

Biology of Northern Hemisphere Pilot Whales

A COLLECTION OF PAPERS

Edited by

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Preface

This volume in our special issue series arises out of discussions in the sub-committee on small cetaceans of the IWC's Scientific Committee since 1985 and particularly in 1987 (*Rep. int. Whal. Commn* 38:117–119), 1989 (*Rep. int. Whal. Commn* 40:144–8) and 1991 (*Rep. int. Whal. Commn* 42: 180–2, 197–200). It makes a welcome addition to our series and to the literature on pilot whales in the Northern Hemisphere, especially the North Atlantic.

G.P. Donovan Series Editor 16 November 1993

Cover Photograph Short-finned pilot whale, Globicephala macrorhynchus, off the coast of Tenerife, Canary Islands, Spain. Photo courtesy of J.R. and S.L. Heimlich-Boran, DELPHIS, Cambridge, UK.

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13 [1991]-Genetic Ecology of Whales and Dolphins. Ed. A.R. Hoelzel. i-ix + 311pp.; ISBN 0 906975 25 5

Introduction

At its 1991 meeting, the IWC Scientific Committee, through its sub-committee on small cetaceans, undertook a major review of the status of stocks of small cetaceans that are subjected to significant directed and incidental takes (1992, *Rep. int. Whal. Commn* 42: 178–228). The review included takes of *Globicephala macrorhynchus*, the short-finned pilot whale, in Japanese waters (*ibid.* pp. 180–2) and takes of *G. melas*¹, the long-finned pilot whale, in Faroese waters (*ibid.* pp. 197–200). While the Committee reported that 'there is no detectable evidence that the stock size of pilot whales appearing in the Faroese area has been affected by the drive fishery' (*ibid.* p. 198), it has expressed concern since 1986 over the status of the stocks of short-finned pilot whales taken off Japan (*ibid.* p. 182).

The first (and larger) section of this volume mainly concerns papers arising out of a field programme to examine catches of long-finned pilot whales taken in the Faroese fishery. The opening paper to the volume provides a general introduction to the field studies carried out between July 1986 and July 1988. A further twelve papers discuss the analyses of the resultant data, including external characteristics (Bloch *et al.*) age and growth parameters (Bloch *et al.*, Lockyer), genetic studies and social organisation (Amos *et al.*, Andersen), reproductive biology (Martin and Rothery, Desportes *et al.*), feeding and energetics (Desportes and Mouritsen, Lockyer), pollution (Borrell and Aguilar, Aguilar *et al.*, Caurant *et al.*) and parasitology (Raga and Balbuena).

At this point it is worth acknowledging the debt that many of these studies owe to the pioneering work of David Sergeant. His paper on the biology of the long-finned pilot whale based on information obtained from the Newfoundland fishery, published in 1962, remains a classic of its kind. Some twenty years later work of similar stature was being published for the short-finned pilot whale by Toshio Kasuya, based on samples collected from Japanese fisheries.

It is interesting to note that despite the more rigorous and sophisticated practical and analytical techniques available to the international team at the Faroes, many of the analyses confirm the results obtained by Sergeant.

The Faroese studies have provided some fascinating new information about the biology of the pilot whale, particularly in terms of its social organisation and reproductive biology. They also underline the need for co-operative studies across disciplines. Interpretation of many of the results would have been far less thorough if information on the age and reproductive status of almost all animals had not been

¹ Following Jones *et al.* (1986, Revised checklist of North American mammals north of Mexico, *Occ. Pap. Mus. Texas Tech. Univ.* 107, 1–22), we use the latin name *Globicephala melas.* Prior to 1990, the 1WC had used the name *Globicephala melaena*.

known. However, much remains to be done if we are to begin to fully understand the biology of pilot whales. A striking feature of many of the studies is that our understanding and ability to interpret the results would be greatly enhanced if our knowledge of the stock identity of the animals taken in the fishery was greater. This applies not only to the work arising out of the field sampling but also to attempts to look at the historical trends in catches (Hoydal and Lastein, Zachariassen) and relate these to the first direct estimates of current population size (Buckland *et al.*) and other information on distribution (Payne *et al.*) and fishery interactions (Fairfield *et al.*).

The final three papers in the volume concern the short-finned pilot whale in the North Pacific, two of them continuing Kasuya's major series of papers on exploitation and biology in Japanese waters, consolidating and expanding on earlier work.

We would like to thank the following scientists who acted as reviewers of papers in the volume: A. Aguayo-L, A. Aguilar, W. Amos, C.S. Baker, H.W. Braham, S.T. Buckland, I. Christensen, A. Collet, J.G. Cooke, D.I. Gibson, P.S. Hammond, R. Hoelzel, T. Kasuya, S.D. Kraus, F. Larsen, C. Lockyer, H. Marsh, A.R. Martin, M.K. Marx, W.F. Perrin, P. Palsbøll, R.R. Reeves, P.J.H. Reijnders, D.E. Sergeant, T.D. Smith, G. Víkingsson, G.T. Waring.

Special thanks should also go to Helen Coulson, who keeps track of the manuscripts and who types in and prepares many of the revised manuscripts; Stella Duff who oversees the proof reading; Julie Creek who helps Helen with the manuscripts and typesets all the tables; Helen Richardson, who helped with the proof reading and artwork; and the staff of Black Bear Press.

> G.P. Donovan C.H. Lockyer A.R. Martin *Cambridge, November 1993*

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North Atlantic



Map of the Faroe Islands reproduced with permission of the Danish Geodetic Institute, Copenhagen, no. A53-91

An Introduction to Studies of the Ecology and Status of the Long-finned Pilot Whale (*Globicephala melas*) off the Faroe Islands, 1986 – 1988

D. Bloch¹, G. Desportes¹, R. Mouritsen², S. Skaaning¹ and E. Stefansson¹

ABSTRACT

The long-finned pilot whale, Globicephala melas Traill, is harvested off the Faroe Islands (in the northeastern Atlantic) for local subsistence purposes. From July 1986 to July 1988, an international team examined 40 of a total of 43 schools of pilot whales landed in the islands (3.470 whales of the 3.617 whales landed). The purpose of the project was to examine the status of the exploited population and aspects of its life history, including feeding, ecological energetics, pollutant loads, parasitology and population genetics. This paper summarises the project, the laboratories involved and the relevant methodology. It also examines some basic information (sex and length distributions) about the schools and compares this with information available throughout the history of the fishery. The landed schools were mostly monospecific, but mixed schools with bottlenose dolphins (Tursiops truncatus) and Atlantic white-sided dolphins (Lagenorhynchus acutus) sometimes occurred. During the study period, 16 of the 21 authorised whaling bays were used. On 12 occasions, particular districts were closed temporarily for periods from between 0.5 and 3.5 months. The average school size was 81.7 \pm 6.6 individuals (mean \pm SE). This is smaller than the average size over the total period 1709–1990 (149.3 \pm 3.5), but it does correspond with some periods within that time. No clear seasonality in school size was detected. The overall sex ratio was 1.58 ± 0.05 (females to males) and no correlation with school size or month was apparent. The average school consisted of 46% immatures of both sexes, 12% pregnant females, 24% lactating females, and a maximum 12% adult males. The final 6% of whales consisted of adult females, either resting or senescent, or simultaneously pregnant and lactating.

KEYWORDS: PILOT WHALES-LONG-FINNED; NORTH ATLANTIC; WHALING MODERN; AGE/LENGTH DISTRIBUTIONS; REPRODUCTION; BEHAVIOUR-SOCIAL; SEX RATIO; BOTTLENOSE DOLPHIN; WHITE-SIDED DOLPHIN.

INTRODUCTION

The long-finned pilot whale, *Globicephala melas* Traill, is harvested in the eastern North Atlantic by Faroe Islanders in a traditional subsistence hunt. The hunt is believed to date back more than 1,100 years (Thorsteinsson, 1986) and the regulated division of the catch provides the longest series of continuous records known to exist for the catch of any wild animal. Written statistics, found in tax accounts, date back to 1584, the only gap being from 1640 to 1709 (Bjørk, 1956). An examination of these revealed long-term (approximately 120 years) cycles in the frequency of catches (Joensen and Zachariassen, 1982; Hoydal, 1986; 1987; Bloch *et al.*, 1990b; Zachariassen, 1993).

When seen in the vicinity of the islands, entire schools are driven to authorised whaling bays by small fishing boats and are slaughtered there. This is carried out under the guidance of 'grind-foremen' (four men elected for five years in each whaling bay by the village councils) who act with the authority of the chief district officer. Although detailed

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² Fisheries Laboratory, FR-100 Tórshavn, Faroe Islands

³ In addition, unsuccessful attempts were made to develop electronic reading with the help of BICO, the Danish Department of *Olympus* Microscopes.

regulations exist, to date no quotas have been set for the fishery. However, whaling districts are closed by government order when the needs of the particular community are met. The meat and blubber are used for human consumption and shared free among the local inhabitants, and no factory processing or export occurs.

The year-round drive fishery presents a unique opportunity to obtain important data on the ecology of the long-finned pilot whale in these waters, particularly as whole schools containing animals of both sexes, at different ages and stages of sexual maturity are available for sampling. In fact, Faroese pilot whaling has provided material for various biological observations and studies for a long time (Svabo, 1783; Lyngbye, 1817; Irminger, 1846; Høst, 1875; Müller, 1882; 1883; Williamson, 1947; Harrison, 1949; Ryggi, 1960; Joensen, 1962; Moore *et al.*, 1978; Joensen and Zachariassen, 1982; Desportes, 1985; Sergeant, 1986; Hoydal, 1987; Bloch, 1992), but no thorough study of the exploited population or the impact of the fishery on the population(s) has previously been undertaken.

In the summer of 1984, during a sampling period of two months, the first two authors established the framework for a large scale research project. In 1986, under the auspices of the IWC and UNEP, the Faroese Government initiated a comprehensive survey of the exploited population(s) and between July 1986 and July 1988, an international scientific team examined almost all landed schools (40 out of 43). This international research programme was intended to provide information essential to understanding the distributional, behavioural, social and ecological dynamics of the exploited stock or stocks (Desportes, 1988; 1990; Desportes *et al.*, 1993a). Future management policies for the fishery will be based on the results of this research.

The study was complemented in June-August 1987, and again in June-August 1989, with Faroese participation in the international North Atlantic Sightings Surveys for which the pilot whale was one of the target species (Joyce *et al.*, 1990; Buckland *et al.*, 1993).

This paper provides an introduction to the project and the laboratories involved and describes the initial sampling and laboratory procedures used. It describes the geographical and seasonal distribution of the catches and the size, sex ratio and composition of the schools. It also presents some of the primary data characterising the schools and compares this with the historical data available. Detailed accounts of the various projects are presented in a series of papers in this volume (Amos *et al.*, 1993; Andersen, 1993; Bloch *et al.*, 1993a; b; Borrell and Aguilar, 1993; Caurant *et al.*, 1993; Desportes and Mouritsen, 1993; Desportes *et al.*, 1993b; Hoydal and Lastein, 1993; Lockyer, 1993; Martin and Rothery, 1993; Raga and Balbuena, 1993; Zachariassen, 1993).

The Faroese word for both a school of pilot whales and the activity of pilot whaling in general, is *grind* (pronounced with a short 'i' as in 'window'). It is used in both senses throughout this paper. In the results and analyses presented here, the results are expressed as mean \pm standard error and the term 'significant' is used solely in the statistical sense of differences significant at the 5% level.

MATERIALS

In the two-year period of sampling, 47 notifications of grinds were recorded, of which 43 were followed by landings. A total of 3,617 pilot whales were caught, of which 3,470 (40 grinds) were examined. Bloch *et al.* (1990a) provide a detailed description of the grind and in particular the 43 occurring between July 1986 and July 1988. A list of these grinds is given in Table 1.

Table 1

List of the pilot whale schools, including the sex ratio, landed in the Faroe Islands in the period July 1986 -July 1988. No samples were collected from the drives marked '#' and the schools marked with '*' indicate that only a part of a larger school was beached.

No.	Date	Location	Male	Female	Female/Male ratio
1	10 July 1986	Gøta	17	24	1.41
2	12 July	Leynar	56	79	1.41
3	30 July	Bøur *	19	35	1.84
4	11 September	Sandur *	95	125	1.32
5	15 September	Øravik	46	72	1.53
6	25 September	Ġøta	11	18	1.64
7	27 September	Viðvík	8	8	1.00
8	26 October	Funningsfjørður *	15	19	1.27
9	1 November	Miðvágur	69	105	1.52
10	11 November	Fuglafjørður	24	31	1.29
11	14 November	Hvalvík	12	20	1.67
12	15 November	Vestmanna	54	69	1.28
13	24 November	Hvalvík	27	50	1.85
14	28 November	Fuglafjørður	31	40	1.29
15	6 December	Gøta	29	56	1.93
16	23 December	Tórshavn	53	65	1.23
17	22 January 1987	Hvannasund	64	88	1.38
18	23 January	Vágur	50	106	2.12
19	31 January	Leynar	9	17	1.89
20	7 February	Hvalvík	28	52	1.86
21	23 March	Leynar *	19	45	2.37
22	10 April	Tórshavn	72	118	1.64
23	21 April	Fuglafjørður	29	39	1.34
24	16 May	Vágur	14	21	1.50
25	22 July	Leynar	31	59	1.90
26	24 July	Miðvágur	45	57	1.27
27	28 July #	Sandur			
28	2 August	Miðvágur	19	28	1.47
29	19 August	Vágur *	17	28	1.65
30	26 August #	Hvannasund*			
31	29 August	Klaksvik *	4	9	2.25
32	18 September	Vágur	5	10	2.00
33	8 October	Tórshavn	15	30	2.00
34	20 October	Vágur	16	23	1.44
35	24 October	Hvalvík	30	42	1.40
36	22 January 1988 #	Funningsfjørður			
37	17 February	Tórshavn	24	35	1.46
38	13 March	Miðvágur	29	28	0.97
39	1 April #	Hvalba			
40	4 April	Bøur	45	66	1.47
41	29 April	Hvannasund *	55	83	1.51
42	4 May	Tórshavn			
43	10 June	Leynar	26	40	1.54
Total	43 drives	3,052 whales	1,212	1,840	$1.58 \pm 0.05 (N = 38)$

Most of the examined pods comprised solely pilot whales. However, on three occasions they were mixed with other species (Bloch and Hoydal, 1989; 1990): once (grind no. 25) with a single bottlenose dolphin (*Tursiops truncatus*) and twice (grind nos 20 (60 dolphins) and 39 (544 dolphins)) with Atlantic white-sided dolphins (*Lagenorhynchus acutus*). It is not uncommon in Faroese pilot whaling that one of these two species is found within a pilot whale school, or that white-sided dolphins beach just in front of pilot whales, but in a separate group. Pilot whales are known to often mix with other cetacean species (e.g. Evans, 1980; Bloch and Lockyer, 1988).

METHODS

The team

The project was carried out under the leadership of D. Bloch of the Faroese Museum of Natural History (FN). C. Lockyer of the Sea Mammal Research Unit (SMRU), Cambridge, UK was the scientific adviser. G. Desportes (FN) coordinated the field work and sampling, while practical matters were the responsibility of R. Mouritsen, seconded for two years from the Faroese Fisheries Laboratory. The Faroese Government through K. Hoydal, Director of Fisheries, facilitated the programme, particularly by taking care of all the travel, sampling and accomodation expenses and providing technical and personal assistance.

The continuous sampling which began on 1 July 1986 was carried out by the two resident scientists, Bloch and Desportes, greatly aided by FN staff. Just over half of the schools (22 out of 40) were examined only by the resident team (scientist/s and four FN staff) who maintained and ensured continuous sampling for the entire team. The non-resident scientists who took a direct part in the summer field sampling are shown in Table 2, as are scientists for whom samples were obtained.

The nature of the sampling (see below), made it necessary to have a large, experienced team ready round-the-clock. Apart from the permanent team, other assistants were involved, 59 from FN and 17 from other institutions.

Name	Examined school no.: in total
D. Bloch	1-6. 8-17, 19-26, 28-30, 32-33, 37-38, 40-43: 35 schools
G. Desportes	1-14, 16-20, 24-26, 28-35, 37-38, 43: 33 schools
C. Lockyer	3, 32: 2 schools
F. Jean-Caurant	1-7: 7 schools
L. W. Andersen	1-4, 6, 25-26, 28-31: 11 schools
A.R. Martin	1-2, 8-9: 4 schools
W. Amos	3, 5-7, 25-26: 6 schools
J. Balbuena	25-26, 28-35: 10 schools
A. Raga	28-31: 4 schools
A Aguilar	28: 1 school

Table 2

Details of the scientists involved in the examination of each school. The number of the catch refers to Table 1.

