one of the 'tastiest' to birds (usually gulls and petrels) and perhaps foxes and mice; specimens are rapidly attacked and skeletonised (see Goodall *et al.*, 1985). This may take from several hours to a week. Despite the cold TF climate, the flippers and shoulder blades, pelvic bones, floating and sternal ribs and then the mandibles are soon lost. However, even in a skeletonised condition, the dorsal fin often remains attached by a strip of tissue to the body, allowing identification to sex in the case of very large fins. The next step in the process of decomposition is the separation of the skull from the postcranial skeleton and then the division of the latter in the pelvic region (Schäfer, 1972). The vertebrae may be scattered along the beach and the heavier skull left on the upper beach by the highest tides. The rapidity of this disintegration should be taken into account when carrying out regular beach surveys in areas where these animals might strand or be captured. Nearly all the biological data for this species to date come from stranded or captured animals.

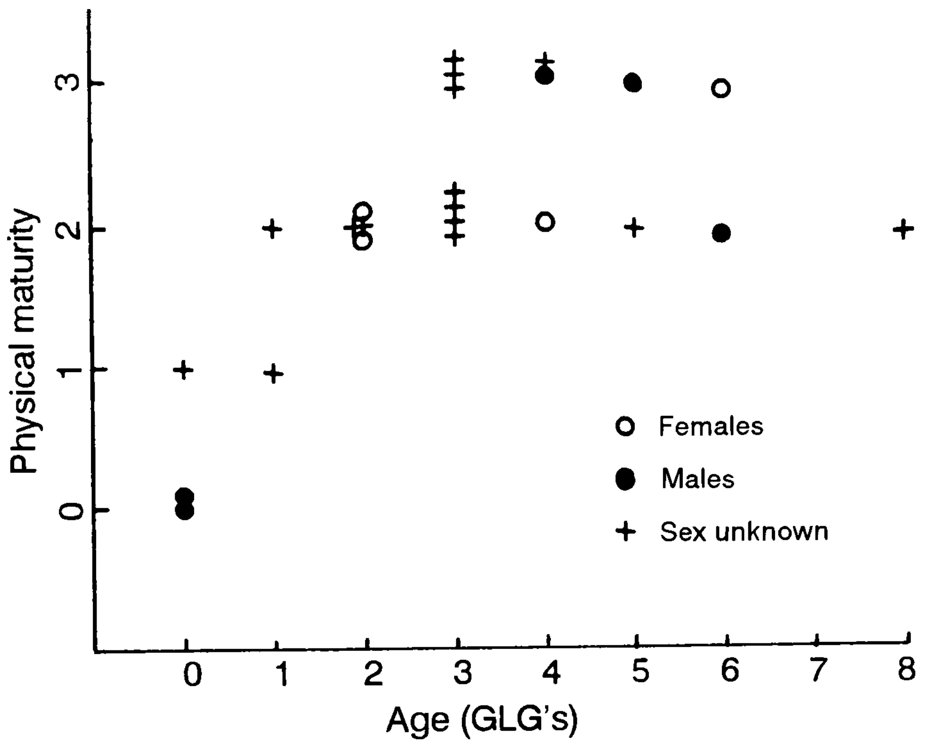


Fig. 17. Age at physical maturity distribution for specimens of *A. dioptrica*.

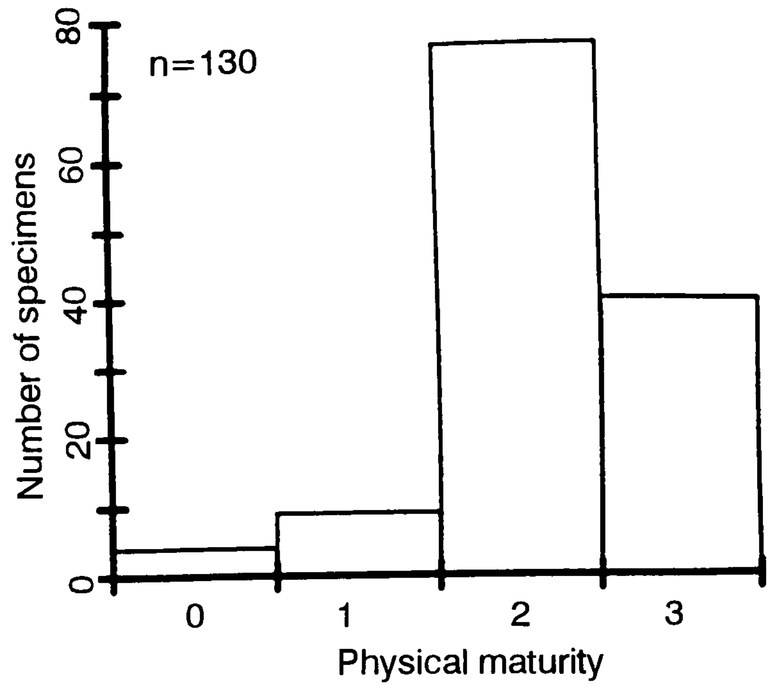


Fig. 18. Distribution of physical maturity classes in specimens of *A. dioptrica* from Tierra del Fuego, based on epiphyseal fusion of the vertebrae. Class 0, neonates; class 1, juveniles; class 2, subadults; class 3, physically adult animals. The database includes both skeletons with skulls and postcranial skeletons without skulls.

HABITAT

The spectacled porpoise has been assumed to be an inshore animal (Brownell, 1974; 1975), probably because it was known only from strandings and because of the large size of its vertebrae; oceanic dolphins usually have vertebrae with short centra and long processes (A. Myrick, pers. comm.). However, the vertebrae of *A. dioptrica*, like those of beaked whales, are porous and fat-filled when compared to those of dolphins. The finding of skulls on widely-separated offshore islands and sightings at sea have shown that the spectacled porpoise is circumpolar in sub-Antarctic and cool-temperate latitudes (Barnes, 1985; Brownell *et al.*, 1989; Reeves and Leatherwood, 1994). Two specimens were found and several sightings were made near or south of the Antarctic Convergence (Fig. 1).

The sightings reported by Kasamatsu *et al.* (1990) were in deep waters far from land. Sea temperatures for those sightings ranged from 5° to 9°C. Sea surface temperatures off Tierra del Fuego are 4°–9°C in the Canal Beagle and 5°–12°C off the northeast coast. Off Uruguay and southern Brazil, waters are much warmer, giving a fairly large temperature range for the species.

The first three specimens were found on the shores of river estuaries and a live specimen and a sighting occurred in bays of the Canal Beagle. Most of the specimens from TF came from the gently sloping mudflats of southwestern Bahía San Sebastián. Nothing else is known about the preferred habitat of this animal.

BEHAVIOUR

Although this species strands or is taken in nets frequently off southeastern South America, it is seldom seen in the wild there. Nothing is known of its seasonal movements, abundance, stock identity or behaviour. Its sounds have never been recorded (Herman and Tavolga, 1980).

There is no evidence thus far that the species mass strands. On two occasions a female and calf were found on the beach, but all other recent records have been of single animals. Beach-worn specimens found together may or may not have stranded together; although near each other on the beach, they may have been deposited there by tides and eddies a different times.

All sightings to date have been of only one to three animals, with only one sighting c two large animals with a calf. This species probably does not form large schools (Baker, 1983; Kasamatsu *et al.*, 1990).

Live stranding

Three of the seven fresh specimens came ashore alive (Lahille, 1912; Fraser, 1968; Goodall, 1978). The latter specimen (RNP 670) was a calf with unerupted teeth but a healed umbilicus found on 25 March 1978 at Puerto Harberton, in the eastern Canal Beagle. It had a deep puncture wound on the head and many healed scars on the body. Having no facilities to keep a live animal, we tied a cloth and a light line about the tailstock and followed it around the bay in a boat until it tired and sank.

Breathing times, under stress out of the water, were from 7–11 breaths per minute (mean 8.2). Once in the water, the rate slowed to 4–7 breaths a minute (mean 5.6). The porpoise swam unobtrusively with a slow, rolling motion, arching its back strongly on each dive. The head was not raised above the water and there was no splashing. A ‘footprint’ was visible after each shallow dive (Fig. 19). The white of the lower body was visible only from directly above; the grey flippers appeared white under water. Cawthorn (1975) noted that the dorsal fin is prominent when these animals dive.

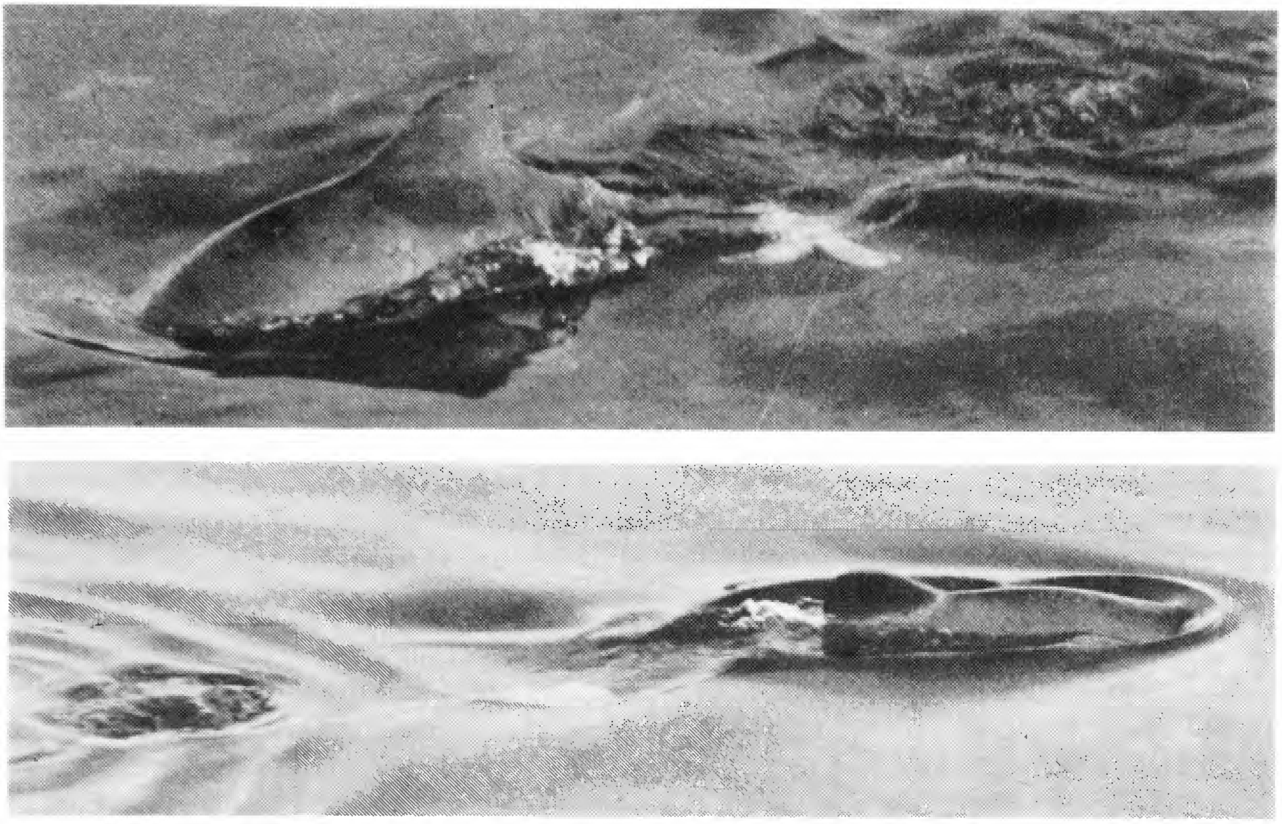


Fig. 19. Surfacing pattern of a spectacled porpoise calf, RNP 670, showing the 'footprint' left behind. The white in the upper photograph is a cloth and light line around the tailstock. Notice the similarity to *Cephalorhynchus eutropia* (Goodall *et al.*, 1988c, p.245).

Food habits

Goodall and Galeazzi (1985) reviewed the food habits of small cetaceans south of 30°S; there were no records for *A. dioptrica*. The two stomachs examined in this study (RNP 412, 658) contained only one nematode each. The stomachs and intestine of RNP 1703 contained only one nematode and a small piece of algae. The stomachs of specimen CNP 116 found at Puerto Madryn were almost empty, but contained some anchovy (*Eugraulis* sp.) and small crustaceans, possibly stomatopods (A.P. Purgue, pers. comm.). These are the first stomach contents known for the species.

Statements in popular guides that spectacled porpoises eat fish and 'probably cuttlefish' (e.g. Mörzer-Bruyns, 1971, repeated by others) were not based on data.

Predators

Killer whales, leopard seals and sharks are probably the main predators of this species. A killer whale that stranded near Barra do Chuí, Río Grande do Sul, Brazil (33°45′S) contained a few remains of two porpoises, possibly of this species (Dalla Rosa *et al.*, 1994; E.R. Secchi, pers. comm.).

EXPLOITATION

Deliberate take

The first known specimen came ashore alive and was offered by a fishmonger to the Museo Nacional in Buenos Aires (Lahille, 1912). The second and third were 'gathered in by fishermen' in the waters of the Río Santiago (Bruch, 1916). The Wilkins specimen also came ashore alive at a whaling station on South Georgia, where it was promptly 'killed by the cook and cut open' (implying that it was eaten). Several whaling captains told Wilkins that they 'sometimes shoot them with rifles for food' (Fraser, 1968). Praderi (1971) reported that fishermen on the Atlantic coast of Uruguay sometimes hunted this species and could easily recognise its pigmentation.

Exploitation of the spectacled porpoise for food and implements began long before it was studied scientifically. Remains of this species and others were found during archeological excavations of aboriginal kitchen middens at Túnel on the Canal Beagle aged over 6,000 years before present (Piana *et al.*, 1985) and vertebrae were found in a disturbed midden on Isla de los Estados aged *ca* 1,400 years (RNP 1270a).

There is no known deliberate exploitation of this species at present, although if the animals are in inshore waters they might be taken for crab bait in southern Chile. We have not heard of this species being directly harpooned for this fishery. Neither these nor any other cetaceans are used for food in Argentina.

Shore-based gillnet fishing

Several of the specimens in the Tierra del Fuego collection were taken incidentally in shore-based gillnets for fish (Goodall, 1978; Goodall and Cameron, 1980; Goodall *et al.*, 1988b; 1990a; b; 1994). This artisanal fishery takes place on mudflats with great tidal range (8–10.5m), where nets attached to fixed posts set perpendicular to the shore are lifted by their floats in the rising tide and lay on the tidal flats at low water. The fishery occurs in northeastern Tierra del Fuego and southern Santa Cruz, Argentina, and occasionally in the easternmost part of the Strait of Magellan, Chile. Since most of the fishermen have

Table 6

Localities in Argentine Tierra del Fuego, from north to south, where gillnets are set in the tidal zone, mainly from October to April, compared to the number of specimens (Cr = cranial and P.Cr. = postcranial) of spectacled porpoise found (to May 1995). A dash means fishing does not occur; an asterisk indicates that the nets are placed only occasionally. No. of sets refers to the usual number set.

Locality	No. sets	Cr.	P.Cr	Type of coast	Wave action
Cabo Espíritu Santo	0-4	2	2	High cliffs, few beaches	Very active
Río Alfa, Beta-R. Cullen	1*	-	1	High cliffs, few beaches	Very active
Río Cullen-Páramo	1*	1	-	High cliffs, few beaches	Very active
Península Páramo, ocean	2-4*	1	1	Sand, shingle, low beach	Very active
Bahía San Sebastián				Large, shallow bay open to E	
Pen. Páramo, bay	6-10	1	3	Patagonian shingle[1]	Very active
30-45km	-	1	1	Mud flats, channels	Passive
20-30km	-	7	2	Mud flats, few channels	Passive
10-20km	-	32	8	Mud flats, few channels	Passive
5-10km	-	31	31	Gravel, sand	Medium
0-5km	2-6	10	7	Gravel, sand	Medium
Los Chorillos	-	6	2	Cliffs behind sand beach	Active
Ea Sara, Campos 15, 17	1-8*	6	2	Sand beach	Very active
Paso Cholgas-Río Chico	10-25	7	5	Sand beach	Very active
Cabo Domingo-Río Grande	1-6	1	2	Sand beach	Very active
C. Peñas-Pta. María-R. Fuego	2-6	38	24	Cape with slight bay, sand, gravel, shingle	Very active
R. Fuego-Río Ewan	1-2*	2	-	Gravel, shingle	Active
Harberton, Canal Beagle	-	1 live	-	Stone, rocks	Passive

[1] Patagonian shingle covers large areas of coast with uniform, sea-worn stones, 2-4cm in diameter

other jobs, the nets may remain in place for several days, or be taken away to set up during weekends and holidays. The localities used along the Fuegian coast change slightly each season, mainly from October to April. Shore-based artisanal fishing increased from 1988 to 1991 due to economic pressures and has since expanded with the use of off-road vehicles and all-terrain-cycles to bring fishermen to areas of difficult access (Goodall *et al.*, 1995).

The extent of incidental exploitation of this species is unknown. We are certain of the capture of only a few specimens of *A. dioptrica* (Goodall *et al.*, 1994). Four additional animals were caught in a net in November 1989, of which we obtained only one. In plotting fishing areas against 'stranding' sites (Fig. 3) and typical fishing localities with number of specimens (Table 6), the areas seem to coincide. Most specimens were found in the southwest part of Bahía San Sebastián, a large, open, east-facing bay, and from Cabo Peñas to Río Fuego, less defined, open, southeast-facing bays. There could be several reasons for this: (a) the porpoises are taken in fisheries in these areas; (b) animals which died in nets could float to other areas; (c) oceanic animals not used to imperceptibly rising coastlines are trapped or stranded there; or (d) floating animals which died at sea are naturally dropped off there by currents. The inshore currents are southeast along the northeast coast of TF, while the Falkland (Malvinas) Current offshore flows northward. Eddies and gyros may form in these bays, dropping off floating debris as they are slowed.

Klinowska (1991) confused this species with *P. spinipinnis* in reporting deaths in nets set for *centolla*, *Lithodes antarctica*. *Centolla* has not been fished with nets since 1976 and we have no records of *A. dioptrica* being taken before then.

Oceanic fishing

Offshore fishing in the southwestern South Atlantic, where most spectacled porpoises have been found, has increased regularly over the last ten years. The main fishing types include bottom trawlers and jiggers that operate over the continental shelf and long-liners operating over the shelf edge and in deep waters. Although there are no specific reports of captures of spectacled porpoises in these fisheries, they may be taken as most ships do not report their incidental catch. Specimen CNP 116 had lacerations and internal haemorraghing typical of animals captured in nets. It was probably taken some distance to the south, kept for a time in the hold, then dumped overboard near Puerto Madryn, where it was found (A.P. Purgue, pers. comm.). The interaction of marine mammals with these fisheries off Argentina is under study (Crespo *et al.*, 1994a; b).

Captivity

To our knowledge no spectacled porpoises have been held in aquaria.

CONSERVATION AND MANAGEMENT

All cetaceans are protected in Argentina. In 1993, Law 101 of the recently formed (1991) Province of Tierra del Fuego prohibits the hunting, sale or industrial use of pinnipeds, cetaceans, guanacos, native foxes and all native birds. However, neither national nor provincial laws address incidental captures or strandings and there are few enforcement measures as yet. The other countries potentially involved, except for Uruguay, (i.e. Australia, Brazil, Chile, France, New Zealand, United Kingdom) have some degree of marine mammal protection (Klinowska, 1991). The spectacled porpoise is on Appendix II of CITES and classified as 'insufficiently known' (Crespo, 1991).

The status of this species is uncertain in all areas (IWC, 1991; Reeves and Leatherwood, 1994) and 'none of the information on abundance or biology required for conservation and management is available for any part of the range' (Klinowska, 1991).

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An Annotated Bibliography of the Spectacled Porpoise, *Australophocaena dioptrica* is given as an Annex to this paper, beginning overleaf.

Annex
An Annotated Bibliography of the Spectacled Porpoise, *Australophocaena dioptrica*

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INTRODUCTION

The spectacled porpoise, *Australophocaena (Phocoena) dioptrica*, is a Southern Hemisphere species which has been considered one of the rarest of mammals (Brownell, 1974). Only in the last 20 years have enough specimens accumulated to permit new clues to its biology. At first thought to occur only in the southwestern South Atlantic, newer specimens extended its range to New Zealand and the southern Indian Ocean; at the present state of knowledge, this species is circumpolar in sub-Antarctic waters and extends further north along the Atlantic coast of southern South America (Goodall, 1995). Since many of the publications on this species are in Spanish and/or difficult to obtain, this annotated list of references should help both the new and experienced student of cetaceans. The references are given in chronological order with those within each year in alphabetical order.

Museum codes

Argentina: CNP, Centro Nacional Patagónico, Puerto Madryn, Chubut; MLP, Museo de la Plata, La Plata; MACN, Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires; RNP, the Goodall collection, Ushuaia; UBA, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires; Australia: NMV, National Museum of Victoria, Melbourne; TM, Tasmanian Museum, Hobart; *Chile*: IPPA, Instituto de la Patagonia, Punta Arenas; MNHN-S, Museo Nacional de Historia Natural, Santiago; *New Zealand*: NMNZ, National Museum of New Zealand (now The Museum of New Zealand Te Papa Tongarewa); *United Kingdom*: BMNH, British Museum (Natural History); *Uruguay*: ZVC, Facultad de Humanidades y Ciencias, Montevideo.

CHRONOLOGICAL BIBLIOGRAPHY

Forster, G. 1777. *Voyage Round the World in his Britannic Majesty's Sloop* Resolution *Commanded by Capt. James Cook During the Years 1872, 3, 4 and 5.* White, B., Robson, J., Elmsly, P. and Robinson, G. 607pp.

[Not seen; cited in Marelli, 1922.] Vol. II says that porpoises with dorsal fins not undercut were seen at 52° and 54°5′S off South America. [Although this report is vague, it may have been the first sighting of *A. dioptrica*.]

Philippi, R.A. 1893. Los delfines de la punta austral de la América del Sur. *An. Mus. Nac. Chile, Sec. 1, Zool.* 6:1–18. [In Spanish].

At the end of winter of 1888, Philippi received the skin of a 149cm '*tunina*' from D. Federico Godoy of Concepción, caught in Bahía de Talcahuano. Philippi named the animal *Phocaena obtusata* and it was deposited in MNHN-S. His figure shows an animal shaped like a porpoise with five short white stripes up the side, but 'the skin, that I received, had lost in various parts its epidermis, so that it was necessary to paint the embalmed animal'. [Over the years there was controversy as to whether this specimen was

Phocoena dioptrica or a *Cephalorhynchus* until Goodall and Cameron had it radiographed in 1978 (see Goodall *et al.*, 1988). They confirmed that the type of specimen of *Phocaena obtusata* is a specimen of Cephalorhynchus, most probably *C. eutropia*.]

Racovitza, E.G. 1902. Cétacés. ***Expédition antarctique belge, résultats de voyage du S.Y. Belgica en 1897–99.*** **Zoología. [In French].**
P. 60: 'Forster (1777) mentions that twice porpoises that have a dorsal fin that is unmarked (not pointed or undercut?) were seen around 52° and 54°S in the South American sector. It is possible in these cases that it refers to a species of the genus *Phocaena*, therefore there exists an Antarctic species of this genus'. [Not seen; cited in Marelli, 1922.]

True, F.W. 1903. On species of South American Delphinidae described by Dr R.A. Philippi in 1893 and 1896. ***Proc. Biol. Soc. Wash.*** **16:133–44.**
P. 139. In referring to *Phocaena obtusata*, True found that 'This remarkable species is quite unlike any porpoise with which I am acquainted especially as regards colouration'. He could not decide what genus it should be and looked forward to new information. He felt the animal was immature. On p. 143 he gave the probable identity as *Cephalorhynchus ? obtusata* (Philippi).

Lahille, F. 1912. Nota preliminar sobre una nueva especie de marsopa del Río de la Plata (*Phocaena dioptrica*). ***An. Mus. Nac. B. Aires*** **23:269–78. [In Spanish].**
Lahille describes the '*focena de anteojos*', *Phocaena dioptrica*, from an animal which came ashore alive on 28 July 1911 at Punta Colares, Quilmes, Río de la Plata near Buenos Aires and was taken to the Museo Nacional de Historia Natural [now MACN]. The animal was a 186cm, 85kg female containing a 48.4cm, 1.6kg female foetus; the latter was preserved in alcohol. The adult had a small mouth with 19–19/20–21 teeth, some without alveoli. The dorsal fin was triangular with a convex posterior margin; the anterior border was thicker and had a single line of small compressed tubercules. The colour pattern was a lustrous black and white, with black lips and almost imperceptible lines from the mouth to flipper. A black eye patch surrounded by a thin white line, like spectacles, gave the specific name. The flipper was white above with light gray borders. The tail stock was white [in the drawing and in the foetus the upper border is black]; the flukes were black above and white below; the lower surface has gray edges and blackish lines radiating from the notch. The foetus was 'almost near birth'. The vertebral formula was C7, T13, L15, Ca 33=68, with four cervicals fused. Plates 6 (Figs 1–2) and 7 (Fig. 3) show the adult, plate 8, the foetus, and plate 9, a comparison with other Phocoenids [but not *P. obtusata*, although he mentions Philippi's paper]. Measurements of both adult and fetus are given in detail. He stated that several scientists would study the specimen [but only one other paper was published – Gallardo, 1913].

Gallardo, A. 1913. Notas sobre la anatomía del aparato espiracular, laringe y hioides de dos delfines: *Phocaena dioptrica* Lahille y *Lagenorhynchus fitzroyi* (Waterhouse) Flower. ***An. Mus. Nac. B. Aires*** **24:235–45. [In Spanish].**
The first work on the anatomy of this species gives further measurements of the head of the Lahille specimen, blubber thickness (2cm) and a description of the blowhole complex, larynx and hyoids. A few nematodes were found in the respiratory sacs. There are 17 figures, including a saggittal plane of the head, the larynx, tongue and hyoid bones.

Bruch, C. 1916. El macho de *Phocaena dioptrica* Lah. ***Physis (B. Aires)*** **2:461–2. [In Spanish].**
A very brief report on the second and third specimens known of this species, a 186cm pregnant female taken by fishermen at Río Santiago on 14 August 1912 and a 204cm male

taken there in September 1913. This first male to be found has an unusually large dorsal fin. The female contained a 'full term' female foetus. Both animals are illustrated and the external measurements of the male are given, but those of the female are of Lahille's animal. [Although not mentioned in the brief text, both skeletons are on exhibition in MLP beside painted body casts of the specimens.]

Marelli, C. 1922a. *Phocaena Stornii* sp.n., una nueva especie de marsopa del mar austral argentino. :3–14. Resultados de la Primera Expedición a Tierra del Fuego (1921) enviada por la Facultad de Ciencias Exactas, Físicas y Naturales de la Universidad Nacional de Buenos Aires. [In Spanish].
The fourth specimen (not counting the Lahille fetus) of this species is a cranium found on the coast of Tierra del Fuego during the summer of 1921. Marelli gives the first illustrations, measurements and description of the cranium (Figs. 1–3, 5) and teeth (Fig. 4). There were 15 functional teeth on each side and four hidden in the gum. He compares his specimen with crania of *P. spinipinnis, P. Philippii, P. phocaena* and the *P. dioptrica* Bruch specimen [although he calls it Lahille's] in MLP. Deciding that his is different, he names it *P. Stornii* in honour of the director of the Argentine Naval School, Segundo Storni. [formerly UBA M-116, now MACN 16407.]

Marelli, C. 1922b. *Phocaena stornii* sp.n., una nueva especie de marsopa del mar austral argentino. *An. Soc. Sci. Cient. Argent.* 94:229–40. [In Spanish].
An exact reprint of the above, with a note saying that the first report on the expedition begins on p. 59.

Allen, G.M. 1925. Burmeister's porpoise (*Phocoena spinipinnis*). *Bull. Mus. Comp. Zool.* 67:251–61.
P. 255 discusses Philippi's *P. obtusata* , 'almost certainly a female' of *P. dioptrica* and that 'his name should, with little doubt, replace *dioptrica*. His figure shows a similar form with the same enormous dorsal fin, and the sharply defined white belly'. Allen felt that the vertical white bars could be due to the folding of the skin in packing and the only discrepancy was the black flipper.

Fraser, F.C. 1938. Whales and dolphins. *In:* J.R. Norman and F.C. Fraser (eds.) *Giant Fishes, Whales and Dolphins.* 1st. Edn. Putnam, London.
[This edition not seen] Hershkovitz (1966) gives 'p. 312, fig. 80 (animal) South Atlantic: River Plate to South Georgia; characters; may be same as *P. obtusata*'. Re-issued in 1948 (see below).

Cabrera, A. and Yepes, J. 1940. *Mamíferos Sud-Americanos.* Hist. Nat. Ediar, Buenos Aires. 370pp.
[This edition not seen] Hershkovitz (1966) says that on p. 300 the distribution is given as Río de la Plata and the local name *marsopa de anteojos*. Re-issued in 1960 (see below).

Hamilton, J.E. 1941. A rare porpoise of the South Atlantic, *Phocaena dioptrica* (Lahille, 1912). *Discovery Rep.* 21:229–34.
By 1941, only four specimens of the spectacled porpoise had been found [Hamilton mentions three, not including *P. stornii*]. This paper reports two more, a 135.9cm immature female collected by H. Wilkins at South Georgia in 1923 [should read 1922] during the Quest [Shackleton-Rowett] Expedition, and a 185.5cm 'skeletonised' animal from the Falkland (Malvinas) Islands, collected by a shepherd, G. Butler. Hamilton

describes the pigmentation of the young animal, comparing it to those of Lahille and Bruch; the Wilkins animal is more like the Lahille fetus in that the tail stock and appendages are darker and the flipper stripe evident; these may get lighter with age. Hamilton gives a detailed description of the skull (which he thought was the first) and skeleton, with the first photographs of the latter, comparing them to those of *P. phocaena* and *P. spinipinnis*. The vertebral count is C7 (five fused), D13, L16, Ca32. Epiphyses were unfused from Th1 to Ca13. Table 1 gives all known body measurements (five animals plus fetus), while Table 2 gives skull measurements of the two new specimens.

Carcelles, A. 1948. Los cetáceos en las aguas argentinas. *Rev. Mus. Arg. Cienc. Nat. B. Aires* Publ. Extra 238:5–10. [In Spanish].

Brief description of the *marsopa de anteojos* giving its habitat as Río de la Plata and an illustration of Lahille's animal. The author states that a plaster model of the head of this porpoise is on exhibit in the Museo de Puerto Quequén, Provincia de Buenos Aires.

Fraser, F.C. 1948. Whales and dolphins. pp. 201–360. *In:* J.R. Norman and F.C. Fraser (eds.) *Giant Fishes, Whales and Dolphins*. 2nd. Edn. Putman, London. 376pp.

P. 312 gives a short description, range (River Plate to South Georgia), form, pigmentation pattern (especially that of the animal from South Georgia) and number of teeth (19–21). The species may be the same as *P. obtusata*. Illustration (p. 313) of Lahille's animal with white flukes.

Hamilton, J.E. 1952. Cetacea of the Falkland Islands. *Comun. Zool. Mus. Hist. Nat. Montev.* 5(66):1–6.

Brief mention of the skull and most of skeleton of the 185.5cm animal collected on West Falkland (Hamilton, 1941), calling it 'adult'. The specimen is in BMNH. Another [the seventh] specimen was described to Hamilton by someone who had seen it stranded.

Sanderson, I.L. 1956. *Follow the Whale*. Little, Brown & Co., Boston. 423pp.

There is no mention of this species in the text, but p.395 shows an illustration of Lahille's specimen (from Fraser, 1948).

Ringuelet, R.A. and Aramburu, R.H. 1957. Enumeración sistemática de los vertebrados de la Provincia de Buenos Aires. *Min. As. Arg. Prov. B. Aires* 119:1–94.

In Spanish. On p.81, *Phocaena dioptrica* is briefly listed as *marsopa de dos colores, marsopa de anteojos*.

Norris, K.S. and McFarland, W.N. 1958. A new porpoise of the genus *Phocoena* from the Gulf of California. *J. Mammal.* 39(1):22–39.

The authors (p. 32) review the characters and feel that *P. storni* is a synonym of *P. dioptrica*, as the few differences can be due to individual variation or the old age of the specimen; some teeth could have been lost. Distribution (p. 34) is along the South Atlantic coast of South America; 'species is little known and its range probably far exceeds that reported'.

Cabrera, A. and Yepes, J. 1960. *Mamíferos Sud-Americanos*. Hist. Nat. Ediar, Buenos Aires. 370pp.

In Spanish. This species is called *marsopa bicolor* or *marsopa de anteojos*. There is a short description of the pigmentation; the number of teeth, 27 on each side, is unsubstantiated. The species is cited only for the Río de la Plata.

Cabrera, A. 1961. Catálogo de los mamíferos de América del Sur. *Rev. Mus. Argent. Cienc. Nat. Zool.* 4(2):603–25. [In Spanish].
This general work gives *Phocoena stornii* Marelli as a synonym of *P. dioptrica*. The author defines the habitat as southwestern Atlantic, lists the type locality and says that sometimes these porpoises enter estuaries.

Carvalho, C.T. 1963. Sobre um boto comun no litoral do Brasil (Cetacea, Delphinidae). *Rev. Bras. Biol.* 23(3):263–76.
[Not seen. Number 253 in Truitt, 1974] 'used for comparison' with a dolphin from Brazil.

Davies, J.L. 1963. The antitropical factor in cetacean speciation. *Evolution* 17(1):107–16.
P. 111. The genus *Phocaena* is one of the most interesting showing antitropical distribution. *P. dioptrica* is known only from the Atlantic sector of South America south of the Río de la Plata.

Scheffer, V.B. and Rice, D.W. 1963. A list of the marine mammals of the world. *US Fish Wildl. Serv. Spec. Sci. Rep. Fish.* 431:1–12.
P. 5 mentions only 'South Atlantic: Argentina, Falkland Islands, and South Georgia'.

Yablokov, A.V. 1963. Types of colour of the Cetacea. *Bull. Moscow Soc. Nat. Biol* Dep. Fish. Res. Board Transl. Ser. No. 1239.
[Not seen; cited in Mitchell, 1970] One of the clearly marked species of delphinoids; may be recognised intraspecifically by visual signals.

Fraser, F.C. 1964. Whales and whaling. pp. 191–205. *In:* R. Priestly (ed.) *Antarctic Research: A Review of British Scientific Achievement in Antarctica.* Butterworths, London. 360pp.
P. 193 lists the first five specimens known, three from the River Plate and one each from South Georgia and Falklands. Length to 204cm. Nothing is known of food, migration, reproductive behaviour, parasites.... 'Five specimens!' Description of pigmentation and illustration with black flukes and tail stock.

Walker, E.P. (ed.). 1964. *Mammals of the World.* John Hopkins Press, Baltimore.
P. 1129, under porpoises, gives distribution only, from La Plata River of South America to South Georgia.

Harrison, R.J. and King, J.E. (eds.). 1965. *Marine Mammals.* Hutchinson University Library, London. 192pp.
In the discussion of the Phocoenidae (pp. 40–41), there is a brief mention of the spectacled porpoise (*P. dioptrica*) of South America.

Fraser, F.C. 1966. Comments on the Delphinoidea. pp. 7–31. *In:* K.S. Norris (ed.) *Whales, Dolphins and Porpoises.* University of California Press, Berkeley and Los Angeles. 789pp.
Brief mention of members of the genus *Phocoena*, and that there are no adequate series of specimens of the two Southern Hemisphere members.

Hershkovitz, P. 1966. Catalog of living whales. *Smithson. Bull.* 246:1–259.
P. 102 gives the list of publications to date. *Phocaena Stornii* Marelli, 1922 is given as a synonym, *Phocaena obtusata* Philippi, 1893 and *Cephalorhynchus ? obtusata* True, 1903 are given as questionable synonyms. These last are given as synonyms of *C. eutropia*, p.

75. The type of *P. dioptrica* is the female foetus preserved in spirits at MACN. Type locality, Punta Colares, near Quilmes, Río de la Plata. Distribution, South Atlantic from 34°40'S to Tierra del Fuego, Falklands and South Georgia. If *P. obtusata* is the same, the range would include the west coast south of 36°S.

Fraser, F.C. 1968. Notes on a specimen of *Phocoena dioptrica* from South Georgia. *Br. Antarct. Surv. Bull.* 16:51–6.
In this important paper, Fraser gives more details of the Wilkins female from Leith Harbour, South Georgia (Hamilton, 1941). The skeleton is BMNH 1922.11.3.1. He shows the original drawing, measurements and pigmentation notes taken by Wilkins on the beach on 1 May 1922. The animal came ashore alive at the whaling station and was killed by the cook. The whaling captains claimed the species was seen in schools about 16km offshore; they sometimes shot them for food. Fraser reviews the five occurrences. External measurements of three specimens, pigmentation and a detailed discussion are given. 'The difference... in the dorsal fin of male and female is of an order not encountered elsewhere in the Phocoenae.... more nearly comparable with that found in the killer whale....' After comparing proportions, he feels 'that the dorsal fin of the male grows heterogonically at a rate in excess of that of the female to produce in the adult male a notable expression of sexual dimorphism'. Fraser reviews the views of True (1903) and Allen (1925) on *P. obtusata*, indicating that the Wilkins animal has a dark flipper and that the pigmentation of *P. obtusata* 'is so trenchantly different from that of *P. dioptrica* that it would be inadvisable, until further evidence is forthcoming, to give [it] priority....' He agrees that *P. stornii* should be a synonym.

Matthews, L.H. (ed.). 1968. *The Whale*. Simon & Schuster, New York. 287pp.
On page 78, under a brief paragraph on the genus *Phocoena*, the author mentions the 'spectacled porpoise (*P. dioptrica*) from western South Atlantic waters'.

Poulter, T.C. 1968. Marine mammals. pp. 435–65. *In:* T.A. Sebeok (ed.) *Animal Communication: Techniques of Study and Results of Research*. Indiana University Press, Indiana.
P. 438 mentions *P. dioptrica* in the list of species and that there are recordings for the genus [*P. phocoena*], which produces both echolocation and communication signals.

Rice, D.W. and Schaffer, V.B. 1968. A list of the marine mammals of the world. *US Fish Wildl. Serv. Spec. Sci. Rep. Fish.* 579:1–16.
Page 10 reads only '*P. dioptrica* Lahille, 1912 (spectacled porpoise). Coast of Argentina, the Falkland Islands and South Georgia'.

Mitchell, E.D. 1970. Pigmentation pattern evolution in delphinid cetaceans: An essay in adaptive coloration. *Can. J. Zool.* 48(4):717–40.
P. 731 mentions only the disruptive pigmentation, which may give protection from predators, camouflage during predation or in some other situation.

Marcuzzi, G. and Pilleri, G. 1971. On the zoology of Cetacea. *Invest. Cetacea* 3(1):101–70 +7 plates.
Brief (three lines) mention of distribution, 'antiboreal American subregion of the antiboreal coastal region'. The map illustrates distribution from Río de la Plata to South Georgia, but not the southern part of South America. It occurs in 'cold-stenothermal' waters.

Matthews, L.H. 1971. Whales and dolphins. pp. 224–54. *In:* Vol. 2. *The Life of Mammals.* Universe Books, New York.
P. 242 gives two brief lines on *P. dioptrica* pigmentation.

Mörzer-Bruyns, W.F.J. 1971. *Field Guide of Whales and Dolphins.* C.A. Meese, Amsterdam. 258pp.
P. 38 gives distribution ('Patagonia to South Georgia'), length (1.5m), teeth, pigmentation, biotope ('cold inshore waters of the Falkland Current'). The author also gives data unsubstantiated by research, such as weight (54kg), food ('fish and probably cuttlefish') and speed ('probably maximum 8 knots').

Pilleri, G. 1971. *Biologish-Anatomische Forschungsreise nach Uruguay zum Studium des La Plata-Delphins, Pontoporia blainvillei.* Hirnanatomisches Institut, Berne. 27pp.
[Not seen; number 132 in Truitt, 1974.]

Praderi, R. 1971. Contribución al conocimiento del género *Phocoena* (Cetacea, Phocoenidae). *Rev. Mus. Argent. Cienc. Nat. 'Bernardino Rivadavia' Inst. Nac. Invest. Cienc. Nat. Zool.* 7(2):251–66. [In Spanish].
A careful review of the species with synonymy, description of earlier specimens and the new one from Uruguay (Praderi and Palerm, below). He presents two more incomplete crania, MACN 292 from the Atlantic coast of Argentina, collected by M. Eguía 30 Dec. 1899 and MACN 7–45, with the same indefinite locality, collected by M. Albieri 1 Sep. 1907. Review of external characters with measurements of five animals, and of the crania with measurements of eight. CBLs range from 244 to 315mm. Photographs of MACN 292 and the Uruguaian cranium. Bruch's female is MLP 1202 and the male MLP 1201; Wilkins' is BMNH 1922.11.2.1, Hamilton's BMNH 1939.9.30.1. The skull of Lahille's specimen was lost and measurements never published. That of Marelli is missing [later found at UBA, number M-116]. The species is sometimes captured off Uruguay.

Praderi, R. and Palerm, E. 1971. Hallazgo de *Phocoena dioptrica* Lahille (Cetacea, Delphinidae) en la costa Uruguaya. *Bol. Soc. Zool. Uruguay* 1:19–21. [In Spanish].
This paper presents the first specimen for Uruguay and the northernmost known to date, a 200cm male found by E. Palerm and L. Lecour on 28 October 1945 at Balneario Lagomar, on the Río de la Plata. Because of decomposition, only the total length and cranial measurements are given. There is a short review of differences with other species of the genus. The cranium and mandibles (ZVC M.850) represent the seventh specimen known.

Nishiwaki, M. 1972. General Biology. pp. 3–204. *In:* S.H. Ridgway (ed.) *Mammals of the Sea: Biology and Medicine.* Chas Thomas, Springfield, Illinois. 812pp.
P. 121 gives a review of the shape, pigmentation, number of vertebrae, etc. 'This is a rare species and the few specimens ... collected to date were all found off South America from the La Plata River to South Georgia Island'.

Pilleri, G. and Gihr, M. 1972. Burmeister's porpoise *Phocoena spinipinnis* Burmeister 1865, off the Punta del Diablo, Uruguay. *Invest. Cetacea* 4:163–72.
The authors compare the skulls of two *P. spinipinnis* from Uruguay with two *P. dioptrica* in the British Museum (Hamilton's, Wilkins') and five skulls of *P. phocoena.* Neurocranium height is highest in *P. dioptrica*, its zygomatic width is wider; *P. spinipinnis* has the largest temporal fossa. Measurements are given.

Ximenez, A., Langguth, A. and Praderi, R. 1972. Lista sistemática de los mamíferos del Uruguay. ***An. Mus. Nac. Hist. Nat. Montev.*** **7(5):1–49. [In Spanish].**
P. 32 gives a synonymy with author and site of collection. At this date, only seven specimens are known [this should have read nine], five from the Río de la Plata. The location of the Uruguayan specimen is given. If *P. obtusata* is proved to be of this species, the distribution would be amplified to the coast of Chile.

Brownell, R.L., Jr. 1974. Small odontocetes of the Antarctic. pp. 13–9. ***In:*** **V. Bushnell (ed.)** ***Antarctic Mammals. Antarctic Map Folio Series. Folio 18.*** **American Geographical Society, New York. 19pp.**
This species is discussed on p. 15. Known only from the western South Atlantic (Plate 8), from 34°52'S in Uruguay to Tierra del Fuego and South Georgia, and from nine specimens, it 'is one of the rarest and most poorly known delphinoids'. There are no published observations of live animals; little is known of its life history and ecology. Two females had near-term fetuses in July and August, so calving may be in the austral spring. [Although he gives lengths for females as 188, 191 and 193cm, only two of 186cm had been published.] [Must be RLB measurements – La Plata Museum specimen?]

Brownell, R.L., Jr. 1975. ***Phocoena dioptrica. Mamm. Species*** **66:1–3.**
This review of knowledge on this species gives details of pigmentation, differences of skull from *P. phocoena*, general characteristics, selected external measurements of two animals, and distribution (Uruguay to Tierra del Fuego and South Georgia, with no specimens known from the centre of the range). It is the only *Phocoena* species to occur around offshore islands. Vertebral and phalangeal counts, reproduction and the lack of knowledge of its ecology are discussed. At this time, only 10 occurrences are known, with eight cranial specimens; the holotype has disappeared, but its foetus is preserved in alcohol at MACN. There is a review of the controversy over the identity of *P. obtusata*; Brownell concludes it is a *Cephalorhynchus*. The most concise and informative work to date, the paper includes illustrations of one of the casts and skeletons at La Plata, the skull, mandibles and earbones, as well as a distribution map. [He gives the length of the Lahille female as 191 instead of 186cm.]

Donoso-Barros, R. 1975. Contribución al conocimiento de los cetáceos vivientes y fósiles del Territorio de Chile. ***Gayana (Zoología)*** **36:1–127. [In Spanish].**
The author gives a short review of the family Phocoenidae and the genus *Phocoena*. He gives his reasons (pp. 52–54), based mainly on pigmentation, for considering that *P. obtusata* Philippi, 1893, and *P. dioptrica* Lahille, 1912 are the same species. After examining the Philippi skin in the Santiago Museum and the two Bruch specimens in the La Plata museum, he gives priority to the name *P. obtusata*. The distribution would thus be from 'south of the Río de la Plata continuing along the Atlantic coast, Islas Malvinas, Georgia del Sur, Estrecho de Magallanes, Pacific to Talcahuano'.

Mitchell, E.D. 1975a. ***IUCN Monograph.*** **No. 3.** ***Porpoise, Dolphin and Small Whale Fisheries of the World: Status and Problems.*** **International Union for Conservation of Nature and Natural Resources, Morges, Switzerland. 129pp.**
P. 129 deals with *Phocoena* spp. This species is reviewed in one line: '...*Phocoena dioptrica*, the Spectacled Porpoise, is distributed in the western South Atlantic, but there is no information about its biology or possible exploitation'.

Mitchell, E. 1975b. Report of the Meeting on Smaller Cetaceans, Montreal April 1–11, 1974. *J. Fish. Res. Board Can.* 32(7):889–983.
This concise, up to date review gives the known distribution of the 10 occurrences (from Brownell, 1974), the lengths of the two Bruch specimens and Lahille's fetus. It states that nothing is known of stocks, feeding, nutrition, behaviour, exploitation, or relation of species to habitat.

Frost, P.G.H. and Best, P.B. 1976. Design and application of a coded format for recording observations of cetaceans at sea. *S. Afr. J. Antarct. Res.* 6:9–14.
A sighting of 4–5 animals, possibly of this species, was made on 2 April 1976 at 49°29'S, 70°15'E in the southern Indian Ocean from the M.S. *Marion Dufresne* (p. 10). P. 12 mentions dolphins with dark backs and triangular dorsal fins in the Golf du Morbihan, Kerguelen Island.

Langguth, A. 1976. *Lista de las especies de vertebrados del Uruguay.* Museo Nacional de Historia Natural, Montevideo. 58pp.
This species is listed on p. 5.

Baker, A.N. 1977. Spectacled porpoise, *Phocoena dioptrica*, new to the subantarctic Pacific Ocean. *NZ J. Mar. Freshwater Res.* 11(2):401–6.
In January 1975, a NMNZ expedition found a bleached cranium with teeth at Sandy Bay, Enderby Island, Auckland Islands (50°40'S, 166°10'E), which proved to be *P. dioptrica*, known only from 10 records in the western South Atlantic. Apart from South America, there are no other Phocoenid records for the South Pacific. Photographs, measurements and reason for the determination are given. The CBL is 310mm (the second largest recorded for the species) and there are 19 teeth per side. *P. dioptrica* possibly has a circumpolar distribution in subantarctic latitudes. The specimen is NMNZ Mam. 1670.

Goodall, R.N.P. 1977. Preliminary report on the small cetaceans stranded on the coasts of Tierra del Fuego. *Rep. int. Whal. Commn* 27:505.
Mentions 46 specimens of *Phocoena dioptrica* collected on beaches in Tierra del Fuego. More skeletal material is found of this species than any other, and it is assumed to be common in the area.

International Whaling Commission. 1977. Report of the sub-committee on small cetaceans, London, June 1976. *Rep. int. Whal. Commn* 27:474–84.
P. 476 mentions that 'Goodall (Paper L24) reports many stranded specimens from Tierra del Fuego'.

Nishiwaki, M. 1977. Distribution of toothed whales in the Antarctic Ocean. pp. 783–91. *In:* G.A. Llano (ed.) *Adaptions Within Antarctic Ecosystems. Proceedings of the Third SCAR Symposium on Antarctic Biology.* Smithsonian Institution, Gulf Publishing Co., Houston. 1252pp.
Fig. 6 on p. 791 shows the distribution of the two Southern Hemisphere Phocoenids. *P. dioptrica* 'goes south over the Antarctic Convergence... [the specimen from South Georgia]. I would hope that in the near future additional information will be added....' P. 783, '... a rare species of the western South Atlantic'.

Rice, D.W. 1977. A list of the marine mammals of the world (third edition). *NOAA Tech. Rep. NMFS SSRF* 711:1–75.
P. 10 is a repeat of Rice and Scheffer, 1968.

Sielfeld, W., Venegas, C. and Atalah, A. 1977. Consideraciones acerca del estado de los mamíferos marinos en Chile. *An. Inst. Patagonia* 8:297–312. [In Spanish].

On p. 299, *Phocoena dioptrica* is listed among the marine mammals of Chile, on the basis of *P. obtusata*, the name which should have priority.

Clarke, R., Aguayo, A. and Bastulto del Campo, S. 1978. Whale observation and whale marking off the coast of Chile in 1964. *Sci. Rep. Whales Res. Inst., Tokyo* 30:117–77.

In trying to identify 'porpoises' seen at sea (pp. 153–156) the authors review what is known of the two Southern Hemisphere species and give a good summary of the controversy over *P. obtusata. P. dioptrica* should be easily recognised at sea, with its distinct black and white and sexually dimorphic dorsal fin.

Goodall, R.N.P. 1978. Report on the small cetaceans stranded on the coasts of Tierra del Fuego. *Sci. Rep. Whales Res. Inst., Tokyo* 30:197–230.

Pp. 216–219 state that only eleven specimens were formerly known, 10 of them from Uruguay to Tierra del Fuego in the southwestern South Atlantic and one from New Zealand, with only two possible sightings. This report gives a detailed listing of 112 new specimens (11 complete skeletons, 76 skulls and 25 postcranial elements) gathered during beach surveys in Tierra del Fuego. Most of these are beach-worn bones, but six were entire enough for total lengths and one was alive. Two suckling animals were found in February and March. At least one specimen was taken incidentally in shore set-nets. At this stage, *P. dioptrica* is the species most abundant in the collection of Fuegian specimens. Photograph of skull.

International Whaling Commission. 1978. Report of the standing sub-committee on small cetaceans. *Rep. int. Whal. Commn* 28:79–82.

P. 81 mentions that Baker, 1977, reported a cranium from the Auckland Islands, and that Cawthorn reported 'a sighting of two pairs of porpoises northeast and northwest of the Auckland Islands in March 1977'. These are the first records from the Pacific Ocean.

Matthews, L.H. (ed.). 1978. *The World Naturalist Series. The Natural History of the Whale.* Weidenfeld & Nicholson, London. 219pp.

On p. 43 there is a brief mention of the pigmentation and range.

Organisation of American States. (ed.). 1978. *Informe Final de la Reunión de Expertos Sobre Conservación de Mamíferos Marinos y sus Ecosistemas.* CIECC, Puerto Madryn, Chubut. 54pp.

In Spanish. A brief note on p. 8 says population unknown, of coastal habits, taken incidentally in nets in Tierra del Fuego.

Venegas, C. and Sielfeld, W. 1978. Registros de *Mesoplodon layardii* y otros cetáceos en Magallanes. *An. Inst. Patagonia* 9:71–177. [In Spanish].

P. 176 reviews the pros and cons of the validity of the name *P. obtusata*, saying that they (Sielfeld *et al.*, 1977a;b) felt that it might be synonymous with *P. dioptrica*, as stated by Donoso-Barros (1975) even though True (1903) and Brownell (1975) felt otherwise. They state that Goodall and Cameron (in prep.) have proved it to be a *Cephalorhynchus*. The first *P. dioptrica* for Chile are then the Goodall specimens (RNP 703–5, 710) from Bahía Lomas [Strait of Magellan] which were donated to the IPPA collection.

Goodall, R.N.P. and Cameron, I.S. 1979. *Phocoena dioptrica*, una nueva especie para aguas chilenas. *Rev. Mus. Argent. Cienc. Nat. 'Bernardino Rivadavia' Inst. Nac. Invest. Cienc. Nat. Zool.* 12(11):143–52. [In Spanish].
This paper gives a detailed review and list of the eleven specimens known up to 1977 (not including the 112 cited in Goodall, 1978), as well as several probable sightings. The authors consider *P. obtusata* to be a *Cephalorhynchus*, and on that basis present the first specimens of *P. dioptrica* for Chilean waters, four beach-worn crania collected at Bahía Lomas on the south shore of the Strait of Magellan. The work includes a map of the eastern strait, three views of skulls and photographs of caudal vertebrae.

Goodall, R.N.P. and Polkinghorn, J.T. 1979. Preliminary report on sightings of small cetaceans off southern South America and the Antarctic Peninsula. Paper SC/31/SM2 presented to the IWC Scientific Committee meeting, June 1979 (unpublished). 10pp.
A probable sighting is reported of five animals off Golfo San Jorge, Patagonia, although not by an experienced observer.

Goodall, R.N.P. and Cameron, I.S. 1980. Exploitation of small cetaceans off southern South America. *Rep. int. Whal. Commn* 30:445–50.
P. 447. From December 1975 to March 1979, at least two *P. dioptrica* were taken in shore-based gillnets; mortality was probably much higher.

Herman, L.M. and Tavolga, W.N. 1980. The communication systems of cetaceans. pp. 149–209. *In:* L.M. Herman (ed.) *Cetacean Behavior: Mechanisms and Functions*. John Wiley & Sons, New York. xiii+463pp.
P. dioptrica is included in Table 4, p. 165, as one of the cetacean species which probably do not whistle, but for which there is no data. In a footnote, 'D. Caldwell and Caldwell (1977) say all Phocoenidae are nonwhistlers'.

Sielfeld, W. 1980. Mamíferos marinos en colecciones y museos de Chile. *An. Inst. Patagonia* 11:272–80.
P. 277 gives a list of four specimens, IPPA-CE 35–38, all beach worn skulls, from Bahía Lomas, Tierra del Fuego [donated by the Goodall team]. [These specimens are in the private collection of Goodall.]

Heintzelman, D.S. 1981. *A World Guide to Whales, Dolphins, and Porpoises*. Winchester Press, Tulsa, Oklahoma. 156pp.
P. 42 deals with this species. Length is given as 1.5m, weight 54kg, food is fish, habitat cold waters inshore, distribution South Atlantic from Río de la Plata to S. Georgia. Possibly in South Pacific south of 36°S. [Nearly all this data is unfounded; neither weight nor any stomach contents had been reported. The Pacific record is on the basis of *P. obtusata*.]

Watson, L. 1981. *Sea Guide to Whales of the World*. Hutchinson, London. 302pp.
The description on pp. 196–7 has several errors. Watson has confused the early specimens [the animal caught by J. de Gaetano was the one described by Lahille, 1912; its foetus is in spirits, but no other specimen is]. The illustration shows a dark flipper stripe running from the angle of mouth to tip of flipper. The posterior ribs are supposed to be 'extraordinarily wide and flat', like those of *Caperea* . Food is fish and squid [no stomach contents had been reported]. Distribution, at that time, was 'cold inshore waters of the Falkland Current'.

Ellis, R. 1982a. *Dolphins and Porpoises*. Alpfred A. Knopf, New York. 270pp.
Pp. 197–199 give a good review of this species. The author describes the variation reported by different authors in flipper, fluke and tail stock pigmentation, the large dorsal fin in males, and the meaning of the scientific name. Nine specimens to 1974 are mentioned, as well as the skull from New Zealand and the many specimens from Tierra del Fuego. Brownell (1974) had recommended beach surveys, which have been implemented; now at-sea observations are needed. 'We know something now about where they die, but very little about how and where they live'. Illustrations on p. 198.

Ellis, R. 1982b. Marine mammals, a sea guide. *Whalewatcher* (special publication):26.
There is a brief description of pigmentation and localities, 'suggesting a circumpolar distribution', but 'you have to be in the region of Cape Horn or Tierra del Fuego to see it'.

Gaskin, D.E. 1982. *The Ecology of Whales and Dolphins*. Heinemann, London. 459pp.
The range of *P. dioptrica* overlaps with *P. spinipinnis* off southeastern South America and it has been found south of New Zealand (map, p. 228). Pp. 229–231 discuss Phocoenid evolution.

Baker, A.N. 1983. *Whales and Dolphins of New Zealand and Australia. An Identification Guide*. Victoria University Press, Wellington, NZ. 133pp.
P. 119. The only true porpoise found in the southwest Pacific. Description, pigmentation, illustration and drawing of skull. The species was rare until recently. A 1975 skull from the Auckland Islands is in NMNZ and 'another skull, collected years ago at MacQuarie Island but not recognised', is in NMV. There have been possible sightings at Kerguelen and the Auckland Islands. Probably restricted to the circumpolar subantarctic. [This species was not listed in Baker's 1972 edition, *New Zealand Whales and Dolphins*.]

Leatherwood, S. and Reeves, R.R. 1983. *The Sierra Club Handbook of Whales and Dolphins*. Sierra Club Books, San Francisco. xvii+302pp.
Pp. 271–2 give a good description of the pigmentation, size (the largest member of the genus, to 2.2m). 'A 50cm foetus was judged to be near term, but the size at birth is unknown'. The small flippers, large triangular dorsal fin, 'exaggerated in adult males' and pigmentation are distinctive. They give the usual distribution including the Pacific Ocean near New Zealand's subantarctic islands; sightings are mentioned south of Tasmania. There is a single record from the Indian Ocean, from Kerguelen. 'The species may be circumpolar in subantarctic latitudes, perhaps concentrating around offshore islands as well as along continental coasts'. '...known to die accidentally in fishing gear'.

Sielfeld, K.W. 1983. *Mamíferos Marinos de Chile*. Ediciones de la Universidad de Chile, Santiago. 199pp.
In Spanish. The common name given is *marsopa anteojillo*. The type specimen, a description, and distribution (including the first for Chile) are given in detail. Nothing is known of its behaviour, reproduction, food or habitat. *P. obtusata* was thought to be this species, but Goodall and Cameron have shown that it is not. The four Goodall specimens at IPPA are listed, as well as an exterior and palatine region illustration.

Fordyce, R.E., Mattlin, R.H. and Dixon, J.M. 1984. Second record of spectacled porpoise from subantarctic Southwest Pacific. *Sci. Rep. Whales Res. Inst., Tokyo* 35:159–64.
The authors report an incomplete skull of a subadult *P. dioptrica* collected at Cataline Point, Macquarie Island (54°30'S, 159°00'E) on 24 July 1957 and recently discovered in the

collection of the National Museum of Victoria (NMV C10323). Skull measurements, photographs and differences with other species of Phocoenidae are given. This is the second 'positive occurrence outside southern South American waters' and indicates a circumpolar distribution in subantarctic latitudes.

Gaskin, D.E., Smith, G.J.D., Watson, A.P., Yasui, W.Y. and Yurick, D.B. 1984. Reproduction in the porpoises (Phocoenidae): implications for management. *Rep. int. Whal. Commn* (special issue 6):135–48.
The population biology of *P. dioptrica* (southern South America and the New Zealand subantarctic), *P. sinus* and *P. spinipinnis* 'is best described as virtually unknown'. Age determination studies have not been carried out. Two females of 186 and 191cm [both were 186] were pregnant; two males 200 and 204 were physically mature [Brownell, 1975 says 'adult on basis of size']. There is no published information on life span. The authors wisely consider 'that a 48.4cm foetus... was 'near-term' should be treated with considerable caution'.

Lichter, A.A. and Hooper, A. 1984. *Guía para el reconocimiento de los cetáceos del Mar Argentino*. Fundación Vida Silvestre Argentina. 96pp.
P. 55 repeats some of unfounded data of the other guides, such as average length, 165cm, average weight, 50kg. Brief description of pigmentation; the male dorsal fin is not mentioned. The specimens for Argentina are cited. Drawing of the skull and pigmentation are given.

Minisean, S.M., Balcomb, K.C. and Foster, L. 1984. *The World's Whales: The Complete Illustrated Guide*. Smithsonian Books, Washington D.C. 224pp.
There is a very good illustration; the text states that only 10 specimens are known and gives the usual description, pointing out the gaps in our knowledge.

Barnes, L.G. 1985. Evolution, taxonomy and antitropical distributions of the porpoises (Phocoenidae, Mammalia). *Mar. Mammal Sci.* 1(2):149–65.
A definitive work on the Phocoenidae, this paper deals with the six extant species, history of names for the group, cranial characters and the fossil record. The characters of the two subfamilies are detailed; the author feels that *Phocoena dioptrica* should be moved from the Phocoeninae to the Phocoenoidinae, but not in the genus *Phocoenoides*, the only genera in the subfamily. He therefore forms a new genus, *Australophocaena* ('southern porpoise') for this species. Characters are given for *A. dioptrica*, which is both more primitive and more derived than *Phocoenoides dalli*; this mix 'indicates that they have probably evolved separately for a considerable period of time'. *A. dioptrica* appears to be an offshore animal and may be the antitropical counterpart of *P. dalli*. The pigmentation and skulls of the two are illustrated. There is a discussion of fossil relations within the Phocoenidae, which probably originated in the temperate latitudes of the North Pacific Ocean.

Bonner, W.N. and Laws, R.M. 1985. Marine mammals. pp. 401–57. *In:* W. Fischer and J.C. Hureau (eds.) FAO Species Identification Sheets for Fishery Purposes. Vol. 2:233–479. ***Southern Ocean (Fishing areas 48, 58 and 88) (CCAMLR Convention Area)*. FAO, Rome. Prepared and published with the support of the Commission for the Conservation of Antarctic Marine Living Resources.**
Pp. 414–5 and the key on p. 437 deal with this species. Description (but doesn't mention large dorsal fin of male), flippers may be white or black. Shows flipper stripe. 'Within the

Southern Ocean, only one specimen is known from South Georgia'. South Atlantic and New Zealand distribution given; distribution map.

Dawson, S. 1985. *The New Zealand Whale and Dolphin Digest.* Brick Row Publishing Co. Ltd, Auckland, NZ. 130pp.
Pp. 125–6. This is one of the smallest New Zealand cetaceans and the only porpoise found there. The description is good except for the very dark flipper stripe, that the flukes are sharply pointed, and that 'it eats both fish and squid'. They are known almost entirely from strandings; 'it may be decades before another stray Spectacled Porpoise turns up again on the New Zealand coast'.

Goodall, R.N.P. and Galeazzi, A.R. 1985. Review of the food habits of the cetaceans of the Antarctic and sub-Antarctic. pp. 566–72. *In:* W.R. Siegfried, P.R. Condy and R.M. Laws (eds.) *Fourth SCAR Symposium on Antarctic Biology – Nutrient Cycles and Food Chains.* Antarctic Nutrient Cycles and Food Webs. Springer-Verlag, Heidelberg. 700pp.
P. dioptrica has been found at or near the Antarctic Convergence. Although over 131 strandings or captures are known, only two stomachs have been examined and they were empty except for one nematode.

Piana, E., Orquera, L., Goodall, R.N.P., Galeazzi, A.R. and Sobral, A.P. 1985. Cetacean remains in Beagle Channel shell middens. Sixth Biennial Conference on the Biology of Marine Mammals, Vancouver, Canada, 22–26 November [Abstract] (unpublished). p.64.
Bones of *P. dioptrica* were found in shell middens at Túnel, on the north coast of the Beagle Channel, Tierra del Fuego, carbon-dated at 6,000 years before present.

Daniel, M. and Baker, A.N. 1986. *Collins Guide to the Mammals of New Zealand.* Collins, Auckland and London. 228pp.
P. 204 gives a short description of the species but does not mention the tall dorsal fin in the male. The colour description is that of Lahille. Distribution southern South America, Falklands, South Georgia, Kerguelen, Macquarie and Auckland Islands. Most strandings are singles; nothing is known about its biology or behaviour.

Brownell, R.L., Jr., Findley, L.T., Vidal, O., Robles, A. and Manzanilla, N.S. 1987. External morphology and pigmentation of the vaquita, *Phocoena sinus* (Cetacea: Mammalia). *Mar. Mammal Sci.* 3(1):22–30.
P. 23 mentions only that *P. dioptrica* has been placed in a separate genus, *Australophocaena*.

Goodall, R.N.P. and Galeazzi, A.R. 1987. Strandings on the coasts of the province of Santa Cruz, Argentina – a preliminary look. Abstracts, Seventh Biennial Conference on the Biology of Marine Mammals, 5–9 December 1987, Miami, Florida, (unpublished). p.26.
Of 58 specimens collected in beach surveys of the southern coasts of the province in 1983 and 1986, only four were of this species, two cranial and two postcranial. This abstract is repeated in 1988: Resúmenes, III Reunión de Trabajo de Especialistas en Mamíferos Acuáticos de América del Sur, Montevideo, Uruguay, 25–30 July 1988. p. 34.

Guiler, E.R., Burton, H.R. and Gales, N.J. 1987. On three odontocete skulls from Heard Island. *Sci. Rep. Whales Res. Inst., Tokyo* 38:117–24.
The authors report a cranium without teeth or mandibles found on the beach of Heard Island. Although they determine it as a specimen of *Phocoena spinipinnis*, the skull

illustrated (p. 120) is clearly of *A. dioptrica* (see Brownell *et al.*, 1988). The finding of this cranium, TM A 1411, extends the distribution of the spectacled porpoise to the southern Indian Ocean, and it is the second specimen from south of the Antarctic Convergence.

Purgue, A. 1987. Facial complex description of the spectacled porpoise *Phocoena dioptrica* Lahille 1912. Mammalia: Cetacea (unpublished). 19pp.[1]
The facial anatomy of *P. phocoena* has been well described. This paper gives a careful description of the nasal passages, diveraticula, nasal musculature and melon of a 205cm male *P. dioptrica* found at 42°47'S 65°00'W near Puerto Madryn, Chubut, Field number 850802. The animal was physically sub-adult (on the basis of epiphyseal fusion). Excellent illustrations of the nasal passages and colour pattern of the head. [This animal is also reported by Pagnoni and Saba, 1989, below.]

Goodall, R.N.P., Galeazzi, A.R., Leatherwood, S., Miller, K.W., Cameron, I.S., Kastelein, R.K. and Sobral, A.P. 1988a. Studies of Commerson's dolphins, *Cephalorhynchus commersonii*, off Tierra del Fuego, 1976–1984, with a review of information on the species in the South Atlantic. *Rep. int. Whal. Commn* (special issue 9):3–70.
P. 10. 'During the first few years of the Tierra del Fuego stranding salvage program, spectacled porpoises ... were found most often, but... after eight years, the collection included more specimens of Commerson's dolphins than any of the other 20 species of small cetaceans known to date from subantarctic waters of South America'.

Goodall, R.N.P., Galeazzi, A.R. and Lichter, A.A. 1988b. Exploitation of small cetaceans off Argentina 1979–1986. *Rep. int. Whal. Commn* 38:407–10.
Some of the many beach specimens of *P. dioptrica* may have died in shore-based gillnets. Known take was two from 1976–1979 and three from 1979–1980; most causes of death are unknown.

Goodall, R.N.P., Norris, K.S., Galeazzi, A.R., Oporto, J.A. and Cameron, I.S. 1988c. On the Chilean dolphin, *Cephalorhynchus eutropia* (Gray, 1846). *Rep. int. Whal. Commn* (special issue 9):197–257.
One paragraph on p. 202 briefly describes the controversy over the identity of *Phocoena obtusata* and indicates that Philippi's specimen in Santiago is really a specimen of *Cephalorhynchus eutropia*. *P. obtusata* is included under the latter species in the Synonymy on p. 206.

Goodall, R.N.P., Sobral, A.P., Labal de Vinuesa, M. and Cameron, I.S. 1988d. On *Phocoena obtusata*, with a comparison of certain diagnostic characters in South American phocoenids and the genus *Cephalorhynchus*. *Rep. int. Whal. Commn* (special issue 9):259–76.
The authors review the background on the strange species *Phocoena obtusata* described by R.A. Philippi in 1893, which some cetologists believed to be a specimen of *A. dioptrica* (thus extending the distribution to central Chile) and others a species of *Cephalorhynchus*. On a visit to Santiago, the authors found the specimen, took radiographs of the osseous material within the dried, varnished skin and compared them to *A. dioptrica*, *P. spinipinnis*, *C. commersonii* and *C. eutropia*. The flipper bones show without doubt that this specimen is a *Cephalorhynchus*, most probably *C. eutropia*. Drawings of pigmentation and flippers, photographs of the specimen, tracings of appendages, and graphs compare the four species.

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[1] Available from R.N.P. Goodall.

International Whaling Commission. 1988. Report of the sub-committee on small cetaceans. *Rep. int. Whal. Commn* 38:117–25.
P. dioptrica may be taken incidentally in nets in Argentina. The editor draws attention to the proposed placement of this species in a new genus, *Australophocaena* (Barnes, 1985).

Lichter, A.A. and Goodall, R.N.P. 1988. Argentina. Progress report on cetacean research, June 1984 to April 1987. *Rep. int. Whal. Commn* 38:173–6.
During this time span, six new specimens of *P. dioptrica* were collected on Tierra del Fuego and four in the Province of Santa Cruz, Argentina.