Time available for sampling

The research project was well received amongst the Faroese community and care was taken to maintain this goodwill by carrying out sampling with minimal disturbance to the killing operation and the meat distribution.

Faroese pilot whaling is sporadic and opportunistic and it is impossible to forecast when and where a grind will take place. However, to obtain maximum scientific value, the examination of a school should begin during killing. Thus the sampling team had to receive notification of a grind as early as possible in order to reach the whaling bay in good time (see Fig. 1). During the study period, therefore, one member of the resident team was in constant radio contact with the Tórshavn Fire Brigade, and chief district police





officers, grind foremen, police and the public were asked to pass on the grind message either directly or to the fire station as soon as they received it. This was done efficiently and promptly and all the grinds were reached in reasonable time, so that even with travelling times of up to three hours (and the availability of ferries) 20 of the grinds were reached in time for blood samples to be collected. Blood sampling had to be carried out during the actual killing of the whales, just after the first incision had been made, as it would not have been possible later due to the drop in blood pressure. The team collected blood from as many whales as possible without disturbing or prolonging the killing. In no case was killing delayed to wait for the presence of a scientific team member.

Main sampling (measurements, reproductive sampling etc., see below) began as soon as the whales were hauled up to the upper part of the beach or on to a wharf, and had to stop when local residents arrived to claim their shares. Depending on the number of whales and the efficiency of the division of shares, this usually ranged from four to eight hours.

The fact that the whales are taken for human consumption had to be considered during the sampling and consequently the meat and cutting-up area could not be spoiled in any way, for example by chemicals. The traditional method of cutting up the animal was strictly followed even though this was not necessarily the most efficient or quickest approach from a scientific point of view.



Plate I. A pilot whale in the Farocs. Tags from both blood sampling and the normal scientific tags can be seen in the cutting line in the neck. Photo: Ole Wich.

Sampling procedures

Blood sampling

The target whales for blood sampling were marked with strong waterproof tags on the back at the neck incision (Plate I). Blood was collected (by teams of two) from the carotids/jugulars in 50ml tubes containing Natrium Heparine previously prepared in the laboratory, kept at -25° C until use and maintained at 5°C in coolers during field work.

In the laboratory, the blood samples were divided into three parts. One part was used fresh, the other two were frozen at -25° C, after separation.

The main sampling

Before the main sampling began, all the whales were marked (or re-marked if blood samples had been taken) with a consecutive number which became the 'scientific number' of the whale. A whale would later be identified in the archives and the database by this number together with the date of the grind.

Tagging was carried out using a set of plastic waterproof labels, one of which was a dymotag attached to the jaw, that was resistant to hot water (see 'TEETH' below). One label remained on the animal throughout the sampling while the others were used to identify individual samples. The set of tags was prepared in advance in the laboratory and re-used from grind to grind.

SEX, LENGTH, OFFICIAL NUMBER, SKINN VALUE

Sex and total body length were recorded for each whale together with their numbers (scientific and blood tags).

During a grind, local assessors give each whale an official number and evaluate the live weight of the animal in *skinn* (for details see Bloch and Zachariassen, 1989). On average, one *skinn* weighs 72kg, i.e. 38kg meat and 34kg blubber. The *skinn* is recorded in the long-term series of catch statistics. It was recorded here in an attempt to enable long-term catch statistics to be incorporated into modern statistics.

Table 3

Readers of teeth from the different schools of pilot whales. The numbers of the catches refer to Table 1. * Represents only a sub-set.

.W. Andersen, 4,6,7,21	C. Lockyer, 3-4, 6-7, 10-11, 17, 21
D. Bloch, 1-43	T. Kasuya, 3,4*,11,23
G. Desportes, 3,17*	T. Waters, 3, 17

TEETH

Teeth were collected by sawing off or severing the tip of the lower mandible. The jaw was then wrapped in a perforated plastic bag with its dymo number.

Several methods of tooth preparation were attempted (Lockyer *et al.*, 1987)³. The one chosen was similar to that of Kasuya and Matsui (1984). The teeth were extracted after allowing the jaw to rot in a heated pressurised cabinet for about a fortnight. This method does not damage the cementum or dentine as does the boiling of the teeth. Eight of the best teeth were then defatted for several hours in a solution of one third chloroform and two thirds 70% alcohol. Two of the teeth were then mounted on a wooden block with epoxy resin and bisected longitudinally, using a diamond rotating saw.

Tooth processing was carried out at the FN and readings were made by several scientists (Table 3).

EXTERNAL CHARACTERS

Attention was paid to any special external marks such as wounds or bites (Plate II), lamprey marks (Plate III), squid marks around the mouth (Plate IV), or the occurrence of ectoparasites. For six grinds, the appearance of 'fighting' marks was systematically recorded. The marks, as well as the teeth *in situ*, were counted and photographed. The presence or absence of the postdorsal fin saddle and the postorbital blaze were systematically recorded for two entire schools.



Plate II A pilot whale in the Faroes showing a wound containing whale lice (Isocyamus delphini). Photo: Ole Wich.



Plate III. Marks from lampreys (Cyclostomata) on the skin of a pilot whale in the Faroe Islands. Photo: Ole Wich.



Plate IV. Marks from squid on the skin of a pilot whale in the Faroes. Photo: Ole Wich.



Plate V. Weighing a pilot whale using the balance point in the dorsal fin. Faroe Islands. Photo: Ole Wich.

WEIGHT

When possible, the total weight of the whales was recorded by means of a lorry crane equipped with a balance. Two kinds were used, an electronic waterproof balance which could weigh up to five tonnes to the nearest kg, and a tensile link balance which could weigh up to one tonne (up to two tonnes if a special device was available). The balance

point of a pilot whale is the dorsal fin and so the weighing device was placed through a hole cut in the middle of the dorsal fin (Plate V).

A total of 32 whales, of both sexes and various sizes, from ten different months and 20 different grinds, was brought back to the laboratory for more detailed sampling. These whales were weighed in pieces to the nearest 100g using either a lorry or a tripod, and the balances mentioned above.

Total weight and weight in pieces were mainly used for comparing the traditional assessment method with biological variables (Bloch and Zachariassen, 1989) and for growth and energetic analyses.

GIRTH MEASUREMENTS AND BLUBBER THICKNESS

These measurements were usually taken in connection with the weighing of whole whales and the tissue sampling (at least ten whales of different sizes for any target school). Girth measurements were taken to the nearest cm from six different places on the whale, and blubber thickness from seven places to the nearest mm. Details are given in Lockyer and Waters (1987).

OTHER MEASUREMENTS

A number of morphological features were measured to the nearest cm (usually in connection with girth measurements) and were systematically collected for 29 schools.

- (i) half of the span of the fluke, and its length from where the fluke protrudes from the backbone;
- (ii) the maximum proximal and the length from the maxilla to the tip (only one flipper from each whale was measured, because the landed whales always are turned over on one side);
- (iii) the caudal height of the dorsal fin, and its length from where it protrudes from the backbone.

Furthermore, certain measurements (foremost part of the skull to eye, eye to anus and anus to fluke notch) for all 59 whales from one grind were measured to the nearest cm in order to study body growth and compare the assessment with biological variables (Bloch and Zachariassen, 1989) and to compare with the Newfoundland long-finned pilot whales (Bloch and Lastein, 1993).

GONADS AND THE REPRODUCTIVE TRACT

The reproductive status was recorded for each whale: for females as either immature, lactating, pregnant and lactating, pregnant non-lactating or resting (i.e. not obviously pregnant or lactating); for males as either immature or mature.

From all mature animals and usually all immature animals, both ovaries or at least one testis (including the epididymis) were systematically sampled. Ovaries were usually labelled as left or right.

The largest width of one mammary gland and the diameter of each uterine cornus were measured to the nearest mm.

In each female with a corpus luteum, the foetus was carefully searched for. Where one was found, it was sexed, measured and weighed in the field (the accuracy of these data depended on the size of the foetus) when possible. Very small foetuses were brought back to the laboratory for closer examination and sampling. Sex was determined by means of macroscopic observation and/or histological examination and/or use of sex chromatin bodies.

All reproductive tissues or organs were preserved in two successive baths of 10% buffered formalin for further processing.

TISSUE SAMPLES

Whales were dissected in the traditional way by means of transventral cuts, 30–40cm apart (Plate VI).

The samples, usually collected in connection with blood sampling and collected from other animals where possible were: a piece of skin, blubber and meat, taken ventrally from the transventral cut behind the dorsal fin; the middle slice of one kidney; the posterior part of a liver lobe; mammary tissue, milk and placenta from pregnant or lactating females (all samples weighing about 200g); both adrenals (from July 1987); samples of urine, faeces, lung, and heart were sometimes collected. All were individually wrapped in plastic bags.

The intensity of the sampling varied from grind to grind, according to the allotted time for sampling and the number of people involved in the sampling team. The minimum sample taken from nearly all whales was a piece of skin, especially from pregnant females and foetuses.

The tissue samples were later sorted in the laboratory to be distributed or mailed to the relevant laboratories.



Plate VI. People cutting up pilot whales in the traditional way with transventral cuts, 30-40cm apart. Photo: Ole Wich.

STOMACHS

Stomachs from all whales up to and including three *skinn*, i.e. about 3m, were sampled, as well as about ten from larger whales of both sexes. The stomachs were either examined as soon as possible for stomach contents and parasites or frozen for later examination.

PARASITES AND CYSTS

When cysts or pathological tissues were observed, these were sampled. Endoparasites were systematically sampled from the summer of 1987. About 15 whales per grind were surveyed. This involved a close examination of lungs, liver, sinuses, digestive tract, kidneys, mammary glands and the general body cavity. The occurrence and abundance of ectoparasite infestation was also investigated (Plate II).

SKELETON

After the cutting up of the whale carcasses, examination of the vertebral column of selected whales was conducted. Bone samples were also collected from 35 whales.

PACK1NG

All samples were placed in plastic bags as soon as they were collected; the ovaries and jaws in perforated bags, the rest in normal plastic bags. A label removed from the scientific tags on the neck of each whale was placed in every plastic bag.

The database

Table 4 summarises the numbers of samples and measurements taken by grind. The Zoological Department of the Tórshavn Natural History Museum coded all the basic data onto a database (DBASE III PLUS) and the dataset was made available to all the contributing parties.

RESULTS

Reliability of length measurements

All measurements were made following the standard of Norris (1961). The only exception was the fluke, where, for convenience, only half the span and the length rather than the width, were measured.

For some grinds only a part of a larger school was beached (marked by an * in Table 1), and this may influence the length and sex distributions. Pooling data among schools requires that they do not differ significantly from the average in length or sex distribution. They did not do so for either the length (F=1.2; p>0.3) or the sex (F=0.6; p>0.2) distributions, nor was any significant difference in body length found for the schools from month to month (F=1.1; p>0.3).

Body length was measured to the nearest cm, from the foremost part of the skull to the fluke notch, in a straight line parallel to the backbone. In order to examine consistency and accuracy in measurements the total lengths of 50 whales were taken three times, and the dorsal fin, one flipper and the fluke of 27 whales measured twice from one school on Sandoy, on 28 September 1988 (i.e. outside the study period). The test included different persons taking the same measurements or repeated readings by the same person. In some cases a 'systematic' reading fault had occurred, e.g. the incorrect reading of 10 and sometimes 50 or 100cm. For the latter two, the *skinn* values were of great assistance in correcting the inaccuracies. If the 50/100cm incorrect readings are not included, the test revealed that for total length 36% of the measurements varied ≤ 5 cm, with 98% <10cm in variation. All measurements varied $\leq 5\%$ from the total length (Fig. 2).

Of the remaining measurements, the most accurate were those for dorsal fin height and the flipper and fluke measurements. The length of the dorsal fin, not surprisingly, showed the most variation as it is the least well defined on the body: 42% varied $\leq 5\%$ with 77% $\leq 10\%$ of the dorsal fin length (Fig. 3).

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Fig. 2. Reliability of total length measurements (n=50).



Fig. 3. Reliability of dorsal fin, flipper and fluke measurements (L=length; H=height; W=width; N=27).

Only four of all the dorsal fin height, flipper and fluke measurements displayed a variation of 25–30cm, which can easily be identified as wrong when compared with other whales of similar size. Between 89–96% varied less than 4cm, or 52–85% of the measurements varied $\leq 5\%$ of the total length. A description and analysis of the external characters and measurements is given in Bloch *et al.* (1993b).

Length distribution by sex

The range in observed lengths of males was 174–625cm with two peaks, the first at 353cm and the second at 552cm, representing immature and mature males (Bloch *et al.*, 1993a; Desportes *et al.*, 1993b); the mean length was 421cm ± 3.2 cm (n=1,211). For females the length range was 163–512cm, again with two peaks, the immatures at 299cm and the matures at 432cm; the mean was 388cm ± 1.7 cm (n=1,836). Similar length distributions with two peaks for each sex have been found in previous studies from the North Atlantic (Joensen, 1962; Moore *et al.*, 1978; Sergeant, 1986; Martin *et al.*, 1987; Kasuya *et al.*, 1988; Bloch, 1992; Zachariassen, 1993). Further comparisons between the eastern and western part of the North Atlantic have been made by Bloch *et al.* (1993a) and Bloch and Lastein (1993).

Pooled length distributions by sex are shown in Fig. 4. It shows the expected pattern with males reaching greater lengths than females (113cm in this sample). Data by individual schools are given in Table 5 and Fig. 5.

[Text continues on p. 21]



Fig. 4. The length to sex distribution of all sampled whales during the study period (n=3.047).

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			Males			Females	
No.	Number	Range	Mean	SE	Range	Mean	SE
1	41	197-577	393	31.3	182-451	380	15.8
2	140	176-586	416	14.6	193-468	386	7.0
3	54	234-582	430	26.5	193-465	385	11.7
4	220	185-620	425	12.3	171-500	39	17.8
5	119	206-597	372	16.7	185-478	395	8.6
6	29	200-582	416	34.9	267-456	406	11.1
7	16	261-555	400	38.1	313-438	389	15.0
8	35	223-585	372	27.4	192-457	366	18.7
9	175	195-614	442	14.5	163-473	373	8.1
10	55	226-586	401	21.6	217-455	375	12.3
11	33	196-553	345	34.9	246-474	404	14.3
12	139	174-586	408	16.8	166-483	377	10.3
13	77	224-607	469	24.5	179-482	393	11.3
14	71	210-545	374	16.3	235-456	384	9.6
15	86	236-598	455	19.9	177-485	379	10.4
16	117	222-625	434	16.6	210-482	385	9.6
17	153	175-610	431	14.9	179-482	378	8.1
18	156	210-602	415	15.0	185-470	380	7.0
19	26	316-589	470	31.4	185-483	386	19. 9
20	80	232-623	417	23.8	237-475	395	10.4
21	64	226-535	372	20.3	177-460	3 67	11.5
22	190	210-600	417	11.4	218-470	390	5.9
23	68	227-612	432	22.5	247-473	395	9.5
24	38	310-589	439	29.6	238-459	386	16.2
25	90	283-625	458	20.8	242-495	408	7.0
26	102	202-585	399	15.6	202-483	407	8.8
28	47	245-606	417	25.3	231-487	413	12.8
29	45	290-600	442	23.3	190-4 8 0	372	15.2
31	13	251-588	44 0	76.9	184-465	375	36.5
32	15	260-498	365	49.3	278-447	392	21.3
33	45	218-574	399	25.3	201-465	386	13.0
34	39	1 88-59 0	442	31.1	190-478	386	18.6
35	72	209- 599	429	22.5	200-464	378	11.4
37	59	230-580	430	24.2	252-465	397	11.1
38	57	274-575	435	18.9	216-467	396	12.3
40	111	260-575	411	13.6	207-476	39 0	8.4
41	138	211-620	440	13.1	207-512	405	7.0
43	66	281-615	452	20.8	303-472	401	8.4
	3,046	174-625	421	3.2	163-512	388	1.7

List of the length distribution of the different pilot whale schools landed in the Faroe Islands in the period July 1986 - July 1988

School size

The average grind size from 1709–1990 was 149.3 \pm 3.5 whales per school (n=1,646; range 1–1,200 whales, see Table 6 and Zachariassen, 1993). During the study period, although the number of schools was high, most were relatively small (mean 84.5 \pm 8.3 whales; n=43; range 13–220). If the full calendar years 1986–88 are considered, the picture remains the same (mean 81.7 \pm 6.6 whales, n=59). These values are similar to those obtained for Newfoundland between 1949 and 1959 (85 whales, n=85 – Sergeant, 1962).