Brownell, R.L., Jr., Heyning, J.E. and Perrin, W.F. 1989. A porpoise, *Australophocaena dioptrica*, previously identified as *Phocoena spinipinnis*, from Heard Island. *Mar. Mammal Sci.* 5(2):193–5.
The authors show that the cranium from Heard Island (Guiler *et al.*, 1987) is a specimen of *A. dioptrica*, giving the skull characteristics of this species and differences with *P. spinipinnis*. From the photographs, they find that the rostral length was incorrectly taken and they indicate that the posterior teeth in these species are in a shallow alveolar goove and easily lost, giving low tooth counts. They review the distribution of both species; that of *A. dioptrica* is 'the cool-temperate waters of the southern ocean in subarctic latitudes'.

Goodall, R.N.P. 1989. The lost whales of Tierra del Fuego. *Oceanus* 32(1):89–95.
This paper gives a description of the study of strandings in Tierra del Fuego, begun in 1974 with skulls of this species. By 1989, the *A. dioptrica* collection had 136 crania (20% of total cetaceans) and 103 postcranial skeletons. Only one animal was fresh and pigmentation could be seen on only two or three others. Sex could be determined for only five males and four females. Formerly considered coastal, the species is found near offshore islands and may be more pelagic than supposed; coastal species usually do not strand and this one strands often.

Lichter, A.A. and Goodall, R.N.P. 1989. Argentina. Progress report on cetacean research, May 1987 to April 1988. *Rep. int. Whal. Commn* 39:169–71.
P. 170 lists seven new specimens from Tierra del Fuego.

Pagnoni, G. and Saba, S. 1989. New record of the spectacle porpoise. *Mar. Mammal Sci.* 5(2):201–2.
This note reports a 202cm, 115kg male specimen from Puerto Madryn, Chubut, Argentina (CNP 116), giving external measurements and an age of six years by E. Crespo. This paper somehow missed the review process. In addition to misspellings (Chabut, spectacle), it claims that although several specimens were reported since 1889 [the species was only discovered in 1912], this is the first description of a specimen south of Río Santiago, and that it is the fifth adult [although Purgue, 1987 says the vertebral epiphyses were unfused] and second male found since the holotype was described. Most of the papers listed above are ignored; the only references are Lahille, 1912; Bruch, 1916 [listed in text but not in the references], Praderi, 1971 and Brownell, 1975.

Goodall, R.N.P. 1990. Notas sobre la biología de la marsopa de anteojos, *Australophocaena dioptrica*. *Reun. Trab. Esp. Mamif. Acuat. Am. Sud [Abstracts only]* IV:28. [In Spanish].
A summary of the unpublished version of Goodall, 1995 (this volume).

Goodall, R.N.P., Iñiguez, M. and Sutton, P. 1990a. Capture of small cetaceans in gillnets off the province of Santa Cruz, Argentina. Abstracts, IWC Symposium on Mortality of Cetaceans in Passive Nets and Traps, La Jolla, California, October 1990 (unpublished). p.13.
Bones of this species were found in localities where fishing takes place with fixed gillnets; they may have been taken in nets. Specimens of *A. dioptrica* found on the beach could have come from passive nets set from shore.

Goodall, R.N.P., Schiavini, A.C.M. and Fermani, C. 1990b. Mortality of small cetaceans in nets off Tierra del Fuego, Argentina. Abstracts, IWC Symposium on Mortality of Cetaceans in Passive Fishing Nets and Traps, La Jolla, CA, 12–20 October 1990. p.12.
Taken occasionally in gillnets set from shore, second to *Cephalorhynchus commersonii* in numbers found.

Kasamatsu, F., Joyce, G.G., Ensor, P. and Mermoz, J. 1990. Current occurrence of cetacea in the Southern Hemisphere; results from the IWC/IDCR Southern Hemisphere minke whale assessment cruises, 1978/79–1987/88. Paper SC/42/O 15 presented to the IWC Scientific Committee, June 1990 (unpublished). 77pp.
[Not seen] During IWC/IDCR Southern Hemisphere Minke Whale Assessment Cruises from 1978/79 to 1987/88, five sightings (11 animals) were made from 54° to 59°S, south and east of New Zealand and south of South America. Sea surface temperatures ranged from 5.5–9.5°C. School size ranged from 1–2 and a calf was seen with two adults (IWC, 1991).

Capozzo, H.L. and Junín, M. 1991. Estado de conservación de los mamíferos marinos del Atlántico Sudoccidental. Mares Regionales: Informes y estudios del Programa de Mares Regionales del PNUMA no. 138 (UNEP). 250pp. [In Spanish].
P. 190 shows a formerly unpublished photograph of the front portion of a spectacled porpoise from the photographic archives of MACN, with no other details. [After some research H.P. Castello (pers. comm.) found that the animal, which, from other photos, appears to be a large female, was found by people from a school in Mar del Plata, Argentina. The photograph is by Martín Duellio Jurado, who sent it to the museum in Buenos Aires; the envelope is stamped 31 December 1925. There is no other information on this specimen. MACN has three photos of the body and three of the skull.]

Crespo, E. 1991. Marsopa de anteojos *Australophocaena dioptrica* (Lahille, 1912). pp. 31–2. *In:* H.L. Capozzo and M. Junín (eds.) *Estado de Conservación de los Mamíferos Marinos del Atlántico Sudoccidental. Informes y Estudios del Programa de Mares Regionales del PNUMA. No. 138.* UNEP. 250pp. [In Spanish].
A. dioptrica is in CITES Appendix II. It is protected in Argentina but there is little control. Distribution; mention of the 202cm 115kg male from Puerto Madryn, which had six GLGs; no studies were done on food or sexual maturity. The species has been taken in beach nets in southern Patagonia and Tierra del Fuego. It might be killed for crab bait [although it does not seem common in that area] but amounts are unknown. Population abundance estimates are needed. Its behaviour is unknown and the species has not been kept in captivity. There is a list of common names in several languages. [The 202cm specimen is the same porpoise described by Pagnoni and Saba, 1898.]

International Whaling Commission. 1992. Report of the Scientific Committee, Annex G. Report of the sub-committee on small cetaceans. *Rep. int. Whal. Commn* 42:178–234.
Two documents were reviewed. Kasamatsu and Joyce reported five sightings (11 animals) during IWC/IDCR Southern Hemisphere Minke Whale Assessment Cruises from 54° to

59°S south and east of New Zealand and south of South America. Data in Goodall (1990a) are summarised. The early specimens were collected by fishermen and there is an incidental take in gillnets.

Klinowska, M. (ed.). 1991. *Dolphins, Porpoises and Whales of the World. The IUCN Red Data Book.* IUCN, Gland, Switzerland and Cambridge, UK. viii + 429pp.
A good review (without including Goodall, 1990) which points out some new aspects, such as 'None of the information on population, stocks or biology required for conservation and management is available for any part of the range. Research is urgently needed .... It is not clear ... whether the island populations are isolated ... or whether there is some contact between them'. The beach collections in Tierra del Fuego show how 'perceptions of the relative abundance ... can be altered in a short time, once recorders are present in the right place'. This porpoise is in Appendix II of CITES. While not as rare as once thought, 'it is certainly among the least known'. No specimens are known to have been kept in captivity. [The sightings she quotes for Goodall and Polkinghorn (1979) were those for *P. spinipinnis,* not this species.]

Schiavini, A.C.M. and Goodall, R.N.P. 1991. Growth structures on the teeth of spectacled porpoise *Australophocaena dioptrica.* Abstracts, Ninth Biennial Conference on the Biology of Marine Mammals, 5–9 December 1991, Chicago, IL, (unpublished). p.61.
Tooth structures were formerly undescribed for this species. GLGs were examined for 25 animals from Tierra del Fuego, 5 females, 5 males and 15 of unknown sex. In females there is a change in layering after the second or third GLG, suggesting an early sexual maturation, as in other porpoises. No gonads are available for this species. A 183cm female with 8 GLGs was found in a net with a neonate. The maximum number of GLGs was 13 [evidently a misprint for 8] in females and 6 in males.

Lichter, A.A. (ed.). 1992a. *Huellas en la Arena, Sombras en el Mar. Los Mamíferos Marinos de la Argentina y la Antártida.* Ediciones Terra Nova, Buenos Aires. 288pp.
In Spanish. Pp. 30–31 with illustration by G. Harris. Few specimens known until 1975, it has now been found from Uruguay to near Cape Horn, from the eastern Strait of Magellan to South Georgia, the Auckland, Heard and Macquarie Islands, with sightings near Auckland and in the Drake Passage. Description of size, pigmentation, captures; stomach contents unknown.

Lichter, A.A. (ed.). 1992b. *Tracks in the Sand, Shadows on the Sea. Marine mammals of Argentina and Antarctica.* Ediciones Terra Nova, Buenos Aires. 288pp. [English translation].
Translation of the above.

Pinedo, M.C., Weber Rosas, F.C. and Marmontel, M. 1992. *Cetáceos e Pinípedes do Brasil: uma revisao dos registros e guía para identificaçao das espécies.* UNEP/FUA, Manaus. 213pp. [In Portuguese].
Pp. 150–152. This species is included as a possible species for Brazil. The review of size, pigmentation, distribution, etc. is the usual from other sources.

Massoia, E. and Chebez, J.C. 1993. *Mamíferos Silvestres del Archipiélago Fueguino.* L.O.L.A., Buenos Aires. 261pp.
In Spanish. P.168, description, P.169, illustration, a mixture of animals, with Lahille's light flipper and Wilkins' flipper stripe. Deals mostly with distribution of specimens from

the Province of Buenos Aires and Tierra del Fuego. The species figures in Appendix II of CITES. Several caught in nets (citing Goodall papers). Nothing on biology or other data.

Rosel, P.E., Haygood, M.G. and Perrin, W.F. 1993. A molecular phylogeny for the Phocoenids: conflict and congruence with morphology. Abstracts, Tenth Biennial Conference on the Biology of Marine Mammals. 11–15 November 1993, Galveston, Texas, (unpublished). p.92.

The systematic relationships among the six species of Phocoenidae were investigated through mitochondrial DNA. These show a close relationship between *P. spinipinnis* and *P. sinus* and an association of these with *A. dioptrica*. This 'is not in concordance with a recent morphological reclassification of *A. dioptrica* and bears further study'. [A revised version of the full paper is in press in *Mol. Phylogen. Evol.* 4(3)].

Crespo, E.A., Corcuera, J.F. and López Cazorla, A. 1994a. Interactions between marine mammals and fisheries in some coastal fishing areas of Argentina. *Rep. int. Whal. Commn* (special issue 15):269–81.

Between Golfo San Matías and Golfo San Jorge, bottom and mid-water trawls for shrimp and hake may capture this species, among others. Mortality is low, but fishing effort is high and increasing. In Santa Cruz province south of Puerto Deseado, gillnets used for *róbalo* take this species; in Tierra del Fuego, gillnets for *róbalo*, hake and silverside trap spectacled porpoises.

Crespo, E.A., Reyes, L., Koen, M. and García, N. 1994b. Interacciones entre mamíferos marinos y pesquerías en el litoral norpatagónico. *An. Reun. Trab. Esp. Mamif. Acuat.* IV:89–95. [In Spanish].

Fishing takes place with 130–140 ships operating in waters off Chubut and northern Santa Cruz, Argentina, with bottom and mid-water trawl nets for fish, squid and shrimp. If the more valuable shrimp are found, fish are discarded overboard. The authors cite the capture of *A. dioptrica* without details of specimens. The species is also taken in passive nets in Tierra del Fuego.

Crespo, E.A., Schiavini, A.C.M., Pérez Macri, G., Reyes, L. and Dans, S. 1994c. Estudios sobre determinación de edad en mamíferos marinos del Atlántico sudoccidental. *An. Reun. Trab. Esp. Mamif. Acuat.* IV:31–9. [In Spanish].

P. 39 describes the methods used to study the teeth of one animal from CNP and 25 from Tierra del Fuego (Schiavini and Goodall, 1991). The prenatal dentine is homogeneous, the neonatal line clearly visible. The GLGs in postnatal dentine have a wide dark band and a narrow light band. Some teeth have many accessory bands which make reading difficult. The width is reduced in females after the second or third GLG. GLGs could not be read in cementum. GLGs varied between 2 and 13 [misprint for 8] in females and 6 in males.

Dalla Rosa, L., Secchi, E.R. and Zerbini, A.N. 1994. Variaçao nos itens alimentares de Orca, *Orcinus orca*, no sul do Brasil. Abstracts, Anais da 6a Reuniao de Trabalho de Especialistas em Mamíferos Aquáticos da América do Sul, Florianópolis, Brasil, 24–28 October 1994 (unpublished). p.73. [In Portuguese].

Remains of two Phocoenids, an adult and a foetus, were found in stomach contents of a 566cm male killer whale stranded on 2 October 1993 at Barra do Chui (33°45′S). [The only Phocoenids in these waters are *A. dioptrica* and *P. spinipinnis*.]

Goodall, R.N.P., Schiavini, A.C.M. and Fermani, C. 1994. Net fisheries and net mortality of small cetaceans off Tierra del Fuego, Argentina. *Rep. int. Whal. Commn* (special issue 15):295–304.
The authors have recalculated exploitation data from earlier papers. Only four *A. dioptrica* were positively taken in nets, but at least another 30 were probably taken in a 15 year period.

Reeves, R.R. and Leatherwood, S. (eds.). 1994. *Dolphins, Porpoises, and Whales: 1994–1998 Action Plan for the Conservation of Cetaceans.* IUCN, Gland, Switzerland. 92pp.
P. 33. The review: 'This small porpoise has a fairly broad distribution in subantarctic and cold temperate waters of the Southern Ocean. The degree of mixing among populations that occur near large islands and island groups ... is uncertain, as are the degrees of mixing between the groups and the population(s) along the South American mainland .... Sightings made far offshore between 54° and 59°S latitude ... suggest that some movement across expanses of open ocean may occur. These porpoises are very poorly known, and their status is uncertain in all areas. Some mortality occurs in fishing gear ... but its scale relative to population abundance and rate of increase is completely unknown'.

Curry, B.E., Mead, J.G. and Purgue, A.P. 1994. The occurrence of calculi in the nasal diverticula of porpoises (*Phocoenidae*). *Mar. Mammal Sci.* 10(1):81–6.
Biomineral concretions or calculi were found in the nasofrontal and posterior nasal sacs of three harbour porpoises, one Burmeister's porpoise, four Dall's porpoises, and one spectacled porpoise. The specimen of spectacled porpoise is the same animal reported on by Pagnoni and Saba, 1989.

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Age Determination Workshop

Harbour porpoise in the Bay of Funday, Canada.
Photo courtesy of John Y. Wang, Porpoise Rescue Program

Report of the Harbour Porpoise Age Determination Workshop, Oslo, 21–23 May 1990

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ABSTRACT

A workshop on age determination in harbour porpoises (*Phocoena phocoena*) was held in Oslo, Norway, 21–23 May 1990. During the workshop, the principles of formation of dental layers were reviewed, as were the growth layer patterns in odontocete teeth and evidence for interpreting the layering patterns as annual. Specific information on how to estimate age in harbour porpoises, identify anomalous mineralisation patterns and use the teeth for discriminating stocks was also presented. An experiment was conducted to test for within- and between-reader variability in age estimates in a sample of teeth provided at the workshop. The teeth were read by three people with experience and four people with little or no experience in harbour porpoise age estimation. An analysis of variance of the experimental results showed more variation for inexperienced readers than for experienced and more for older animals than younger. For the experienced readers, the reliability of age reading for animals less than five years of age was high. The pooled standard deviation was in this case 0.32yrs, which was made up of contributions from pure error, between-section and between-reader variability, in increasing order of importance. This report includes all presentations, results of the experiment and a series of annotated photos of harbour porpoise tooth sections.

INTRODUCTION

The harbour porpoise, *Phocoena phocoena* (Linnaeus, 1758), is common in Scandinavian waters. Little attention has been paid to this species, despite the severe reduction in the abundance of porpoises in the North and Baltic Seas reported by several authors (cited by

Gaskin, 1984). When the Scientific Committee of the International Whaling Commission (IWC) assessed the status of porpoises in 1983, the sub-committee on small cetaceans concluded that it is possible that a significant population decline has occurred in the Baltic and North Sea region and recommended that research be initiated in these areas (IWC, 1984). This concern has been reiterated more recently (e.g. IWC, 1992).

In order to stimulate research on harbour porpoise, the European Cetacean Society (ECS) established a Working Group on this species (Broekema and Smeenk, 1987) and arranged a workshop on the harbour porpoise in Cambridge, England, November 1988, aimed at standardising the sampling and measuring procedures for examination of stranded or incidentally caught porpoises (Kinze, 1989).

In 1988, the World Wide Fund for Nature (WWF) funded a three year programme of harbour porpoise research in Scandinavia, with individual projects in Denmark, Sweden and Norway. Since 1989, porpoise research in Norway has been coordinated by the Norwegian Marine Mammal Research Programme, 1989–1993. Examination of porpoises from incidental catches and strandings are important elements of research in Scandinavia. Analysis of growth and reproductive data and further studies of population biology require a reliable method for age estimation of the animals.

Although there have been previous studies of harbour porpoise age determination in Scandinavia (Grue Nielsen, 1972), this early work was not continued. The Norwegian Institute for Nature Research (NINA) therefore developed a technique for processing porpoise teeth, based on modifications of the techniques routinely used for the age determination of terrestrial mammals (Kvam, 1995). The techniques applied by NINA are, in principle, similar to the methods used at the Sea Mammal Research Unit (SMRU) in the United Kingdom and at the Southwest Fisheries Science Center (SWFSC) in the USA, where age estimation of harbour porpoises has been a matter of routine for some years.

In order to further improve the methods of age estimation of harbour porpoises, this workshop was convened in Oslo, 21–23 May 1990. It was hosted by NINA and funded by the Norwegian Council for Fisheries Research through the Norwegian Marine Mammal Research Programme.

The aims of the workshop were to share the knowledge of scientists experienced in age estimation, to provide training under the supervision of the experienced scientists and to make the techniques available to institutions where porpoise research is now evolving. A further and equally important objective was to assess and improve reliability in harbour porpoise age determination. This report presents the results from the workshop, including the presentations, experimental results and a series of annotated photographs of harbour porpoise tooth sections. These photographs show how teeth can develop in different age classes and illustrate the importance of obtaining good on-centre tooth sections.

The Workshop adopted the terminology agreed at the International Conference on Determining Age of Odontocete Cetaceans and Sirenians held in September 1978 in La Jolla, USA (Perrin and Myrick, 1980).

SUMMARY OF PRESENTATIONS

Langvatn (NINA) reviewed the present status of knowledge on the principles in formation and zonation of dentine and cementum in mammalian teeth. He summarised different approaches to age determination and the evaluation of age distributions in mammal populations. He also addressed the question of the biochemical mechanisms underlying the mineralisation of bone and teeth. The intermittent deposition patterns in incremental lines in teeth were discussed in relation to the hypothetical influence of hormone systems such as PTH, calcitonin and Vitamin D. In most areas our knowledge of the biochemistry involved in the formation of zones in mammalian teeth is poor, making it difficult to establish an objective rationale for interpreting the zonation. Agreed and consistent age characters are only available for some mammal species and even then, mainly on an empirical basis. In conclusion he emphasised that experimental work is necessary to reveal the functional relationships between environmental cycles, stress, the physiological cycles of the animals and the biochemical processes responsible for the incremental lines observed in teeth. Only then can a proper understanding and interpretation of age characters in mineralised tissues be achieved.

Hohn (SWFSC) reviewed the structures observed in odontocete teeth and similarities and differences between dental growth layers in dolphins, porpoises and whales. She also discussed the similarities and differences between odontocete teeth and teeth from terrestrial mammals in the context of age determination. Most notably, odontocete teeth are generally homodont, there are no deciduous teeth and dentine is usually relied upon more than cement to obtain age estimates; in terrestrial mammals, cement is often used exclusively.

Lockyer (SMRU) reviewed the evidence for the annual deposition rate of GLGs (growth layer groups) in odontocete teeth, referring to data for bottlenose dolphins (*Tursiops truncatus* – e.g. Myrick and Cornell, 1990) and killer whales (*Orcinus orca* – e.g. Myrick *et al.*, 1988) as well as referring to her own studies of captive short-finned pilot whales, *Globicephala macrorhynchus*, which had been time-marked throughout life with tetracycline medication. Tetracycline leaves a permanent fluorescent residue in the teeth at the time of administration (later visible in reflected ultraviolet light), which can then be used to identify specific time periods in the tooth and calculate incremental deposition rates of tissue. The methods used to carry out such studies were described.

Da Silva (University of Cambridge) presented preliminary information on an age estimation study in the boto or Amazon River dolphin, *Inia geoffrensis*, from Brazil, in order to provide a comparison of the layering pattern in porpoise teeth with those from a different family and completely different environment. Problems in determining the best method for preparing teeth from *Inia* were similar to those encountered for other species at the beginning of such studies.

Hohn discussed the interpretation of the layering patterns in porpoise teeth, i.e. what constitutes a GLG, how to distinguish a GLG boundary layer from an accessory layer and ages at which errors are most likely to occur. The use of the absolute thickness of GLGs is a useful guide for correctly identifying them, as is the relative size of adjacent GLGs. About mid-way through the first GLG, there is often a distinct accessory layer that may incorrectly be interpreted as the boundary between the first and second GLGs. This error may be reduced by noting where along the length of the tooth the layer meets the edge of the tooth at the cement. The accessory layer meets this point about midway between the base of the neonatal line and the bottom of the tooth (if the animal is greater than 2yrs old), representing a tooth that has erupted only partially. The first GLG extends almost the full length of the tooth. Some difficulty in interpreting GLGs also seems to occur at about age 3–4, when marker lines and unusual staining within the GLGs, and an increase in thickness of the more recently deposited GLG, are more likely to be found. Finally, the narrow layers around the pulp cavity in old animals are thought to be GLGs and should be counted for age estimation.

Hohn found that harbour porpoise teeth from California, the Bay of Fundy and the UK are different with respect to the clarity of boundary layers and the stainability of those layers (lightly or darkly stained). These characters, as well as others, may be useful in broadly distinguishing stocks.

Lockyer reviewed work, pioneered and being carried out by Myrick at the Southwest Fisheries Science Center (SWFSC), on the investigation of mineralisation anomalies in teeth as a means of identifying stress (however caused) during the animal's lifetime (Myrick, 1988). Examples and the implied causes of stress were presented, including 'parturition' lines (Klevezal' and Myrick, 1984), hypocalcified lines associated with the *El Niño* phenomenon off Peru (Manzanilla, 1989) and 'suckling' lines (Bengtson, 1988) in dentine. Stress was identified as being linked with a number of factors including reproduction, feeding, captivity and fishery pressure.

Five major categories of mineralisation anomaly were defined: pulp stones, marker lines, mineralisation interference, dentinal resorption and cemental disturbance. These categories are broadly based on the criteria used by Myrick (1988).

Lockyer referred to recent studies on mineralisation anomalies in pilot whale teeth, using examples from this species and also from harbour porpoise to demonstrate the different types of anomaly. She presented preliminary results of an investigation on approximately 50 porpoise teeth from each of the three locations: United Kingdom, Bay of Fundy (Canada) and southern California. Comparisons between the regions, allowing for differences in age and sex, demonstrated that there were significant variations in the incidence of certain types of anomalies. In particular dentinal resorption and mineralisation interference had comparatively high levels of incidence in California while marker lines were more prominent in Canadian teeth. The interpretation of these findings is at present uncertain, but may indicate either genetic stock differences or different types and levels of environmental stress.

Hohn also described the methods for preparing sections of teeth at the SWFSC. To obtain stained thin sections, teeth are decalcified in a commercial decalcifying agent (RDO), sectioned on a freezing microtome to 26μm, stained in haematoxylin, 'blued' in a weak ammonia solution and mounted in 100% glycerin. For harbour porpoises, two teeth are prepared for each specimen: one cut in the traditional plane (parallel to the mandible) so that the sections are spatulate in appearance; and one in the bucco-lingual plane resulting in sections that appear more like dolphin teeth. Age estimates are the same for each orientation, although at times the GLGs in one orientation, usually the 'dolphin' cut, are clearer. The dolphin cut also has the advantage of providing more depth of tooth for obtaining a good section. Hohn emphasised the importance of producing mid-longitudinal (on-centre or central) cuts to obtain the most reliable age estimates. When teeth are bent or twisted, whichever orientation of cut is likely to section the largest central area of the pulp cavity should be used.

For comparison, Kvam (NINA) outlined the methods used at NINA for preparing sections of harbour porpoise teeth. The teeth are decalcified in 5% HNO_3 for five hours, then cut into 20μm thin sections using a freezing microtome. The sections are cut in a plane parallel to the mandible and the thin sections are stained in *Mayers* haemalun for 45 minutes before mounting. The laboratory procedures followed at NINA and the SWFSC are in many aspects identical.

AN EXPERIMENT TO ASSESS THE RELIABILITY OF HARBOUR PORPOISE AGE DETERMINATION

Experimental design

In order to assess the extent and sources of variation in harbour porpoise age determination, an experiment was set up during the workshop. The teeth used for the experiment were all from animals incidentally caught in Norwegian coastal fisheries in the period May-July 1988, collected as a part of WWFs Project Porpoise and processed by NINA as outlined by Kvam. Five series (coded A-E) of tooth sections (coded A1, A2,..B1, B2.., etc.) were arranged in sets. The teeth were read by a group of three experienced age readers (A. Hohn, T. Kvam and C. Lockyer) and a group (H. Aarefjord, M. Addink, S. Kaarstad and M. Kingsley) with little or no previous experience. Three of the series of teeth (B, C, D) comprised replicate teeth from the same 21 animals, while the two other series were from different animals. The three replicate series were cut to thicknesses of 15(B), 20(C) and 30(D)μm. The two non-identical series were included to minimise the risk of remembering from one series to another.

Each of the experienced readers read each of the five series once and one of the three identical series a second time i.e. four age estimates were produced by each reader for each animal in the replicated series. Two of the inexperienced readers read each of the replicate series four times prior to the workshop. The other two inexperienced readers read teeth only during the workshop – one in a design identical to the experienced readers while the other completed only two of the four sets of readings. The numbers of readings in each series are shown in Table 1; the readings in both groups totalled 882 repetitive age estimates of 21 different animals.

Table 1

The number of readings of series B, C and D. Each of these series was a duplicate, containing tooth sections from 21 different harbour porpoises.

	Number of readings of each series						
	Experienced readers			Inexperienced readers			
Series	1	2	3	1	2	3	4
B	2	1	1	4	4	1	1
C	1	2	1	4	4	2	1
D	1	1	2	4	4	1	0

Results

The analysis of results focussed on the replicate series (B, C and D).

Experienced readers

Table 2 (3-way ANOVA: reader × series × animal) shows that most of the variation of the age estimates was, as one would expect, between animals. The standard deviation (SD) of the pure error was estimated as 0.40 (i.e. given the tooth section, independent replicate readings by one experienced reader will vary with SD of 0.4yrs). Most of this variation was, however, due to two old animals in the sample (see animals no. 10 and 13 in Table 3; Figs 1, 3 and 4). This was also true for the between-reader variation.

The mean age (and SD) for all readings for an animal are given in Table 3. For 11 of the 21 animals, there was no within- or between-reader variation in age estimates. These 11 animals ranged from 1–4yrs of age. Of the remaining 10 animals, the largest variation occurred in the two oldest animals (no. 10 – mean age 8.6yrs, range = 7–10yrs; and no. 13 – mean age 13.4yrs, range = 11–16yrs). For six of the 10, much of the variation resulted from rounding error introduced when animals were placed in the nearest whole age class (e.g. 1.9 being rounded to 2) for analysis. These rounded age classes were not necessarily those intended by the reader, resulting in increased within- and between-reader variation.

Table 2

Analysis of variance table for the 3-way layout with model Age = Reader + Series + Animal + Reader x Animal, calculated from glm of MINITAB (1989).

Source	DF	Adj.SS	Adj.MS
Experienced readers			
Reader	2	2.79	1.40
Series	2	0.56	0.28
Animal	20	2062.55	103.13
Rdr x animal	40	20.81	0.52
Error	184	29.86	0.16
Total	248		
Inexperienced readers			
Reader	3	33.59	11.20
Series	2	7.07	3.53
Animal	20	1195.80	59.79
Rdr x animal	60	171.35	2.86
Error	545	223.65	0.41
Total	630		

Table 3

The number of age estimates and the mean age and standard deviation (SD) for each animal in the experimental sample. Estimates were made by two groups of readers: those with experience and those with little or no experience.

Animal number	Experienced readers			Inexperienced readers		
	No. of readings	Mean age	SD	No. of readings	Mean age	SD
1	12	2.00	0.00	30	2.00	0.00
2	12	3.00	0.00	30	2.97	0.18
3	12	1.00	0.00	30	1.00	0.00
4	12	1.00	0.00	30	0.97	0.49
5	12	0.75	0.45	30	0.27	0.45
6	12	2.33	0.49	30	1.00	1.26
7	12	2.00	0.00	30	1.87	0.43
8	12	1.00	0.00	30	1.07	0.37
9	12	3.00	0.00	30	2.27	0.83
10	12	13.42	1.51	30	6.23	2.81
11	12	1.92	0.67	30	1.17	0.38
12	12	0.92	0.29	30	0.40	0.50
13	10[1]	8.60	0.97	29[2]	6.45	1.48
14	12	2.00	0.00	30	1.77	0.57
15	12	4.00	0.00	30	3.84	0.37
16	11[2]	1.18	0.60	30	0.47	0.57
17	12	1.08	0.29	30	1.57	0.57
18	12	1.58	0.52	30	1.63	0.56
19	12	1.00	0.00	30	1.10	0.31
20	12	1.00	0.00	30	1.00	0.00
21	12	2.58	0.52	30	2.13	0.35

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[1] Tooth section from this animal were rejected twice due to poor quality.

[2] Tooth sections from this animal were rejected once due to poor quality.

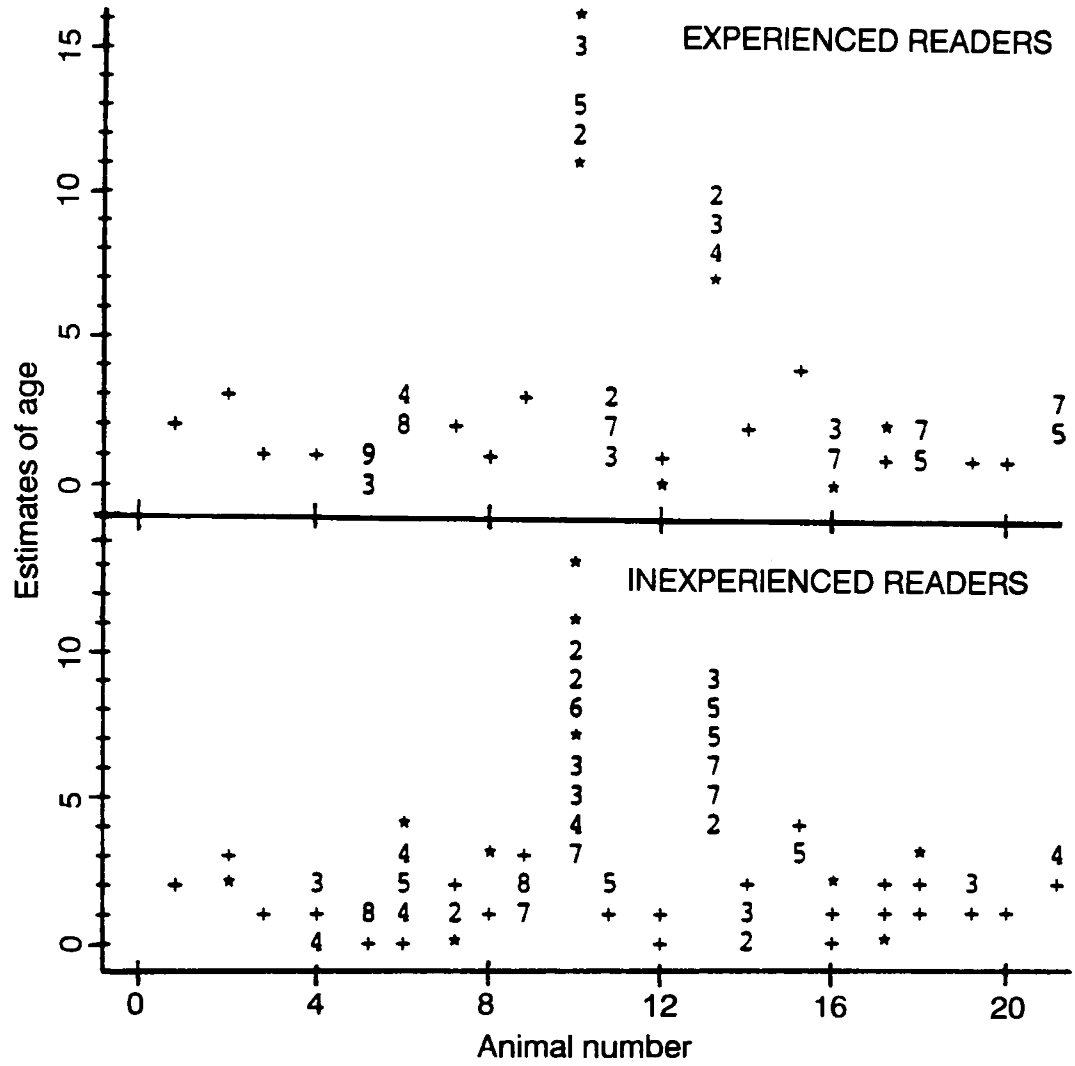


Fig. 1. Repetitive age estimates on tooth sections from 21 animals (harbour porpoise). The numbers in columns represent the number of times a particular age was estimated for an animal. An '*' represents one reading, a '+' more than nine readings. Complete consensus in estimates between readers and series is designated by a single '+'. The upper figure shows estimates made by three experienced readers (a total of 12 repetitive readings per animal except for animals 13 and 15). The lower figure shows estimates made by four inexperienced readers (a total of 30 repetitive readings per animal).

For the additional two animals, the within-reader error was low while there was as much as a year difference between readers. Rounding errors were also part of the apparent within- and between-reader error for these two specimens.

The pooled SD of 0.49yrs over series and experienced readers obtained from Table 3, comprised SD = 1.3yrs for the two old animals and SD = 0.32yrs for animals less than five years of age.

Table 3 shows that the variability between readers was mainly due to the two old animals. The between-reader variability dominates the pure error and the between-series variability. The pooled SD of 0.32yrs for animals <5yrs showed that the reliability of age readings by the experienced readers was high for these age classes.

The within-reader overall mean age estimates (pooled over all readings for all animals) showed close agreement, differing by only 0.3yrs (from 2.5–2.8yrs of age) between readers and 0.1yrs (2.57–2.67yrs of age) between series.

(Text continues on page 479)

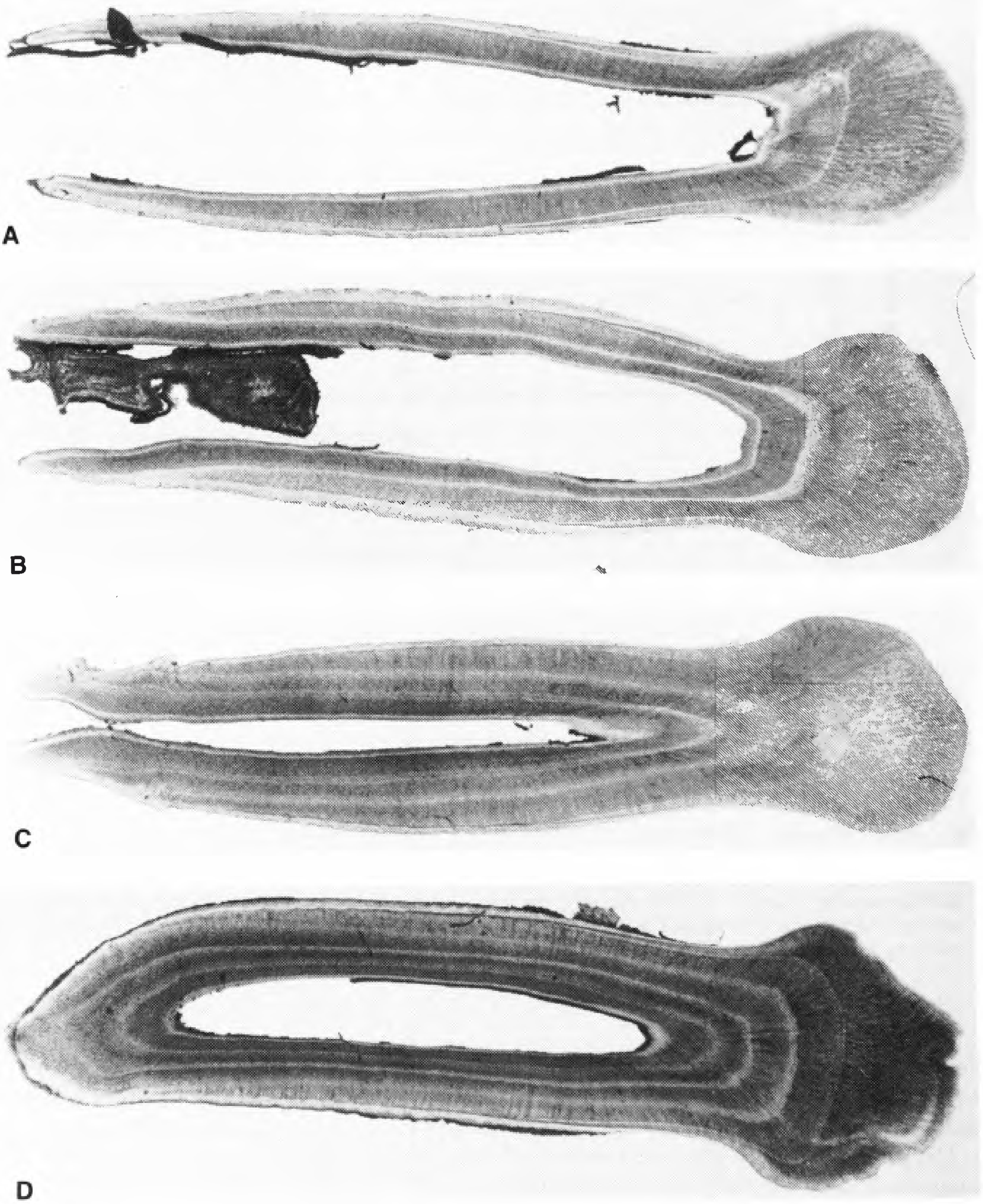
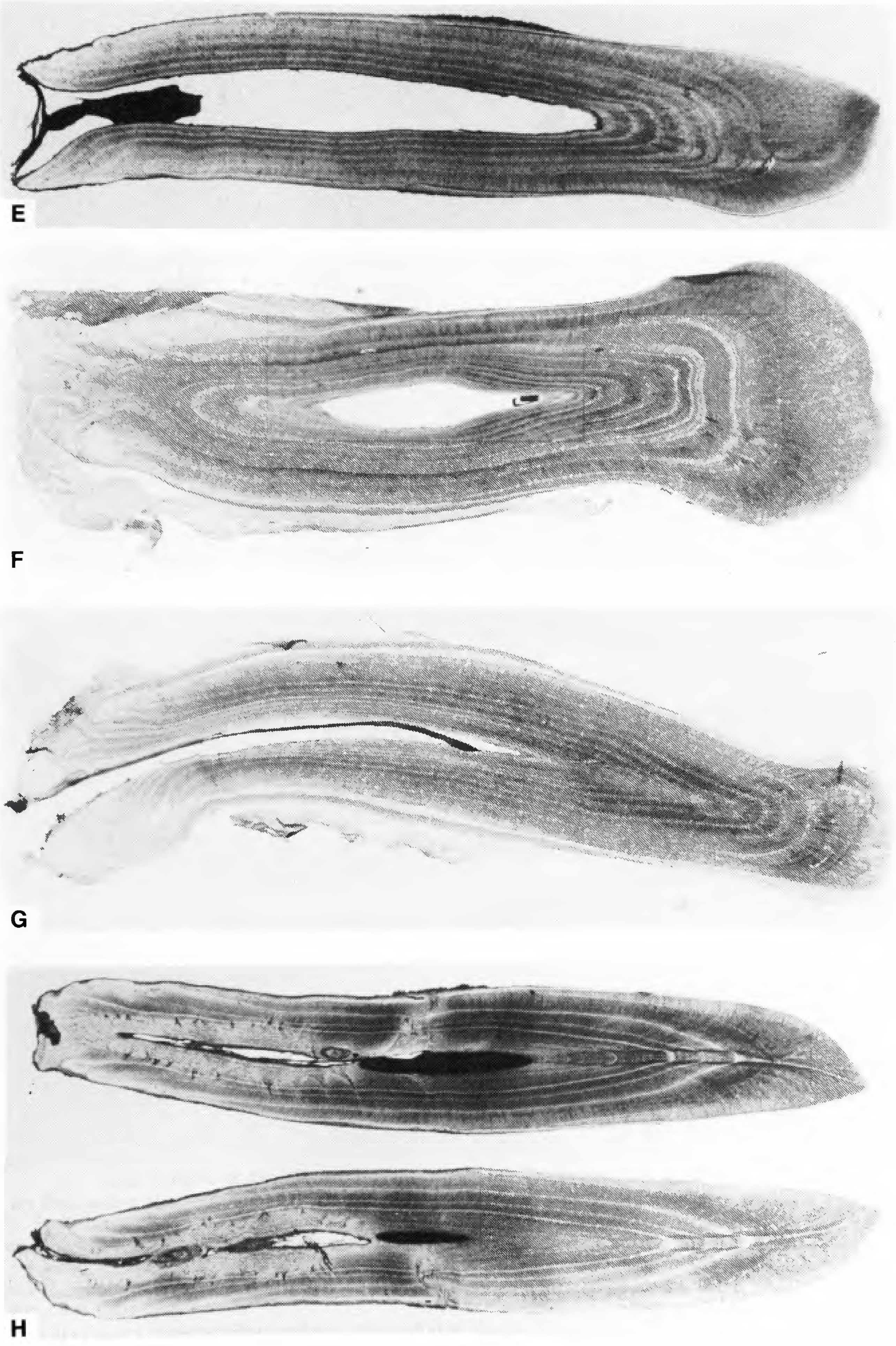


Fig. 2. Ontogenetic series of harbour porpoise teeth.
A. 1 year-old. No.3 Total agreement among both experienced readers and inexperienced readers.
B. 2 year-old. No.1 Total agreement among both experienced readers and inexperienced readers.
C. 3 year-old. No.2.
D. 4 year-old. No.15.
E. 5 year-old. 89–007 Notice the grainy dentine.
F. 9 year-old. 88–069.
G. 10 year-old. 88–074 'British' type of clarity and stainability of boundary layers.
H. 13 year-old. 88–022 'Bay of Fundy' type of clarity and stainability of boundary layers. The tooth is not completely decalcified, it is anomalous and dolphin cut.


E
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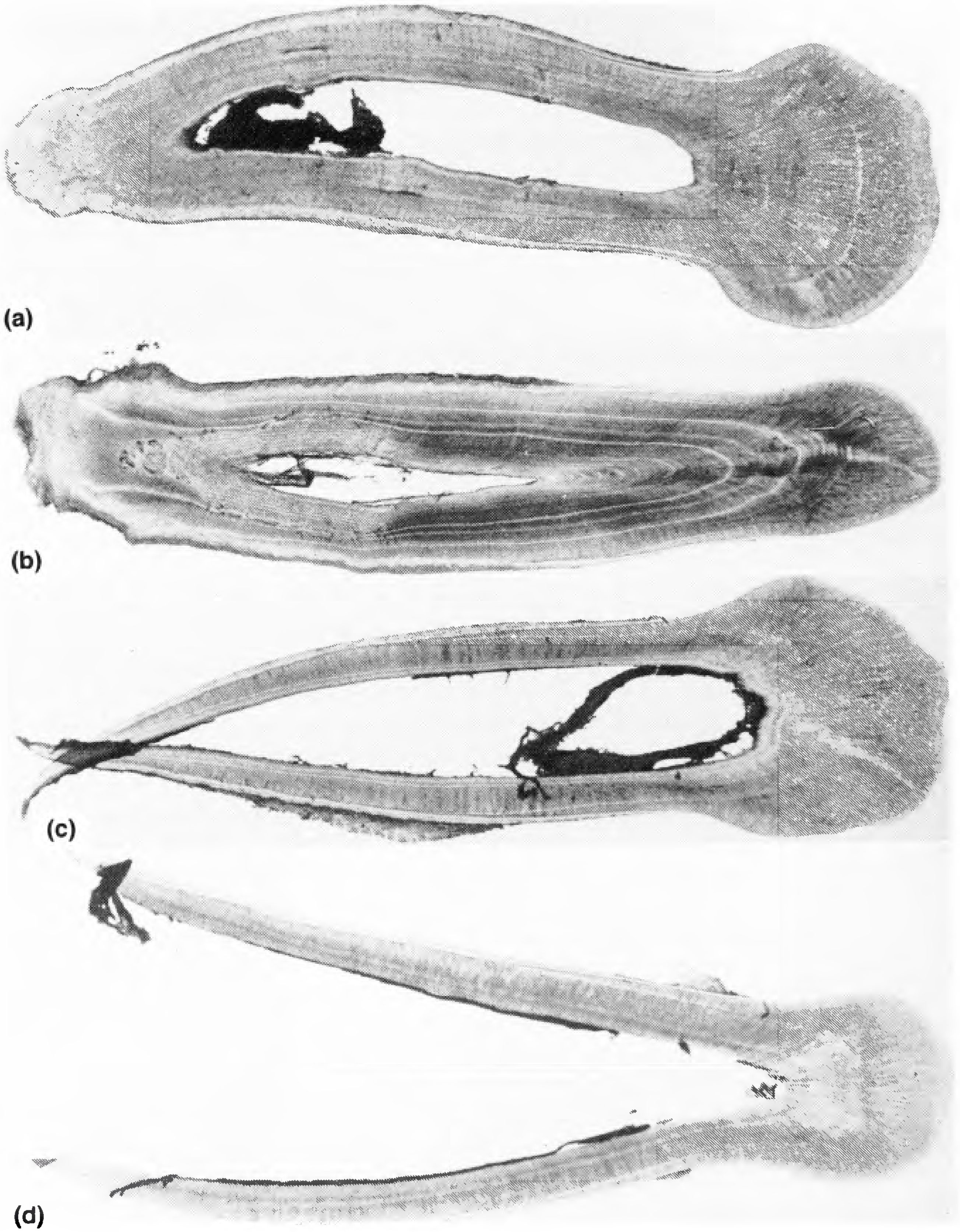
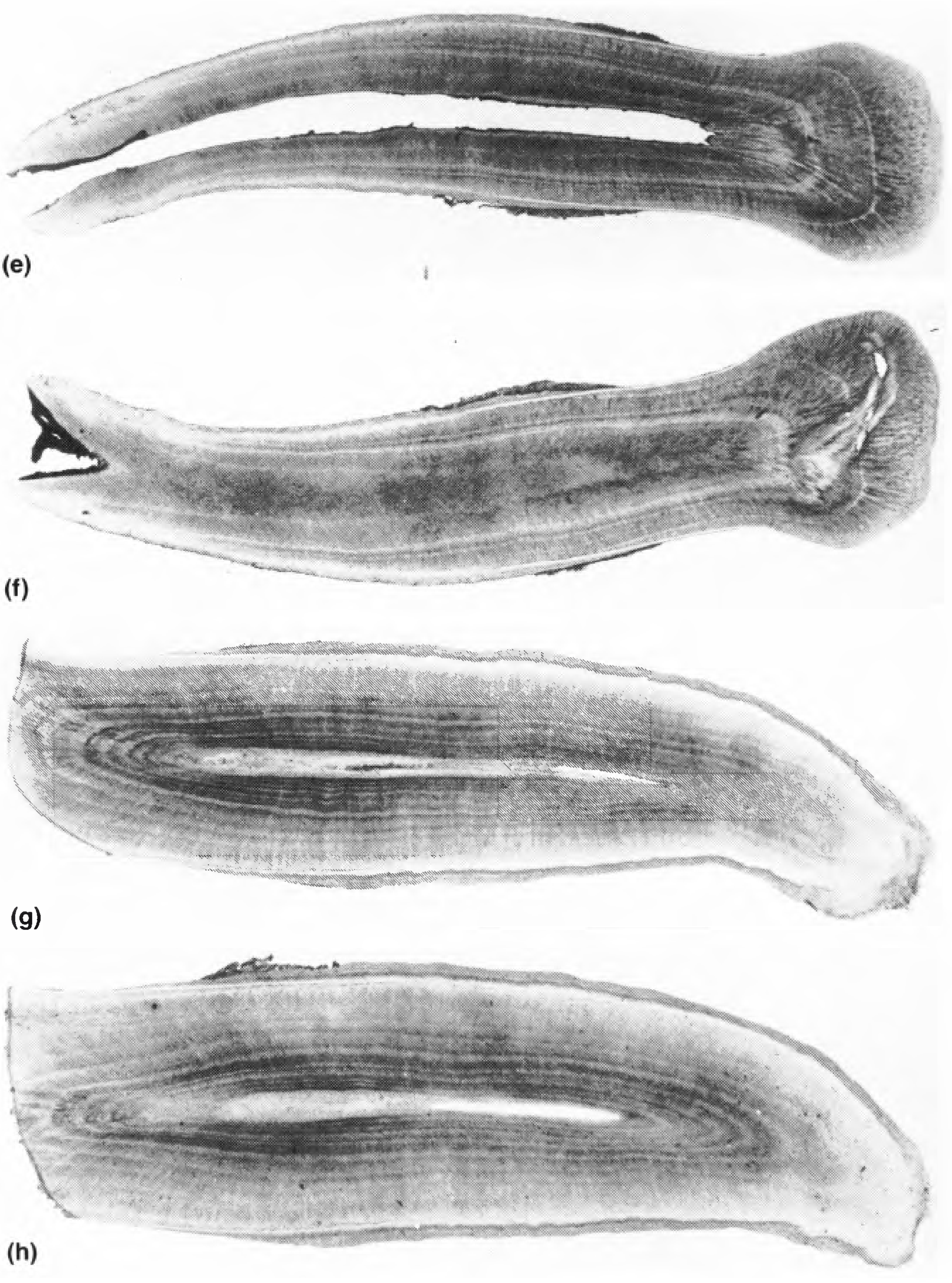


Fig. 3. Photographs of some harbour porpoise teeth for which it was difficult to estimate age.
(a) No. 6. 3–4 indistinct layers therefore it is difficult to interpret. Experienced readers disagreed on estimates.
(b) No. 10. 15 year-old. Inexperienced readers estimated 6 years, the mean of the experienced readers was about 13 using low-power microscopes.
(c) No. 17. 1 year-old. Inexperienced reader estimates were higher than those of experienced readers – possibly due to accessory layer.
(d) No. 18. 1–2 year-old. Second GLG ends at edge of pulp cavity, readings split between 1 and 2 GLGs.

Fig. 4. Photographs of two tooth sections from the same animal (harbour porpoise).
No. 16. 1 year-old: (a) On-centre section with very clear first GLG. (b) Off-centre section with first GLG boundary not visible.
No. 7. 2 year-old: (c) First boundary layer very distinct, second not. (d) Off-centre, second boundary layer even less clear.

continued overleaf



No. 9. 3 year-old: (e) Mostly on-centre preparation, good section with clear GLGs. (f) Off-centre.
No. 13. 13 year-old: (g) Old animal, mean for experienced readers during experiment was 8.6yrs, but when examined under high-power microscope, AH and CL think it is about 13. This illustrates the importance of using an appropriate microscope or risk missing fine layers. (h) Poor section of tooth that had difficult layers to read even in a good section; this section appears to be OK because lots of layers are visible, but the fine layers around pulp cavity are not visible and age would almost certainly be underestimated.

Inexperienced readers

As with the experienced readers, most of the variation was between animals (3-way ANOVA: reader × series × animal, Table 2). The between-reader variability was much larger than the within-reader variability.

The SD of the mean age estimates within animals pooled across all inexperienced readers was greater than for experienced readers, except for three animals (nos. 11, 16 and 21 – Table 3). In the two older animals the mean age estimates between the experienced and inexperienced readers were quite different. The pooled SD for the entire sample was 2.133, with 34% of the error contributed by the two old animals. In inexperienced readers the age estimates for these old animals ranged from 3–13yrs (overall mean = 6.2 vs 13.4yrs for the experienced readers) and 4–9yrs (overall mean = 6.4 vs 8.6yrs for the experienced readers).

The within-reader overall mean age estimates (pooled over all readings for all animals) varied 0.7yrs between readers, from 1.77 to 2.45yrs and 0.3yrs (from 1.97 to 2.23yrs) between series.

For three animals (nos. 1, 3 and 20), there was complete agreement among all experienced and inexperienced readers (Fig. 2 no. 3(A) and no. 1(B)).

DISCUSSION

The experiment revealed that experience in estimating age, whether in odontocetes or in terrestrial mammals, increased the precision of age estimates and resulted in greater similarity in estimates between other experienced readers. Within- and between-reader imprecision was greatest in old animals and in sections that were poorly prepared. Two of the experienced readers declined to read sections that they considered too poor to allow them to make reliable age estimate. The teeth were either cut off-centre or were poorly sectioned and were from animals 13 and 16 (Fig. 4). They were rejected once and twice respectively in the total of 12 repetitive readings by the experienced readers.

As several (2–15) tooth sections from each animal were presented the reader had to choose which ones to read. Experienced readers were more able to determine the quality of the sections and had a higher probability of choosing the best and, thereby, the same tooth sections during each reading than the inexperienced group. This may partly explain the generally lower SD values for the readings of the experienced group.

Teeth from some animals were clearly easier to read than teeth from other animals and these teeth are not likely to cause many errors in age estimation. In some animals, however (e.g. animal 6 – Fig. 3) GLGs were not distinct and experience becomes important in interpreting the layering patterns. In that animal inexperienced readers had difficulty in recognising any GLGs whilst experienced readers had difficulty in deciding between 2 or 3 years of age.

In particular, inexperienced readers seemed reluctant to count all of the GLGs in older animals, thereby underestimating the age. Animal 10, which, after discussion amongst the experienced readers was subsequently determined to have a best age estimate of 15 years, had mean age estimates of 6.23 and 13.42yrs for the inexperienced and experienced group. This illustrates how differently the two groups estimated age from the teeth of old animals.

For all but three animals (17, 18 and 19) age estimates made by the inexperienced group were lower than those made by the experienced group. The animals with higher age estimates were all between 1 and 2 years of age. One likely reason the inexperienced group had slightly higher age estimates for these was the counting of accessory layers as annual layers (e.g. Fig. 3 no. 17).

Some apparent error resulted from rounding up to the next age class for animals nearing the end of an annual layer, as the question of using only whole layers was inadvertently not addressed before the experiment began. Nonetheless, the age estimates from experienced readers were, for most animals, precise both within- and between-readers and series, even with some of the sections being off-centre and intended for use in this experiment only. For experienced readers, the overall reliability in age estimates for animals less than five years of age was high, with a pooled SD of about one third of a year.

There was total agreement on the age of three animals, two one year olds and one three year old. It is therefore probable that harbour porpoises with few annual layers are the easiest to read both for experienced and inexperienced readers. The reverse appears to be true for many dolphin species.

RECOMMENDATIONS FROM THE WORKSHOP

1. Standardisation of readings

A. Protocol for obtaining age estimates from harbour porpoise teeth

The workshop recommended that the scientists at the workshop most experienced in harbour porpoise age determination (Hohn and Lockyer) compile a Protocol for Obtaining Age Estimates to be included in the workshop report. The protocol is given as Appendix 3.

B. Use of a standard set of teeth

The methodology for estimating age needs to be the same for all investigators for comparability of demographic parameters. One method by which this may be possible is to have a standard set of teeth with GLGs determined and an estimated age assigned. A set of teeth from the sample examined in Oslo has been chosen for use for this purpose. The teeth have been photographed, GLGs marked and likely sources of error identified. This series of photographs is readily available from NINA, Oslo, Norway.

C. Exchange of tooth sections

From time to time it is useful even for experienced readers to obtain a second opinion regarding age estimates to verify the consistent application of criteria. For inexperienced readers, the exchange of material with experienced readers is extremely important.

D. Known-age and tetracycline-marked animals

Although samples from few known-age and tetracycline-marked harbour porpoise currently exist, the circulation of teeth from these specimens would contribute to the calibration of GLGs in porpoise teeth and the training of people for estimating age from them. Further experimental tetracycline marking of harbour porpoises for calibration of GLGs is encouraged.

2. Use of teeth for discriminating stocks

Some evidence suggests that the characteristics of GLGs seem to differ in animals from various regions. In addition, the relative occurrence of mineralisation anomalies varies geographically. These factors may be inherent to the individual or influenced by environmental variables, which could include forms of stress. There may also be an average or modal form of GLGs or anomaly pattern that is stock-specific, due to either genetic or environmental causes, that would allow stocks to be broadly discriminated on the basis of those characteristics. Further research using tooth characteristics as a means of stock discrimination is recommended.

3. Cause of layering patterns

The physiological and biochemical basis of layer deposition, in relation to age and mineralisation anomalies, remains unknown. Such information might provide support for the interpretation of annual layers as in tooth sections, help explain the similarities and differences in tooth-layer patterns between stocks and suggest the mechanism for anomalous mineralisation patterns. Research on the physiological and biochemical basis of layer deposition is recommended.

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Appendix 1

AGENDA

Monday, 21 May 1990
Session 1
Opening of the workshop.
Address of welcome:
— Professor Lars Walløe, Chairman of the Norwegian Marine Mammal Research Programme.
— Vera Selnes, WWF Norway.

Rolf Langvatn: What do we know about principles in formation and zonation of dentine and cementum in mammalian teeth?

Session 2
Christina Lockyer/Aleta A. Hohn: Age determination in odontocetes. Similarities and differences between species. An overview.

Aleta A. Hohn: The harbour porpoise tooth. Specific characteristics and heterogeneity in zonation in porpoises from different geographic areas.

Session 3
Christina Lockyer: Impact of environmental factors and major life events on zonation in odontocete teeth, with reference to harbour porpoise teeth.

Vera de Silva: Preliminary study on age determination of the Amazon dolphin, *Inia geoffrensis*.

Aleta A. Hohn: Laboratory procedures and techniques for handling, storing and processing porpoise teeth.

Tor Kvam: Procedures and techniques applied by NINA for cutting, staining and mounting porpoise teeth.

Tuesday, 22 May 1990
Sessions 4–8
Practical demonstration and reading of age material.

Session 9
How reliable is the age determination of harbour porpoise?
Presentation and discussion of the results of the practical sessions.

Closure of the workshop.

Appendix 2

LIST OF PARTICIPANTS

CANADA
Michael Kingsley

DENMARK
Carl Chr. Kinze

FAROE ISLANDS
Dorete Bloch

NETHERLANDS
Marjan Addink

NORWAY
Hilde Aarefjord
Arne Bjørge
Sølvi Kaarstad
Lars Kleivane
Sigrid Kvaal
Tor Kvam
Rolf Langvatn
Karl A. Rødland
Tore Solheim
Tore Schweder

SWEDEN
Ingalill Lindstedt
Fredrik Petterson

UNITED KINGDOM
Anthony R. Martin
Simon Northridge
Vera da Silva

USA
Aleta, A. Hohn
Christina Lockyer

Appendix 3

PROTOCOL FOR OBTAINING AGE ESTIMATES FROM HARBOUR PORPOISE TEETH

Aleta A. Hohn and Christina Lockyer

(1) Preparation of sections

(A) Orientation of cut

Traditionally, porpoise teeth have been sectioned in a plane parallel to the mandible. An alternative is to section them in the bucco-lingual plane, producing sections that are more similar in appearance to sections from delphinid teeth. The methods give the same age estimates, although generally the dolphin-type orientation provides more opportunity for producing a good-quality section.

(B) Quality of sections

In the context of preparation techniques, this is the most important aspect of obtaining a good age estimate. It is imperative that teeth be sectioned through the centre axis of the pulp cavity and apex of the crown. Many errors in age estimation result from sections that have been sectioned 'off-centre'.

The person preparing the tooth sections should know what constitutes a good section and be able to identify GLGs well enough to determine if the quality of the section is acceptable for age estimation.

(C) Mounting sections

One slide (with multiple sections) per animal is usually sufficient, providing that the optimal sections are mounted. For age estimation only good-quality sections need to be mounted (off-centre sections may introduce error, see above). Off-centre sections that contain interesting mineralisation anomalies or other features may also be worth mounting.

(D) Number of teeth per specimen

If the quality of the section is good, it should be necessary to examine only one tooth from each animal.

(2) Examination of tooth sections

(A) Read without access to data

Reading should be done without access to biological data for the specimen in order to eliminate possible bias in the age estimate.

(B) Use both dentine and cement

In the harbour porpoise, the dentine usually is preferable to the cement for estimating age. There are, however, special cases where the dentine can be difficult if not useless for estimating anything but minimum age and a better estimate can be obtained from cement. For example, in very old animals, in specimens in which there are many mineralisation anomalies in the dentine obscuring the GLGs and in specimens in which the teeth are bent or twisted making good on-centre sections in the dentine impossible, the cement must be used to obtain a good estimate of age.

(C) Mapping GLGs

Inexperienced readers, especially, may find it useful to serially list the type of layers identified in the tooth section, including all major darkly stained (D) and lightly stained (L) layers, as well as accessory layers (a) (Kvam *et al.*, 1989). For example, an animal estimated to be 1 year old with an accessory layer in the first GLG might appear as 'aDL'. This procedure would assist in identification of main boundary layers between GLGs, as distinct from accessory layers and be useful for explaining to another person the main structures seen in a tooth section.

(D) Multiple readings

Teeth should be read on more than one occasion, with readings separated by at least a day to avoid fatigue and remembering individual slides.

(E) Comments about the sections

Comments about the quality of the preparation, the clarity of GLGs and occurrence of accessory layers, and other interesting characteristics in the tooth, such as a particularly distinct marker line, often turn out to be useful later in evaluating the reliability of age estimates and identifying problem teeth especially when estimates from more than one reading are disparate.

(3) Estimation of age

(A) Use of dentine and cement

At times, dentinal and cemental counts will not be identical. In order to obtain the best age estimate when both dentine and cement have been read, one must evaluate the quality of the layering patterns in each tissue and make a judgement about which tissue is better. This situation is most likely to occur in old animals and where mineralisation anomalies have obscured dentinal GLGs.

(B) Single vs. multiple readers

B.1 THE LONE READER

After two readings, compare the age estimates. If they agree, then accept that value as the age estimate. If they do not agree, read the sections again independently of the previous estimates. If two of the three readings agree, use those as the age estimate. If there is no consensus, examine the sections again with the various age estimates and biological data from the specimens to help determine the most likely biological age.

B.2 MULTIPLE READERS

The goal should be to have two experienced readers; more than this is probably unnecessary.

Each reader reads once, then the readings are compared. If the estimates are in agreement, use that value as the age estimate. If the estimates are disparate, the readers should re-examine the sections together, discuss the criteria used by each to obtain the estimates and come to an agreement. When an agreement cannot be reached, the biological data for the specimen may be used to help interpret the most likely biological age.

(C) Acceptable levels of variation in age estimates

The effect of imprecision in age estimates depends on the species and the age of the individual. In short-lived, early-maturing species such as the harbour porpoise, a variation of even one year can be significant in estimating demographic parameters. The effect is even greater if the specimen is relatively young because the error will affect estimates of age at sexual maturation and growth rates of early postnatal animals.

One source of imprecision (and possibly bias) may result from age estimates which are rounded to the nearest whole year, for example, when an animal estimated to be 1.9 years of age is, in some cases, placed as a 2 year old because it was taken near the time of year when animals are born. If age is systematically rounded up by one reader and not by another, there will be an apparent disparity of one year in the age estimates. This difference could translate into significant differences in demographic parameters. Because rounding up places an animal in a new age class, it is inadvisable to do so.

While only complete GLGs should be counted for determining age class, partial GLGs (e.g. 0.5 yrs, 1.2 yrs, 1.9 yrs) are more accurate for determining growth rates and helping to verify age estimates when date of death is known and birth is seasonal, as in harbour porpoise.

A more difficult source of imprecision to address is that which occurs when an agreement on the age estimate cannot be reached. In harbour porpoises, many differences in age estimates occur between ages 3–5 and in old animals. The former occurs because the layers that form at or about the age at sexual maturation seem to be different in character. In old animals, it can be difficult to distinguish each GLG because GLGs become quite narrow and indistinct because of mineralisation anomalies. Up to the age of five in harbour porpoises, a systematic variation of one year is unacceptable.

(4) Limitations on the use of age estimates – teeth with poor layers

Some teeth have very poor layers due to individual variation in the clarity of growth layers or preparations that have resulted in sections that are not readable with any reliability. In the former case and in the latter case when additional teeth are not available for sectioning, a decision should be made that a reliable age estimate cannot be obtained and the specimen cannot be incorporated into any demographic parameter estimates.

Such age estimates can be used, however, when age data are needed to categorise specimens into general age groups, such as newborn, juvenile, adult and the very old, especially as most of the cases in which it is difficult to obtain reliable age estimates will be for old animals. For example, harbour porpoises estimated to have more than 10 GLGs can be included as very old animals for analyses of the relative occurrence of mineralisation anomalies in teeth or for determining the asymptotic length in the population.

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Papers

Age Determination of Mammals – Some Aspects of Biochemistry and Physiological Mechanisms Relating to Deposition of Incremental Lines in Dental Tissues

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ABSTRACT

This article poses some basic questions pertaining to the biological nature of incremental lines in teeth, used as age criteria in mammals. The structure and chemical composition of teeth is presented and discussed in relation to physiological and biochemical mechanisms assumed to regulate calcium and phosphorus metabolism and the process of mineralisation in teeth. Mechanisms responsible for deposition of incremental lines in teeth are not well understood. Empirical observations regarding environmental factors that may influence this process raise new questions and call for critical interpretation of presumed age criteria. The need for experimental reference studies is emphasised.

INTRODUCTION

Being able to determine the age of animals is a fundamental requirement for many aspects of ecological and physiological research. For example, knowledge of ontogenetic stages (or age) is important in the reliable interpretation of animal performance, metabolic capacity and behavioural patterns. In addition, for long lived species, realistic population dynamic models are dependent on age-specific information related to demographic parameters concerning reproduction and mortality.

The importance of age determination in biological research is reflected in the numerous publications on age assessment techniques (see Morris, 1972 for a review). The two main approaches applied are:

(1) statistical analysis and models based on distributions of age-related characteristics such as body weights and linear size dimensions, skeletal proportions and anatomic maturity (e.g. epiphysical lines, tooth eruption patterns, cranial sutures), size and weight of organs (e.g. eye lenses, testes, uteri) and anatomical degradation (e.g. tooth wear);

(2) observation and measurement of age criteria such as bone zonation; rings in horns; zonation in baleen and solid ear plugs in whales and incremental lines in tooth cementum and dentine.

It should be emphasised that specific criteria and approaches show varying accuracy and applicability among different species (Klevezal' and Mina, 1973) and that combinations of criteria used on the same material may be a useful approach to arrive at the best possible age estimate (Maat, 1987; Solem, 1988; Jacobsen and Reiner, 1989). Some age characteristics are relative indices (Morris, 1972), whereas specific anatomical criteria may provide accurate and reliable age-estimates in some species but not in all (see Geist, 1966;

Hemming, 1969; Hoefs and König, 1984). Distributions of relative age indices may serve the purpose of comparison between populations and between groups within populations (Peterson and Ballard, 1983) and may provide a basis for deductive appraisals on the population level. Accurate age criteria provide an opportunity for higher resolution in studies of age related problems, thus being more suitable for inductive approaches on an individual or group level.

Incremental lines in teeth represent fairly accurate and reliable age criteria in many mammals (Morris, 1978) including odontocete cetaceans (Donovan, 1985; Perrin and Myrick, 1980) and this paper will summarise aspects of biochemical and physiological processes pertaining to teeth as the source of information on age. The information referred to is primarily extracted from Ganong (1975), Jenkins (1978) and Campion *et al.* (1989).

Teeth are rigid and lasting, but still dynamic and living structures that reflect cyclic and metabolic events in the life of an individual. Teeth are readily available from dead animals and easy to preserve for processing and analysis.

Incremental lines have been observed in the dental tissues of all mammals investigated (Grue and Jensen, 1979) and on an empirical basis such lines have, in many cases, proved to be virtual annuli. However, a number of questions arise:

— What is the biochemical and histological nature of incremental lines?
— What are the biochemical and physiological processes responsible for their deposition?
— What are the ultimate factor(s) triggering deposition of incremental lines?
— Are all dark-staining zones in dentine and cementum responses to the same ultimate factors and proximate biochemical and physiological mechanisms?
— How do factors like photo-period, energy balance, hormone levels, nutritional cycles and environmental stress influence deposition of incremental lines?

Many more questions of this sort remain and as yet the answers are not always adequate.

STRUCTURE AND CHEMICAL COMPOSITION OF TEETH

Teeth are specialised bony structures with minerals deposited on a matrix of collagen fibres. The histological structure of teeth differs from skeletal bone and in the teeth themselves four main types of dental tissue can be distinguished (Fig. 1).

Ameloblasts play a central role in the synthesis and secretion of a lightly-mineralised organic framework that eventually matures and mineralises more completely to become enamel. Formation of the matrix by ameloblasts is dependent on the presence of a thin dentine layer which seems to act as an organiser of the ameloblasts and induces enamel matrix formation. Formation of enamel thus takes place from the amelodentinal junction (Jenkins, 1978).