Fig. 6. The average composition of 38 long-finned pilot whale schools examined during the study period (n=3,018): 1 = Immature males; 2 = M I males; 3 = M II males; 4 = M III males; 5 = Immature females; 6 = Mature females with no more information; 7 = Pregnant females with no more information; 8 = Pregnant and lactating females; 9 = Pregnant, non lactating females; 10 = Lactating females; 11 = Resting females, i.e. mature females which are not pregnant or lactating. The division of the males in M I-III is according to Desportes *et al.* (1993b).



Fig. 7. The average monthly composition of 38 long-finned pilot whale schools examined during the study period (n=3,018). The division of mature males as M 11 and M 111 is according to Desportes *et al.* (1993b).

School composition

In the 'average' school (Fig. 6; n=3,018 whales; n=38 grinds) there are 46% immatures, 12% pregnant females and 24% lactating females; a maximum of 12% are mature males (male groups M II + M III, according to Desportes *et al.*, 1993b). An examination of the pooled data by month (Fig. 7) reveals clear differences in the period from March to September, the first part including the peak conception period followed by peaks in numbers pregnant and parturition. Details of the structure in the schools among the mating section of the whales are treated by Desportes *et al.* (1993b) who conclude that further studies are needed before, in particular, the role of mature males within the school becomes clear.

Sex ratios

The sex ratio is significantly biased towards females (z=1,141; p<0.001; n=3,046), comprising 60% females or a ratio of 1:1.58 ±0.05 (n=38) of the total number of whales with a range of 49–70% (or 0.97–2.37, see Table 1). These findings agree well with those previously found for the Faroes (58% – Bloch, 1992; 60% – Joensen, 1962) and other areas of the North Atlantic, including Iceland (68% – Sigurjónsson *et al.*, 1993), Orkney (55% – de Kock, 1956), Great Britain (62% – Martin *et al.*, 1987) and Newfoundland (65% – Kasuya *et al.*, 1988; Zachariassen, 1993).

The sex ratio in relation to age (Fig. 8) shows a significant positive slope (r=0.68; t=5.75) caused by differences in observed maximum ages (46 years for males and 59 years for females – Bloch *et al.*, 1993a). Thus the sex ratio increases with age in favour of females.



Fig. 8. The ratio between females and males compared according to age (n=2,418; r=0.68; t=5.75).



Fig. 9. The ratio between females and males in schools of different sizes (n=3,046; r=0.14; t=0.86).



Fig. 10. The ratio between females and males according to month (n=3,046; r=0.15; t=0.92).
The sex ratio shows no correlation with either school size (Fig. 9; r=0.14) or month (Fig. 10; r=0.15). Thus the peak reproductive season (April to July) does not influence the overall sex ratio in the school (Desportes *et al.*, 1993b) as might be expected in a social structure where the sexually active males migrate between schools (Danielsdottir *et al.*, 1992; Andersen, 1993).

DISCUSSION

Factors affecting the geographical distribution of the sample *Available sampling sites*

The Faroe Islands are divided into nine grind districts, with overlaps, i.e. areas which receive shares from pilot whales beached in the authorised whaling bays (Joensen, 1976; Joensen, 1981; Bloch *et al.*, 1990a). In that way each member of every household gets a 'home share', even those who are temporarily away fishing. Not all Faroese bays provide suitable topographic conditions for a grind (Svabo, 1783; Müller, 1882) and experience over the centuries has shown which ones offer the best chance for a 'good' grind. The first written regulations appeared in 1832 and since then they have been revised several times concurrent with changes in the community. At present, 22 bays have been authorised for whaling (Executive Order no. 107, 21 November 1989) and the most recent whaling regulations outline the responsible authorities, the procedure of the drive, beaching, slaughtering, valuation and division of the catch, and penalties for breaches.

During the sampling period 1986–8, 16 out of 22 authorised whaling bays were used between one and five times (Fig. 1–2). The five bays not used were Saksun, Norðskála, Húsavík, Trongisvágur and Fámjin. Saksun has only been used three times since records began (Zachariassen, 1993) and was de-authorised on 21 November 1989. Norðskála is very close to Hvalvík, which was used four times (Table 1). Their relative use depends on the whales – when they come from the north Nordskála is used and when they come from the south Hvalvík is used. Húsavík was under consideration for grind no. 22 but sea conditions were unsuitable. Only one grind took place in northern Suduroy and that was at Hvalba, not Trongisvágur (no. 39). Fámjin, which was also not used, is only used when absolutely necessary because of the dangerous surf conditions.

Vestmanna was only used once (grind no. 12), after which it was closed. It was reauthorised according to the new executive order from November 1989, after successful improvements and extensions to the existing beach had been made. Similar improvements have also been made to the beaches in Funningsfjørður and Tórshavn.

Closed districts

Since 1982, whenever the supply of blubber and meat is considered adequate by the chief district officer in agreement with the grind-foremen in the district, that district has been closed by an executive order until the meat and blubber is consumed. During the sampling period, the following districts were closed for periods ranging from 0.5 to 3.5 months (see Fig. 1 for their location):

1986: Hvannasund, Klaksvík, Viðvík, Sandoy.

- 1987: Tórshavn, Miðvágur, Bøur, Leynar, Sandoy.
- 1988: Tórshavn, Miðvágur, Bøur.

It is known that grinds were observed from the closed districts, but only a few were reported, and no attempts were made to drive them.

The closure of districts may of course affect the geographical and seasonal distribution of the catches. This can be illustrated by considering three examples, Miðvágur, Tórshavn and Leynar. The village of Miðvágur on Vágoy had the highest proportion of catches between 1709 and 1990 (15.0% of all beached grinds; 17.9% of all whales). For the period 1929–90, which includes the latest peak occurrence and the two year study period, the values were 9.7% of grinds and 10.7% of landed whales, giving an annual average catch of 1.08 grinds or 168.3 whales (Bloch *et al.*, 1990b; Zachariassen, 1993). During the study period, Miðvágur had four grinds (401 whales). Although, the village had, in fact, a greater supply than average despite the periods of closure, it should be noted that grinds were definitely observed from this district which under other circumstances might have been taken.

The population of the capital, Tórshavn, on the island of Streymoy, has grown dramatically in recent years. This means that today, many more boats and people are able to take part in a grind compared with many small villages. Boats from the capital are often able to reach schools before village boats and thus can take the grind to Tórshavn. Therefore, despite being closed for two periods in the three years examined, Tórshavn had five grinds containing 568 whales (the average yearly figures for grinds and individual animals for the period 1929–90 are 1.1 and 127.7).

The whaling bay Leynar, also on the island of Streymoy, was first used in 1909, but the local topographical conditions seldom give this bay an advantage over Vestmanna, located a little further north. However, during the study period, Vestmanna was closed most of the time for improvements (see above), so Leynar was used more often than usual with five grinds (381 whales), while the annual average over the 1929–90 period was 0.2 grinds (15.2 whales).

These examples show that the distribution of grinds can change over time with the closing of districts and changes in the community structure. Any detailed examination of the long-term statistics should take account of such changes in local population structure.

Temporal distribution

During the study period there were a greater number of small schools and a wider monthly spread than the overall average long-term series, 1709–1990 (Fig. 11); the peak months over the whole period were July-September (Zachariassen, 1993). However, seasonal distribution has also changed considerably throughout the long-term series. The 1709–1990 period can be divided into five sub-periods, following the *ca* 120 year periodicity in occurrence of pilot whales in Faroese waters. The periods with peaks in occurrences were from about 1709–1750, 1800–1880 and 1935-present, separated by periods of low occurrence between 1750–1800 and 1880–1935 (Zachariassen, 1993). The period 1750–1800, one of the lowest in the occurrence of pilot whales, also had a monthly distribution similar to the study period (Fig. 12), although it is not possible from the older material to determine whether the period represented a rise or fall in the curve. The present period is at the beginning of a descending period, close to the previous peak.

This periodicity in occurrence of pilot whales around the Faroe Islands appears to be related to the occurrence of their favourite prey, the squid *Todarodes sagitatus*. Although no squid were caught in the Faroes in 1986 or 1988, and only a small amount in 1987, they were known to be out on the banks (Desportes and Mouritsen, 1993). As early as the late 19th century, Müller (1882, p.4; 1883, p.21) mentioned the relationship between surface water temperature, and squid and pilot whale abundance. This pattern is also known from Newfoundland, where Rumage (1983) mentions that pilot whales feed on squid and that the fewer the squid in the area, the smaller the schools of whales seen were.



Fig. 11. Monthly distribution of pilot whale catches in the Faroes in the period 1986–1988 (n-4,818), compared with all catches 1709–1990 (n=223,707).



• Fig. 12. Monthly distribution of pilot whale catches examined during the study period (n=3,635).

Table 6

	1709- 1990	1966- 1985	1986	1 987	1988	1986-8
No. of whales Average school size No. of schools Range	235,649 149 1,646 1-1,200	30,101 128 235 1-644	1,677 84 20 16-207	1,451 76 19 5-225	1,690 84 20 15-183	4,818 82 59 5-225
Annual no. of schools Range	5.9 0-23	11.8 3-21	20	19	20	20 19-20
No. of months included Range	12 0-12	3-10	8	9	11	9.3 8-11

The average school size, number of schools and months used for the period 1709-1990, 1986-1985, and from 1986-1988, separately and compared. Data from the period 1709-1990 are taken from Zachariassen (1993), while the data from 1966-85 are from Hoydal and Lastein (1993).

Recent studies on the circulation of the water masses in the northern part of the northeast Atlantic (Hansen, 1985; Hansen *et al.*, 1988), the long-time series in surface temperature (Hansen and Meincke, 1984) and anomalies caused by eddies of cold water close to the Faroes (Hansen and Zachariassen, 1977; Hansen and Meincke, 1979) confirm the correlation between the periodically long-term differences in water temperature around the Faroe Islands, and the occurrence of the squid prey and the long-finned pilot whale. A further, more detailed analysis of the long-term data may reveal more interesting details of the occurrence of the whales around the Faroes (Hoydal and Lastein, 1993).

School size

Periods of low occurrence have been characterised by relatively few schools which have a larger number of animals, whereas in the peak periods, the number of schools was greater but the mean school size was smaller than the average (Table 6). The observed school sizes and numbers for the study period fit well with this pattern.

Recorded school sizes of landed pilot whales in the Faroes can be compared with the records of stranded pilot whales from other areas and with observed 'offshore' observations, in particular from the recent North Atlantic Sightings Surveys (e.g. Buckland *et al.*, 1993). In the North Atlantic, information exists for schools from Newfoundland, Iceland, Ireland, Great Britain, The Netherlands, Spain and the Mediterranean Sea (Fraser, 1946; 1953; de Kock, 1956; Husson and van Bree, 1972; 1976; O'Riordan, 1975; Evans, 1980; van Bree and Smeenk, 1982; McBrearty, 1986; Smeenk, 1986; Klinowska, 1987; Martin *et al.*, 1987; Nores and Peréz, 1988; Kastelein *et al.*, 1990; Sigurjónsson *et al.*, 1993). Further afield, information from the South Atlantic is available (e.g. Aguayo, 1975; Ross, 1984; Crespo *et al.*, 1985; Goodall and Galeazzi, 1987). In all areas, school sizes vary considerably, usually ranging from single individuals to no more than 200, although occasional groups of up to 300 whales have been reported.

Comparisons of the different offshore observations show a range from single individuals to more than 1,000 in both the North and South Atlantic (Fraser, 1934; Evans, 1980; McBrearty, 1986; Sanpera and Jover, 1987; Gunnlaugsson *et al.*, 1988; Kasamatsu *et al.*, 1988; Larsen *et al.*, 1989; Lens *et al.*, 1989; Joyce *et al.*, 1990; Sigurjónsson and Gunnlaugsson, 1990; Lens, 1991).

The available information shows that most of the schools landed in the Faroes are within the observed school sizes from other parts of the North Atlantic. However, the known problems with estimating the school sizes offshore (Joyce *et al.*, 1990) may be reflected in the observation that, out of all landed pilot whales from the period 1709–1990, 157 grinds (9.5%) containing 29% of all landed whales, exceed the number of landed or observed school sizes mentioned elsewhere. The drive of up to 1,200 whales landed on 9 October 1940 on Sandoy is the largest recorded Faroese grind (Zachariassen, 1993).

A detailed examination of the correlations between the occurrence of pilot whales and the oceanographical conditions over time around the Faroes may help to elucidate the relationship between the numbers of schools and school sizes (Hoydal and Lastein, 1993).

CONCLUSION

A comparison of the data obtained from the grinds examined during the study period, with the available data from the history of the fishery, suggests that the grinds fit in well with the observed patterns over the long-term series and revealed no biases that would affect the general nature of the conclusions that can be drawn from the study programme.

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Distribution and Abundance of Long-Finned Pilot Whales in the North Atlantic, Estimated From NASS-87 and NASS-89 Data

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ABSTRACT

During the summers of 1987 and 1989, large scale transect surveys were conducted throughout the North Atlantic by several national agencies in Denmark (off Greenland), Faroe Islands, Iceland, Norway and Spain (North Atlantic Sightings Surveys, NASS-87 and NASS-89). This paper analyses the pilot whale (*Globicephala melas*) survey data collected by three Icelandic and one Faroese survey vessel in 1987, and four Icelandic, one Faroese and one Spanish vessel in 1989. Norwegian survey vessels operated north and cast of this area in both years, but only five groups (three primary sightings) were observed in 1989 and none in 1987. Furthermore, no sightings were made in the area north and northeast of Iceland, thus indicating that the joint surveys covered the northernmost areas of pilot whale distribution east of 42°W. The area further to the west was not covered in either survey. The coastal European waters between 42–52°N were covered by the Spanish vessel in 1989. Sightings made in 1989 by the Icelandic vessels tended to be at the southernmost boundaries of the survey area.

The present data were examined with respect to several potential stratification factors, namely geographic block, Beaufort (i.e. wind speed), vessel and school size, but sample size precluded stratification by all these factors simultaneously. The encounter rate was generally lower in the 1987 survey than in 1989, but the difference was not statistically significant. The total estimate for the 1989 survey, covering a wider area and further to the south than in 1987, was 778,000 (CV=0.295). This is regarded as the best available estimate of the total stock of long-finned pilot whales in the northeastern North Atlantic Ocean, although small numbers occur outside the NASS survey areas. The paper discusses potential biases in the abundance estimates, and the problems of estimating pilot whale abundance from sightings data.

KEYWORDS: PILOT WHALES—LONG-FINNED; NORTH ATLANTIC; ASSESSMENT; DISTRIBUTION; SURVEY.

INTRODUCTION

Distribution of pilot whales

Mitchell (1975b) reviewed the status and distribution of the long-finned pilot whale (*Globicephala melas*) in the North Atlantic. It is common from Northwest Africa (and the Mediterranean) to Cape Hatteras and north to Greenland, Iceland and the Barents Sea. Its close relative, the short-finned pilot whale (*G. macrorhynchus*) has a more southerly distribution and is rarely seen north of Cape Hatteras in the west and north of Madeira, off Northwest Africa, in the east. Brown's (1961) summary of observations made from ocean weather ships, merchant vessels and other ships, provides information on the oceanic range of this species as far south as 45°N in the central area of the North Atlantic,

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suggesting their occurrence throughout the year in oceanic waters between 45° and 50°N and probably in all longitudes from the Bay of Biscay to Newfoundland.

In the European part of the Northeast Atlantic, sightings reveal a distribution from the western basin of the Mediterranean east of Gibraltar to Corsica (Müller, 1882; McBrearty et al., 1986) to Greenland (Kapel, 1975), with an inshore occurrence especially in late summer and autumn months (Joensen and Zachariassen, 1982; Desportes, 1983; Bloch et al., 1989a). Strandings have frequently occurred on the coasts of Ireland and Great Britain (de Kock, 1956; Fraser, 1974; O'Riordan, 1975; Martin et al., 1987) with an increasing number in this century (Sheldrick, 1976). Concentrations have been recorded in the Bay of Biscay, the southwestern coasts of Britain and Ireland, and in the more northern areas near the Hebrides, Shetland and the Faroe Islands (Evans, 1980; 1987; McBrearty et al., 1986).

Abundance and status

Joensen and Zachariassen (1982) and Hoydal (1986; 1987) reviewed information on the distribution and abundance of North Atlantic pilot whales with reference to the well documented catch history from the Faroe Islands. Although the data did not permit estimation of stock size, Hoydal concluded that there were no signs of overexploitation in the stock exploited from the Faroes, despite average catches in the range 800–2,000 p.a. over three centuries. In contrast, the industrial pilot whale drive-fishery off Newfoundland after the Second World War appeared to cause drastic changes in local abundance before it ceased in the late 1970s (Mercer, 1975).