Dentinogenesis occurs in two stages. Initially an unmineralised collagenous matrix (predentine) is formed. The predentine then becomes mineralised at a sharp boundary (i.e. the dentine-predentine junction). The first layer of dentine deposited is called mantle dentine and is formed by pulp cells. The rest of the dentine (circumpulpar dentine) differs from mantle dentine in the way the collagen fibres are orientated and this part is formed and mineralised by odontoblasts. Since the deposition of dentine takes place from the amelodentinal junction and the dentine layer grows thicker with age, the pulp chamber gradually becomes smaller. Mineralisation of dentine includes the formation of spheric, inorganic calcospherites, beginning in the part of the matrix which occupies the tip of the cusps. It then extends in conical increments throughout the crown and into the roots (Dellmann and Brown, 1976; Jenkins, 1978).

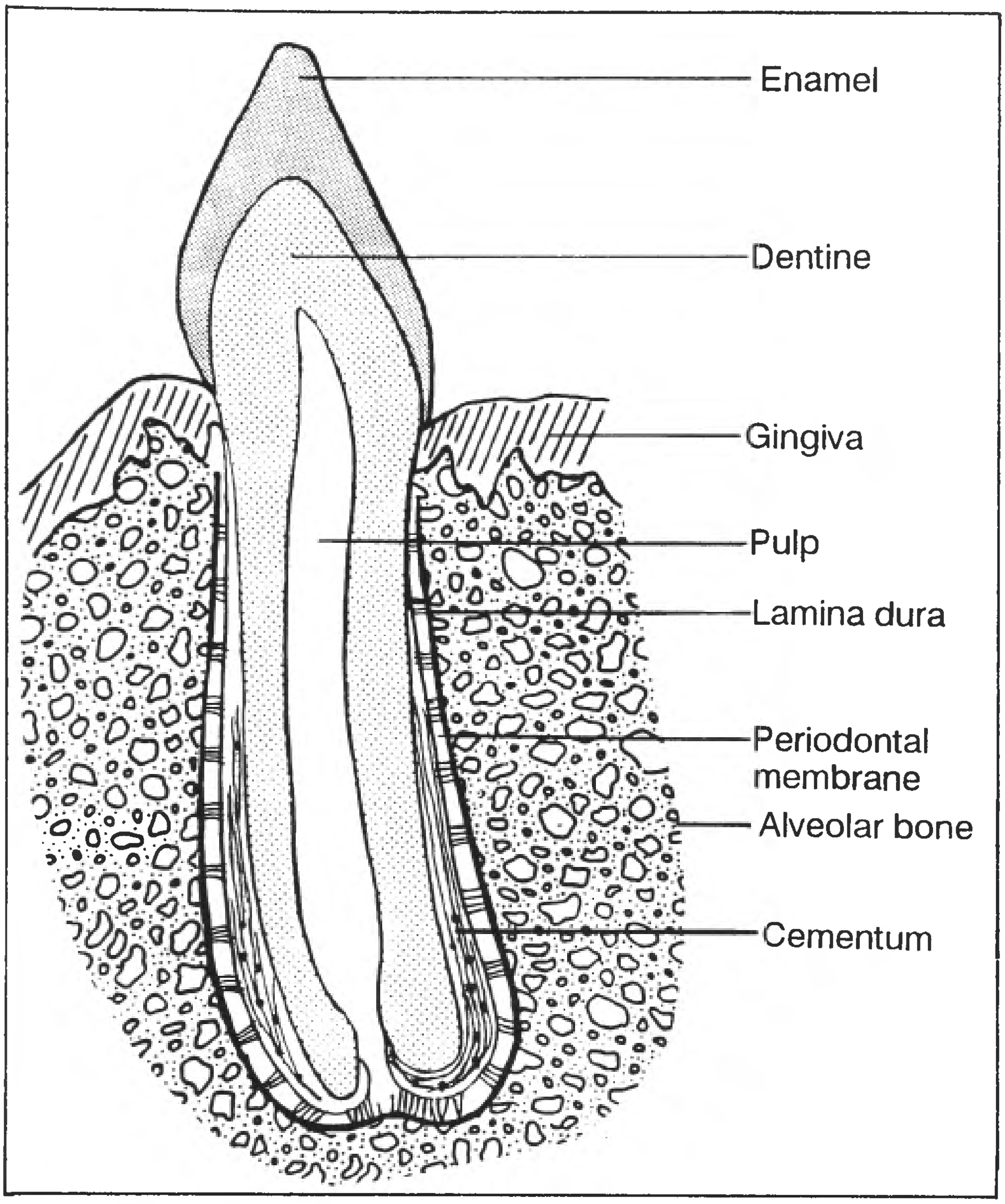

Fig. 1. Main histological structures in teeth.

Dental pulp is composed of connective tissue cells and fibres, matrix and numerous blood vessels and nerves. Odontoblasts are found in the peripheral part of the pulp cavity as a layer of columnar cells.

Dental cementum, probably of special interest in the age determination of animals, covers the outside of the root. Unlike enamel and dentine, cementum is deposited from the periodontal membrane and appears as a layer with lamellae running parallel to the direction of the root. Cementum is divided into two types – the cell free, primary cementum usually covering the coronal third of the root and the cell-containing, secondary cementum which covers the apical two-thirds and bifurcations of multi-rooted teeth. Both types of cementum contain collagen fibres of the periodontal membrane embedded in them (Dellmann and Brown, 1976).

The presence of lamellae indicates that cementum is formed intermittently. It is formed by cells called cementoblasts similar to osteoblasts, which lie between the edge of the periodontal membrane and a thin layer of uncalcified *precementum*. These cells become surrounded by the cementum they have produced and are then present in the *lacunae*

(Jenkins, 1978). Cementum formation continues throughout life. The increase is greatest in the apical region and least in the cervical region. That which forms after eruption tends to be of the cell-containing variety. The cells in the outer part of the cementum are oval in shape and contain prominent nuclei.

Occlusal stress influences both the amount of cementum laid down and its arrangement. In functioning teeth, cementum is deposited in a dense compact form, either as regular lamellae, or in some teeth, as a series of projections from the cementum already present. In both types, many periodontal fibres are embedded in the outer layers. In non-functioning teeth, however, although the cementum may be thicker than in teeth receiving occlusal stress, it is more diffuse and there are few fibres attached to it. The increase in the thickness of cementum is compensated for by a reduction in the thickness of the periodontal membrane and not by the resorption of bone, a fact which probably explains the observation that the periodontal membrane becomes thinner in advancing age and in teeth without antagonists. Under experimental conditions of stress, such as large doses of parathyroid hormone, cementum may be resorbed by the cementocytes in a reaction similar to osteocytic osteolysis in bone (Spencer, 1989).

The function of cementum is to provide an attachment for the fibres of the periodontal membrane. As the tooth moves in eruption or in physiological mesial drift, groups of fibres become detached from the cementum and degenerate. New fibres are continually being formed to replace them and re-attachment is made to the layer of secondary cementum being laid down at the time. Cementum growth can be very pronounced in the apical region of the tooth. In effect, it lengthens the root and may compensate for loss of enamel resulting from attrition. Cementum is not dependent on the pulp and dentine for its nutrition and therefore continues to function even if the pulp is dead. For this reason a pulpless tooth is retained because its periodontal membranes is inserted into the still vital cementum.

The composition of enamel and dentine-cementum differs significantly. Enamel is the hardest tissue in the body, containing 95% minerals (Fig. 2). Dentine and cementum contain relatively more organic matter but the minerals are deposited with different crystal patterns compared to enamel. The chemical composition of dentine and cementum is rather similar, although cementum has slightly lower ash content (approximately 26% calcium and 13% phosphorus). Table 1 shows approximate figures for major mineral components and organic matter in human teeth (Jenkins, 1978).

The inorganic composition of mineralised tissues varies between and within tissues, and there is still some debate about structural details. However, there is general agreement that the main constituent is the crystalline form of calcium phosphate (apatite), probably with the exception of enamel. The general formula for crystalline apatite is $Ca_{10}(PO_4)_6X_2$ and in biological material hydroxyapatite ($X{=}OH$) is the most common form. Along with apatite some amorphous calcium phosphate also occurs (Jenkins, 1978).

Collagen fibres are the main component of organic matter in teeth and are formed by fibroblasts, osteoblasts and odontoblasts. Four amino acids (glycine, proline, alanin and hydroxproline) make up approximately 60% of the collagen content where altogether 18 amino acids have been identified. The complete macromolecule in collagen (tropocollagen) consists of three strands of polypeptide chains arranged as a triple helix. Tropocollagen molecules readily polymerise both end-to-end and side-by-side to form collagen fibrils and may in turn attach to collagen fibres (Jenkins, 1978). Like other proteins, polypeptides containing proline (collagen precursors) are formed by ribosomes on the endoplasmatic reticulum. Aggregations of polyribosomes have been observed and it is possible that this occurs because the fibrous collagen precursors become ravelled with each other and engulf the ribosomes. However, a more likely explanation is that the

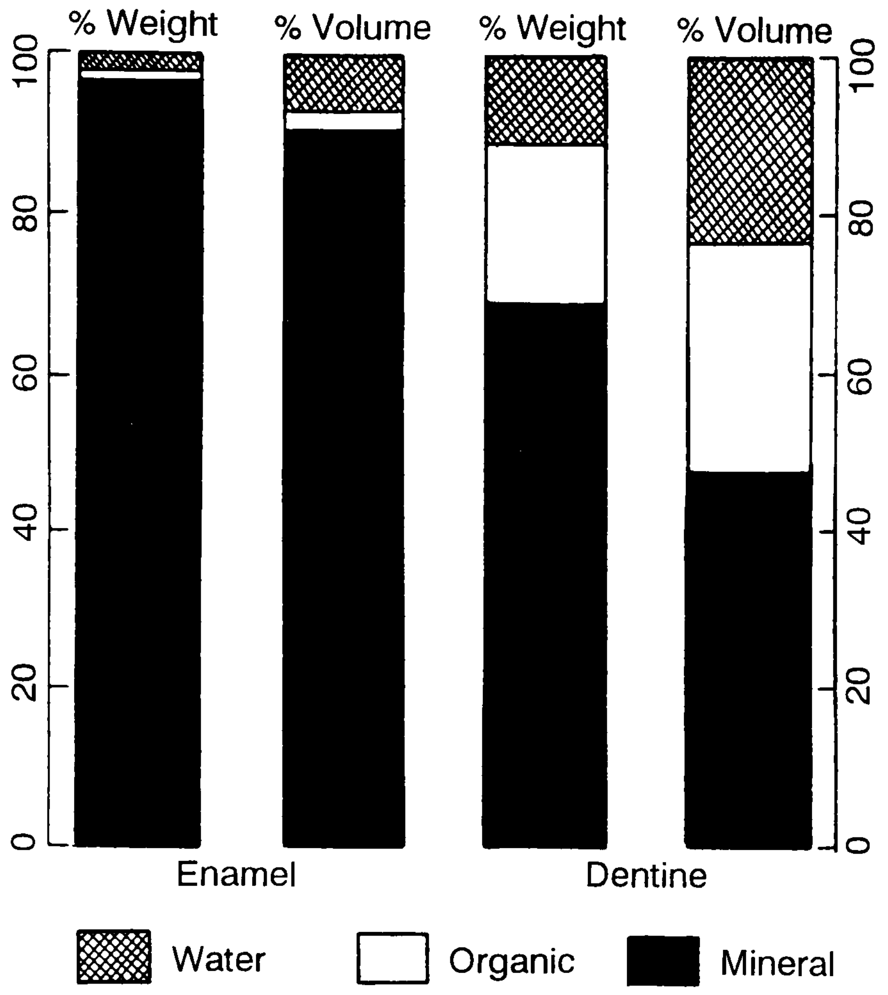

Fig. 2. Relative proportions of water, inorganic matter and organic matter in enamel and dentin (after Jenkins, 1978).

chains formed by neighbouring ribosomes interact to form larger chains, and possibly the observed triple helices before being released from their ribosome (Jenkins, 1978). Consequently the fibrils link the ribosomes together. Formation of collagen fibres from polypeptide chains is a complicated process involving several amino acids and enzyme systems. Parts of the process take place within cells, while the final stages, i.e. the establishment of insoluble structures, is mainly an extracellular process. The many stages and mechanisms involved in collagen synthesis probably expose the whole system to variations in and the impact of many metabolic, hormonal and dietary factors.

REGULATION OF CALCIUM AND PHOSPHORUS METABOLISM

Although few minerals are involved in the development of dental tissues, the process of mineralisation as a whole is complex due to the number of minerotropic hormones and growth factors involved. Maintenance and regulation of calcium and phosphorus plasma levels is of great importance with respect to tooth and bone formation as well as the general vitality and development of the individual (Ganong, 1975).

The metabolism of calcium and phosphorus, with respect to plasma levels, is closely linked. Some factors which modify calcium absorption influence the cells involved in the process, while other factors increase or decrease the solubility of calcium and phosphate (pH levels), thereby altering the amounts available for absorption. Because formation of

Table 1

Approximate composition of chemical components in enamel and dentine expressed in different ways. (After Jenkins, 1978). Note that the second column of figures refers to P and the fourth to CO_2, whereas the tooth contains PO_4 and CO_3. This explains why the figures do not add up to 100%.

	Ca	P	Mg	CO_2	Organic matter	Comments
(1) As a percentage of dry weight						
Enamel	36	17	0.45	2.5	1.3	(a) Tooth material heated to about 105°C until weight constant. Some water removed but 'bound' water retained. (b) The large differences between the figures for enamel and dentine are due to the higher organic and water contents of dentine.
Dentine	27	13	1.4	3.3	20	
(2) As a percentage of ash						
Enamel	38	18	0.45	None	None	(a) Tooth material heated strongly - all water removed, organic matter destroyed and CO_2 driven off from carbonates. (b) Note that in this material the only major difference between enamel and dentine is in the magnesium content.
Dentine	38	18	1.9	None	None	
(3) As a percentage of inorganic material						
Enamel	37.8	17.7	0.45	2.5	None	(a) Tooth material boiled with 3% KOH in ethylene glycol which removes organic matter and water but leaves carbonates intact. (b) In dentine, the figures given are those actually found, but they are lower than would be expected, probably because some Ca and P is dissolved by the reagent.
Dentine	35.5	16.7	1.8	3.9	None	
(4) As a present in the tooth of a living animal (calculated)						
Enamel	35	16.5	0.4	2.5	1.1	(a) Actual analysis of fresh tooth material is technically difficult. These approximate figures are calculated from those given in (1) above assuming: (i) that enamel contains 4% water, (ii) that dentine contains 10% water.
Dentine	24	11.5	0.9	3.0	21.0	

insoluble calcium phosphate is one factor in reducing absorption, it seems clear that absorption of neither ion can be considered alone. If, for example, calcium absorption is increased, the calcium concentration in the intestine is reduced. Then, according to the law of mass action, the tendency for calcium to precipitate with phosphate is diminished, thereby indirectly favouring the absorption of phosphate also (Jenkins, 1978).

The active transport of calcium from the intestine is increased by vitamin D, a group of closely relating sterols produced by the action of ultraviolet radiation on certain provitamins in mammals. Vitamin D_3, especially important in humans, is produced in the skin from 7-dehydrocholesterol by the action of sunlight. Vitamin D_3 is carried to the liver where it is converted to a metabolite of the vitamin, 25-hydroxycholecalciferol (25-OHCC). 25-OHCC is converted in turn in the kidney into the physiologically active metabolite 1,25-dihydroxycholecalciferol (1,25-DiOHCC), also called calcitriol, which acts as a hormone (Ganong, 1975; Spencer, 1989).

There is still some controversy as to the detailed mechanisms of action by calcitriol on the calcium and phosphate metabolism (Jenkins, 1978). However, generally it is accepted that calcitriol increases intestinal absorption of calcium and phosphorus, stimulates resorption of bone by osteoclasts and stimulates renal retention of phosphate. It functions primarily to maintain normal plasma concentrations of calcium, but may effect the formation of bone and dental tissues by providing an adequate supply of calcium and phosphorus for mineralisation. Calcitriol has several effects on osteoblasts, although a direct stimulatory role on osteoblast proliferation is doubtful. Calcitriol may also reduce collagen synthesis through an action of transcription due to the concomitant decrease in procollagen m-RNA and it may increase somatomedin C production by osteoblasts (Spencer, 1989).

The parathyroid hormone (PTH) also plays an important role in calcium and phosphate metabolism. In addition to raising plasma calcium levels through mobilising calcium from bone, PTH also decreases plasma phosphate and increases phosphate excretion and calcium reabsorption in the urine. It is possible that the primary effect of PTH under normal conditions is to rise plasma levels of calcium via the kidney and gut, and thereby to favour bone formation. PTH may act synergetically with calcitriol in the effect on bone resorption, but no calcium seems to be mobilised from teeth by PTH alone. PTH may also increase the formation of calcitriol, thus contributing to calcium absorption from the intestine. Secretion of PTH from the parathyroid glands varies inversely with the plasma-ionised calcium level (Ganong, 1975; Spencer, 1989).

The third principal hormone involved in calcium and phosphorus metabolism is calcitonin, secreted mainly by the C-cells of the thyroid gland. Its function is to maintain a normal plasma calcium level. An increase in this normal level triggers a release of calcitonin, which leads to renal excretion of calcium and decreased resorption of bone. The latter is accomplished by a direct inhibition of osteoclasts. Calcitonin is the only substance known to do this and osteoblasts are not required. Calcitonin does not appear to have any effect on osteoblasts. While calcitonin lowers circulating calcium and phosphate levels, it probably has no effect on magnesium, at least in humans. There is evidence that calcitonin acts by inhibiting the active transport of calcium from bone cells into the extra cellular fluids. It does not appear to affect cyclic AMP or the genetic mechanisms regulating protein synthesis. The hormone is more active in young individuals (Jenkins, 1978; Spencer, 1989).

In addition to calcitriol, PTH and calcitonin, several other hormones, growth factors and physiological conditions influence calcium and phosphorus metabolism, as well as the process of mineralisation in general. However, although correlations and functional mechanisms in isolated processes have been demonstrated for many relationships, there are as yet no comprehensive models explaining interactions and causality more generally. Compounds such as sex steroids (testosterone, oestrogen), growth hormones, insulin, thyroid hormones, glucocorticoids, prostaglandins and proteins or peptides produced by osteoblasts may directly or indirectly influence the formation of bone and dental tissues. In addition, Table 2 shows the effect of some growth factors on bone formation. Growth factors are principally peptides or proteins which usually operate as paracrines or autocrines, but may also act as endocrines. They interact with specific cell surface receptors and initiate intracellular events that lead to mitosis or differentiation. However, other specialised cell functions such as collagen synthesis can be stimulated or inhibited. Thus far, no effects on mineralisation as such have been reported (Jenkins, 1978).

Although many factors and mechanisms influencing bone formation and calcium and phosphorus metabolism in general have been indicated above, the specific influence on dental tissues may differ. Nevertheless, the complicated interactions and the many participating factors involved expose the process of calcium and phosphorus metabolism, protein synthesis and mineralisation so that cyclic events in the environment, metabolic cycles and endogenous rhythms may trigger biochemical and physiological actions that influence the deposition of incremental lines in dentin and cementum.

MINERALISATION

Mineralisation is a complicated process, and although we have a reasonable understanding of the main correlations and sequences in the process, there are still many unsolved questions, especially concerning timing and regulation. Mineralisation includes the deposition of calcium and phosphate as well as protein metabolism. The key questions have been – how does mineralisation take place and why does it occur only in bone and teeth? After all the precursors and participating chemical compounds in mineralised tissue circulate throughout the whole body.

Table 2

The effects of some growth factors on bone (after Spencer, 1989).

	Osteoblast synthesis		Osteoclastic resorption
	DNA	Collagen	
Somatomedian C(EGF-1)*	+	-	-
IGF-II	+	+	
Prostaglandins*	+	+[a]	+
EGF	+	-	+
TGFα			+
TGF-β_1	+	-	+
PDGF	+	+[b]	+
FGF(α,β)	+	-	
IL-1(α,β)*	+	+	+
TNF			-
Interferon-γ	-	-	-
M-CSF*			+
Bone derived growth factor (β_2-microglobulin)	+?		
Bone morphogenic protein	+	+	

* Produced by osteoblasts.

[a] High doses (-).

[b] Nonspecific effect.

Many hypotheses and theories have been put forward to explain this (see Jenkins, 1978 for a review). Two of the best known theories are probably: the 'boosting' theory (phosphatase-theory); and the more recent 'seeding' theory.

The 'boosting theory' assumes that enzyme activity raises concentrations of calcium and phosphate ions and according to the law of mass action this should lead to precipitation of crystals, especially if an 'apatite-like' nucleus were present in the tissue (epitaxy).

The 'seeding theory' in its early version was presented on the basis of *in vitro* experimental observations that collagen, with its 640Å wide bands, seemed to induce the deposition of apatite-crystals on these surface bands. Differences in the collagen structure between mineralising and non-mineralising tissues have been demonstrated, but even so, no explanation is completely satisfactory, and other hypotheses including the involvement of inhibitor-substances like polypeptides in non-mineralising tissues were suggested. Other factors cited to explain the mineralisation process included chondroitin sulphate (promotor and inhabitant), lipid substances and phosphoproteins (see Jenkins, 1978 for details).

Following the discovery in the 1960s of two types of vesicles occurring in cartilage, a fairly unifying theory for the process of mineralisation in terms of biochemical mechanisms has been suggested. These vesicles appear in two forms, one round or ovoid (Type I), the other irregular in shape, bounded by a trimellar membrane (Type II). Type I vesicles occurring in tissues with mineralisation well advanced are found to contain apatite crystals that grow and coalesce until the whole matrix is mineralised. The apatite crystals are closely associated with a matrix of organic matter.

Type II vesicles sometimes contain ribosomes and have an internal structure resembling cytoplasm. They contain alkaline phosphates and ATPase, enzymes characteristic of the membranes of cartilage cells and lipids, chiefly phosphatidylserine, a substance previously shown in the lipids of the calcifying front. This substance has a strong affinity for calcium, especially in the presence of phosphate, and it is tempting to speculate that it is important in concentrating calcium ions, thus acting as a seed.

It seems that Type II vesicles may promote mineralisation in several ways involving all the hypotheses proposed over the last 50 years. The alkaline phosphatase has pyrophosphatase activity and it converts the inhibitor pyrophosphate into orthophosphate thus removing its inhibitory power and simultaneously converting it into a booster by increasing the concentration of orthophosphate. The lipid may attract calcium ions, this action being favoured by the orthophosphate which, in turn, will be available to convert the calcium into calcium phosphate.

The discovery of vesicles, in particular, the fact that they seem able to act both as a booster and as a seed, provided a reasonable solution to the problem of mineralisation. However, some difficulties remain. Electron micrographs of dentine give the impression that the crystals extend beyond the membranes of the vesicles and coalesce with other crystals emerging from other vesicles, engulfing collagen in the process. Any orientation with collagen seems to be an incidental secondary process. Also, apatite crystals are formed very early in mineralisation and before the crystals become associated with collagen. There seems to be no mechanism for the formation of the amorphous calcium phosphate (Jenkins, 1978).

The relationship of calcium phosphate formation in the vesicles to its presence within the collagen fibres is another unresolved problem. One picture of mineralisation which links vesicles and collagen suggests that amorphous calcium phosphate is precipitated in the vesicle and, being more soluble than hydroxyapatite, calcium phosphate is then dissolved by unknown mechanisms in the tissue fluid surrounding the cells of the mineralising tissue. The calcium and phosphate ions then diffuse into the collagen fibre because, in the mineralising tissues, the spaces between the fibres are large enough to permit these ions to enter, where they form hydroxyapatite by a seeding process. In other words, the vesicles carry out a concentrating process which provides the collagen with sufficient ions to form hydroxyapatite crystals (Jenkins, 1978).

The presence of vesicles in a tissue, along with collagen macromolecules surrounded by spaces sufficiently large enough to allow ions to diffuse between them provides the most reasonable interpretation of why mineralisation occurs only in certain tissues. The spaces between the collagen molecules in bone and dentine average 6Å, which is 3Å larger than in tendon. This difference may explain why mineral ions enter collagen in bone and dentine but not elsewhere. The space between the molecules in tendons is smaller than the diameter of the phosphate 4Å, suggesting that it could not enter tendon fibrils but could permeate the larger spaces between bone collagen fibrils and thus precipitate as apatite within these fibrils (Jenkins, 1978; Campion *et al.*, 1989).

FACTORS INFLUENCING THE DEPOSITION OF INCREMENTAL LINES

The presence of lamellae and incremental lines in dental tissues indicate an intermittent deposition pattern. Such a pattern may take place for various reasons, but is primarily a result of the variation in the rate of either mineral deposition or collagen synthesis, or a combination of the two.

As mentioned, it has been demonstrated empirically in many species that some incremental lines are virtual annuli (Morris, 1972). These lines usually appear as dark stains and are more conspicuous than the thinner and lighter lines which occur between annuli. Generally it is accepted that these 'primary lines' are more regular and developed in arctic and temperate regions, whereas animals from tropical and sub-tropical regions show a more diffuse picture. Indications are that 'primary lines' are deposited according to the number of dry seasons in tropical regions, whereas one line per year is the rule in temperate and arctic regions. Incremental lines also appear more distinct in oceanic environments (Klevezal' and Mina, 1973).

Information on when incremental lines are laid down during the year is important with respect to what factors ultimately may cause the intermittent deposition pattern. Observations in the literature (e.g. Grue and Jensen, 1979) show great variations among species as to when annuli develop. However, within species there is a certain consistency and although the period during which lines develop may take several months, it tends to peak during certain seasons. For many species, e.g. many temperate cervids, annuli seem to develop during a period of declining and low physical condition. In most cases neither sex nor breeding cycles *per se* seem to have any profound effect on the character or timing of the annual cementum layers.

Within species, the distinctness of incremental lines, in particular annuli, seems to increase with increasing variation in severity of climatic conditions between seasons, as well as increased variation in nutritional supply during the year. Within the distribution area of a particular species, the distinctness of incremental lines tends to correlate with higher latitudes. Time of formation of incremental lines for a particular species appears fairly synchronised throughout its distribution range, allowing for a six month difference between the two hemispheres.

Geographical and climatic factors alone can hardly explain the general picture of intermittent growth in dental tissues, since within the same geographic region, different species show great variation in distinctness and timing of the development of incremental lines (Klevezal' and Mina, 1973). Thus, if photoperiodicity was to be an ultimate factor the deposition of incremental lines, its influence on more proximate factors and mechanisms must be different and/or induce a different timing in various species. Photoperiodicity cannot be a causative factor in equatorial regions with constant day length (and minor differences in monthly mean temperatures), but incremental lines are still found in animal teeth from this region. Some authors speculate that a basic biological, endogenous rhythm is responsible for the deposition of primary lines or annuli, while environmental and/or dietary conditions may induce the thinner and less distinct secondary lines, sometimes merging with the former (Jenkins, 1978; Campion *et al.*, 1989; Spencer, 1989).

In most species, growth rate and weight gain varies between seasons and plasma levels of many hormones show a cyclic pattern throughout the year, thus functionally appearing to fit this picture. Variation in FSH, thyroid hormones, growth hormones, prolactin, sex hormones, vitamin D and others, with metabolic activity and differential growth, seems too consistent and systematic to be disregarded in the search for possible steps in the chain of mechanisms that induce and regulate deposition of incremental lines in teeth. From an evolutionary point of view it is not surprising that the trends mentioned intercorrelate with seasonal changes in climatic conditions, nutritional supply and various forms of environmental or metabolic stress. Perhaps the cyclic shedding and growth of cervid antlers could provide hypotheses of how to further elucidate the problem of the deposition of incremental lines in teeth. Antler growth is known to include many of the same factors presumed present in mineralisation of teeth, like photoperiodic influence, endogenous rhythms, hormones, growth factors, minerals, collagen synthesis and specific nutrients, and antlers lend themselves conveniently to experiments.

CONCLUSION

This review has not tried to answer the questions posed in the introduction. However, it has probably managed to indicate how complicated the causalities are regarding age criteria and deposition of incremental lines in teeth. Age determination of mammals should be practised with a clear understanding of the limitations inherent in the available methods.

Reliable age assessment of animals is of great importance both in biological research and management and there is clearly a need for wide ranging physiological studies of metabolism and its interactions with environmental factors. Experiments should be carried out to achieve a better understanding of how the ageing process is perpetuated and expressed in mineralising tissues. The answers would be of great benefit to the biological sciences in general, human medicine included (Scott and Levy, 1982; Solem, 1989).

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A Review of Factors Involved in Zonation in Odontocete Teeth, and an Investigation of the Likely Impact of Environmental Factors and Major Life Events on Harbour Porpoise Tooth Structure

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ABSTRACT

Variation in zonation and Growth Layer Group (GLG) formation and underlying causes are reviewed. Five different types of anomaly were investigated in the teeth of harbour porpoise (*Phocoena phocoena*): pulp stones, mineralisation interference, marker lines, dentinal resorption and cemental disturbance. Samples of approximately 50 teeth from British Isles, Denmark, Canada, Norway and California were studied and findings compared. The incidence of all anomalies increased with age through natural persistence in the teeth. No differences in incidence of anomalies were found between the sexes, but significant differences in incidence by region for four anomaly types (excluding pulp stones) were observed. Similarities were seen between teeth from the British Isles and Denmark, and between Canada and Norway, which could not be explained by geographical proximity. Various hypotheses concerning environmental factors, including pollution and life history events, were discussed as the possible causes of these anomalies and their different levels of incidence. The most promising result appears to be a possible link between marker lines and life history events, a hypothesis which is open to experimental testing, with the use of tetracycline time-marking techniques of teeth and known-history captive animals.

KEYWORDS: HARBOUR PORPOISE; TEETH; STOCK IDENTITY; BIOLOGICAL PARAMETERS; AGEING; PHYSIOLOGY; POLLUTION

INTRODUCTION

Teeth, as one of the hard tissues of the body, have been extensively used for determining age in mammals (and also many other animals; e.g. Klevezal', 1980). The use of teeth in age determination in cetaceans has been both addressed generally (Perrin and Myrick, 1980) and more specifically for porpoises in the report of this workshop (Bjørge *et al.*, 1995) also Nielsen (1972), Gaskin and Blair (1977) and Hohn and Lockyer (1995).

The harbour porpoise has, for a cetacean, a relatively short life-span of about 12 years and an early age of sexual maturation of 3–4 years (Gaskin, 1977; Gaskin *et al.*, 1984; Hohn and Brownell, 1990; Martin *et al.*, 1990; Read, 1990; Kinze *et al.*, 1990). The teeth have proved to be a reliable means of relating demographic parameters to age (Perrin and Myrick, 1980) and the question to be explored in this paper is that of whether or not more than just age can be determined from the teeth.

Potential information that might be inferred from teeth include general health, maturity, sex, reproductive history and the occurrence of environmental events affecting general status. The possibility of such interpretations from variations in zonation and Growth Layer Group (GLG – Perrin and Myrick, 1980) patterns in teeth have been raised by several researchers over the years, each studying different mammals (e.g. Klevezal' and Myrick, 1984; Bengtson, 1988).

The importance of the ability to interpret life history events from teeth is that it would provide an insight into the past performance of individuals – at least for the survivors. An historical perspective is often lacking for populations because of inconsistency, or absence, of monitoring and/or records. When records are available, they only provide information for a particular point in time rather than life history. Life history has to be determined from a combination of information from several individuals at different life stages, all subjected to different stresses at different points in their life history.

If the interpretation of tooth zonation patterns can identify age at sexual maturation, parturition and 'time-marks' associated with environmental events and other crises, it would be a powerful tool for long-term monitoring and modelling, reducing the need to have access to historic material.

This paper reviews the underlying principles of tooth zonation and explores the use of zonation patterns in estimating demographic parameters, identifying life history events and the general health of porpoises.

PRINCIPLES INVOLVED IN ZONATION IN TEETH

Formation and development of teeth

Teeth are composed of living tissue which continues growing throughout the life of the animal. In some mammals (e.g. rodents) the continuous growth is evident, whereas in others (e.g. humans) the continued growth is often only evident in the repair of damaged dental tissue (Avery, 1976a). Both the live pulp and the odontoblasts (formative cells) retain the capability of growth and repair as long as the tooth remains alive. Once the pulp dies, additional growth of the dentine is no longer possible. The general pattern of hard tissue differentiation into dentine, enamel and cementum, surrounding the pulp, has been described by Langvatn (1995) and Perrin and Myrick (1980). Generally, cetacean teeth are homodont and are present throughout life (there are no deciduous teeth) increasing in size with age.

The first most visible character in the tooth, used as a baseline in age determination, is the *neonatal line*, present in the dentine. This appears as a hypocalcified incremental line, caused by the hormonal stresses occurring at birth (Avery, 1976a). The line represents the beginning of life as an independent individual, and is equivalent to age 0 years.

Incremental growth and GLG verification

Following birth, incremental growth in the dentine accumulates on a daily basis, visible under suitable magnification as the *lines of Ebner*. The progression of incremental growth tends to be regular, but variations do occur. Some of these lines, *lines of Owen* (hereafter termed 'marker lines'), appear more pronounced than others. They are usually hypocalcified and are caused by interference in the mineralisation process (Avery, 1976a).

Mineralisation occurs parallel to the tubules in the dentine, but lags behind the growth of the newly formed matrix or predentine. The tubules are formed by cytoplasmic processes at the pulpal surface, arising from the odontoblasts. The matrix of the dentine is collagen fibrils and mucopolysaccharides. The mineral component deposited in teeth is hydroxyapatite, $3Ca_3(PO_4)_2.Ca(OH)_2$. The laminations in the dentine and/or cementum have generally been defined in terms of mineralisation density and/or quality (Boyde, 1980): high and low, a contiguous pair of which constitute a growth layer group or GLG. This is, of course, a simplification of the real situation where accessory laminae of varying mineralisation density and thickness are frequently observed, as discussed by Myrick (1984). The main problem is how to interpret laminae in relation to real time, i.e. what constitutes a daily, lunar and annual growth layer. In general the hypo- and hypercalcification that results in marker lines arises from systemic interference in the calcification process.

The cementum also grows after birth, with the production of incremental lines (Grue and Jensen, 1979), which have been found suitable for age determination in both terrestrial and marine mammals. The cementum forms from cementoblasts and accumulates in apposition to the dentine in the root of the tooth (Armitage, 1976). The most recently formed cement is adjacent to the gum tissue. Grue and Jensen (1979) found variations in the pattern of cemental deposition with double lines and irregular widths of incremental bands; but, unlike dentine, no unusual incremental lines similar to the marker lines were observed.

The periodic growth of dentine and cement in teeth is well documented (Perrin and Myrick, 1980; Grue and Jensen, 1979), normally coinciding with an annual incremental rate of accumulation. The annual growth has been described as a GLG, or some multiple thereof. A GLG comprises the incremental series of daily lines, lunar lines, accessory lines and whatever else has formed during the year. The GLG has a defined boundary and is distinguishable as a separate zone.

The true incremental rate of growth of laminae has been investigated and established directly for some marine mammal species by studying teeth from known-history captive (and free-living) cetaceans (Hohn *et al.*, 1989) and the judicious use of tetracycline antibiotic administrations to 'time-mark' hard tissues, i.e. dentine and cementum in teeth, as well as bone (Yagi *et al.*, 1963; Best, 1976; Domning and Myrick, 1980; Gurevich *et al.*, 1980; Myrick *et al.*, 1984; 1988; Myrick and Cornell, 1990). The tetracycline drugs are incorporated into the mineral element of the teeth and appear as a fluorescent band under reflected UV light. By administering a series of doses of tetracycline over time, the incremental rate of growth in teeth can be accurately assessed (Perrin and Myrick, 1980; Lockyer, 1993; Hohn *et al.*, 1989; Myrick and Cornell, 1990).

In her review, Klevezal' (1980) concluded, that for odontocetes, growth layers in both dentine and cementum are the result of seasonal growth rhythms, and that the special pattern of an annual GLG is determined by 'the form of the intraseasonal growth rhythms of an individual'. This has been established for terrestrial mammals (Grue and Jensen, 1979). Growth patterns in individuals are determined by hormonal variations, many of which are in turn, sensitive to seasonal influence, e.g. day length on the hypothalamus. Clearly, any factor which is powerful enough to interfere with what is essentially a seasonal hormonally linked response could potentially affect the formation pattern in teeth. If this is the case, interference should be visible as variations in zonation and mineralisation.

Manifestation of the effects of stress in hard tissues

As noted above, the hypo- or hyper-mineralisation of dentinal tissues may appear as a distinctive band in the tooth. The types of stress or interference which might be ascribed to causing this are various. Lockyer (1993) reported the coincidence of such lines with the event of being taken into captivity in short-finned pilot whales, *Globicephala macrorhynchus*. Apart from the general stress to the animal at this time, health problems of weight loss and actual infection often arise as a result of a period of inadequate food intake soon after captivity. The period of adaptation to new feeding habits and diet often appeared to be prolonged.

Klevezal' and Myrick (1984) reported the appearance of 'deeply dark-stained layers' (DSL) in dolphin (*Stenella* sp.) teeth and ascribed them to parturition events in females, perhaps related to hormonal changes and/or nutritional demands.

Manzanilla (1989) reported a correlation in timing of the appearance of hypocalcified dentinal layers in the teeth of female dusky dolphins, *Lagenorhynchus obscurus*, off Peru, with the El Niño event of 1982/83. The anomalous layer, described as the 'El Niño mark'

(ENM) comprised a pair of hypocalcified incremental layers about 75μm wide within the 1983 GLG. The feature appeared predominantly, but not exclusively, in adult females. The primary prey of the dusky dolphin was anchoveta (*Engraulis ringens*), the stocks of which collapsed during the El Niño period. Manzanilla ascribed dietary deficiencies as the cause of the tooth anomalies. Teeth of other species did nôt display ENM's, but were feeding on a different prey source. This is the first convincing evidence of a connection between tooth anomalies and environmental factors. Bengtson (1988) reported the appearance of 'suckling' lines in teeth of fur seal mothers and their pups, *Arctocephalus gazella*, coincident with episodic suckling from the mother. The occurrence of these lines in association with nursing would appear to be directly related to the periodic calcium and nutrient transfer.

Thus in each of the above cases, the appearance of marker lines might be associated with interruption or change in regular feeding habits.

Lockyer (1993) reported the appearance of such marker lines in the teeth of free-living long-finned pilot whales (*G. melas*) mass-stranded off Iceland and Faroes, and the independent correlation of appearance of such lines in particular years in animals separated both in time and geographic space in the northeast Atlantic. This may be indicative of an external environmental crisis, similar in impact to the El Niño event off Peru.

Documented effects of stress on hard tissues in marine mammals are rare and generally open to some debate. Myrick (1988) has investigated the likely effects of stress induced by repeated setting on dolphins with tuna purse seine nets in the eastern tropical Pacific (ETP). By comparing two populations in the ETP, Myrick showed that the events of frequency of being entrapped in nets and the incidence of certain types of resorption of dentine were related. Resorption has been linked to stress which may cause variation of Ca^{++} ions in the blood and the sudden requirement for extra ions to be drawn off from reservoirs in the body such as hard tissues as well as mitochondria. However, in severe cases of resorption, the collagen matrix is also resorbed. Animals that regularly undergo extended periods of stress such as hibernation, e.g. black bears, show alternating patterns of resorption and subsequent repair (Myrick, 1988). The repair tissue is generally randomly organised, unlike the regular tubule formation and is often more similar to bone.

Boschma (1950) investigated the possibility that resorption was caused by physical external pressure, such as that from adjacent or opposing teeth in sperm whale, but reached no firm conclusions. Such physical pressure can create resorption (Boyde, 1984) and the rate of erosion depends on the orientation and density of the mineralised tissue. However, Boyde *et al.* (1984) have demonstrated that resorption resulting in typical *Howship's lacunae*, could be experimentally created *in vitro* using sperm whale dentine and osteoclasts from rabbit foetuses. Resorption *in vivo* by this mechanism is clearly a physiological process; perhaps systemic as well as local and has nothing in common with physical erosion.

A correlation between organochlorine contaminants (DDT and PCB) and pathological changes in the bone of harbour seals (*Phoca vitulina*) in German waters, has been observed (Stede and Stede, 1990). The changes were manifested in the form of osteoporosis and bone lesions, with the loss of alveolar bone in the mandibles and maxillae. Such loss of tissue can be part of a resorptive process. Similar changes in bone were reported for grey seals (*Halichoerus grypus*) from the Baltic (Bergman *et al.*, 1986). Skull material of Baltic grey seals collected after 1960 showed a significantly higher incidence of pathological bone lesions than for the pre-1950 material (Zakharov and Yablokov, 1990). The exact process is uncertain, but in the case of PCBs, is thought to be caused by the disturbance of steroid hormone chemical interference (Safe, 1984). Overproduction of glucocorticoid hormones depresses collagen formation, the natural matrix of bone and other hard tissues such as teeth. A form of mineralisation interference and cemental disturbance could perhaps occur in teeth as a result of such interference, but would be evident at the time of formation of new tissue rather than resorption from existing tissue.

Grue and Jensen (1979), initiated studies to investigate variations in cemental deposition patterns with factors of nutrition and body condition, environmental crisis, climate (temperature), sex and reproductive status. Their results, including a review of data from other sources, were inconclusive. They reported that in general sex and reproductive status did not appear to affect cemental deposition. The only factor that appeared to be linked with clarity and definition of incremental lines was cool temperature (broadly linked with high geographic latitude) – perhaps because of greater extremes of light intensities and hormonal response to the strong seasonal cycles experienced. The biggest problem in interpreting variations in cemental deposition is that physical stresses on the teeth initiate cementum build-up in order to strengthen the hold on the tooth in its socket in the jaw – changes which may have nothing to do with physiological stresses. Thus, irregularities in cemental thickness may be almost entirely linked to physical factors e.g. feeding and foraging tactics. Pathological changes in the cementum are a different matter, but were not addressed by Grue and Jensen (1979). Myrick (1988) addressed the possibility of resorption in cementum as a response to physiological stress in both terrestrial and marine mammals. He reported close links between stress and resorption, and noted that resorption in teeth frequently involved both dentine and cement, indicating a systemic cause rather than a local physical one.

Anomalies and abnormalities in teeth

Any approach which assumes a constant regular growth pattern in teeth is greatly oversimplified. Detailed examination of teeth of many mammals reveals that events may occur which appear to create systemic rather than local disturbances in the regular deposition of laminae in the teeth (Myrick, 1988). Such disturbances may be termed mineralisation anomalies. In cetacean teeth they range from 'foreign' inclusions in the teeth, such as bone-true osteodentine (Best, 1966), to tooth-originating materials such as 'pulp stones', frequently labelled as 'osteodentine' (Boschma, 1938; Nishiwaki *et al.*, 1958), and further complexities such as distinct laminae, defined by virtue of their unusual appearance and affinity for stain – 'deeply dark-stained layer (DSL)', as identified and described by Klevezal' and Myrick (1984), and Myrick (1991); and various degrees of interference in mineralisation as well as actual resorption of dentinal and cemental tissue (Boschma, 1950; Myrick, 1988). Many of these characteristics have also been scored by Akin (1988), in an attempt to discriminate stocks, with inconclusive results.

Akin (1988) explored the theme of 'individuality' in teeth of spinner dolphins (*Stenella longirostris*), comparing GLG patterns and general tooth morphology between stocks of supposedly different origins and geographical location. Klevezal' and Tormosov (1971) also used characteristics of the dentinal layers to distinguish between groups of sperm whales (*Physeter catodon*). They used specific characters in the teeth to identify populations, but rather than consider the possible reasons for differences, assumed that they were genetic. However, it is clear that any differences found might be related to the environmental experiences of the animals rather than any genetic differentiation.

Although the various types of anomaly may be inter-related and affected by the same internal and/or external factors, each may differentially respond in the severity of the response to such factors. Recent literature (e.g. Myrick, 1988) and that detailing causes of changes in tooth structure (Johannessen, 1964; Nikiforuk and Fraser, 1979; Jensen *et al.*, 1981), suggest that the resorption and transformation of existing dentinal tissues may be elicited by a severe long-term or continuing change in physiological state, probably coincident hormone imbalance which either exacerbates any pre-existing hereditary-based tendencies or initiates a chronic hypocalcaemic condition. Other anomalies such as marker lines may be clear-cut responses to discrete short-term problems, even recurrent ones if recovery is prompt, in growth and nutritional status. Situations of intermediate severity may result in varying irregularities such as mineralisation interference. All these conditions assume a systemic cause rather than a purely local one specific to the tooth such as gum infection or parasites. Myrick (1988) has proposed theoretical models of the effects of supra-threshold and chronic cyclic sub-threshold stressors on Ca^{++} balance and the mode of Ca^{++} recruitment into the blood. The evidence for a systemic cause of anomalies in pilot whale teeth was strengthened by the appearance of the same anomalies in duplicate sets of teeth (Lockyer, 1993).

MATERIALS

Samples of teeth were examined from porpoises obtained from California, Newfoundland, Norway, the British Isles and Denmark. They represent the following oceanic regions: Northeast Pacific, Northwest Atlantic, Northeast Atlantic and North Sea. Each sample comprised about 50 animals and included both sexes. The data, grouped into age categories of juvenile (0–2 years), young mature (3–6 years), and old (≥7 years) and sex are presented in Table 1. Of the total sample of 278 animals, there were 146 males and 125 females and 7 for which the sex was unknown. Length and reproductive status were also known.

Samples examined were from the following years and locations: British samples were collected from predominantly stranded animals, some of which may have originated as bycatch and represented mainly years 1988–90, with a range 1985–1991; Canadian samples were all from 1987 and were all bycatch; Danish samples were predominantly bycatch in seasons 1987–89; Norwegian samples were predominantly bycatch and were from years 1988 and 1989; Californian samples were a mixture of strandings and bycatch, and represented a wide period from early 1980's to 1989, but mainly from 1987–1989. The majority of specimens were therefore of bycatch origin and in the years 1987–1989.

Two teeth from each individual were available for preparation from California, Canada and the British Isles. The teeth were received in one of several ways: extracted from the jaw and only roughly cleaned but dried; preserved in 10% neutral formalin, usually still in

Table 1

Sample size of teeth used for mineralisation anomaly analysis, by age group, sex and geographic area.

	British Isles		Canada		California		Denmark		Norway	
Age group	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
0-2yr	13	11	9	13	15	13	21	9	7	15
3-6yr	11	13	8	15	9	11	6	8	12	3
≥ 7yr	10	2	2	3	3	2	12	7	8	0
0-20yr	34	26	19	31	27	26	39	24	27	18
Total including unknown sex	61		50		56		64		47	

the jaw; or frozen in the jaw. Samples from Norway and Denmark were already prepared as thin stained sections of decalcified teeth. California teeth were already prepared by Aleta Hohn. Once prepared, all teeth were examined both for age and anomalies, without reference to biological information about the animal.

METHODS

Tooth preparation

Once cleaned, teeth were sorted on the basis of appearance, into approximate age categories of neonate, young, young adult, old and very old, mainly to select for tooth size and volume, which affects treatment time. The teeth were then placed in perforated plastic histological baskets with labels and decalcified in RDO, a commercially prepared mixture of acids, for 2–8 hours, depending on the tooth volume. Decalcified teeth were flexible and rubbery in texture and were rinsed in running water for several hours. Fixation in 10% buffered formalin was then carried out and the teeth then stored temporarily in distilled water.

The teeth were sectioned on a CO_2-freezing stage of a sledge microtome at 20–25μm thickness. One tooth was cut at right angles to the jaw (the dolphin-cut) and the other parallel to the jaw (the porpoise cut), as described by Hohn and Lockyer (1995). Both teeth were cut through the crown and root so that the cut passed centrally through the pulp chamber. Sections selected as most central and complete were then stained in the histological baskets in Haematoxylin for approximately 15 minutes. The sections were then 'blued' in weak ammonia solution, rinsed in distilled water and then dehydrated in 70% alcohol before floating onto 5% gelatin-coated slides. The mounted sections were air-dried briefly on a slide warmer and immediately mounted permanently using Protex under a glass coverslip. All Protex-mounted sections required several days on a slide warmer to completely harden off.

Age determination

The sectioned and stained decalcified teeth were examined under a binocular microscope in plain transmitted light with magnification power ×10-×50. This was found to be adequate for the task of GLG counting. All teeth, including duplicates, were examined at least twice, using the criteria as described in the Appendix 1 of this volume.

Criteria used for classifying anomalies

Anomalies have been classified following the criteria used by Lockyer (1993) and Myrick (1988).

Pulp stones – discrete nodules containing concentric rings in the dentine (Fig. 1a), equivalent to the false denticles described by Avery (1976b) and frequently arising around blood vessels in the pulp. These structures may also remain free in the pulp rather than embedded in dentine.

Mineralisation interference – irregularities in the lamina formation emanating from differential inhibition and/or activation of odontoblasts at the mineralisation front (normally, the pulp cavity edge), causing realignment of the dentinal tubules and resulting in wavey lines, squirls and asymmetry (Fig. 1b), which disrupt usual patterns yet do not prevent continuous lamina formation (Myrick, 1988).

Marker lines – both in dentine and often cementum: discrete laminae which are regular yet noticeably different in appearance from the boundary layers in morphology and affinity for stain (Fig. 1c), either totally unstaining or deeply staining – equivalent to the

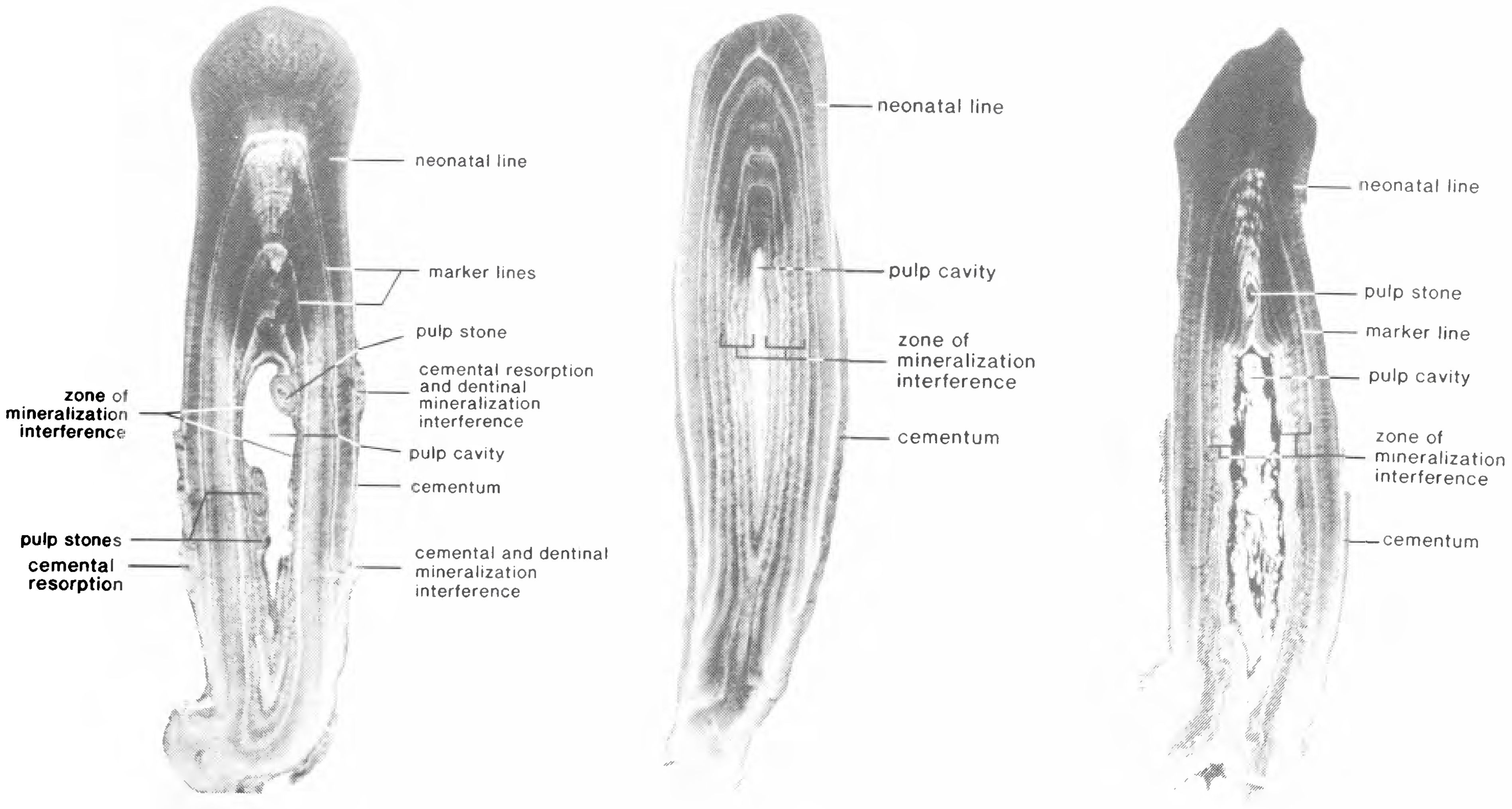
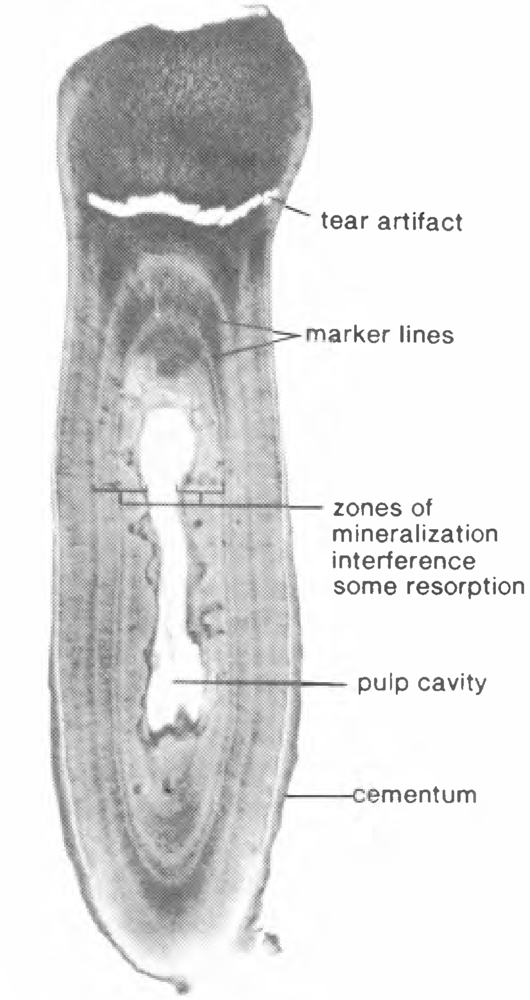


Fig. 1 (a) Porpoise tooth section showing pulp stones. Other mineralisation problems are also indicated, including marker lines as in Fig. 1c and cemental problems as illustrated in Fig. 1e. (b) Porpoise tooth section showing several GLG's where mineralisation interference at the mineralisation front has resulted in irregular boundary lines. (c) Porpoise tooth section showing a clear example of a marker line. Other mineralisation problems are also indicated, including mineralisation interference and a pulp stone.



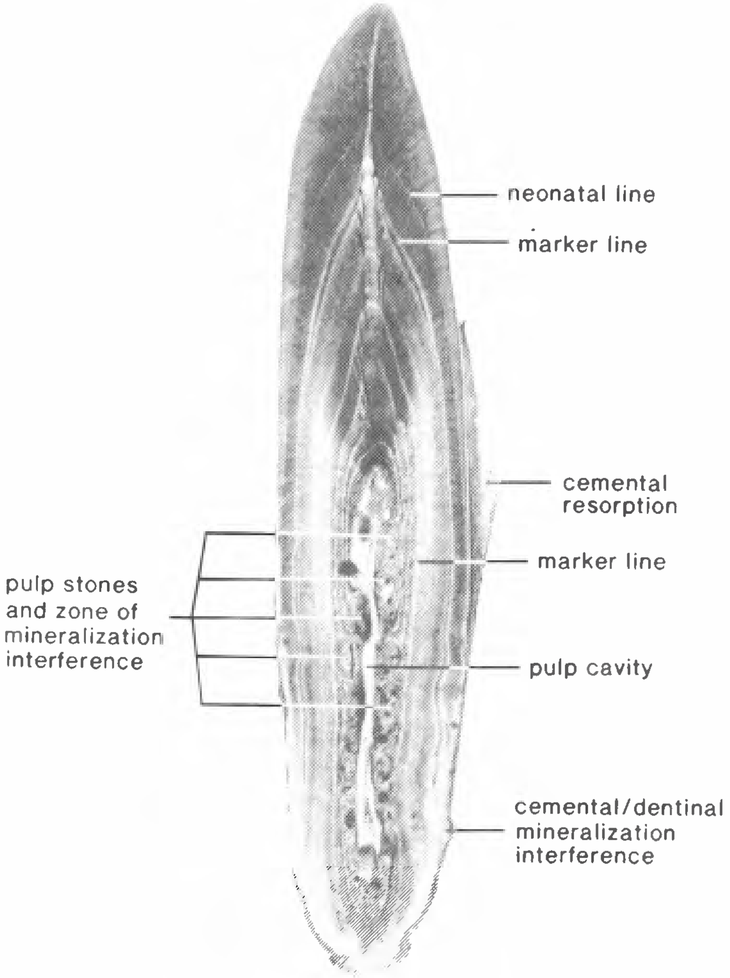


Fig. 1d. Porpoise tooth section showing dentinal resorption adjacent to the pulp cavity. Mineralisation interference is also present.

Fig. 1e. Porpoise tooth section illustrating problems in cementum formation. Pulp stones, marker lines and other mineralisation problems are also present.

DSL's and maturational layers described by Klevezal' and Myrick (1984) and the lines of Owen (Avery, 1976a).

Dentinal resorption – actual erosion and frequent repair of existing regular laminated dentinal tissue, resulting in an amorphous and/or globular appearance (Fig. 1d), frequently with holes, cutting across and into regular tissue (Myrick, 1988).

Cemental disturbance – any anomalous appearance of the usual laminated cemental tissue (Fig. 1e), including mineralisation interference and resorption (Myrick, 1988). Cemental resorption may progress into the dentine (Armitage, 1976) and may also result from local infection. Prodigious local deposition of cementum may occur if there are excessive or unequal forces on the tooth and may occur irregularly around the root in relation to the forces experienced (Armitage, 1976).

Characterisation of anomalies

Each tooth specimen examined was scored for the five anomalies defined above. Where pulp stones were observed, their number and relative position in the tooth were recorded. Mineralisation interference was noted in relation to the GLG's and age from initial occurrence. The number and position of marker lines were noted. The extent and position of dentinal resorption were recorded in the tooth and cemental disturbance was noted as any irregularity in formation. In severe cases of dentinal resorption and cemental disturbance, the anomaly involved both dentinal and cemental tissues.

RESULTS AND DISCUSSION

Comparability of samples by age and sex

Age frequency distribution

Initial analyses included comparisons of age frequency distributions between areas and sexes by means of Kolmogorov-Smirnov (K-S) tests (Zar, 1984). Results indicated that within areas, there were no significant differences in age frequency distribution by sex. Comparing areas, there were no significant differences in age frequency by sex or sexes combined.

Sex ratios and anomaly incidence

The total number of occurrences of different types of anomalies were recorded for each sex for all areas combined. The anomalies were then divided into each of the five anomaly types. The expectation was that there would be the same proportion of anomaly type in both sexes. The percentage of total anomalies by sex (170 male and 127 female cases; 57.2% male), was not significantly different ($chi^2=0.715$, $p>0.25$, $df=1$) from the percentage of animals in the sample by sex (146 males and 125 females; 53.9% male).

All areas have been combined to maintain a reasonable sample size, with the assumption that if any sex differences exist, they will be manifested in every area. This assumption is important, because as Table 1 shows, the sex ratios are not the same in each area. The assumption that there are no differences in anomaly incidence between males and females appears to be correct for this sample ($chi^2=6.087$, $p>0.1$, $df=4$), but it is perhaps too early to reach a firm general conclusion because of other assumptions made which have yet to be tested.

Table 2

Percentage incidence of mineralisation anomalies in porpoise teeth by age and geographic area.

Anomaly	Age group	British Isles	Canada	California	Denmark	Norway
Pulp stones	0-2yr	0	9.1	0	0	0
	3-6yr	4.2	4.3	15.0	7.1	6.7
	≥7yr	38.5	20.0	0	10.5	12.5
Mineralisation interference	0-2yr	4.2	27.3	34.5	6.45	8.3
	3-6yr	12.5	13.0	60.0	21.4	26.7
	≥7yr	23.1	60.0	57.0	26.3	50.0
Marker lines	0-2yr	0	13.6	6.9	0	20.8
	3-6yr	29.2	52.2	35.0	42.85	60.0
	≥7yr	38.5	100.0	85.7	52.6	100.0
Dentinal resorption	0-2yr	0	0	10.3	0	0
	3-6yr	16.7	0	45.0	14.3	0
	≥7yr	15.4	0	28.6	15.8	0
Cemental disturbance	0-2yr	16.7	22.7	41.4	58.1	25.0
	3-6yr	54.2	34.5	45.0	78.6	46.7
	≥7yr	53.8	60.0	85.7	68.4	50.0

Incidence of anomalies

Table 2 shows the percentage occurrence of the five different types of anomalies by area and age group. As expected, all anomalies tend to increase with age simply by virtue of their persistence in the teeth. However, the pattern of increase is not regular for pulp stones. The generally low incidence (Table 2), suggests that occurrence may be both uncommon and spontaneous. However, pulp stones originate from and may remain free in the pulp for long periods before becoming embedded in the dentine. The method of tooth preparation means that the pulp is not always evident. Thus pulp stones are only recorded when they are embedded. Pulp stones may form at an early age but not embed until later, if at all. Their appearance in the dentine would then be irregular, even though the incidence of pulp stones would normally be expected to increase with age (Avery, 1976b).

The most frequently occurring anomalies were mineralisation interference, cemental disturbance and marker lines, all of which increased with age. Cemental disturbance (including various unspecified forms such as uneven depositional thickness, resorption and other abnormalities) appeared to have a fairly high, often similar, incidence, in all age groups. The most common form of disturbance was uneven thickness.

Geographic region

All age groups were combined to examine presence/absence of anomaly types by geographical region. The hypothesis that anomaly incidence is similar in all geographical regions has been tested by chi^2-tests for the total sample of 278 animals. Results are presented below, using a $p<0.05$ level for significance.

Pulp stones

Only 19 (6.8%) animals of the total sample of 278 had pulp stones. The occurrence of pulp stones appears to be random i.e. not associated with geographic area (chi^2=1.915, $p>0.75$, df=4). It does not therefore appear that pulp stones are a useful indicator of stress in porpoises. Avery (1976b) found that in humans, whilst incidence increased with age, pulp stones were present in healthy teeth from healthy individuals. The cause of such stones and their fate are not understood.

Mineralisation interference

A total of 65 (23.4%, $n=278$) animals showed mineralisation interference. The chi^2-test results (17.453, with $p<0.005$, df=4) rejected the hypothesis that all animals were from a single sample. Incidences for the British Isles and Denmark were generally low and similar at 11–16%. The incidence was higher in Norway and Canada at 21–24%, and highest in California at 46%.

Marker lines

A total of 85 (30.6%, $n=278$) animals had marker lines. Chi^2-test results (12.792, with $p<0.025$, df=4) rejected the hypothesis that all animals were from a single sample. The overall incidence of marker lines was similar in the British Isles (20%), Denmark (25%) and California (27%). However, if age is taken into account (Table 2) the British Isles' samples had the lowest record of marker lines in ≥7yr old animals, whereas the incidence for Californian animals was much higher. The highest overall incidence was in animals from Canada (40%) and Norway (47%); Table 2 shows that all old animals from these two regions have marker lines.

Dentinal resorption

Relatively few (25, 9%) of the 278 animals showed dentinal resorption. The chi^2-test results (27.517, with $p<0.001$, df=4) again rejected the hypothesis that all animals were from a single sample. There was no dentinal resorption in teeth from either Canada or Norway, a low incidence in animals from Denmark (8%) and the British Isles (10%), and a high incidence in California (25%). Reference to Table 2 indicates that there is an incidence of this type of anomaly in all age groups from California, unlike the Danish and British samples.

Cemental disturbance

Almost half (126, 45.3%) of the sample showed cemental disturbance. Chi^2-test results (16.908, with $p<0.005$, df=4) were again significant. The lowest incidence was observed for Norway (36%) and the British Isles (39%), and the highest incidence for Denmark (66%). The high incidence relative to other recorded anomalies and the relatively high incidence in all age groups, suggests that these 'anomalies' may be usual and perhaps be a response to physical pressure and abrasion of the teeth, as well as other causes.

Environment and life history

Lockyer (1993) investigated potential correlations between marker lines, age and timing of occurrence in pilot whales. An unusually high incidence of marker lines corresponding to particular years was observed but no strong correlation with particular ages. For harbour porpoises, each region was scored for the age band where a marker line appeared, by the age class of the animal. The results are given in Table 3. The general pattern was for modal peaks at age 1 year for young animals and adolescent/young adults, and 2–4 years for older adults. Overall, the modal peaks were 1 year and 3 years. However, the Danish teeth showed a clear peak at 2 years. No animals with marker lines in the 0–2 years age group were recorded for Denmark and the British Isles.

Table 3

Modal age peaks, observed for marker lines in porpoise teeth, by geographic region.

Locality	Juveniles (0-2yr)	Adolescents and young adults (3-6yr)	Older adults (≥7yr)	All age groups (0-15yr)	Range of ages
British Isles	0	1	3	1 and 3	1-4
Denmark	0	2	2	2	1-8
Norway	1	1	4	1	1-6
Canada	1	1	2	1	1-4
California	1	1, 2 and 3	3	1 and 3	1-6
All regions	1	1	2 and 3	1	1-8

The years of sampling were very variable, ranging over many years in California, Denmark and the British Isles. Sorting for year class and incidence of marker lines was neither feasible nor useful, because sample sizes were too small and the majority of animals were not sufficiently long-lived, thus further reducing the sample size by year class. The pattern of peaks of occurrence in year one to two (age 0–1 years) and years three to five (age 2–4 years) is so consistent that it may be linked to life history events. According to Gaskin *et al.* (1984) weaning occurs at ca 8 months and this might be related to the marker line close to age 1 year. The second peak at age 2–4 years may be linked to sexual maturation. The age at attainment of age at sexual maturity varies with area, but may also vary with sex and over time (Read, 1990), but is certainly within this range (Gaskin *et al.*, 1984). The younger modal age of appearance of marker lines in adults from Canada may be a reflection of an earlier age at sexual maturity (*ca* 3 years) than in other areas (Read, 1990). The age at sexual maturity off California is over 4 years (Hohn and Brownell, 1990). In the British Isles, the age at sexual maturity is uncertain, but is at least 2 years (Martin *et al.*, 1990). Off Denmark, the age at sexual maturity has been reported as 3–4 years (Sørensen and Kinze, 1990). No information is available for Norway.

Whilst there are marker lines which appear at other ages throughout life, these are far fewer. The fact that the peaks occur at times that are close to major life history events (weaning and sexual maturation – neither of which are 'knife-edge' events), warrants further detailed investigation, especially in animals whose history is known.

Regional differences in anomaly incidence

California, Canada and the European countries represent at least three distinct geographic populations. There is evidence from a number of sources for additional stock distinction (IWC, 1995) e.g. from morphometrics (Yurick, 1977; Kinze, 1985; 1990; Yurick and Gaskin, 1987), comparative behavioural ecology (Barlow, 1987; Barlow and Hanan, 1995) and genetic and isozyme studies (Omura, 1953; Kapel, 1985).

The present study has revealed significant regional differences in the incidence of some anomalies. Mineralisation interference and marker lines appear to be linked and may represent physiologically-based differences between regions. Other types, particularly cemental disturbance, may be caused, at least partly, by some physical stress. The one anomaly type, dentinal resorption, which can most easily be explained by physiological stress also appeared to vary geographically and to not occur in the two northernmost regions. Pulp stones clearly do not provide a useful tool for evaluating stress of any form because of the low incidence and the irregular appearance in the dentine. Thus the three anomalies which are most likely to be useful for this purpose are mineralisation interference, marker lines and dentinal resorption.

In Table 4, the results for the different regions are ordered according to anomaly incidence. A cursory examination reveals similarities in occurrence for the British Isles and Denmark, and Canada and Norway; California was unlike any other region. The similarity between Britain and Denmark could be attributed to geographical closeness (there is some common sea area in the southern North Sea) and also, whilst some stock differences have been reported between the Baltic and North Seas (Kinze, 1985; 1990), there may be seasonal mingling in winter as suggested by Andersen (1990) from electrophoretic enzyme analysis.

The similarities between Norway and Canada are less easy to explain. Andersen (1990) found significant differences between Northwest and Northeast Atlantic animals using isozyme analysis, consistent with a clear separation of stocks. The similarities in anomaly

Table 4

Percentage incidence of mineralisation anomalies in porpoise teeth by geographic area.

Locality	Pulp stones	Mineralisation interference	Marker lines	Dentinal resorption	Cementel disturbance
British Isles	9.8	11.5	19.7	9.8	39.3
Denmark	4.7	15.6	25.0	7.8	65.6
Norway	4.2	21.3	46.8	0	36.2
Canada	8.0	24.0	40.0	0	32.0
California	7.1	46.4	26.8	25.0	48.2

incidence are, therefore, not likely to be caused by genetic factors. One common factor here is sea temperature, even though latitude is different. Grue and Jensen (1979) observed that teeth from colder areas showed clearer definition of laminae than those from warmer areas and sub-tropics: perhaps marker lines do not show as clearly in teeth from warmer waters.

Other possible factors causing variation in anomaly incidence, require further examination include pollution and diet.

Life history events

Another feature of marker lines is that they may be associated with life history events. As noted above, the high proportion of marker lines in year one and between two and four GLGs, may be linked with weaning and sexual maturation. Correlation with other events may be difficult and the possibility for long-term monitoring of the environment not feasible because of the relatively short life of the species.