Mitchell (1975a) suggested that since both these fisheries operated concurrently, but only the Newfoundland fishery collapsed, this suggested some separation of stocks. However, Sergeant (1986) noted that in the period 1948 to 1971 the catches at Newfoundland somewhat resembled the catches at the Faroe Islands, and that catches off the Faroes subsequently continued at a low level until 1976, after which they increased steadily. He considered that this, along with a simultaneous increase in the frequency of mass strandings in recent years in the western North Atlantic, indicated a trans-Atlantic connection of this species. Evans (1987) gives data on a substantial increase in both strandings and sightings of pilot whales in British and Irish waters since the 1950s, which concurs with Hoydal's (1986) observations of apparent increase in abundance reflected in higher catches in recent years.

Surveys

Before 1987, the only systematic vessel surveys for cetaceans in the northeastern Atlantic were carried out in limited areas and were of relatively short duration (Iceland, e.g. Sigurjónsson, 1983; 1985; Martin *et al.*, 1984; Norway, e.g. Øien and Christensen, 1985; Spain, e.g. Aguilar *et al.*, 1983; Sanpera *et al.*, 1984; 1985; Sanpera and Jover, 1986). Similarly, systematic aerial surveys covered only limited coastal areas (Iceland, e.g. Hiby *et al.*, 1984; Gunnlaugsson *et al.*, 1988; West Greenland, e.g. Larsen, 1984; 1985; 1986). In the Northwest Atlantic (the Newfoundland-Labrador area), a line-transect aerial survey directed towards humpback (*Megaptera novaeangliae*), fin (*Balaenoptera physalus*) and long-finned pilot whales was conducted in 1980 (Hay, 1982), and during 1978–82 cetacean aerial surveys were conducted on the shelf waters of the northeastern United States and shipboard surveys during 1980–88 (CeTAP, 1982; Payne *et al.*, 1993). Many of these surveys were not specifically designed to yield estimates of stock size and have suffered from their sporadic nature both in time and space, covering only a fraction of the species' summer ranges at a time.

In 1987, several interested national laboratories met to organise a joint North Atlantic Sightings Survey (NASS-87) to be implemented in June-August 1987 in the area bounded by Spitzbergen and the Barents Sea in the north and the Spanish coast in the south, and between West Greenland in the west and the Norwegian coast in the east (Anonymous, 1987a; b). A further survey (NASS-89) took place in the summer of 1989 (Anonymous, 1988; 1989a; b). This paper analyses the pilot whale data from both surveys collected by the Icelandic and Faroese vessels, and that from the NASS-89 survey collected by the Spanish vessel.

Although not included in the analyses of this paper, 11 pilot whale groups, comprising in total 123 animals, were detected during the Spanish cruise for NASS-87. These occurred between 44°N and 52°N, and between 11°W and 18°W, and were spread through most of the survey area (Lens *et al.*, 1989). No pilot whales were detected during Norwegian cruises for NASS-87 (Øritsland *et al.*, 1989) and only five groups were observed in 1989 (Øien, pers. comm.). The Norwegian data are also not included in the analysis here.

The pilot whale sightings data from the Icelandic and Faroese cruises in 1987 were first analysed by Bloch *et al.* (1989b). The analyses of NASS-87 data presented here are more extensive, are carried out using more conventional methods and yield revised abundance estimates.

METHODS

Vessels and ship methodology

During June and July 1987, three Icelandic vessels surveyed Icelandic and adjacent waters (Fig. 1). They were Arni Friðriksson (referred to here as AF), Skírnir (Sk) and Keflvikingur (Ke). The Faroese vessel Hvítaklettur surveyed Faroese and adjacent waters (Fig. 1) from June to August. In 1989, four Icelandic vessels surveyed Icelandic and adjacent waters (Fig. 2) during July and August: Arni Friðriksson (AF), Bardinn, which was the same vessel as Skírnir in 1987, so will be referred to as Sk here, Hvalur 8 (Hv8) and Hvalur 9 (Hv9). A Faroese vessel, the Olavur Halgi, surveyed Faroese and adjacent waters to the west (see Fig. 3).

The design and conduct of these surveys have been described in detail (Sigurjónsson *et al.*, 1989; 1991; Joyce *et al.*, 1990 and Lens, 1991). It is not repeated here.

Data and analyses

Only primary sightings¹ of pilot whales were analysed. The recorded sighting angles and distances to pilot whale schools were smeared and transformed to perpendicular distance intervals using smearing method (2) of Buckland and Anganuzzi (1988). The hazard-rate model (Buckland, 1985; 1987) was fitted to the smeared perpendicular distances, truncated at 0.65 n.miles.

School size

Where available, analyses were carried out using the 'best' estimates of school size. For all vessels in 1987, high, low and best estimates of school size were usually recorded. For these data, if a best estimate was not recorded, the mean of the low and high estimate was used. If there was no best or high estimate, the low estimate was used. In 1989, the Faroese

¹ Sightings made when a vessel is searching 'on effort', i.e. when searching is the primary activity. Sightings made while other activities are being carried out (e.g. sailing towards a sighting to confirm its species identity or school size) are termed 'secondary' sightings.



Fig. 1. Blocks in which there was Icelandic and/or Faroese effort in 1987. Faroese blocks are delineated by broken lines. Icelandic block 7 overlapped slightly with Faroese block 17. Sightings of pilot whales are indicated by crosses.

vessel again recorded high, low and best estimates. However, the Icelandic vessels recorded either a best estimate or a low and a high estimate. In this case, the best estimate was used if available; otherwise the low estimate was used. Analyses were also carried out after replacing the low estimate by the mean of the low and high estimates, to assess the impact on the final abundance estimate. For the Spanish data, the best estimate for each school was analysed.

Stratification

Data from the Icelandic NASS-89 cruises were analysed to determine an appropriate methodology for estimating pilot whale abundance. Sample sizes were too small for the NASS-87 survey and for the Faroese and Spanish NASS-89 cruises to allow adequate assessment of different stratification options from those data alone.

Several potential stratification factors were identified: geographic block, Beaufort (i.e. wind speed), vessel and school size. Ideally stratification should be by all of these factors, but sample size considerations preclude this, so stratification was initially carried out for each candidate factor in turn. To assess the effect of Beaufort, the average school size, encounter rate and effective search half-widths were estimated for each Beaufort (0–6) in turn, ignoring other possible stratification factors. Given the small sample sizes, this was



Fig. 2. Blocks in which there was Icelandic and/or Faroese effort in 1989. Faroese blocks are delineated by broken lines. Icelandic block 88 overlapped with Faroese block 20. Sightings of pilot whales are indicated by crosses.



Fig. 3. Blocks in which there was Spanish effort in 1989. Block 21 is to the west of 15°W, and block 22 to the east. Sightings of pilot whales are indicated by crosses.

repeated, grouping together data from Beauforts 0–2 and 3–6. Standard errors (SE) were calculated for each estimate and z-tests carried out to assess whether there were significant differences in estimates at different Beauforts. The SE for mean school size was calculated as sample standard deviation (SD) divided by the square root of the sample size. For encounter rate, the rate per day was calculated, and the sample variance of these rates, weighted by daily effort was used following the empirical method described by Burnham *et al.* (1980). The SE for the effective search half-width was obtained using likelihood methods, via the information matrix. A similar analysis was carried out for each stratification factor. As these factors are confounded with each other and the above approach ignores interactions between them, analyses were supplemented by knowledge of likely effects of the different factors on the three components of estimation to determine an appropriate stratification (see below).

Abundance within strata

Within a stratum the abundance N was estimated by (Burnham et al., 1980)

$$\hat{N} = \frac{n.\hat{f}(0).\bar{s}.A}{2L} ,$$
 (1)

with

$$v\hat{a}r(\hat{N}) = \hat{N}^2 \cdot \left[\frac{v\hat{a}r(n)}{n^2} + \frac{v\hat{a}r\{\hat{f}(0)\}}{\{\hat{f}(0)\}^2} + \frac{v\hat{a}r(\bar{s})}{\bar{s}^2}\right],$$
(2)

where

n = number of sightings after truncation,

 $\hat{f}(0)$ = estimated probability density of perpendicular distances, evaluated at zero,

 \bar{s} = mean group size,

L = distance covered by the vessel while on effort,

A = size of the area containing the population of N animals.

The encounter rate is then defined as n/L and the effective search half-width is $1/\hat{f}(0)$.

Where abundance estimates were combined across strata for which a common value of f(0) was assumed, the variance of the combined estimate was calculated allowing for the covariance between the individual estimates. If instead the individual abundance estimates were assumed to be independent, variances would be underestimated.

When the coefficient of variation (CV) of an abundance estimate \hat{N} is large, a poor, possibly negative, lower confidence limit can be obtained if the estimate is assumed to be normally distributed. Here, \hat{N} was assumed to have a log normal distribution and a 95% confidence interval was estimated using the method of Burnham *et al.* (1987, p.212):

 $(\hat{N}/C, \hat{N} \cdot C) \tag{3}$

where

$$C = \exp\left[1.96. \sqrt{\left\{ \hat{var}(\log_e \hat{N}) \right\}}\right]$$
(4)

and

$$v\hat{a}r (\log_e \hat{N}) = \log_e \left[1 + \frac{v\hat{a}r(\hat{N})}{\hat{N}^2}\right]$$

Treatment of aggregations

Pilot whales often occur in large, loose aggregations of subgroups. For all cruises but one, the whole aggregation was treated as a single sighting. In 1987, vessel Ke recorded data by

subgroup, making it possible to estimate abundance treating aggregations two ways: first by taking subgroups as schools, and second by taking the aggregation as the school, located at the recorded position of the first subgroup detected. By taking the ratio of the estimate from the first method to that from the second, a correction factor was obtained. An SE and confidence interval for the correction factor were found by segregating the sightings and effort data by day, block, Beaufort and cloud cover category, bootstrapping from the resulting units, and applying the two estimation methods to each of 399 bootstrap replicates. This yields 399 estimates of the correction factor; their SD is an estimate of the SE of the correction factor, and the tenth smallest and tenth largest estimates provide a 95% 'percentile' confidence interval.

RESULTS

Distribution

The distribution of sightings is given in Figs 1-3.

Abundance

The effects of Beaufort on parameter estimates are summarised in Table 1. The effective search half-width did not vary significantly with Beaufort category. Indeed, the estimated width was greater at higher Beaufort, the reverse of what might be expected and thus it seems reasonable to assume that the effective search half-width is independent of sea state for these data. There was some evidence that encounter rate varied with Beaufort, but the results were inconsistent, with low encounter rates at Beauforts 0 and 5, and high encounter rates at Beauforts 2 and 3. This probably occurred because the geographic areas with high densities of pilot whales were predominantly surveyed during Beauforts 2 and 3 while Beauforts 0 and 5 were recorded mostly in areas of low density. There was no indication of variation in mean school size with Beaufort. Thus, data were pooled across Beaufort for all subsequent analyses.

Parameter estimates are shown by block in Table 2. Sample sizes were too small to allow stratification of effective search half-width by block. There was strong evidence of differences in encounter rates among geographic blocks. Small sample size does not rule

Table 1

Number of sightings (after truncation but before smearing), effective search half-width, encounter rate and mean school size by sea state, Icelandic pilot whale data, NASS-89. Standard errors in parentheses. Values in the same column with different superscript letters differ significantly (p < 0.05). Thus the encounter rates at Beauforts 2 and 3 were significantly higher than those at Beauforts 0 and 5, but no other differences in this table were significant.

Beaufort	Number of sightings, n	Effective search half-width (nm)	Encounter rate (schools/100nm)	Mean school size, s
0	1	-	0.31 (0.39) ^a	7.0 (-)
1	12	$0.140(0.114)^{a}$	$1.10(0.71)^{ab}$	$24.3(8.0)^{a}$
2	34	$0.113(0.062)^{a}$	1.95 (0.56) ^b	$29.4(6.4)^{a}$
3	28	0.207 (0.072) ^a	1.59 (0.35) ^b	$19.9(2.7)^{a}$
4	10	$0.268(0.136)^{3}$	$0.72(0.40)^{ab}$	$32.6(9.9)^{a}$
5	1	-	$0.08(0.13)^{a}$	100.0 (` - ´)
6	4	-	0.62 (0.46) ^{ab}	24.0 (6.3) ^{°a}
0-2	47	$0.113(0.053)^{\alpha}$	$1.48(0.36)^{\alpha}$	$27.7(5.1)^{\alpha}$
3-6	43	$0.221 (0.063)^{lpha}$	$0.84(0.14)^{\alpha}$	$25.1(3.5)^{\alpha}$

Table 2

Number of sightings (after truncation but before smearing), encounter rate and mean school size by area, pilot whale data, NASS-89. Standard errors in parentheses. Values in the same column with different superscript letters differ significantly (p < 0.05). Sample sizes were too small to calculate effective search half-width by block.

Nationality	Block	Number of sightings, n	Encounter rate (schools/100nm)	Mean school size, s
Icelandic	36	16	1.50 (0.35) ^{ab}	$23.1(3.9)^{a}$
	40	10	$1.32(0.49)^{abc}$	$17.0(3.8)^{a}$
	50	25	$2.24(0.55)^{a}$	$31.8(8.1)^{a}$
	60	3	$0.33(0.20)^{c}$	83.3 (32.8)
	70	7	$0.81(0.30)^{bcd}$	$19.0(4.3)^{a}$
	88	9	$0.80(0.40)^{bc}$	$21.7 (5.7)^{a}$
	93	2	$0.53(0.28)^{\circ}$	5.0 (0.0)
	94	9	$1.18(0.41)^{abc}$	27.9 (10.2) ^a
	95	9	$0.76(0.28)^{bc}$	22.8 (6.6) ^a
Faroese	10	11	0.70 (0.28)	13.5 (5.1)
Spanish	21	15	$0.92(0.28)^{\alpha}$	$17.7(6.2)^{\alpha}$
-	22	4	$0.22(0.09)^{\beta}$	$10.0 (3.5)^{\alpha}$

out valid estimation of encounter rate and mean school size by block and so we stratified by block for those two parameters. This yields more reliable abundance estimates by block than does an unstratified analysis in which the total abundance estimate is proportioned by block area, although precision may be poor for individual block estimates.

Stratification by block also effectively stratifies the data by vessel, because most blocks were surveyed largely or entirely by a single vessel. As the effective search half-width was not stratified by block, it was necessary to determine whether it should be stratified by vessel. Table 3 shows that there were no significant differences between Icelandic vessels, although the effective search half-width for vessel Hv9 was just a quarter of that for vessel Sk. When the effective search half-width was stratified by vessel, an estimate of 538,000 (CV=0.339) was obtained for the area surveyed by Icelandic vessels in 1989. With no stratification the estimate was 611,000 (CV=0.354). A chi-squared test for differences in the observed perpendicular distance distribution between vessels also proved non-significant, and thus data were pooled across vessel for subsequent estimation of effective search half-width. However, the effective search half-width was stratified by nationality, as different nations used different vessel types and survey methods. A plot of the fitted detection curve for the pooled data from Icelandic vessels in 1989 is shown in Fig. 4a.

The distribution of school size was highly skewed (Table 4). Although large schools influence the final abundance estimate appreciably, too few were detected to allow satisfactory stratification. Parameter estimates are shown by school size in Table 5. School size intervals of 1–10, 11–45 and >45 animals were selected. The first cutpoint was selected because it split the number of schools of at most 45 animals into two groups of equal sample size. The value of 45 was selected because it provided a sample size for 'large schools' that was just sufficient to allow estimation of effective search half-width, and because there was no natural break in recorded school sizes below this value. No significant differences in the effective search half-width was for small schools, as might be expected. However, estimated correlation between school size and (untruncated) perpendicular distance of the school from the trackline was very close to zero (r=0.012; p > 0.1) while the



Fig. 4. Fits of the hazard rate model to the pooled perpendicular distance data.

Table 3

Number of sightings (after truncation but before smearing), effective search half-width, encounter rate and mean school size by vessel, pilot whale data, NASS-89. Standard errors in parentheses. Values in the same column with different superscript letters differ significantly (p < 0.05).

Vessel	Number of sightings, n	Effective search half-width (nm)	Encounter rate (schools/100nm)	Mean school size, s
 Sk	31	$0.323(0.137)^{a}$	1.38 (0.33) ^a	32.6 (7.3) ^a
AF	24	$0.157 (0.092)^{a}$	$0.81(0.21)^{a}$	19.2 (4.2) ^a
Hv8	21	0.150 (0.053) ^a	$1.32(0.44)^{a}$	$25.7 (3.4)^{a}$
Hv9	14	$0.087(0.058)^{a}$	0.97 (0.27) ^a	26.1 (7.6) ^a
All Icelandic	90	$0.163(0.047)^{\alpha}$	$1.09(0.17)^{\alpha}$	$26.4(3.1)^{\alpha}$
Faroese	11	$0.214(0.078)^{\alpha}$	$0.70(0.28)^{\alpha\beta}$	$13.5(5.1)^{\beta}$
Spanish	19	$0.156(0.052)^{\alpha}$	$0.55(0.15)^{\beta}$	$16.1(5.0)^{\alpha\beta}$

Table 4

School sizes (after truncation but before smearing), Icelandic pilot whale data, NASS-89.

School size	1-10	11-20	21-30	31-40	41-50	51-70	71-90	91-120	121-150
Frequency	38	16	15	7	4	1	3	4	2

Table 5

Number of sightings (after truncation but before smearing), effective search half-width and encounter rate by school size, Icelandic pilot whale data, NASS-89. Standard errors in parentheses. Values in the same column with different superscript letters differ significantly (p < 0.05).

School size	Number of sightings, n	Effective search half-width (nm)	Encounter rate (schools/100nm)
1-10	38	$0.143(0.043)^{a}$	$0.44(0.11)^{a}$
11-45	38	$0.272(0.108)^{a}$	$0.47(0.08)^{a}$
>45	14	$0.232(0.158)^{a}$	$0.18(0.04)^{b}$

estimated correlation between log school size and perpendicular distance was in fact negative (r = -0.045; p > 0.1). Given no indication of a relationship between school size and perpendicular distance, subsequent analyses were not stratified by school size.

Abundance estimates under the preferred analysis method are given in Tables 6–8. Plots of the fitted detection curves for the pooled data from Icelandic vessels in 1987, for Faroese 1987 and 1989 data, and for Spanish 1989 data are shown in Figs 4b-e.

The abundance estimate from the Icelandic NASS-89 data is high relative to the estimate from NASS-87 data. This arises both because high abundance estimates were obtained for the southern blocks, which were not covered in 1987, and because estimated abundance was higher on average in 1989 for blocks covered in both surveys. The surveys were carried out earlier in the summer in 1987 than in 1989, so it is possible that more animals are present in the blocks covered in both surveys in late summer. Comparison of Tables 3 and 9 shows that estimated effective search half-widths were narrower for 1989

Year	Block	Number of sightings, n	Size of block (nm ²)	Abundance estimate, Ñ	CV(N)	95% confidence interval
1987	1	1	2542.1	136	1.079	(24, 763)
	2	1	18926.3	271	0.594	(92, 796)
	7	11	75215.1	4651	0.814	(1149, 18819)
	36	6	44172.5	5753	0.707	(1651, 20051)
	88	12	59848.0	11325	0.577	(3960, 32388)
	93	15	21760.7	17339	0.608	(5774, 52066)
	94	10	46092.4	14147	0.781	(3656, 54744)
	95	1	69396 .1	4240	0.778	(1101, 16326)
	All	57	337953.2	57864	0.362	(29074, 115164)
1989	36	16	44172.5	47195	0.408	(21857, 101904)
	40	10	107842.0	74503	0.522	(28484, 194869)
	50	25	9975 0.0	217950	0.458	(92611, 512923)
	60	3	131458.0	112138	0.777	(29157, 431288)
	70	7	88571.0	42109	0.523	(16052, 110461)
	88	9	59848.0	31889	0.633	(10215, 99549)
	93	2	21760.7	1783	0.597	(604, 5260)
	94	9	46092.4	46786	0.579	(16314, 134171)
	95	9	69396.1	37026	0.550	(13528, 101340)
	All	90	668890.7	611378	0.354	(312023,1197933)

Table 6

Table 7

Abundance estimates by block, Faroese pilot whale data, NASS-87 and NASS-89.

Year	Block	Number of sightings, n	Size of block (nm ²)	Abundance estimate, Ñ	CV(N)	95% confidence interval
1987	17	15	29599	55112	0.521	(21108, 143895)
	37	1	69394	4275	0.880	(968, 18871)
	47	3	73492	5392	0.732	(1495, 19453)
	All	19	172485	64779	0.454	(27752, 151209)
1989	10	5	195560	26122	0.689	(7702, 88593)
	20	6	40625	22887	0.898	(5068, 103357)
	All	11	236185	49009	0.614	(16186, 148389)

Table 8

Abundance estimates by block, Spanish pilot whale data, NASS-89.

Year	Block	Number of sightings, n	Size of block (nm ²)	Abundance estimate, N	CV(N)	95% confidence interval
1989	21	15	244390	128080	0.571	(45241, 362604)
	22 All	4 19	170900 415290	12235 140316	0.633 0.541	(3924, 38148) (52015, 378518)

Table 9

Vessel	Number of sightings, <i>n</i>	Effective search half-width (nm)	Encounter rate (schools/100nm)	Mean school size, s
Sk		$0.532(0.097)^{a}$	0.96 (0.27) ^a	31.3 (9.3) ^a
AF Ke	3 24	- 0.264 (0.130) ^a	0.25 (0.09) ^b 0.70 (0.21) ^a	7.7 (2.6) 13.9 (4.3) ^a
All Icelandic Faroese	57 19	$\begin{array}{c} 0.438 \left(0.094 \right)^{\alpha} \\ 0.234 \left(0.023 \right)^{\beta} \end{array}$	$0.74~(0.14)^{lpha}~0.41~(0.17)^{lpha}$	22.7 $(5.3)^{\alpha}$ 102.0(22.6) ^{β}

Number of sightings (after truncation but before smearing), effective search half-width, encounter rate and mean school size by vessel, pilot whale data, NASS-87. Standard errors in parentheses. Values in the same column with different superscript letters differ significantly (p < 0.05).

than 1987, leading to higher abundance estimates. Only vessel Sk detected sufficient pilot whales in both surveys to allow estimation of effective search half-widths by vessel, and these were high relative to other vessels. The estimated search width for vessel Sk was higher in 1987 than in 1989, but the difference was not significant. For the Icelandic data, mean school size was low in 1987 relative to 1989, except for vessel Sk. On average, encounter rates for Icelandic vessels were lower in 1987 than in 1989. If Icelandic blocks 40, 50, 60 and 70 and both Spanish blocks are excluded from analyses, so that the 1989 estimate is broadly comparable with the total estimate from Icelandic and Faroese data, the 1989 estimate is 191,000 animals (CV=0.330), compared with 123,000 animals (CV=0.294) for 1987. These estimates do not differ significantly (p>0.1), so that the observed large differences in abundance estimates for 1987 and 1989 might be explained largely or wholly by the wider area included in the 1989 analyses. If abundance estimates from Icelandic, Faroese and Spanish data are summed, excluding the estimate for Faroese block 20, which is largely within Icelandic block 88, the total abundance for the entire area surveyed during NASS-89 is estimated as 778,000 animals (CV=0.295).

DISCUSSION

General distribution

This is the first time a synoptic view of the entire area has been obtained. The geographical distribution found during the surveys is well in accordance with earlier published observations. For example Christensen (1977) reported a number of sightings off East Greenland from May-August 1974 and a single sighting southwest of Iceland. During a cruise in June-July 1981 at East Greenland and west of Iceland, Sigurjónsson (1983) encountered no pilot whales off Greenland, but observed 16 groups at the edge of the continental shelf and in deep waters west of Iceland. Martin *et al.* (1984) covering the latter area in 1982, located 5 groups of pilot whales. Sigurjónsson (1985) reported two sightings of pilot whales along the East Greenland coast in August 1993, but no animals were observed in any of the deep and shallow water areas covered around Iceland.

In the waters southwest of Iceland sightings of significant numbers of animals were made in both years. The clumped distribution in 1987 is due to unfavourable sightings conditions. The area at the continental edge south of Iceland was the only one resulting in sightings of pilot whales in extensive aerial surveys conducted in Icelandic coastal waters in June-July 1986 (3 sightings of 60 animals) and 1987 (7 sightings of 103 animals). respectively (Gunnlaugsson *et al.*, 1988; Donovan and Gunnlaugsson, 1989). Brown (1961) and McBrearty *et al.* (1986) had reported a number of summer sightings of pilot whales in deep waters farther south of Iceland, as was found in 1989.

The waters to the north, northeast and east of Iceland were covered under relatively good sightings conditions and the absence of pilot whales is in agreement with earlier surveys in these areas (Sigurjónsson, 1983; 1985; Martin *et al.*, 1984; Gunnlaugsson *et al.*, 1988; Donovan and Gunnlaugsson, 1989). Christensen's (1977) single sighting of 10 animals off Langanes, Northeast Iceland, in June 1974 is thus the only sighting so far of the species that far north in these waters. His summary of catches by Norwegian whalers (Christensen, 1975) shows a small number of takes east of Iceland and around Jan Mayen, proving the presence, although in small numbers, of this species in these waters.

A considerable number of sightings were made to the southeast of Iceland in both years. The only previously published sighting was a single group reported by Martin *et al.* (1984). The area further to the southeast, i.e. southwest of the Faroe Islands, had in 1987 by far the greatest occurrence of the species as one might expect given the ongoing fishery in Faroese waters. The fewer sightings in the area in 1989 reflect the level of primary effort and the cruise track. Evans (1980; 1987) reported sightings in the area between the Faroe Islands and the coast of Scotland. The relatively few sightings made during this survey west of Ireland and Great Britain are in conformity with Evans' (1987) observations of relatively low abundance in this area compared to the northernmost area of Scotland.

No pilot whales were seen in 1987 on the Norwegian survey vessels nor during the Norwegian aerial survey, which covered the Norwegian Sea northeast of our study area, the Norwegian coast and the Barents sea (Øritsland *et al.*, 1989), while only five groups were seen in 1989 (Øien, pers. comm.). This indicates that the species is scarce in the northernmost regions of the northeast Atlantic as also indicated by Christensen's (1977) summary of observations made in the different parts of North Atlantic (no pilot whales reported), although McBrearty *et al.* (1986) reported two sightings off North Norway.

In 1987, eleven sightings of 123 animals were made on board the Spanish survey vessel surveying south of 52°N, west of the British Isles and in the Bay of Biscay (Lens *et al.*, 1989), which is in accordance with earlier surveys by Spanish scientists (Aguilar *et al.*, 1983; Sanpera *et al.*, 1984; 1985; Sanpera and Jover, 1986) and from stranding records on the French coast. All were identified as long-finned pilot whales. The survey extended further to the west in 1989 and pilot whales were encountered throughout the area.

Abundance estimate

We regard our estimate of 778,000 (CV=0.295) as the best available estimate of the total stock of long-finned pilot whales in the northeastern Atlantic in summer. As explained in the Results section, the estimates from NASS-87 are lower. Our analyses of Icelandic and Faroese NASS-87 data yield a total estimate of 123,000 animals (CV=0.294). This is comparable with an estimate of 104,000 animals (CV=0.3), derived from estimates of 72,000 (CV=0.4) from Faroese NASS-87 data and 31,900 (CV=0.3) from Icelandic NASS-87 data given by Bloch *et al.* (1989b).

Estimates from the northwestern Atlantic are substantially lower than our estimate. Hay (1982) estimated some 13,000 animals from an aerial survey of the Newfoundland area whilst Payne *et al.* (1993), concluded that there were 10,000–12,000 off the Northeastern coast of the USA. During the aerial survey off West Greenland in 1987, 460 pilot whales were sighted in 18 groups (Larsen *et al.*, 1989), indicating substantial occurrence of the species during the survey period. Although no pilot whales had been observed in earlier aerial surveys (in 1983, 1984 and 1985) in the same area, subsequent surveys have regularly encountered pilot whales. Their seasonal occurrence has also been reported by Christensen (1975; 1977) and Kapel (1975). However no population estimates exist for the area.

Possible biases

There are several potential biases in the abundance estimates. For example, for many schools detected by Icelandic vessels in 1989, no best estimate of school size was recorded. We adopted the conservative approach, using the low estimate when no best estimate was recorded. This gave an abundance estimate from Icelandic data of 611,000 animals (Table 6). If instead the mean of the low and high estimates is used, the corresponding estimate of abundance is 691,000 animals (CV=0.353).

Another source of potential bias is the assumption that all pilot whales on the trackline were detected (g(0)=1). Although pilot whales can dive for up to one hour, Mate (1989) observed that a satellite-monitored radio tagged pilot whale averaged a dive time of 40 seconds. The distance travelled by a sightings vessel in 40 seconds is less than 300m, and pilot whales usually travel in groups that are not entirely synchronised, so that sighting cues occur more frequently than the surfacing rate of a single animal. Thus it seems likely that most pilot whales near the trackline and with a similar surfacing rate to that observed by Mate will be seen, and that g(0) for pilot whale groups will be close to unity. However, pilot whales sometimes show synchronous deep diving behaviour, and in the absence of adequate information on this behaviour, the possibility remains that a significant proportion of animals near the trackline remains undetected.

Perhaps more serious is the potential positive bias in estimates arising because of the method of recording large, loose aggregations of pilot whales. The first detected subgroup of such an aggregation, and hence the aggregation itself, will tend to be recorded closer to the trackline than the centre of gravity of the aggregation (which may explain why no correlation between school size and perpendicular distance was found) and mean school size will be overestimated, since large aggregations, occupying a substantial area, are more likely to be detected than small schools. We endorse strongly the recommendation of Bloch et al. (1989b), that 'as far as practical, every subgroup must be individually recorded and group sizes assessed (preferably while in passing or delayed closing mode) without any extrapolations.' It does not matter that the whole aggregation is not counted, provided most subgroups near the trackline are detected, and their sizes are estimated with reasonable accuracy. Provided robust methods of variance estimation are used, to take account of the strong clustering of subgroups, the analysis should be substantially less biased than an analysis based on aggregations. Using the data from vessel Ke in 1987, which were recorded in this way, a correction factor of 0.824 (CV=0.257; 95% confidence interval [0.330, 1.191]) was obtained. Although the confidence interval includes unity (no correction), it also extends as low as one third, corresponding to a reduction to one third of the uncorrected abundance estimate. The correction factor is an alternative to the solution adopted by Bloch et al. (1989b), who reduced Faroese school size estimates exceeding 100 animals to exactly 100, and Icelandic estimates exceeding 150 animals to exactly 150, in an attempt to reduce the bias caused by recording large schools too close to the trackline. At present, the correction factor is not applied, as it is unclear whether a correction calculated from data for vessel Ke in 1987 is appropriate for other vessels in either 1987 or 1989.

The counts of school size introduce another potential source of bias, especially when vessels operate in passing mode, when underestimation might be anticipated (Bloch *et al.*, 1989b). The decision whether to close with a sighting was made when animals were detected, and larger schools were more likely to be closed with. Thus it is not possible to associate effort with either mode, and mean school size during passing mode cannot be estimated by the observed mean size in closing mode. In future surveys, it might be

advisable to determine in advance whether effort is to be carried out in passing mode or closing mode with respect to pilot whales, so that school size estimates from the two modes can be compared. The possibility of using a helicopter to confirm estimates at least for a proportion of schools might also be considered.

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The Distribution of Pilot Whales (*Globicephala* spp.) in Shelf/Shelf-edge and Slope Waters of the Northeastern United States, 1978–1988

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ABSTRACT

The spatial and temporal distribution of pilot whales (*Globicephala* spp.) in shelf/shelf-edge and slope waters of the northeastern United States is described from 1,033 sightings collected during standardized aerial and shipboard surveys (1978–88). Two species of Globicephala, the long-finned (*G. melas*) and the short-finned pilot whale (*G. macrorhynchus*) occur in the study area. The long-finned pilot whale is the most widespread and abundant. Seasonal movements and distribution of *G. melas* coincide most closely with the abundance of the long-finned squid (*Loligo pealei*) and Atlantic mackerel (*Scomber scombrus*). During latewinter and spring the distribution of pilot whales generally follows the shelf-cdge/slope region between the 100m and 2,000m contours. This corresponds to a general movement northward and onto the shelf from deeper, slope waters. During late-summer and fall the pilot whale sighting distribution is more widespread throughout the shelf.

Two distinct clusters of pilot whale sightings occur in shelf-edge/slope waters of the northeastern United States, May-December. A northward cluster (likely G. melas) is centred north of $40^{\circ}0'N$ (in the Great South Channel-Georges Bank regions). The second cluster of pilot whale sightings occurs in the Mid-Atlantic (south of $38^{\circ}30'N$) at this time, and is considered to be G. macrorhynchus.