Pollution

Although contaminant levels of DDT and PCB are reportedly high in harbour porpoises from Bay of Fundy (Gaskin *et al.*, 1971; 1982; 1983), the levels do not appear to be consistently higher than those for seals off East of England or Denmark where levels are considered 'low' (Law *et al.*, 1989) and are considerably lower than for the Baltic (Helle *et al.*, 1985). Coastal Norway is not known as a polluted area. An interesting point here is that teeth from neither Canada nor Norway have any evidence of dentinal resorption. Mineral resorption is usually associated with pollution (see earlier).

Analyses of contaminant levels in the blubber tissue of harbour porpoise from Denmark have not revealed high levels (Clausen and Andersen, 1985; 1988). However, organochlorine concentrations in blubber from porpoises taken in the Baltic are about twice those recorded from animals from the North Sea (Luckas *et al.*, 1988). The PCB/DDT ratios in blubber have been used to suggest separate stocks from western areas of Denmark (North Sea) and the Baltic (Clausen and Andersen, 1985). Such possibilities highlight the need to obtain contaminant levels for sample animals. Porpoise tissue from animals off West Wales were examined for DDT and PCB's, and were found to have concentrations similar to some animals from the Baltic (Morris *et al.*, 1989). Aguilar and Borrell (1995) reviewed the pollutant levels for porpoises in the Eastern North Atlantic and found considerable variations with high levels off coastal France. It is clear that contaminant levels can vary considerably even within a relatively small area, so that information needs to be very precise when attempting correlations, particularly for a species whose distribution remains very local.

It has been suggested that the high level of incidence of dentinal resorption in Californian teeth may be linked to high pollutant levels in the area (O'Shea *et al.*, 1980). However, more recent evidence indicates that the average pollutant levels in porpoise blubber from this region are only moderately high relative to other geographic regions (Calambokidis and Barlow, 1991) and that it does not constitute a 'hotspot'. Teeth from British and Danish coastal areas show only low incidence of resorption; but as reported above, organochlorine contaminant levels in animals from these areas are generally relatively low.

In summary, dentinal resorption is highest in the Californian sample, and organochlorine levels in porpoises are recorded as moderate from this region. Areas of the North Sea (Denmark and partly Britain) have low to moderate levels of pollutant concentrations recorded in porpoise and a low incidence of resorption was seen in animals from this region. The Norwegian situation on contaminants is not known from direct analysis of porpoise tissues, but it is assumed that levels are low. No resorption was observed in teeth from this region. The reportedly historic (1980s) high level of pollutants reported for some Bay of Fundy porpoises, but with an apparent absence of resorption in teeth, appears to confound a possible correlation of factors, although it is important to recognise that only up-to-date information will be relevant for animals that may live only about 10 years. The significance of dentinal resorption is unknown at this time, but the results here are sufficiently interesting to indicate further investigation on the precise relationship between organochlorine concentrations and dentinal resorption in individual animals.

Clearly generalisations about contaminant levels are inappropriate and misleading, especially as historic levels reported may be both different today and also not directly comparable in methodology used in analysis (Reutergardh and Knap, 1987). Any future analysis attempting a correlation of anomalies and pollutant levels must relate directly to the individuals sampled for any conclusion to be valid.

Currently, therefore, there is no obvious link between anomalies and pollution, but factors such as nutritional status and body condition may be important factors. However, there is little information currently available on this for any area and none that relates to a time series.

Food and feeding

The feeding ecology of porpoise is not well known, but regional differences in feeding habits may directly affect the growth of the teeth, particularly cemental deposition, as mentioned earlier. Feeding habits which create physical strain on the jaw and teeth may initiate cementum build-up. The cause of the difference between British and Danish dolphins in cemental disturbance is unclear. Some similarities in feeding habits and diet may occur seasonally. However, it is the differences which are important and this aspect may merit further investigation.

Off the Bay of Fundy, Canada, porpoises feed on schooling pelagic fish such as herring, *Clupea harengus* (Recchia and Read, 1989). The diet in British and Scandinavian waters, from examination of net-caught animals, also appears to be predominantly pelagic gadoid and clupeid fish (Rae, 1964; Martin *et al.*, 1990; Aarefjord *et al.*, 1995). In Californian waters, the implication from net-entanglement is that fish are the predominant prey taken (Hohn and Brownell, 1990). The general diet of porpoise includes mainly pelagic schooling fish which enter shallow coastal waters to spawn and also squid (Evans, 1987). Porpoises off the Danish coast have been found to contain herring and whiting, *Merlangius merlangius* (Andersen, 1965). Currently there is no information to indicate differences in feeding habits which might lead to variations in tooth structure from physical stress. Porpoises in all areas appear to feed on similar types of fish; this may be due to the fact that the majority of animals investigated were recovered from fishing gear. Therefore, the differences in cemental build-up on teeth cannot be explained by differences in feeding habits, at least with our present knowledge.

In summary, there appears to be no clearcut correlation between any environmental factor and anomalies in teeth. Regional differences cannot be consistently explained by stock differences and similarities occur in stocks which are known to be quite distinct. There appear to be no obvious differences between sexes, unlike in the long-finned pilot whale (Lockyer, 1993). The problem of attempting to identify environmental crises in any particular year or years is complicated in porpoise by the short longevity (little more than a decade), again unlike pilot whales which may live for several decades (Bloch *et al.*, 1993). The real usefulness of recording anomalies in teeth, e.g. marker lines, may be the potential link with life history events. At present this appears to be the one avenue which has real promise and could be tested experimentally with both known-history and captive animals.

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Age Estimation of the Amazon Dolphin, *Inia geoffrensis*, using Laminae in the Teeth

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KEYWORDS: AGE DETERMINATION; TEETH; AMAZON DOLPHIN

INTRODUCTION

Age determination of individuals is essential to the study of population biology. Several methods have been used to estimate age in odontocetes. Among those, the counting of the number of structural layers in the teeth (dentine and cement) or bone is considered the most precise and reliable technique (e.g. Klevezal' and Kleinenberg, 1967; Perrin and Myrick, 1980; Hohn *et al.*, 1989). Although it is generally accepted that potentially the number of growth layer groups can be read in the teeth of all species of odontocetes, results vary widely across species (Perrin and Myrick, 1980). In this study, the first application of a number of age determination techniques to teeth from specimens from the Amazon dolphin, *Inia geoffrensis*, are discussed.

The term growth layer group (GLG) is usually defined as a group of incremental growth layers of opaque and translucent dentine or cement of dolphin teeth (Perrin and Myrick, 1980). GLGs are the most prominent layered component within the tooth (Hohn, 1980) and are recognisable due to cyclic repetition, generally at a constant rate of deposition.

Evidence of annual deposition of growth layers has been shown for various odontocetes, e.g. *Delphinus delphis* (Collet, 1981), *Tursiops truncatus* (Hohn, 1980; Hohn *et al.*, 1989), *Globicephala macrorhynchus* (Lockyer, 1993), *Lagenorhynchus obscurus* (Manzanilla, 1989) and *Phocoena phocoena* (Nielsen, 1972). The Platanistoid dolphins also show an annual deposition of one growth layer group: *Lipotes vexillifer* (Anli and Zhou, 1992), *Platanista gangetica* (Kasuya, 1972) and *Pontoporia blainvillei* (Pinedo, 1991). However, the pattern of deposition of growth layers is not always regular and may vary between species. This may be due to environmental conditions, feeding cycles (Manzanilla, 1989) or endocrine rhythms (Myrick, 1988). There is evidence that two GLGs are deposited annually in the teeth of white whales, *Delphinapterus leucas* (Goren *et al.*, 1987). In general, however, evidence on the rate of dentinal growth in odontocetes has indicated an annual formation rate of one GLG. Hohn (1980) attributes these differences in the periodicity of GLG formation to accessory layers (AL), which are sometimes almost indistinguishable from annual layers.

Inia geoffrensis is the largest of the river dolphins and inhabits the largest riverine ecosystem of the world, the Amazon and Orinoco basins. Inia belongs to the Superfamily Platanistoidea, family Iniidae, and is popularly called boto or pink dolphin. The boto has between 100 and 130 teeth with the number per ramus ranging from 24 to 35, depending on the geographical provenance of the animal. It differs from other modern odontocetes, including other freshwater dolphins, by having two types of teeth. The anterior teeth (the first 14–20 pairs) are conical as in other odontocetes, but the cheek teeth, comprised by the most posterior 8–10 pairs, are of different shape, with one pointed cusp extending from the crown towards the labial side and a depression on the lingual side (Fig. 1). Both types

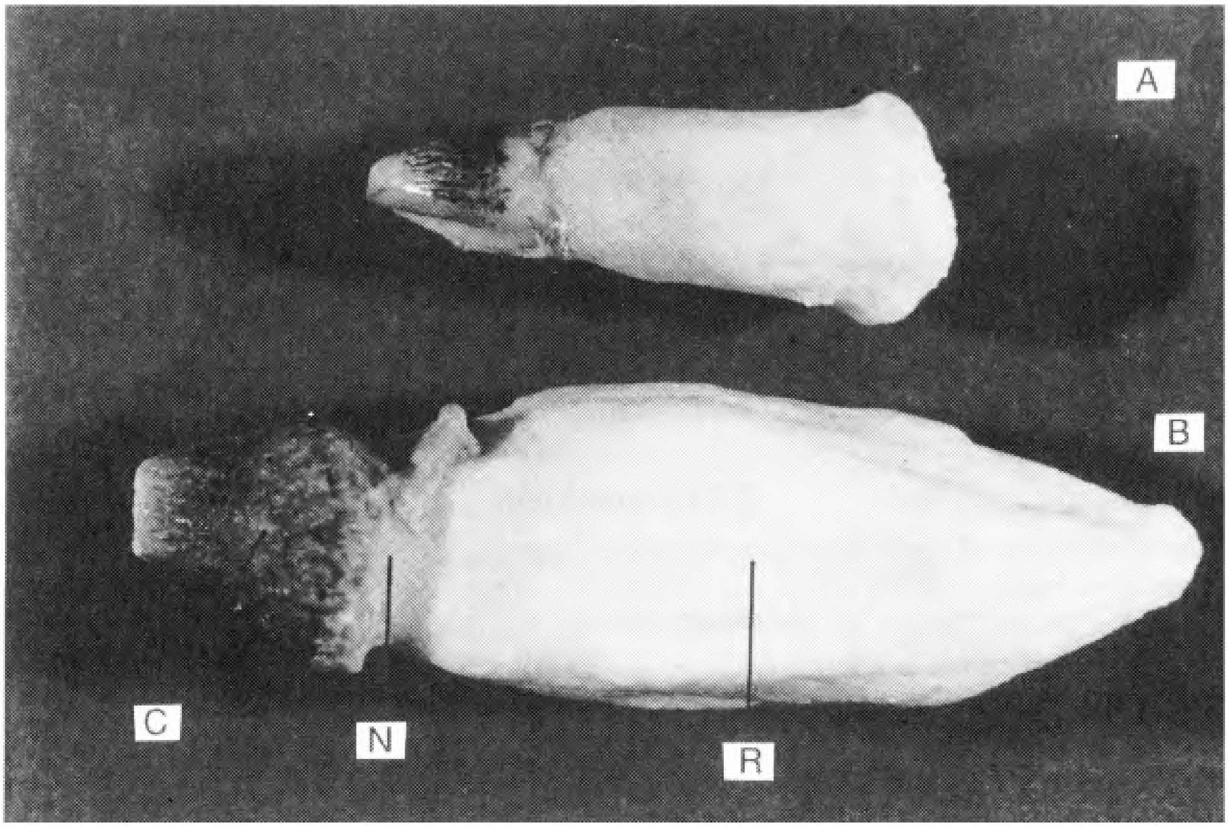


Fig. 1. The figure shows that the two types of teeth in *Inia* each have a single root. The anterior teeth (A) are small and conical. The posterior or cheek teeth (B) have a pointed cusp extending from the crown towards the labial side with a depression on the lingual side; also note the vertical folds on the root. C=crown, R=root, N=neck.

of teeth have a single root, slightly curved in the anterior conical teeth but usually straight in the posterior ones, although some of those have vertical folds around the root. In some young adults and most old animals the roots have a lateral expansion and the teeth are strongly anchored in the bone. All teeth have a rugose outer surface which is caused by a gentle 'wrinkling' of the enamel. They are often discoloured with a light-yellow to a tar-brown colour. No apparent differences exist between the teeth of males and females.

Dental anomalies such as caries, holes, chipping, other pathologies and broken teeth are very common in both sexes. Some individuals show teeth uniformly worn to the gum line. Others have some or all teeth partially worn on only one or on both sides of the jaw due to a severe lateral torsion of the rostrum. Some of the teeth have a cavity on the crown and on the root canal. Sometimes the tooth can be missing and the alveoli filled with osteodentine. A thick tartar ring below the gum line is quite common.

MATERIALS AND METHODS

Specimens examined

The teeth used in this study are from specimens in European, North and South American museums. Collections and catalogue numbers are presented in Appendix 1. Skulls, and consequently the teeth, were submitted to various types of treatment during the process of skull cleaning. Some were boiled, others macerated for several days in water with or without chemicals and washed with bleach or soap. Others are from washed skulls found clean or dry on river banks. After being washed, some skulls were dried in the open air whilst others were dried in ovens at low temperature. Some were stored dry for more than

35 years. Due to these procedures, a large number of teeth became very dry, cracked and split. In several cases, the enamel was cracked and flaking and the dentine soft and porous. In addition, it was also difficult to extract the teeth without breaking them or the skull or jaw when the bones are very dry. For this study, if one or more teeth were already loose, the straightest one was selected and used. Often the tooth easiest to extract was chosen. However, although dental anomalies such as the ones described earlier make it difficult to establish one standard position or area to select one tooth in different animals for ageing purposes, in my experience, the easiest place to extract teeth is in the middle of the lower jaw, just behind the posterior end of the mandibular symphysis.

Of the 186 skulls examined, most (141) had teeth and at least one tooth from each specimen was processed. Information on sex was available for 145 individuals (78 males and 67 females). Of the specimens of known gender, 65 were also of known body length. For a large number of animals only one tooth was available, so that even when the quality of the preparation was not very good, attempts were made to count the GLGs in the dentine, cement or in both structures. Before cutting, all teeth used for age analysis were weighed, measured and photographed when possible, then fixed in 10% formalin for about 24 hours.

Two series of specimens had some information about the method by which skulls were treated. Those include a total of 59 teeth of *Inia* specimens from the Central Amazon (39 males, 15 females and 5 of unknown gender), from the collection of aquatic mammals at INPA, Manaus. Teeth from these specimens were stored in 70% alcohol for several weeks before processing, and were extracted from skulls cleaned either by boiling or by maceration, dried in the open air or in a dessicator, and kept in a dehumidified room. The teeth of 17 specimens (11 adults and 6 immature animals) from the collection of the Museu Paraense Emilio Goeldi (MPEG), in Belém, Parà State, Brazil were extracted from boiled skulls, cleaned with chemical products and stored in a very dry and cold room. All but two skulls (8850 and 12756) were collected between 1916 and 1932. No information on cleaning and storage methods was available for other collections.

Laboratory techniques

Two main techniques for cutting and preparing teeth were used to determine which provides the most successful count of the laminae.

Decalcification and staining techniques

The methodology used to decalcify and stain was based on Myrick *et al.* (1983). Initially, decalcification was attempted by immersing the whole tooth in 10% formic acid. Depending on the size of the tooth, with this solution, decalcification can take several weeks before it is ready to cut. In an attempt to reduce the decalcification time, a commercially available mixture of acids (RDO) was also used. For small teeth or for teeth from young animals, decalcification took about 24 hours. However, in large teeth the crown and the tip of the root tended to be destroyed long before the centre of the tooth was decalcified. To avoid this problem, before immersion in RDO, a central longitudinal section (about 2.0 to 3.5mm thick) was made of each tooth using a low speed diamond circular saw. The slices were then separated into groups according to their density and decalcified in RDO. The decalcification time ranged from 7 to more than 36 hours depending on the density of the tooth. The tooth was considered ready when flexible, bending in the centre.

After being rinsed in running tap water for several hours, the teeth were sectioned longitudinally on a CO_2-freezing microtome from the tip of the root towards the crown to avoid the irregularities and splitting of the tip of the crown after decalcification.

Different thicknesses of sections in relation to stain quality and resolution in reading the layers were used for two kinds of stains (Ehrlich and Mayer's haematoxylin), and various staining times. After staining and washing, the sections were blued in a weak ammonia solution and rinsed in distilled water. The sections were then mounted with 100% glycerine following the procedure described by Hohn *et al.* (1989). Subsequently, permanent slides were prepared using DPX-mountant.

Unstained ground sections

Eight teeth from animals of various ages were prepared by cutting a thin dry slice (0.05–0.1mm) from the centre of the tooth, grinding the slice to translucency at approximately 30μm thickness on a very fine sandpaper sheet and examining it using transmitted light and a dissecting microscope. The slice was then compared with sections from a tooth from the same animal prepared by decalcification and staining. A ground tooth section of an animal from Kamogawa Sea World (KSW-2) was prepared by Kamiya (Anatomical Laboratory, University of Tsukuba, Japan). A whole tooth from that same animal, provided by Tobayama (Kamogawa Sea World, Japan) was prepared in the course of this study by the decalcification and staining process, and compared with the ground tooth section.

Dentinal and cemental layers

GLG counts were made for all teeth in which the quality of the section was good enough to give reliable results. Following the procedure described by Hohn *et al.* (1989) dentinal and cemental layers were read using a *Wild* M3Z dissecting microscope with transmitted light at powers from ×10 to ×50. Cemental layers were also counted using a compound microscope; six readings were made for each section. In the two first readings, the GLGs of the dentine and cement were read together. After intervals varying between 30 and 60 days, either the cement or the dentine was counted again, twice. Readings kindly provided by C. Lockyer (SMRU, Cambridge) were used as references to verify the consistency of the criteria used and to allow comparisons with previous readings. The age was then estimated, without access to the biological data. A figure was accepted when two readings produced similar results. In this study, it is assumed that one GLG represents one year of life of the animal and that the age assigned to each individual (n) is the number of complete years it is thought to have lived. The true age can therefore be between n and $n+1$ years.

The cement of *Inia* teeth is well developed and deposited as continuous layers over most of the tooth, but is generally thicker on the labial side (Fig. 2). Very often, the dentine stains poorly and contains several anomalies that interfere with the counting of the GLGs. Two teeth from each of 12 individuals (6 males, 4 females and 2 of unknown gender) were used to verify if the number of layers in the cement were in accordance with the number of dentinal layers. The growth layers in the cement were counted where the lines were most clear and easily distinguished on each individual tooth.

RESULTS AND DISCUSSION

Staining and unstaining sections

Unstained ground sections did not provide good results for *Inia* teeth. Readings of the slices with thicknesses ranging from 15μ to 35μ were not satisfactory. The opacity of the dentine due to dense mineralisation makes the GLG counting unreliable or even impossible.

Decalcification and staining techniques provided the best readings. For *Inia*, especially when using the posterior and larger teeth, it is essential to cut a central slice in order to

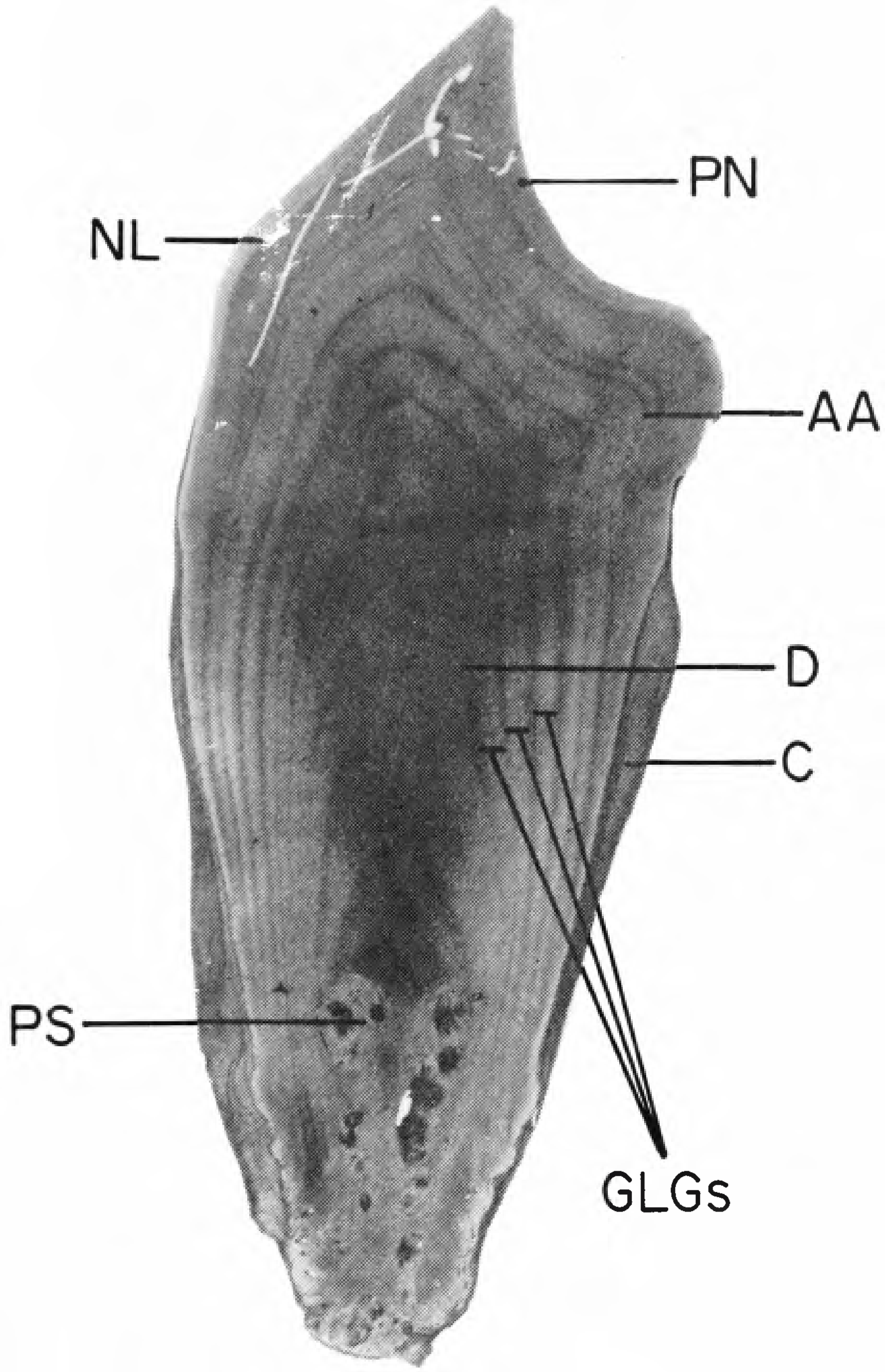


Fig. 2. Longitudinal section of decalcified and stained teeth of *Inia geoffrensis* (female MA 107, 12 dentinal GLGs) from the central Amazon with schematic interpretations of layer patterns. PN=prenatal dentine, NL=neonatal line, C=cement, D=dentine, AA=accessory line, GLGs=growth layer groups, and PS=pulp stone.

achieve even decalcification. After decalcification, the best results were obtained with sections between 20 and 25μ, depending upon the size of the tooth. This thickness permits counting layers from the dentine as well as from the cement and gives a good quality of stain. Thinner slices stain faster but the contrast is not good and the tissue has a tendency to roll up when cutting. For thicker slices it may be necessary to leave them over 24 hours in haematoxylin and they are not always adequately stained. The best contrast between growth layers was found with Mayer's haematoxylin, although the quality of the sections varied even when staining for more than 24 hours.

Dentinal and cemental layers in Inia

In the boto, all teeth erupt at the same time and contain the same number of growth layer groups. When the laminae were clear the number of layers in the dentine and cement was found to be similar in animals within a given age class, showing that dentine continues to be deposited throughout life.

After decalcification, it is sometimes possible to see a very thin enamel layer covering the crown of the tooth. The next layer, the prenatal dentine, is less opaque than the postnatal dentine and in some young individuals shows several conspicuous laminae. The neonatal line is a well-defined translucent layer which usually finishes below the level of the tooth neck. The dentinal GLGs consist of one narrow translucent layer and one broad opaque layer. The identification of the first GLG is the key for correct age estimation, since it is the guideline for the following layers (e.g. Hohn *et al.*, 1989). The two first dentinal growth layers in *Inia* teeth are much broader than the following layers and show several accessory and incremental layers (Fig. 2). These layers are quite distinct and are part of the GLG. However, they can cause problems in discerning GLGs since they can be erroneously considered as boundary layers between GLGs. One of the criteria used to distinguish accessory lines was to follow the line of the GLG until the bottom of the tooth. In most cases accessory layers finished before reaching half the length of the root.

Stained sections of cemental GLGs show stronger contrast than those of the dentine. They consist of a pair of opaque and translucent layers, with numerous fine accessory lines. In some parts of the cement the accessory lines may merge into one single thick dark line and then become separated again further down the tooth (Fig. 3). The cement of adult teeth is generally thicker in the bottom half of the tooth and covers all the root surface. The thickness of the cement is extremely variable among individuals. In some specimens, cemental layers are difficult to count, due to both the variation in thickness and layering structure and the presence of indistinct lines. In some teeth, the GLGs are thin and compressed while in others the GLGs are broad, having the appearance of double layers as described by Klevezal' (1980). In this case they might be wrongly counted as two GLGs. Double layers seem to occur in long-lived mammals where the pattern of seasonal growth changes with age and is not inherent to all members of a population but rather determined by some genetic factor (Klevezal', 1980).

For individuals with teeth showing up to three layers in the dentine, the number of lines in the cement was not easy to differentiate. In teeth with up to 9–10 GLGs, the pulp cavity is not completely occluded, but after 12 GLGs the pulp cavity is usually filled with irregular and anomalous dentine making the use of dentine for age determination more difficult. At this stage, the cemental GLGs may exceed the number of dentinal growth layers and might be used to determine age more precisely. In several individuals, the quality of the teeth was so bad as to be unsuitable for ageing while for others it was only possible to read the layers in the cement.

In other species of odontocetes it is known that the filling of the pulp cavity by dentine, with age, results in growth layers being thinner and closer to each other (Hohn *et al.*, 1989). In *Inia* however, at a very early age, several teeth show an increase in thickness due to the deposition of large amounts of osteodentine on the tip of both sides of the root. In animals with 5–8 GLGs or more, the tip of the root at the bottom of the tooth may join, closing the root canal. The large pulp cavity then becomes gradually filled with an irregular deposition of osteodentine, making the counting of GLGs difficult in older animals.

Comparison of section quality between the laminae of teeth treated with chemical products, boiled or naturally cleaned showed the same range of variation, suggesting that the poor resolution of the laminae in some teeth is not caused by such external factors. Teeth without any severe cleaning treatment also presented inconspicuous lines in the

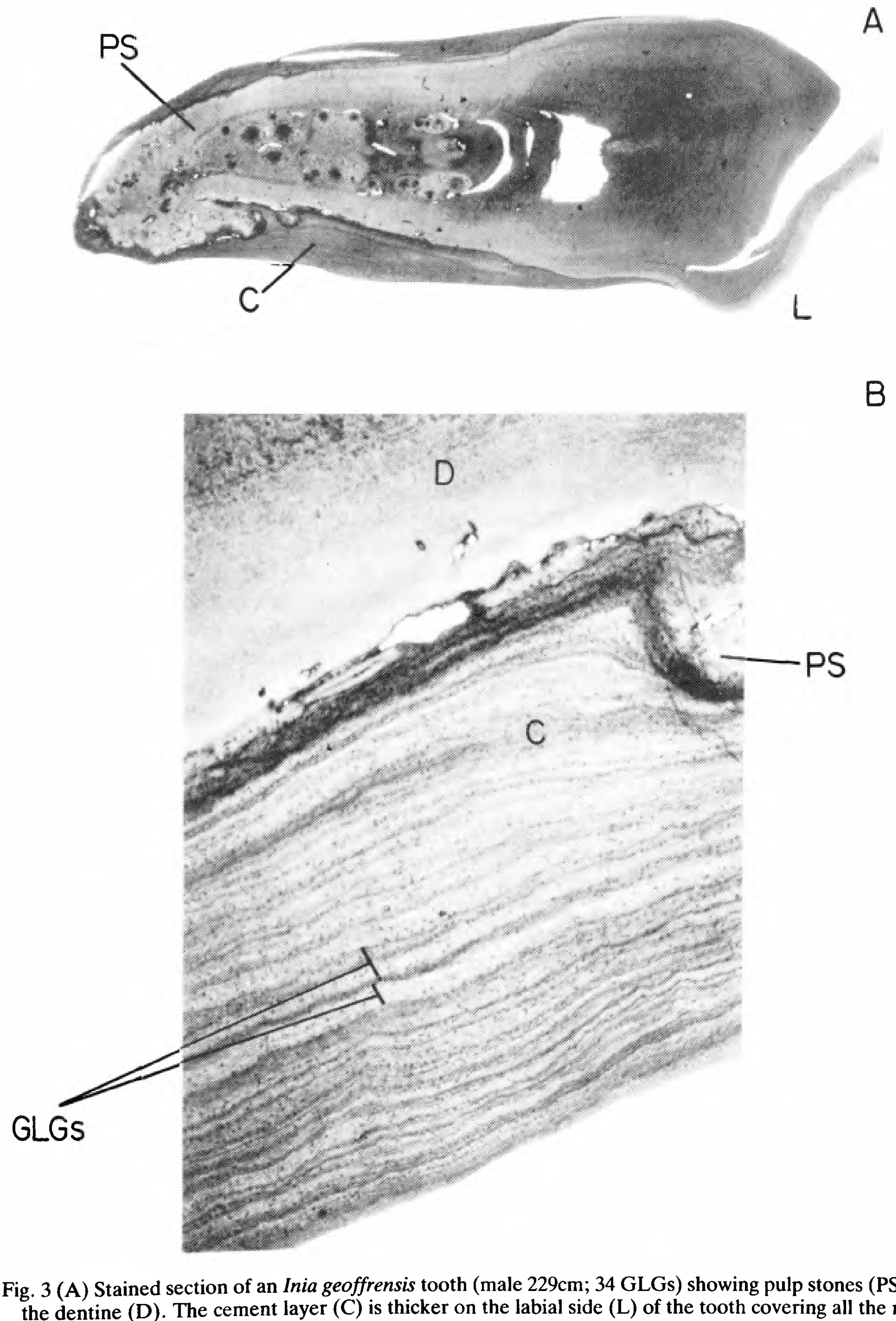


Fig. 3 (A) Stained section of an *Inia geoffrensis* tooth (male 229cm; 34 GLGs) showing pulp stones (PS) in the dentine (D). The cement layer (C) is thicker on the labial side (L) of the tooth covering all the root surface. (B) Detail of the cemental layers of the same tooth showing the 'double layers' (see text). Note that the relatively clear cemental lines allow a reliable estimate of age in a tooth where the dentine is effectively unreadable.

dentine and cement. However, the physical quality of the sections (e.g. lack of cracks) seems better in teeth that have not undergone chemical or boiling treatment.

In the anterior teeth of *Inia*, a centre-line cut is important for good interpretation of the GLGs (Hohn *et al.*, 1989; Hohn, 1990), but was difficult to obtain, mainly due to curvature and some degree of twist. In addition, the non-conical shape of the cheek teeth does not provide the sharp end of the pulp-cavity characteristic of the on-centre cut of conical teeth. According to Hohn (1980; 1990) these might be a source of error in the age estimation of odontocetes, since the off-centre cut accentuates the accessory lines, thus overestimating the number of GLGs. Pinedo (1991), however, found no significant differences in age estimation between close-to-centre cuts and on-centre cuts in *Pontoporia* teeth.

Tooth anomalies

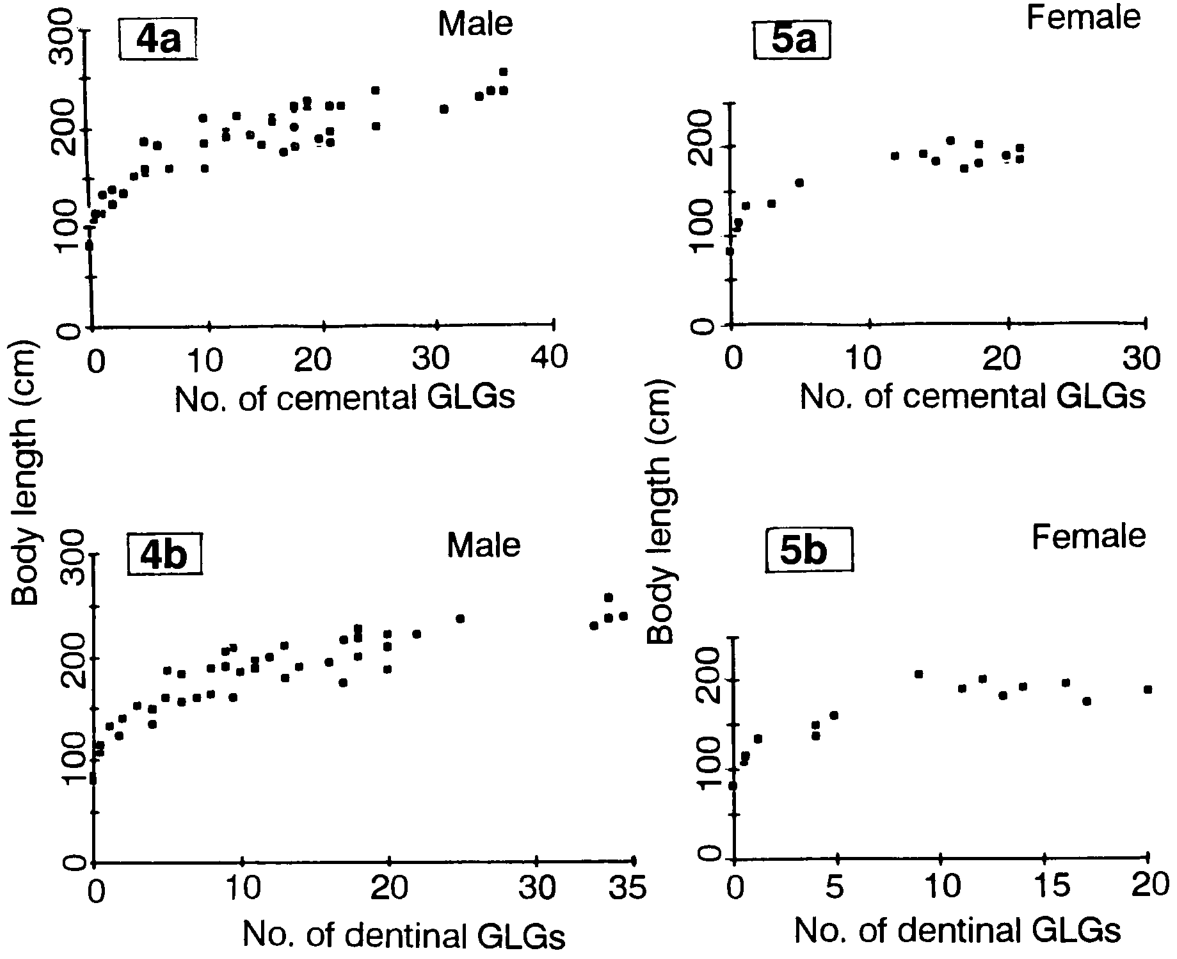
Dentinal anomalies, such as pulp stones, were noticed in most specimens with more than 6–7 GLGs. They consisted of concentric nodules and irregularities (Fig. 2) formed by remnants of epithelial root sheath which have become enclosed in the pulp as a result of disturbance during development (Avery, 1976). These structures are difficult to decalcify and stain, compromising the laminae reading. Mineralisation interference is another anomaly commonly found in the dentine. It consists of irregularities in the dentinal lamina due to inhibition and/or activation of odontoblasts, causing realignment of the dentinal tubules and resulting in waves, squirls and asymmetric lines (Lockyer, 1993). In *Inia*, these anomalies appear simultaneously in several teeth of the same individual. Lockyer (1993) suggests that mineralisation interference might be the result of short-term growth and/or nutritional condition. A third kind of anomaly is the change in direction of the dentinal GLGs which at the bottom of the tooth follow the extension of the roots, while the lines in the centre of the pulp cavity continue to grow concentrically. This growth pattern makes differentiation between the lines in the centre of the tooth and those growing at the bottom difficult.