KEYBOARDS: PILOT WHALE-LONG-FINNED; PILOT WHALE-SHORT-FINNED; NORTH ATLANTIC; SURVEY-AERIAL; SURVEY-SHIP; DISTRIBUTION; FEEDING; SQUID; FISH

INTRODUCTION

Since 1978 there have been two large-scale surveys of cetaceans throughout the shelf waters of the northeastern United States. The Cetacean and Seabird Assessment Program was conducted by the Manomet Bird Observatory from May 1980 through December 1988. These shipboard surveys were designed to provide the National Marine Fisheries Service/Northeast Fisheries Center (hereafter these surveys are referred to as NMFS/ NEFC surveys) with a near-continuous assessment of cetacean and seabird populations in the shelf and shelf-edge waters (generally <200m). These data have been used to monitor small-scale temporal changes in the distribution and relative abundance of these taxa (Payne *et al.*, 1984; 1986). In addition, direct comparison to fisheries data collected concurrently with sighting data have been used to describe trophic interactions between cetaceans and/or seabirds and potential prey (Payne *et al.*, 1986; Smith *et al.*, 1988).

Information on distribution and abundance has also been provided by the Cetacean and Turtle Assessment Program (CETAP), sponsored by the Department of the Interior, Bureau of Land Management. These shelf-wide aerial surveys were conducted from November 1978 to January 1982. The major objectives of CETAP were to provide a spatial overview of cetacean distribution (Hain *et al.*, 1981; 1992; Winn, 1982; Kenney and Winn, 1986), and to estimate the absolute abundance of cetaceans in the study area (Scott

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et al., 1981; Winn, 1982; Kenney *et al.*, 1985; Hain *et al.*, 1992). The resultant data were to be used by federal agencies making decisions about potential development of oil- and gaslease sale tracts (Edel *et al.*, 1981); therefore special attention was paid to these areas (Sørensen *et al.*, 1984).

The CETAP aerial surveys provided the first absolute estimates of cetacean abundance in the shelf waters of the northeastern United States from line-transect surveys. A mean density and variance estimate were computed for each cetacean species within seasonal and regional samples for the entire study area. The collection of NMFS/NEFC shipboard sighting data also followed line-transect procedures (e.g. see Seber, 1973; Burnham *et al.*, 1980), but, thus far, the data have been used only to describe relative densities or abundance of cetaceans in shelf and shelf-edge waters, rather than the absolute densities that were generated by CETAP.

Despite differences in platform and survey objectives, both programs have provided parallel information on the distribution of cetaceans in shelf waters of the northeastern United States. Each survey has identified several regions within the study area as high-density habitats used by the entire cetacean community (Payne *et al.*, 1984; Hain *et al.*, 1985; Kenney and Winn, 1986; Selzer and Payne, 1988; Kenney, 1990). In this paper, we use the combined dataset to describe the spatial and temporal distribution of pilot whales (*Globicephala melas* and *G. macrorhynchus*) within shelf and shelf-edge/slope waters of the northeastern United States.

Because the apparent ranges of the two species overlap in shelf/shelf-edge and slope waters of the northeastern United States between $35^{\circ}0'N$ (Cape Hatteras) and $38^{\circ}0'N$ - $39^{\circ}0'N$, and difficulties in separating these two species in the field, both species have been considered together in recent distributional and abundance analyses (Winn, 1982; Powers and Payne, 1983; Payne *et al.*, 1984; Hain *et al.*, 1985; Kenney and Winn, 1987). We also consider their distributions together, although they are probably seasonally disjunct in the shelf waters of the northeastern United States. This is considered further in the Discussion section.

METHODS

Study area

The NMFS/NEFC study area consisted of all continental shelf and shelf-edge waters between Cape Hatteras and Nova Scotia, Canada less than 910m (212,686 km²), although most of the surveys were conducted in waters <183m. The CETAP surveys also encompassed the entire US outer continental shelf seaward to the 1,820m isobath (278,350 km²). Therefore, the NMFS/NEFC study area was comparable, but slightly smaller in size to the CETAP study area due primarily to less intensive coverage along the shelf-edge. For this paper, the study area has been partitioned into four regions (Fig. 1), the Gulf of Maine, Georges Bank, Southern New England and the Mid-Atlantic (following Payne *et al.*, 1984; 1986). The characteristic oceanographic features of these regions are described below.

The seaward edge of the entire study area is formed by the continental shelf-edge which is cut by several submarine canyons (Fig. 1). Shelf and slope waters meet in a narrow region of sharp temperature and salinity gradients at the shelf-edge/slope front. The front generally intersects the bottom near the 50m contour (Sherman *et al.*, 1988).

Gulf of Maine (GOM)

The GOM is bounded on the northwest by the USA coastline, and on the northeast by the Bay of Fundy and Nova Scotia. The character of the Gulf of Maine is influenced by



Fig. 1. The major regions and subregions of the study area mentioned throughout the text.

relatively cold, fresh surface water (Hopkins and Garfield III, 1979) and deep basins. The maximum depth is 377m in Georges Basin located inside the Northeast Channel north of Georges Bank. The bottom topography of the GOM is bounded on the south and east by two relatively shallow banks, Browns Bank and Georges Bank respectively, essentially making the Gulf a closed basin. The Northeast Channel (depths to 270m) separates Browns Bank from Georges Bank and is the largest passage into the GOM.

Georges Bank (GB)

GB is a broad, relatively shallow area, marked on the northern half by numerous, very shallow shoals (minimum depth about 4m). Water on the central part of the Bank (<60m in depth) is nearly homogeneous due to strong tidal mixing (Hopkins and Garfield III, 1981; Sherman *et al.*, 1988). The northern edge of the Bank has a very steep slope into the GOM, and the southern edge deepens to the continental shelf-edge. The western boundary of GB is formed by the Great South Channel (GSC). To the west of the GSC lie the Southern New England and mid-Atlantic regions.

Southern New England (SNE) and mid-Atlantic (M-A) regions

The SNE and M-A regions are characterized by a gently sloping shelf from the coast to the shelf-edge. The shelf is broad at the GSC, but narrows toward the southwest to Cape Hatteras. The Hudson Canyon, an important submarine feature, cuts across the SNE shelf. The M-A region also includes the mouths of the Delaware and Chesapeake Bays (Fig. 1). Two principal water masses are found in these regions: relatively cool, low-salinity shelf water, which extends 50–70km seaward of the continental shelf-edge; and slope water, which is found seaward of shelf water throughout the region (Sherman *et al.*, 1988).

Collection of sighting data

Shipboard survey effort-NMFS/NEFC

A long-term series of stratified-random, bottom trawl surveys were begun by NMFS/ NEFC in 1963 (Grosslein, 1969; Azarovitz, 1981). In 1976, NMFS/NEFC established the Marine Monitoring Assessment and Prediction Program (MARMAP) to provide annual and seasonal monitoring of the distribution, biomass and population structure of principal biota, and the physical environment on a broad geographical scale (Sherman, 1980). A basic part of the NMFS/NEFC strategy was to develop a multispecies-ecological approach to fisheries management (Grosslein *et al.*, 1980; Sissenwine *et al.*, 1982) by providing a broad-scale monitoring of the ecosystem against which predictive models could be evaluated. In 1980, NMFS/NEFC began placing a dedicated observer on board the surveys to monitor the distribution and abundance of cetaceans and seabirds.

The NMFS/NEFC surveys were designed so that one observer could collect sighting data on several taxa, principally cetaceans and seabirds (the data collection procedures are described in Powers *et al.*, 1980; Payne *et al.*, 1984; 1986; Selzer and Payne, 1988; Smith *et al.*, 1988). Observers were placed on NMFS/NEFC research vessels, principally the R/V Albatross IV and R/V Delaware II, on a non-interference basis and, generally, could not alter the trackline of the vessel during the survey. Observations were recorded by the observer while the ship was moving on a straight course and at a uniform speed along the predetermined trackline between NMFS sampling stations.

The study area was spatially stratified by NMFS/NEFC into individual strata (see Grosslein, 1969), based principally on latitude and depth. The NMFS/NEFC surveys quantified sighting effort as the number of transects surveyed within a strata or sub-region and specified time-interval. The NMFS/NEFC sampling stations were randomly placed within each stratum (roughly in proportion to the size of each stratum, Grosslein, 1969) prior to each survey. Initially, therefore, the amount of time spent obtaining cetacean and seabird sighting data within strata was also considered proportional to the size of each stratum. However, Payne *et al.* (1990) found that NMFS/NEFC sampling effort per strata area generally decreased with an increase in the size of the stratum. The larger strata were undersampled in these surveys. Since these data are biased by uneven effort allocation relative to strata size, they do not provide a basis for the estimation of absolute pilot whale abundance.

Dedicated aerial survey effort-CETAP

Throughout the three-year CETAP study, a number of sampling schemes and time intervals for data collection and analyses were employed, and each year a number of refinements and changes were incorporated into the database management (Edel *et al.*, 1981; Scott *et al.*, 1981; Scott and Gilbert, 1982; Winn, 1982). During 1979, dedicated, random-transect aerial surveys were conducted during each of eight time periods

throughout the year (Edel et al., 1981). During 1980 and 1981, four dedicated surveys were flown each year, usually one per season (Winn, 1982).

The CETAP sampling area was partitioned into blocks of comparable size, then stratified (based principally on depth) into three sub-regions (nearshore, 0–36.6m; shelf, 36.6–91.4m; slope, >91.4m). The CETAP surveys combined the SNE waters with the M-A region, otherwise the methods of regional stratification between the CETAP aerial surveys and the NMFS/NEFC surveys were comparable.

Only the data collected during the dedicated aerial surveys were used by CETAP in estimating absolute abundance. Although data were also collected by CETAP during other surveys (see below) and used to describe patterns of distribution, they could not be corrected for level of effort, and thus to estimate abundance. Nonetheless, we have incorporated them into the combined database used in this paper to describe the seasonal and temporal distribution of pilot whales.

Special aerial surveys-CETAP

During each of the years of the study, special aerial surveys were conducted emphasizing endangered species not adequately sampled by the dedicated surveys, or to characterize species occurrence and abundance in areas of particular importance (i.e. specified lease sale areas). During May 1979, a special right whale (*Eubalaena glacialis*) survey was conducted over the entire GOM and OCS regions immediately south of the GOM (Edel *et al.*, 1981; Winn *et al.*, 1981). During 1980 and 1981, several surveys were conducted during spring and late-summer (Winn, 1982) to obtain data for a better understanding of the distribution of endangered baleen whales. These flights took place in Lease Sale 52 Nomination Area (east of Cape Cod, south through the GSC and eastward over GB; see Winn, 1982), and in the northern GOM and southwestern Scotian Shelf.

Special shipboard surveys-CETAP

During May 1980 and 1981, sighting and quantitative behavioral data were collected on dive duration and frequency for baleen whales (Winn, 1982), during two cruises to waters adjacent to Cape Cod.

Surveys of Opportunity-CETAP

During 1979 and 1980, CETAP placed observers on aircraft and vessels-of-opportunity operating within the study area (Edel *et al.*, 1981; Winn, 1982). The US Coast Guard and NMFS/NEFC provided the majority of vessel platforms. These platforms were supplemented by several institutional research vessels. The aerial portion of this effort was generally provided by the US Coast Guard, Cape Cod, Massachusetts, and continued through 1981. The shipboard component of this effort was discontinued in 1980.

Treatment of sighting data

The number of usable transects varied by season as a function of wind speed; sighting efficiency is affected by environmental conditions, especially sea state (Eberhardt *et al.*, 1979; Holt and Cologne, 1987; Barlow, 1988; Holt, 1988). Scott *et al.* (1981) and Payne *et al.* (1984) found that marine mammal sightings in this database decreased significantly when wind speeds exceeded 17 knots. Therefore only sighting data collected at wind speeds <17 knots were used to examine the distribution of pilot whales.

All pilot whale sightings observed during the CETAP aerial surveys (Nov 1978-Jan 1982) and the NMFS/NEFC shipboard surveys (May 1980-Dec 1988) were combined and treated as one dataset. The spatial distribution of pilot whales throughout the year was examined by grouping the sightings into six, two-month time-periods (i.e. January-

February, March-April, May-June, July-August, September-October, and November-December). Each sighting in the database was weighted by group-size per sighting (i.e. 1-10, 11–30, 31–300, or 301–1,000 individuals per sighting), then overlayed onto a base map of the study area.

Because of differences in survey type and platform between the CETAP and NMFS/ NEFC surveys, and uneven effort allocation in the NMFS/NEFC surveys (Payne *et al.*, 1990), relative densities (sighting data corrected to some measure of standardized effort) could not be used to describe pilot whale distribution with the combined database. Despite this bias, the number of individuals per sighting approach (unweighted by effort) does provide a detailed account of the spatial and temporal distribution of pilot whales in the shelf waters of the northeastern United States.

All base maps were digitized and sighting data overlayed onto the base maps using the PC based mapping-program CAMRIS (Computer Aided Mapping and Resource Inventory System; Ford, 1989).

RESULTS

Sighting effort-NMFS/NEFC surveys

Between May 1980 and January 1988, 18,826 usable transects were conducted throughout the study area. Spatial and temporal coverage varied by NMFS/NEFC survey type:

- (a) approximately 19% of the total number of usable transects were conducted on bottom-trawl surveys between March and November;
- (b) MARMAP or ichthyo- and phyto-plankton surveys provided the most complete seasonal and regional coverage of any type of survey and 55% of the total number of transects conducted between December-February were of this survey type;
- (c) 33% of all survey effort between June and August, occurred on scallop surveys, although these surveys generally excluded the GOM and all outer-shelf waters;
- (d) 14% of the transects occurred on NMFS/NEFC multi-disciplinary surveys (the NORTHEAST MONITORING PROGRAM) which occurred throughout the study area, primarily between June and August.

Regional effort was generally uniform throughout the study period (Smith *et al.*, 1988), ranging between 20% of the total number of transects (n=3,293) which occurred on NMFS/NEFC research surveys on GB, to 25% (n=4,135 transects) throughout the M-A region.

Most (87%) of the total number of usable transects were conducted from March through November: 4,575 (24%) between March and May; 6,766 (36%) between June and August; and 5,052 transects (27%) between September and November. During winter (December-February) over 5,000 transects were conducted but only 47% of these (2,433 or 13% of the total usable transect effort) occurred at wind speeds <17 knots.

Sighting effort-CETAP aerial surveys

The sighting effort for the dedicated aerial surveys (over the 39 month CETAP study period) can be summarized as follows (from Winn, 1982, p. 41):

- (a) sighting effort varied geographically and temporally (within years, between years, and between seasons);
- (b) of the total on-watch miles surveyed, 51% were in 1979, 34% were in 1980, and 15% were in 1981;

- (c) using miles-on-watch as a measure, spring received 39% of the total coverage, summer 31%, fall 17% and winter 12%;
- (d) in general, the area to the east and southeast of Cape Cod received the most coverage, and the areas over eastern GB and through the central GOM received the least;
- (e) the above yearly and seasonal figures give the following overall measure of study area coverage an average of 47% of the study area was surveyed during each of the three spring seasons, 37% during summer, 20% during fall and 14% during winter.

			Mo	onth			
Region	J-F	M-A	M-J	J-A	S-O	N-D	Total
GOM	1	2	87	94	45	39	268
GB	2	2	21	46	47	30	148
SNE	6	36	76	18	16	19	171
M-A	2	16	5	16	3	4	46
SL	15	82	102	79	55	67	400
Total	26	138	291	253	166	159	1.033

Table 1 The number of pilot whale sightings used in the plots of distribution by regions and two-month

period. GOM = Gulf of Maine; GB = Georges Bank; SNE = southern New England; M-A = mid-Atlantic and SL = slope.

Distribution of sightings

There were 1,033 sightings of pilot whales (an estimated 16,155 individuals) in the combined database (Table 1). Pilot whales were observed during every two-month period. Only 26 pilot whale sightings occurred during January-February. Excluding January-February, the range in the number of sightings varied from 138 during March-April to 291 during May-June (Table 1).

The distribution of pilot whale *Globicephala* spp. sightings off the northeastern coast of the United States generally followed the shelf-edge/slope region from Cape Hatteras to the northeastern portion of GB (and onto the Scotian Shelf) (Fig. 2). A total of 400 sightings was made throughout the year in slope waters (200m-2,000m). This represents 39% (400/1,033 sightings) of all pilot whale sightings throughout the year. The overall distribution of sightings also extended from the V-shaped basin of the GSC, along the northern edge of GB to the Northeast Channel (Fig. 2).

The smallest number of pilot whale sightings (n=26) occurred during January-February, when pilot whales were loosely distributed along the shelf-edge/slope region of the study area (Fig. 3). Over one-half of the pilot whale sightings (15/26) during January-February occurred in shelf-edge/slope waters between the 100-2,000m contours (Table 1). Only three sightings occurred on GB and throughout the GOM (Table 1). These data suggest that all near- and mid-shelf areas were unoccupied, generally, by pilot whales at this time.

The number of pilot whale sightings increased from $37^{\circ}N$, north to the Scotian Shelf during mid-spring and summer. Approximately one-half (201/429) of all sightings on the shelf (<200m in depth) from March to June (from Table 1) occurred in the SNE/GB regions. In contrast, only 21 sightings (<5%) occurred on the shelf in the M-A region during the same period (Table 1). The number of sightings increased along the shelf-edge from Norfolk Canyon to the Northeast Channel during March-April (Fig. 4).

[Text continues on p. 60]





Pilot whale sightings were most widespread throughout the study area during May-June (Fig. 5). Sightings north of 40°N were common in the GSC and all over GB during this period (Fig. 5). A total of 291 sightings occurred during May-June (Table 1) due primarily to an increase in the number of sightings in the slope waters of the M-A region over the previous four months (Table 2). During May-June the sighting distribution extended from Cape Hatteras north along the shelf-edge/slope (Fig. 5). However, there was one obvious gap in the sightings pattern located west of the GSC between 40°00'N and 38°40'N (centered on the Hudson Canyon). This resulted in two separate groups of pilot whale sightings: a northern group from the GSC northeast to the Scotian Shelf, and into the GOM through the GSC and the Northeast Channel (mostly north of 40°0'N); and a southern group in the M-A from 39°N (Wilmington Canyon) south to the southern edge of the study area, between the 200–2,000m contours (Fig. 5).

During July-August, 94 pilot whale sightings occurred on GB (Table 1). These sightings were concentrated nearer to the Northeast Channel (Fig. 6) than GB sightings were in May-June. Another large concentration formed in the mid- to upper reaches of the GSC (Fig. 6).

Of all pilot whale sightings in slope waters during July-August, 70% (n=56) occurred in the M-A slope region (Table 2). This large number of M-A/slope sightings first occurred during May-June, peaked in July-August, then remained high throughout the remainder of the year. The northernmost range of these sightings extended to 39°N (east of Delaware Bay), and more importantly, remained spatially segregated from those north of 40°N throughout the year.

There were 166 sightings during September-October (Table 1). During this period, the number of sightings on the central-northeast areas of GB decreased by over one half (Table 1), concurrent with an increase in the number of pilot whale sightings concentrated in the lower GOM (north of GB) and GSC (Fig. 7). During September-October most pilot whales observed in the GSC appeared to be moving southwestward, through the GSC, out of the GOM (from observers notes and personal observations).

By November-December, the only shelf region (<200m) with a noticeable concentration of pilot whale sightings was at the GSC (Fig. 8). However, the distribution of pilot whale sightings in slope waters again extended throughout the study area along the shelf-edge/slope interface, with 67 sightings occurring in slope waters (Table 1). The major concentration of sightings (50/67) occurred in M-A slope waters east of Cape Hatteras (Table 2, Fig. 8). There were no sightings there in January.

Table 2

The number of pilot whale sightings in slope waters partitioned by region and two-month period. SL-GB = slope waters (200-2,000m depth) seaward of Georges Bank; SL-SNE = slope waters seaward of the southern New England region; SL-M-A = slope waters seaward of the mid-Atlantic region.

	Month							
Region	J-F	M-A	M-J	J-A	S-O	N-D	Total	
SI-GB	8	34	40	18	3	12	115	
SI-SNE	5	31	24	5	13	5	83	
Sl-M-A	2	17	3 9	55	39	50	201	
Total	15	82	102	78	55	67	399	




Fig. 8. The distribution of pilot whale *Globicephala* spp. sightings suring November-December in continental shelf/shelf-edge and slope waters of the northeastern United States, 1978-88.

DISCUSSION

Information on the seasonal movements of pilot whales in shelf and shelf-edge/slope waters of the northeastern USA can be obtained from the spatial and temporal distribution of *Globicephala* sightings. The importance of shelf-edge/slope waters to pilot whales cannot be overstated. Kenney and Winn (1986) identified the shelf-edge as a high-use cetacean habitat and pilot whales were a principal species of the cetacean assemblage in these waters (Hain *et al.*, 1985; Kenney and Winn, 1987). Generally, the shelf-edge is an area of increased bottom relief which has been shown to influence the distribution of pilot whales over areas with the steepest bottom topography to their steno-teuthophagic feeding habits.

We also believe that these sighting data allow us to distinguish the distribution of G. *melas* from that of G. *macrorhynchus* in the study area throughout much of the year. This is summarised below.

Distribution and movements of the long-finned pilot whale

The Atlantic or long-finned pilot whale (G. melas) is a common component of the cetacean community in the northwest Atlantic from at least Cape Hatteras, North Carolina (Leatherwood *et al.*, 1976; Hain *et al.*, 1981; Winn, 1982; Payne *et al.*, 1984) north to the Scotian Shelf and eastern Canada and Newfoundland (Sergeant and Fisher, 1957; Sergeant, 1968; Sergeant *et al.*, 1970; Mercer, 1975; Mitchell, 1975; Hay, 1982), Greenland (Kapel, 1975) and Iceland and the Faroe Islands (Sigurjónsson *et al.*, 1989; Bloch *et al.*, 1993). In the waters of the northeastern United States, pilot whales constitute a significant percentage of the entire cetacean biomass for the shelf-edge/slope community (Hain *et al.*, 1985; Kenney and Winn, 1987).

Sightings of the long-finned pilot whale in the study area were made throughout the year. However, as a result of fewer sightings, their distribution appeared less-well defined during mid-winter as it was during other periods of the year. This was at least due in part to an overall reduction of sighting effort at this time of the year when only 14–15.5% of the total effective survey effort occurred. However, it also seems apparent that the distribution of G. melas at this time was scattered, largely shelf-edge and seaward into slope waters.

Waring et al. (1990) observed that the major concentrations of G. melas during winter occurred along the shelf-edge primarily in the SNE/M-A regions from Cape Hatteras north to GB, closely paralleling the known seasonal distribution of long-finned squid (Loligo pealei) at that time (Lange, 1980; Lange and Sissenwine, 1980). Since the seasonal distribution of G. melas followed the distribution of squid spp., Waring et al. (1990) suggested that the long-finned squid was a principal prey item of G. melas in this study area during winter and early-spring.

Fish are considered to be an alternative prey when squid are not available (Mercer, 1967; Mitchell, 1975; Sergeant, 1982). Waring *et al.* (1990), based on stomach contents of trawl-captured *G. melas* and co-occurring distributional data, further suggested that pilot whales were feeding on Atlantic mackerel (*Scomber scombrus*) during winter and early-spring in the SNE/M-A regions (see Fairfield *et al.*, 1993).

From mid-winter through early-spring, the number of *G. melas* sightings increased in the study area. The progression of sightings extended northeastward in shelf-edge/slope waters to the outer perimeter of Georges Bank by March-April, suggesting that the species was moving northward along the shelf-edge/slope interface of the M-A region. Most of the shelf-edge sightings at this time occurred in the SNE region, while most slope sightings extended from the northern M-A to GB.

During May-June, the distribution of *G. melas* was most widespread. They appear to move from the shelf-edge/slope waters onto GB, then into the deeper basins of the GOM located north of GB (Fig. 5). They were most abundant on central GB north along the northern edge of the Bank from May to September (Winn, 1982). This movement onto shelf and nearshore waters during late-spring to early-summer closely parallels that described elsewhere throughout Canada (Sergeant and Fisher, 1957; Sergeant *et al.*, 1970; Mercer, 1975) and may be related to an inshore movement of the short-finned squid (*Illex illecebrosus*) during the warmer months.

The short-finned squid is the near exclusive prey of G. melas off Newfoundland in summer (Sergeant, 1961; 1982; Mercer, 1975). It spawns in slope waters of the northeastern USA, seaward of the continental shelf, during mid-winter (Lange and Sissenwine, 1980), then moves onto the shelf during late-summer and autumn to feed (Lange, 1980). The on-shelf movement of G. melas and its widespread occurrence on GB coincided with the period when squid were most abundant in shelf waters. Waring *et al.*

(1990) suggested that the short-finned squid formed a major prey component of the diet of G, melas on GB and in the GOM during that time.

The apparent clockwise movement of G. melas parallel to the shelf-edge continued through autumn and resulted in a reduced number of sightings as it moved out of the study area below Nova Scotia. Our understanding of the movements of these pilot whales after they leave the study area is incomplete. However, during autumn and winter, they presumeably move southwestward in slope waters, completing a clockwise gyre which will place them back in the M-A/SNE regions by the following spring, when they again move northward in slope waters parallel to the shelf-edge.

The distribution of those G. melas which remain on the shelf (GB/GOM regions) during September-December also shifted southward. Local concentrations of G. melas occurred from the Northeast Channel, down the northern edge of the GB into the GSC during September-October. By November-December, most G. melas located on the shelf are found in the southwestern GOM/Cape Cod Bay to the GSC. Pilot whales observed in the GSC at this time were generally heading southwestward out of the GOM (from observer's notes and personal observations). This southwestward movement out of the GOM during autumn likely facilitated the number and location of mass-stranding events in this region in recent years. All mass-strandings of pilot whales (all were G. melas) in the northeastern USA between 1981–90 occurred at a limited number of locations in the southwestern GOM adjacent to Cape Cod, between October and December (Greg Early, New England Aquarium Stranding Network, pers. comm.). By the end of December, there were few sightings of G. melas north of 40°N or in M-A/SNE waters, further indicating a large-scale movement into slope waters during winter.

Distribution and movements of the short-finned pilot whale

In the northern portion of its western North Atlantic range, the short-finned pilot whale (*G. macrorhynchus*) is sympatric with *G. melas*. The short-finned pilot whale is considered a more tropical species, common south of Cape Hatteras into Caribbean waters (Caldwell and Erdman, 1963; Caldwell and Golley, 1965; Caldwell *et al.*, 1971; Erdman *et al.*, 1973; Caldwell and Caldwell, 1975; Leatherwood *et al.*, 1976) into the Gulf of Mexico (Gunter, 1954; Fritts and Reynolds, 1981; Schmidly, 1981; Fritts *et al.*, 1983; Loehoefner *et al.*, 1989) and south to Venezuela (Leatherwood *et al.*, 1976).

There are few confirmed records of G. macrorhynchus in our study area. Rowlett (1980) reported a sighting of G. macrorhynchus seaward of the Baltimore Canyon ($38^{\circ}6'N$, $73^{\circ}45'W$) during September 1977, and strandings have been reported as far north as New Jersey (Katona *et al.*, 1978; Mead, 1979). Leatherwood *et al.* (1976) suggested that they probably range as far north as Virginia during late-summer and autumn. Winn (1982) also proposed the occurrence of the two Globicephala species in the study area during fall based on the occurrence of calves in both spatially separated northern and southern pilot whale concentrations.

From January through April there was little evidence of a disjunct distribution of pilot whale sightings north of $37^{\circ}N$ (Figs 2 and 3), suggesting that only one pilot whale species G. melas (the northernmost and most commonly observed) was present during that period. However, by May-June, two distinct groups of pilot whale sightings occurred in the study area-one which largely remained in slope waters along the shelf-edge below $38^{\circ}30'N$, and a second whose distribution occurred throughout shelf and shelf-edge/slope waters north of $40^{\circ}0'N$. We believe the large increase in the number of pilot whale sightings in slope waters of the mid-Atlantic between May and December (from Table 2) was due to an incursion of G. macrorhynchus into the study area, during a northward, seasonal extension of their more tropical range south of Cape Hatteras.

We suggest that three major concentrations of G. macrorhynchus formed in the M-A and SNE shelf-edge/slope regions (generally between 200-2,000m water depth) during July-August (Fig. 6)- one east of Cape Hatteras, another east of the mouth of Chesapeake Bay, and the northernmost at approximately 39°N, east of Delaware Bay. This last concentration represented the northernmost range extension of any large concentrations of G. macrorhynchus in the study area (and likely the northwest Atlantic).

From May-December (the period when G. macrorhynchus were most abundant and most separated from concentrations of G. melas) only 23 sightings occurred in shelf/shelfedge waters of the M-A region (Table 1). A total of 145 sightings (or 86% of all sightings in the mid-Atlantic during these months) occurred in M-A slope waters. Unlike G. melas, the short-finned pilot whale did not move onto the shelf but remained in the deeper (Gulf Stream influenced) slope waters of the M-A region.

Throughout autumn, the northern limit of G. macrorhynchus sightings continually retreated southward outside the shelf-edge. The sighting distribution coalesced into a patchy continuum and by December most pilot whale sightings in the mid-Atlantic occurred in slope waters east of Cape Hatteras. During January, G. macrorhynchus again moved south of the study area.

Relative occurrence of G. macrorhynchus vs. G. melas in the study area

These sighting data cannot be used to directly estimate the abundance of G. *macrorhynchus* vs. G. *melas* in the study area. However, by comparing the distribution of sighting data (presented in this paper) with existing abundance data (from Winn, 1982), we can quantify the occurrence of G. *macrorhynchus* relative to the shelf-wide abundance estimate for *Globicephala* spp., during spring-summer.

Shelf/shelf-edge abundance estimates (excluding slope water regions) for pilot whales *Globicephala* spp. during spring and summer ranged between 10,000–12,000 (Winn, 1982). Comparable estimates were provided by Kenney *et al.* (1985) partitioned by CETAP strata. The sighting distribution for *G. macrorhynchus* during these seasons followed CETAP strata Gz, Hz, and Lz (from Kenney *et al.*, 1985). The summed pilot whale estimates for these strata ranged between 1,700–2,300, spring and summer, respectively (from Kenney *et al.*, 1985). Therefore, during that period when two distinct groups of pilot whale sightings occurred in the study area (from sighting data, this paper), the abundance of pilot whales in the M-A region represented 14–23% of the abundance estimate for pilot whales throughout the entire study area at that time. It seems apparent that *G. macrorhynchus* is an abundant, regularly occurring seasonal component of the entire pilot whale spp. community in slope waters along the shelf-edge of the northeastern United States.

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Pilot Whale Catches in the Faroe Islands, 1709–1992

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ABSTRACT

This paper deals with the statistics of the pilot whale catches in the Faroe Islands in the period 1709–1992, when a total of 1,629 grinds (= schools taken) with 240,721 whales was recorded, resulting in yearly averages of 5.74 grinds and 848 whales. In 44 years there were no catches at all, in 17 years there were 15 or more grinds, and the maximum number in one year was 27 grinds (1941). On average there are 147.8 whales per grind, ranging from 40 grinds with a single whale, to 15 grinds with more than 700 whales, and a maximum of 1,200 whales in two grinds (in 1729 and 1940). The grind time series shows, along with an essential year-to-year variation, a large-scale fluctuation with two main peaks around 1710-30 (annual mean - 5.5) and 1830-50 (annual mean - 9.1), and a general high incidence level after 1935 with several narrower peaks, including a 5-year record in 1984-88 with a total of 100 grinds. The total seasonal distribution has a peak in July-August (21.0% \pm 27.6%) and a low in February-March $(2.2\% \pm 1.7\%)$, but a January-July/August-December grouping of grinds varies over time, e.g. in the periods 1890-1930 and 1934-1958 the January-July season accounts for 13% and 52% respectively. A geographical grouping in N-E bays and S-W bays, which for all the period splits the grinds respectively 54% and 46%, shows variations through time, e.g. in the periods 1710-40 and 1890-1930 the N-E bays account for 62% and 15% respectively. The January-July proportion and the N-E bay proportion are correlated, such that with a few exceptions, the two proportions are either low (0-30% in the 4-year periods used) or they are both high (35-70%). High January-July and N-E bay proportions also seem to correspond with a high grind rate. The number of whales per grind varies according to season: 94-126 in the winter (December-March) and 158-163 in July-August. Grind clustering on a time scale of weeks and days seems to occur, e.g. of the 13 grinds in 1979, 8 grinds occur within an eleven-day period in August, and on the same day, 16 July 1992, four grinds were caught. In a simple random model the expected number of multiple-grind days in July-August through the entire period was calculated as 18, compared with the observed 40 multiple-grind days. Along with the abundance variation of pilot whales in the Faroe area, the grind rate will also be influenced by variations in sighting possibilities (such as hours of daylight, weather conditions) and community factors (such as increasing population, changing fishing activities and improvements in vessel and communication technology). The number of grinds in July-September each year in the period 1957-1976 has been compared to the sea-surface temperature in regions West and South-West of the Faroes, where the highest correlation coefficients (0.68–0.74) showed up in the area 57–59°N, 16–32°W. An observed shift from 1966-69 to 1970-74 in the climatic and biological conditions in the North Atlantic coincides with changes in the grind statistics: the annual number of grinds (14.5-5.8), January-July proportion (52%-24%), and the Western bays proportion (29%-45%).

KEYWORDS: NORTH ATLANTIC; PILOT WHALE-LONG-FINNED; WHALING; OCEANOGRAPHY.