Age determination

The procedure used to estimate the age of *Inia* was based on the 'reader's guide to dolphin teeth' presented by Hohn *et al.* (1989). The pattern of GLGs observed for *Inia* is similar to that of other dolphins (see Fig. 1), despite remarkable individual variation in tooth size and GLG width.

The number of dentinal and cemental GLGs ranged from 9–36 in males (with body lengths between 190 and 255cm), with the maximum values corresponding to the age and body size of the largest specimen known from the Amazon Basin (da Silva, 1994). The pulp cavities in the teeth of this animal were completely occluded, with pulp stones present at the base of the dentine and double lines in the cement. Generally, the pulp cavities in males are occluded between 9–11 GLGs. At 10 GLGs the body size in most males is larger than 190cm. For two specimens (males 032 and 16450) the number of GLGs was not consistent with their body size (154 and 155cm, respectively). This result is probably related to the poor quality of the tooth sections of these individuals. Two males with similar body lengths (152 and 156cm) had 3–4 GLGs and 5–6 GLGs, respectively. Females with the same body size had 4–5 GLGs in both the dentine and cement. The oldest female recorded was 21 cemental GLGs in age and measured 196cm in body length. Females with body lengths between 174 and 205cm had between 13–19 GLGs in the dentine and 11–21 in the cement. Some females with 8 dentinal GLGs had occluded pulp cavities while in one immature female with 5 GLGs the pulp cavity was still open.

Figs 4 and 5 show the relationship of body length against the number of GLGs for males and females, respectively. Growth is similar between the sexes until about 170cm in body



Figs 4 and 5. Plot of body length on number of cemental (a) and post-natal dentinal (b) growth layer groups (GLGs) in male and female *Inia geoffrensis*.

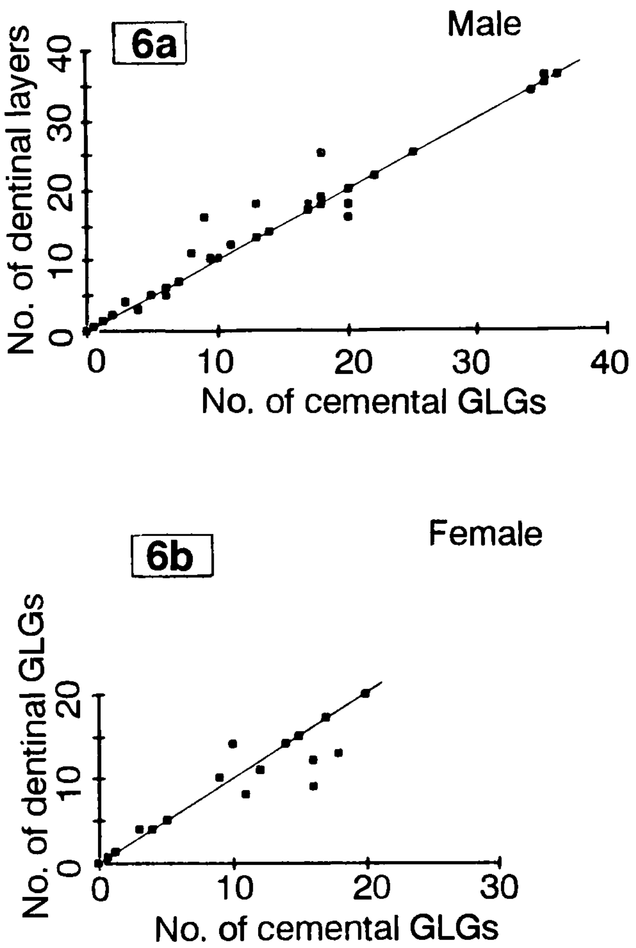


Fig. 6. Relationship between the number of dentinal and cemental growth layer groups (GLGs) in male (a) and female (b) *Inia geoffrensis*. The line of points indicates parity between dentinal and cemental counts.

length, when the growth rate of females is reduced. The maximum body size observed in females ranged from 190 to 205cm and in general they were older than males of the same size. Also males and females at any given age have approximately the same number of dentinal and cemental layers (Fig. 6). This indicates that the rate of layering is about the same for both tissues and both sexes, although in older animals the complexity of dentinal lines particularly due to pulp cavity anomalies is such that they are often uncountable.

CONCLUSIONS

The examination of dentinal and cemental GLGs constitutes a useful technique for age determination in *Inia*. This study revealed that the best method for both the cement and dentine was obtaining decalcified stained sections. However, given the difficulties arising out of irregular tooth structure and problems in obtaining clear differentiation between laminae, other techniques and structures should be explored and compared.

In a given individual, all teeth erupt at the same time and contain the same number of GLGs. Dentinal and cemental layers are generally equivalent in numbers (although with some discrepancies); potentially this permits a good estimation of age.

Postnatal dentine and cement is formed by the deposition of a succession of layers. In *Inia*, the GLG as defined here consists, in the dentine, of annual deposits comprising one narrow translucent layer and one broad opaque layer, with each GLG beginning with the translucent layer. In contrast, the cemental GLG consists of one broad and light layer and one narrow and dark layer.

The rate of growth layer deposition is not yet proven, but results from teeth of captive animals and the similarity of layers with other odontocetes suggests that only one GLG is deposited each year.

Dentinal deposition stops due to the occlusion of the pulp cavity by pulp stones, and at the base of the root by cemental accumulation, at about 10 GLGs in females. In males the occlusion of the pulp cavity occurs much later, with large individual variation. The maximum number of GLGs found in this study was 36 in males and 21 in females.

Ninety (64%) of the 141 teeth from which a decalcified and stained section was examined had readable lines in one or both laminated structures. Of these, 13 (14%) had readable lines only in the dentine, 14 (16%) only in the cement and 63 (70%) in both.

Anomalies usually appeared at the same time in different teeth of the same animal and may be due to a systemic cause, such as a problem with growth or nutrition rather than a problem specific to a particular tooth.

The inconspicuousness of the tooth laminae does not seem to be caused by external factors. Teeth which have not undergone severe treatment in storage or preparation can still present inconspicuous lines in the dentine and/or cement.

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Appendix 1

INSTITUTIONS AND MUSEUM COLLECTIONS (ACRONYMS IN BRACKETS), CATALOGUE NUMBER AND LOCALITY OF COLLECTION OF THE SPECIMENS ANALYSED

Rijksmuseum van Natuurlyke Historie, Leiden (RNHL), specimens 12400 and 12401, from Tucuruí, Pará, Brazil; **Swedish Museum of Natural History** (SMNH), specimens A558294/6648, Rio Solimões; A558295/6929–671, A558296/6930–672, Rio Tocantins; A558297/6931–673, A558300/8300, A558301, Rio Amazonas; A558298/6932–904, A558299/6933–905, Rio Madeira; **Zoologische Staatssammlung**, Munchen (ZSM) 1979/187, unknown locality (market of Manaus), FR 1971 (Private coll.) Manacapurú, Rio Solimões; **Zoologisches Museum Hamburg** (ZMH), 2698–70, Rio Tapajós, Santarém; **Museum of Natural History Paciano** (Umbria, Italy) c/o Dr. G. Pilleri, Switzerland, 433, R. Amazonas, Manacapurú, 832/56 (Grosjean Exped.), Amazon, Brazil, 807, 806, 805, S. Carlos de R. Negro, Venezuela, R. Orinoco, Venezuela, R. Apure, Venezuela; **Los Angeles County Museum of Natural History** (LACM), 72146, Amazonas, Iquitos, Peru, 19588, R. Ucayaly, Peru, 18589, R. Napo, at Marina Cocha, 19590, R. Ucayaly, Peru, 19591, 19593, 19595, 19596, R. Amazonas, Leticia, Colombia, 52457, 54440, 054441, Peru, 54453, R. Orinoco, Venezuela, 27060, R. Amazonas, Leticia, Colombia, 27063, Colombia, 27064, R. Amazonas, Manaus, 28257, R. Guanare, Venezuela, 27067, R. Ucayaly, Peru, 27074, 27075, R. Amazonas, Iquitos, Peru; **San Francisco Academy of Sciences** (SFAS), 13135, 15429, 16637, R. Amazonas, Iquitos, Peru, 16450, 16631, R. Amazonas, Leticia, Colombia; **American Museum of Natural History**, NY (AMNH) 395614 395602, S.F. de Apure, Venezuela, 147503, 147502, 98695, 98695, R. Tamaya, Peru, R. Saimiria, Peru, 95753, R. Tapajós, Brazil, 93415, 93412, 93414, R. Andira, Brasil; **Smithsonian Institution**, Washington, 93416, R. Amazonas, Villa Imperatriz, 239667, R. Tapajos, Santarem, Pará, 395415, S.F. de Apure, 406801, R. Manapiare, Venezuela, 49582, R. Purus, Brazil, s/n 10001, R. Nanay, Peru, 396166, S.F. de Apure, 55517, 395416, R. Ucayaly, Peru. **Museum of Zoology, University of Florida** (MZUF) #1, #2 South America, 1238, 7818, 17518, 17541, 17535, 17540, 15543, 17544, 17545, 18775, 18776, 18777, 18779, 18780, 18778, R. Amazonas, Iquitos, Peru, 17542, R. Napa, Equador, 93413, R. Andira, Brazil; **Academy of Sci. Chicago**, 57819, R. Apure, Venezuela, 51084, R. Tocantins, Brazil, 51083, R. Tapajos, Brazil; **Kamogoa Sea World** (Japan), KSW-2; **Museu Paraense Emilio Goeldi** (MPEG), 4610, 4011, s/n #1, 4606, s/n#2, 4612, 4609, 4607, s/n #3, 4602, 4605, 4603, 4604, 4608, 4642, R. Tapajós, Taperinha, Brazil, 8850, Ilha Caviana, Pará, Brazil, 12756, Rio Xingu, mouth, Brazil; **Museu Nacional do Rio de Janeiro** (MNRJ), Brazil 64230, R. Tapajos, Brazil, 6020, R. Amazonas, Igarapé Cuiabá, 6425, R. Amazonas, Lago Serpa; **Estacion Biologica de Rancho Grande, Maracay**, Venezuela, 1739, R. Arauca, Venezuela, 4128, R. Tamatama, Venezuela, #36, R. Orinoco, Venezuela. **Instituto de Zoologia Tropical** (MBUCV), Caracas, Venezuela, 1–135, R. Apure, 251, R. Orinoco. **Aquatic Mammals Laboratory** (MA)/INPA, 019, 021, 027, 030, 031, 044, 049, 075, 084, R. Japurá, L. Amana, 002, R. Amazonas, Santarém, 004, R. Negro, Brazil, 006, R. Amazonas, P. Janauaca, 011, R. Juruá, Acre, 014, R. Demeni, Barcelos, 022, 061, 076, 095, 096, 116, Praia Grande, R. Negro, 064, Anavilhanas, R. Negro, 027, 030, 066, 070, L. Tefe, R. Japurá, 046, R. Negro, P. do Abiu, 058, R. Solimões, near Coari, 083, Careiro, R. Solimões, 089, R. Tapajós, Curuatuba, 090, 091, 092, 093, 094, 098, 099, 100, 101, 102, 103, 104, 105, 106, 107, 108, 109, 110, 111, R. Tucuruí, 112, Marchantaria, R. Solimões, 115, R. Tapajós, Santarém, 118, R. Guaporé.

Procedures and Techniques Applied by NINA for Cutting, Staining, Mounting and Ageing Porpoise Teeth

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ABSTRACT

Age determination of terrestrial mammals based on growth layers in the teeth has been a routine technique at NINA in Trondheim for many years. This paper describes how this well established technique has been applied and modified for the harbour porpoise.

KEYWORDS: HARBOUR PORPOISE; AGE DETERMINATION

INTRODUCTION

Since the early 1960s, procedures for age determination have been worked out for various animals and are in routine use by the Norwegian Institute for Nature Research (NINA). At first, the technique was focussed on cervids, since knowledge of population structure (age and sex distribution) in these species was important for deciding the pattern of hunting. The laboratory techniques applied for cervids have been published by Reimers and Nordby (1968).

The main focus for the development of age determination methods was later changed from cervids to carnivores. Routines for age determination have been worked out for all carnivores native to Norway. For the lynx (*Lynx lynx*) and wolf (*Canis lupus*), see Kvam (1984) and Kvam and Sørensen (1984). The accuracy of age determination is steadily being improved, partly based on animals of known age. The harbour porpoise is the first marine mammal which has been age determined at NINA.

MATERIALS AND METHODS

Laboratory procedure

The procedure applied for harbour porpoises (*Phocoena phocoena*) is similar to the procedure for cervids published by Reimers and Nordby (1968). But, due to the different size of the teeth and some species-dependent differences, the duration of some steps may differ:

(1) decalcification in 5% nitric acid (HNO_3) – 6 hours;
(2) rinsing in running water – overnight;
(3) sectioning by freezing microtome;
(4) staining by MAYERS HAEMALUN – 45 minutes;
(5) mounting on glass slide using KAISERS GLYCEROL GELATINE; and
(6) interpretation of annual growth layer groups in dentine based on Grue Nielsen (1972) and Perrin and Myrick (1980).

Sectioning

The crown was *not* cut off before sectioning as in terrestrial mammals, which are aged by analysis of annual root cementum. The dentine zones in harbour porpoise teeth are found inside the crown. Consequently, cutting off the crown would mean destruction of the tooth for ageing purposes.

Freezing microtome

Longitudinal sections were produced by a REICHERT-JUNG 1206 with a FRIGOMOBIL electric freezing unit.

Thickness of sections

Sections of harbour porpoise teeth were at first produced in three different thicknesses: 15, 20 and 30μ. The thinnest sections were found to be difficult to mount on glass slides. Sections of 20 and 30μ were just as suitable as 15μ ones for counting dentine zones. However, 20μ may be better than 30μ for reading of cementum zones. Thicknesses of 20–30μ seem to be a suitable standard.

Staining

The recipe for MAYERS HAEMALUN has been chosen from Romeis (1948). Other similar recipes may be found in standard textbooks (e.g. Baker, 1958; 1966; Gray, 1964). The following recipe is applied by NINA:
(1) Haematoxylin, 1g [$C_{16}M_{14}O_6$];
(2) distilled water, 1,000cm [H_2O];
(3) sodium iodate, 0, 2g [$NaIO_3$];
(4) potassium aluminium sulphate, 50g [$KAl(SO_4)_2$];
(5) citric acid, 1g [$C_6H_8O_7 . H_2O$].

Staining for 45 minutes has proved to give good, readable results and seems suitable as standard.

Reading

The interpretation of annual growth layer groups in dentine is based on Grue Nielsen (1972) and Perrin and Myrick (1980).

Age determination of harbour porpoises of 1, 2 and 5 years old is demonstrated in Figs 1, 2 and 3. The light staining neonatal line (N) is formed at birth. Dark and light staining lines are counted inwards from this line. As each year's light staining line is normally developed in July, and parturition normally takes place in June, age in years corresponds directly to the number of light staining lines (L) counted. Approximately 700 harbour porpoises have been aged at NINA since 1989. In some cases, where dentine zones were difficult to read, age was decided by comparison with thickness of dentine and cementum deposits. The number of cementum zones tended not to correspond in all cases with the number of dentine zones (see Fig. 4).

Age determination beyond the age of eight years seems to be very difficult, due to blurring of the light and dark lines as the pulp cavity is filled up.

An example of harbour porpoise age reading is shown in Table 2. A guide to the symbols can be found in Table 1.

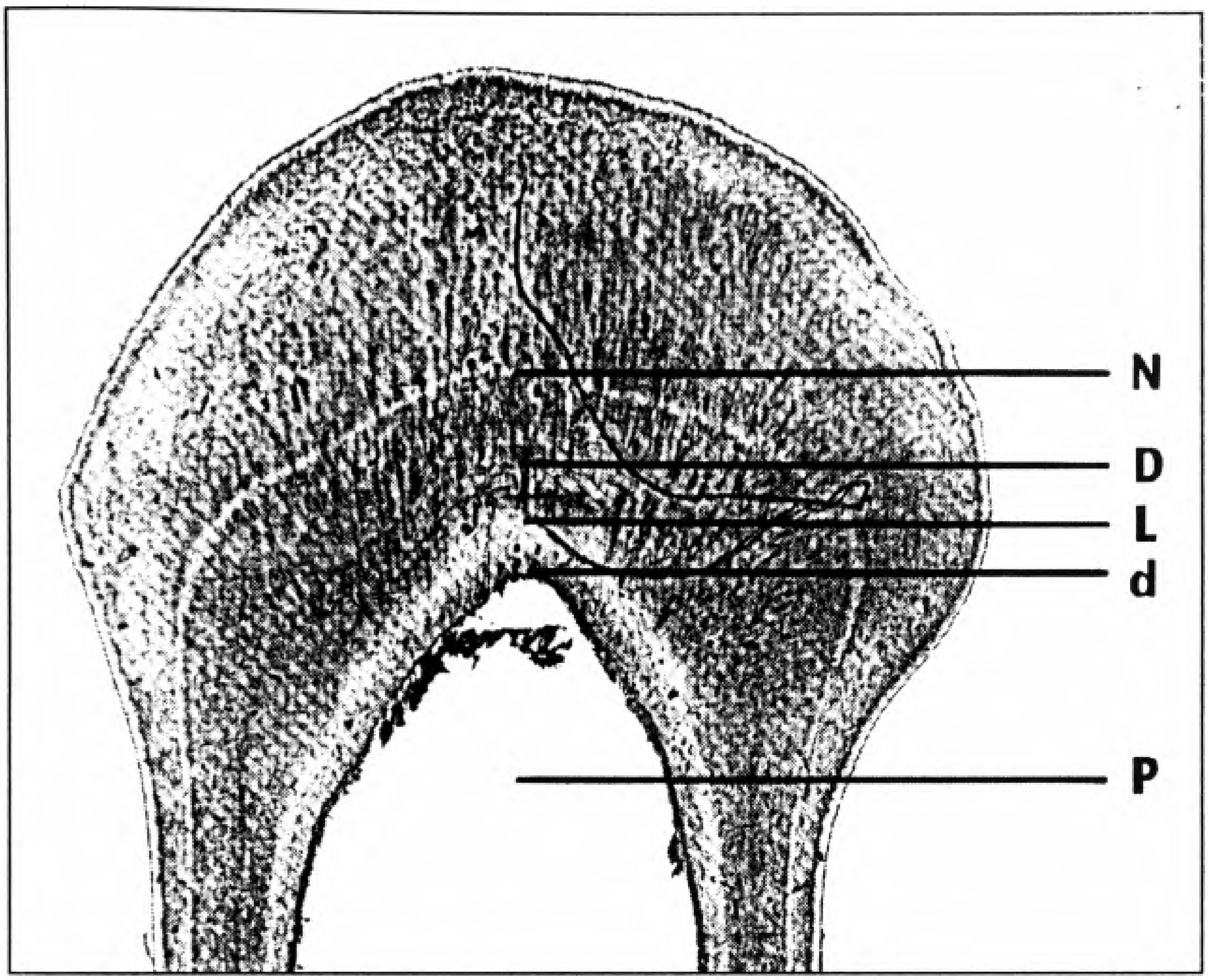

Fig. 1. Photocopy of a thin section microscope slide from No. 88–019. Age determined as 1 year. N = The neonatal line, the first light staining line which is formed around birth. Dark and light staining lines are counted inwards from the neonatal line. One dark staining line, one light line and one narrow dark line surrounding the pulp cavity (P) are marked D, L and d (see guide to symbols in Table 1).

Table 1

Guide to symbols used for standard reading of harbour porpoise age at NINA.

Sex:	1 = male 2 = female	
Age:	Age in years, based on no. of light staining annual dentine layers which normally develop in July. Parturition normally takes place in June.	
Reading:	D: Dark staining dentine zone L: Light staining dentine zone	
	Capital letters:	Distinct, easily recognisable
	Small letters:	Less distinct and narrow zone
	Parenthesis:	Uncertain, diffuse outline
Lines:	No. of light staining dentine lines. Uncertain counting indicated by parenthesis. In such cases age may have been decided by comparison with thickness in dentine and cementum deposits in already aged teeth.	

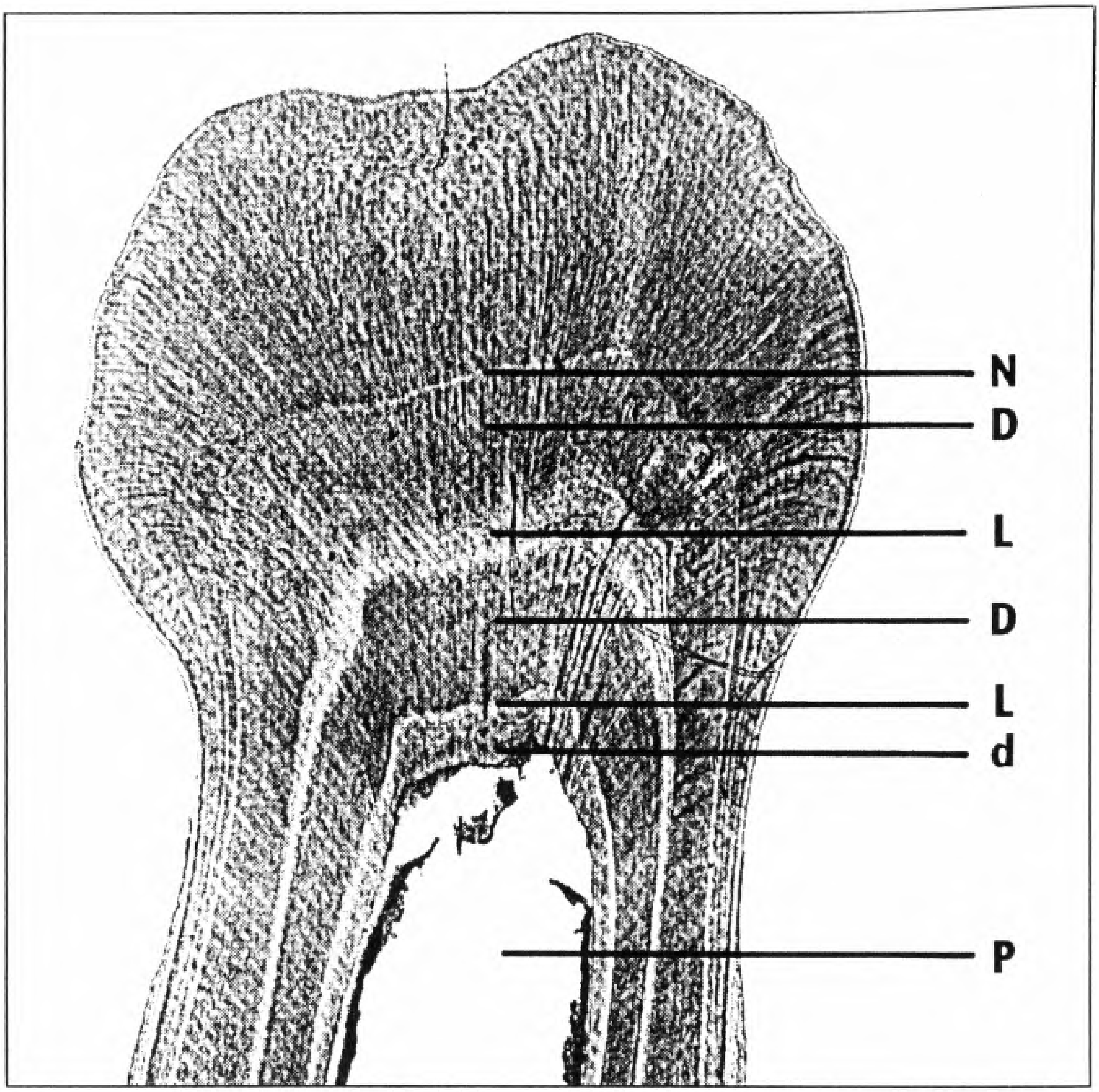

Fig. 2. Photocopy of a thin section microscope slide from No. 88–003. Age determined as 2 years. The dark and light staining lines are marked in the same manner as in Fig. 1: D,L,D,L,d.

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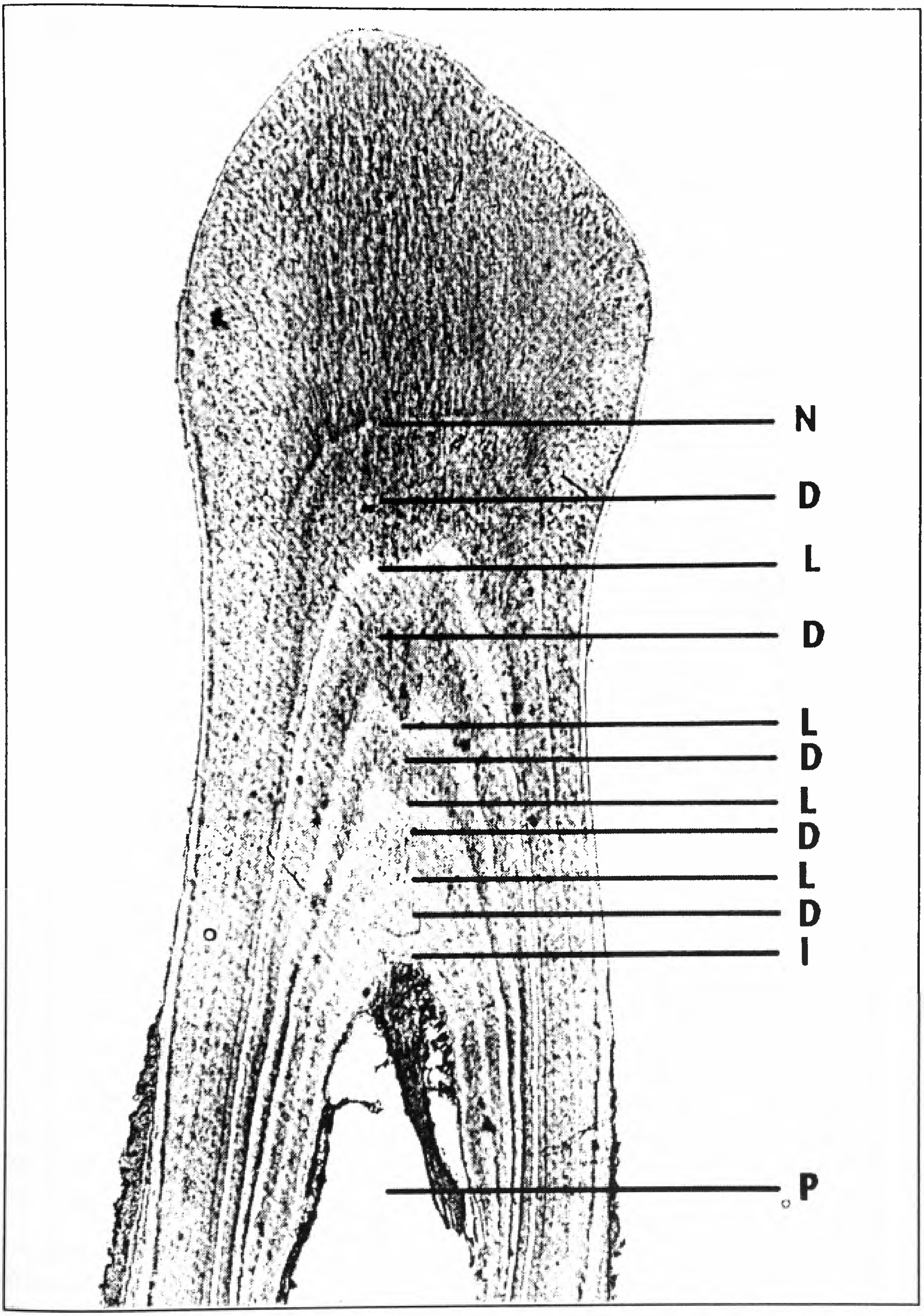

Fig. 3. Photocopy of a thin section microscope slide from No. 88–045. Age determined as 5 years. The dark and light staining lines are marked in the same manner as in Fig. 1: D,L,D,L,D,L,D,L,D,1.

Table 2

Age determination of harbour porpoise (*Phocoena phocoena*) based on annual layers in dentine deposits. Guide to symbols in Table 1.

Reg. no.	Sex	Age	Reading	Lines
88-003	2	2	DLDLd	2
88-005	1	3	DLDLDLd	3
88-008	?	1	Dld	1
88-010	1	1	D(l)	1
88-012	1	1	D(1?)	(1)[1]
88-013	2	2	(DLDL)	2
88-018	2	2	DLDL	2
88-019	?	1	DLd	1
88-021	1	3	DLDLDL	3
88-022	1	8+	DLDLDLDLDldl(dldl)	8
88-023	2	2	(DLDld)	(2)
88-024	2	1	(DL)	(1)
88-026	2	8+	DLDLDLDLDLDLDLDL	8
88-031	2	4	DLDLDLDL	4
88-032	1	2	D(l)D(l)	(2)
88-036	1	1	D(ld)	(1)
88-037	2	1	DLD	1
88-040	1	1	(DLD)	(1)
88-042	1	1	DLd	1
88-043	2	2	DLDL(d)	2
88-044	1	8+	(old!)	(10)[2]
88-045	1	5	DLDLDLDLDl	5
88-047	2	1	DLD	1
88-048	2	3	DLdldld	3

[1] Much postnatal dentine. Approx. 1 year.

[2] 10 light zones observed. Pulpa filled up. Older than 88-002 based on cementum thickness.

DISCUSSION

According to Grue Nielsen (1972) and Perrin and Myrick (1980), various methods have been tested for age determination of harbour porpoise and some methods have proved to be applicable. Similar laboratory procedures have been described by Jensen and Brunberg Nielsen (1968), Nishiwaki and Yagi (1953), Sergeant (1959), Klevezal and Kleinenberg (1967) and Grue and Jensen (1979). According to Grue Nielsen (1972) age determination beyond eight years is very difficult. This has also been experienced in our work. All porpoises older than 8 years have consequently been recorded as 8+.

The reason for this difficulty is that the pulp cavity at age 8+ tends to be so full that dentine zones become less recognisable and very difficult to count. In this phase of life, dentine is layered in the form of osteodentine, which is fairly homogeneous in appearance (Lankaster, 1867).

Longitudinal tooth sections are preferable since they permit the reader to examine the whole length of the tooth in one operation. Cross sections will be more laborious, as more than one section from each tooth has to be examined (Grue Nielsen, 1972).

Dentine zones have been the basis for our age determination of harbour porpoise since cementum zones give unreliable results. This is in correspondence with observations reported by Grue Nielsen (1972). However, cementum deposits have in some cases been

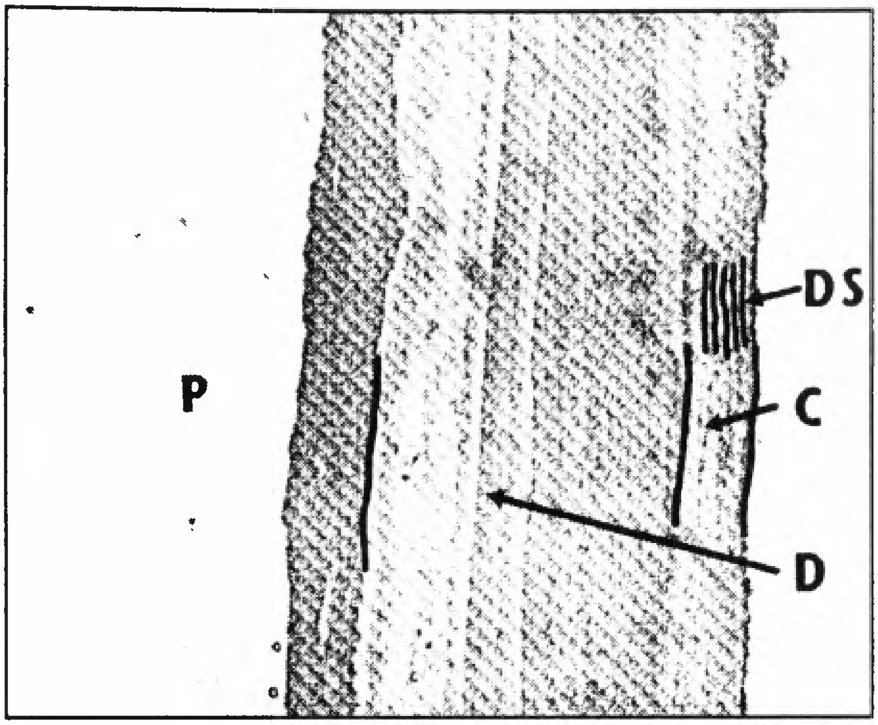

Fig. 4. Photocopy of a thin section microscope slide from No. 88–045. Age determined as 5 years. P = Pulp cavity. D = Dentine. C = Cementum. DS = Dark staining incremental lines in the cementum. Age determination in most terrestrial mammals is based on counts of these annual lines. With skill and patience one may be able to find up to five dark staining zones. That is one too many compared to the dentine growth layer groups. (The fifth line should be found on the outer fringe of the cementum layer). Incremental lines in the cementum of harbour porpoise are very difficult to count and age determination based on these lines is bound to be uncertain.

used for comparison of readings based on indistinct dentine zones with low contrast. Grue Nielsen (1972) also found thickness of cementum deposits to be comparable to age as determined by cementum dentine zones.

Tests were made with three thicknesses of sections: 15, 20 and 30μ. Dentine zones were distinct and easily readable with all three categories. However, 20μ may be an upper limit for proper reading of cementum zones. Since sections of 15 and 20μ are difficult to mount on glass slides and age determination tends to be based on dentine zones, 30μ should be applied as the standard thickness of sections. This is in correspondence with recommendations given by Grue Nielsen (1972).

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