INTRODUCTION

The long-finned pilot whale (*Globicephala melas*) has been exploited in the Faroe Islands since the Norse settlement more than a thousand years ago (Dahl, 1970). The catch is an opportunistic hunt occurring all year round. In Faroese pilot whaling, entire schools sighted in the vicinity of the islands from land or from a boat, are driven ashore by small fishing boats under the guidance of 'foremen', to be dispatched by a group of men waiting on the shore. In Faroese, the word 'grind' denotes both a school of pilot whales, as well as the process of driving and killing the whales. A description of the process of a grind is given in Bloch *et al.* (1990a).

In earlier times, about two-thirds of the catch had to be paid as tax to the church, king and other landowners, which resulted in the recording in official accounts of the numbers and value of all whales caught. These unique statistics date back to 1584 when secular authorities took over the administration of taxation from the monasteries. The statistical series is unbroken from 1709 to the present day (Joensen and Zachariassen, 1982; Bloch *et al.*, 1990b).

The statistics reveal much information on the occurrence of pilot whales off the Faroes. The length of the time series and the large number of whales involved, renders them valuable not only for historians and ethologists, but also for biologists. Joensen and Zachariassen (1982) examined the periods 1584–1640 and 1709–1978. This paper updates the latter period to 1992 and extends the analysis of the entire time series. Some corrections have been made to the 1709–1978 data.

MATERIAL AND METHODS

The statistics include the following information on each grind: locality (i.e. whaling bay); year; month; and number of whales. Information on the whaling day is available for 95% of the grinds after 1800. The main sources of information are Müller (1882; 1883) for the period 1709–1883, Joensen (1962) for 1884–1962, and Joensen and Zachariassen (1982) for 1962–78. Apart from 65 grinds from 1709–31 and 1799–1804, for which the month is not recorded and 6 grinds from the year 1725 for which the location is not recorded, the information is complete. Some corrections have been made to the data for the period 1709–1978 after a thorough examination of the archives; these corrections have been included in this paper together with the data for the period 1979–92 (Table 1), courtesy of Dorete Bloch of the Museum of Natural History in Tórshavn. Some recently-discovered grinds in the old material, as well as new information about one grind which indicates that it was actually two grinds, and other minor corrections have also been incorporated into the present material.

Since 1982, authorities in certain whaling districts have enforced a temporary closure of the district for further hunting (usually for a period of a few months), when those districts were considered to be well-supplied with whale meat (Bloch *et al.*, 1993). In the years 1986, 1987 and 1988 this occurred in, respectively, 4, 5 and 3 districts of 9, with closures lasting from 0.5 to 3.5 months (Bloch *et al.*, 1990a). It is known in some cases that during a temporary closure, a pilot whale school has been observed but not pursued, when in normal circumstances it would probably have been driven ashore and killed. However, no adjustment has been made in the following statistical analysis with respect to this.

The analysis in this paper is based primarily on the number of grinds, which is appropriate in trying to assess the intensity of schools encountered in the Faroes, assuming that on average a certain percentage of schools passing the Faroes are detected and driven ashore. Possibilities for sighting will not necessarily be influenced by the size of the school, but it could be argued that small schools (with a dozen whales or less) are not as easily seen as schools with a hundred whales or more. The proportion of grinds with a dozen whales or less amounts to about 5%, which thus probably underestimates the proportion of pilot whale schools of the same size in the Faroe area.

One way of studying whether catches can be considered as 'independent' events in the statistical sense, is to examine whether any time or whale-bay clusterings are observed on a scale of days. Sometimes a number of schools may be passing the islands at the same time, or, in some cases, when large schools approach the islands, they may split into

several smaller schools. To confirm a possible dependency in the grind time series, an observed clustering must of course exceed that of an intrinsic random model clustering.

The catch data have been grouped into 4-year periods for the greater part of the analysis in this paper. This grouping has been chosen to emphasise longer term variation rather than inter-annual fluctuations. In graphical representations of time series, the values under the time axis are mid-point years representing some of the 4-year periods, e.g. 1710 indicating the period 1709–1712 and 1990 indicating the period 1989–1992. The total period spans 284 years thus accounting for 71 4-year periods.

TIME SERIES AND DISTRIBUTION ANALYSIS

Time series

In all, 1,629 grinds with a total of 240,721 whales were recorded in the 284-year series, resulting in yearly averages of 5.74 grinds and 848 whales. In 44 years there were no catches at all (mostly in the second half of the 18th century) while in 17 years (7 of these in the 1980s) there were 15 or more grinds. The maximum number in one year was 27. On average, there were 147.8 whales per grind, ranging from 40 grinds with only a single whale, to 15 grinds with more than 700 whales. The maximum number of whales in one grind was 1,200 (once in 1729 and once in 1940).

In the grind time series (Fig. 1), a large-scale fluctuation is observed with two main peaks around 1710–30 and 1830–50 and a more diffuse picture after 1935, with a general



Fig. 1. Number of grinds for each 4-year period from 1709 to 1992, showing pronounced fluctuations.

	No. of grinds	Whales per grind		No. of grinds	Whales per grind		No. of grinds	Whales per grind	
1979	13	128.7	1984	21	91.5	1989	14	89.9	
1980	14	198.2	1985	20	129.0	1990	11	83.3	
1981	19	156.5	1986	20	83.9	1991	11	65.5	
1982	15	176.8	1987	19	76.4	1992	14	112.3	
1983	16	105.6	1988	20	84.5				

Table 1	
Statistics of pilot whale catches in the Faroe Islands	1979-92

high incidence level and several narrower peaks. Two low level periods can also be clearly seen, 1750-95 and 1890-1930. In 12 of the last 14 years (i.e. new data) the levels suggest a new peak, increasing from a relatively low level in the mid-1970s. The 79 (=20+20+19+20) grinds in the period 1985-88 (Table 1) is the highest of any of the 4-year periods. Indeed this peak might have been higher, since the authorities banned pilot whale hunting temporarily in some districts (as mentioned above) during this period. This catch rate was exceeded only during the period of the Second World War, with a total of 27 grinds and 4,448 whales in 1941.



Fig. 2. Number of whales per grind for each 4-year period from 1709 to 1992. No bar has been drawn when there were fewer than three grinds in a 4-year period.

Fig. 2 shows the mean number of whales per grind in each 4-year period. When there were only one or two grinds in a non-empty period, no mean is shown. The average number of whales per grind varies from 89 in 1989–92 to 236 in 1872–75. In the last 30 years, the number per grind has been lower than the average. A similar trend was seen in the early years of the eighteenth century. In the late eighteenth century and around 1915–40, grinds contained a larger than average number of whales.

Whaling bays

Experienced whalers have noted that in some years, catches seem to be concentrated in whaling bays in a particular region of the islands. To study this phenomenon, the grinds have been divided into four regional groups: northern (N), eastern (E), southern (S), and western (W) (Table 2, taken from Joensen and Zachariassen, 1982). A clear change in the distribution of catches by whaling bays may indicate a change in the direction from which schools approach the islands, and may thus shed some light on pilot whale migration. In this respect the N/E/S/W grouping was also considered appropriate. To simplify, a further N-E/S-W grouping is used in several comparisons. Pilot whales are found mainly to the south and south-west of the Faroes, this grouping is thought to be more appropriate than a S-E/N-W grouping.

Table 2

Grouping rules of whaling bays (from Joensen and Zachariassen, 1982). The used bay labels are based on the order numbering according to the number of catches for the period 1709-1978, so that is why the higher labels (>16) are not in accordance with the number of catches in the period 1709-1992, shown in (). Bay 34 and 36 are not in the list, since they occurred only once each in the statistics for the period 1584-1640. Number of catches in bays 1-16 are shown in Table 3, together with site names. A map of bay sites are produced in Fig. 3.

Northern bays	2,8,10,14,16,22(8),38(1)
Eastern bays	3,7,12,15,19(11),21(10),25(5),28(4),29(3),32(1),33(1)
Southern bays	4,6,9,13,17(13),23(9),31(2),37(1)
Western bays	1,5,11,18(17),20(7),24(7),26(16),27(15),30(3),35(1),39(1)

The N-E and S-W groups are of a similar extent, 747 grinds in N-E bays and 876 grinds in S-W bays. Fig. 4 includes the frequency time series in these two groups and the time series of N-E percentages. The fluctuations of percentages cannot be attributed to random variation alone, e.g. in the period 1890–1930 N-E bays account for 15% (21/136) of the total, whereas from 1710–40 the value is 62% (88/143). In some periods fluctuations in the total grind number (Fig. 1) as a whole are due to fluctuations in one group, while the other is at an almost constant level, e.g. the 'boom' during the 1940s can be ascribed to a marked peak in the S-W group, when at the same time, for the N-E group, only small changes in the number of grinds are observed.

In all, 37 whaling bays have been used in the entire period, ranging from six bays with one recorded grind, to Midvágur with 247 recorded grinds, equalling 15% of the total catch. The four top-ranked bays (Table 3, Fig. 3) cover 46% of the grinds and 55% of the whales killed. The 21 lowest-ranked bays cover 8.1% of the grinds, but account for only 4.2% of the whales.

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Grind statistics by bay and groups of bays. Information on bay is missing for six grinds (all from 1725). Fig. 3 shows the bay sites.

		Grind fr	equency	Whales p	er grind
Bay	Site	No.	%	Average	Median
	Miðvágur	247	15.2	179.0	134
7	Klaksvík	198	12.2	182.1	123
e	Hvalvík	153	9.5	195.9	165
4	Vágur	145	9.0	143.0	118
5	Vestmanna	138	8.5	144.3	115
9	Hvalba	119	7.4	140.5	101
7	Tórshavn	66	6.2	132.7	101
~	Hvannasund	74	4.6	104.7	80
6	Tvoroyri	50	3.1	128.8	81
10	Funningsfjørður	47	2.9	103.2	55
11	Sandur	45	2.8	119.3	90
12	Gota	42	2.6	153.5	96
13	Fámjin	41	2.5	183.2	176
14	Nesvík	35	2.2	114.6	89
15	Húsavík	29	1.8	143.7	108
16	Fuglafjørður	25	1.6	69.1	55
1-16	≥ 25 grinds	1,487	91.6	154.0	115
17-38	< 25 grinds	136	8.4	77.0	53
Northern bays		389	24.0	142.0	96
Eastern bays		358	22.0	153.4	109
Southern bays		380	23.4	140.5	115
Western bays		496	30.6	154.0	116
N-E bays		747	46.0	147.5	101
S-W bays		876	54.0	148.1	116



Fig. 3. Location of bay sites and the total number of catches in the most frequent bays, showing concentration of catches in a relatively few sites. Numbers are shown in Table 3.



Fig. 4. Number of grinds in N-E and S-W bays for each 4-year period from 1709 to 1992, and corresponding percentages for the N-E proportions.

Seasonal analysis

A division into two seasonal groups has been made – January-July and August-December, making it possible to measure shifts within the main seasonal peak of the pilot whales appearing in July-August. In the January-July group there are 661 grinds and in the August-December group there are 903 grinds; for 65 grinds the month is not recorded. Fig. 5 includes the frequency time series in these two groups and the time series of January-July percentages. Some of the above-mentioned characteristics of the grouping of bays (Fig. 4) are also indicated in the seasonal grouping. The January-July group 'behaves' like the N-E group, especially in the period 1890–1930, where the January-July group accounts for only 15% of the total.



Fig. 5. Number of grinds in January-July and August-December for each 4-year period from 1709 to 1992, and corresponding percentages for the January-July proportions.

To investigate further the connection between bays and seasons, the number of grinds by month is given for each of the four groups of bays (Fig. 6). In all distributions except the one for the eastern bays, August has the highest frequency, from 23% for the northern bays to 34% for the western bays (Table 3). The asymmetrical form of distribution for the eastern bays is different from the more symmetrical distributions for the other groups of bays. Among other characteristics, the winter months November-February have a high frequency (20%) in the northern bays, compared to the November-February frequency in the other bays (8–13%).

Size of the grinds

The number of whales per grind is shown as a histogram (Fig. 7). The lowest interval has the highest frequency: 90 grinds, 40 of which were only single whales. Apart from this



Fig. 6. Number of grinds in each month for the period 1709–1992 according to a geographical grouping of bays, showing some variations of the grind distribution in different bay groups.



Fig. 7. Grouping of grinds according to number of whales (1-9, 10-19, 20-29....) for the period 1709-1992. The three quartiles (Q1, M, Q3) are marked on the whale axis. The 15 grinds with more than 700 whales are not included in the histogram.

interval, the distribution on the whole can be characterised as a unimodal right skewed distribution, with 50-90 as the most typical numbers of whales per grind, and with the following quartiles: 55 (25%), 110 (the median), 194 (75%)). The histogram does not include the 15 largest grinds (with more than 700 whales) that have been recorded, corresponding to 1% of the total number.

The grind-size distributions by the four bay groups (Fig. 8) are quite similar to the total grind size distribution (Fig. 7). The southern bays seem to hold relatively fewer big grinds, and the eastern bays have a lower incidence of single whale grinds. These observations are partly confirmed by the means and the medians shown in Table 3. There appear to be no major differences between the group distributions.



Fig. 8. Grouping of grinds according to number of whales for the period 1709–1992 in four geographical groups of bays, showing distributions with similar features.

The grind-size distributions by month (Fig. 9) show a larger variation in class frequencies, which to some extent is due to the relatively small number of grinds in some months, especially in January-April (25–41 grinds). The winter months November-March seem to hold relatively smaller grinds, but April compared to its adjoining months seems to hold few small grinds. These observations are confirmed by the means and the medians shown in Table 4, e.g. of all months April has the highest median (143) and the highest mean number (165), compared to 110 and 148 respectively for the total distribution.





Whaling bays and seasons

The grind distribution by month in groups of bays (Fig. 6) shows some marked characteristics, such as the relatively large winter frequency in the northern bays, the marked August peak in the western group, and the July peak in the eastern group. To examine this more closely, an XY-plot has been produced (Fig. 10), showing the January-July proportion versus the N-E bay proportion for each 4-year group.

Fig. 10 covers the period 1805-1992, since information on the catch month is sometimes missing in the first half of 18th century, and because of the almost zero incidence of grind in the latter half of that century. The time flow is indicated by the broken line, starting at the point (20%, 50%) for the years 1805-1808, and ending at the point (46%, 36%) for the years 1988-1992.

There seems to be a positive correlation between the January-July proportion and the N-E bays proportion, in the sense that either the two proportions are low (0-30%) or they are both high (35-70%). But there are some marked exceptions, such as (20%, 50%) and (30%, 73%). High January-July and N-E bay proportions also seem to correspond with a high grind rate.



Fig. 10. Comparison of January-July (%) and N-E bays proportion (%) for each 4-year period in 1805–1992. The symbols indicate annual averages (A) of grinds in the 4-year periods: A < 5 (▲); 5 ≤ A < 10 (■); A ≥ 10 (●). The time flow is indicated by the broken line connecting the points. On the whole, the two proportions are either low or they are both high. High January-July and N-E bay proportions also seem to correspond with a high grind rate.

RESULTS AND DISCUSSION

The pilot whale catch rate in the Faroes can be seen as consisting of two main components: (a) the abundance; and (b) the catch effort. The (a) component will partly reflect the variability in the migration pattern and partly the state of the pilot whale stock. The (b) component reflects the sighting intensity and the probability of a sighted school being successfully driven ashore and killed. Components (a) and (b) can probably be considered as independent, although it is possible that in periods with an almost zero catch rate the low probability of sighting pilot whales might influence public interest in pilot whaling and thus diminish the catch effort. This can be shown by one extreme example: Svabo (1783) noted in one case 'not long ago', that due to the immediate lack of suitable equipment, a sighted school could not be killed.

In attempting to explain the fluctuations in the nearly 300 year-long time series of pilot whale catches in the Faroe Islands, it is important to separate these two components. To understand the migration of the pilot whale, it is of special interest to isolate the abundance rate. However, changes in effort in combination with the random noise of the components over this long period, make this difficult.

In Hoydal and Lastein (1993), the univariate time series of pilot whale catches for the period 1709–1984 was fitted to an ARIMA model explaining 32% of the variation in the data. Climatic time-series data based on samples from the Greenland ice-cap have been added as an additional explanatory variable together with the time series of the Faroese catch of bottlenose whales (*Hyperoodon ampullatus*). For the period 1709–1882, the relationship is highly significant, but weaker for the period 1883–1983. A major part of the year-to-year variation remains unexplained.

Sighting

The sighting of pilot whales, which contributes by far the most to the catch effort, is largely incidental; people busy with other occupations may see a school when looking out to sea. Only in a few cases, mostly in former times, is a sighting the result of active searching. Schools of pilot whales are usually spotted from a fishing or transport vessel close enough to the islands that the initiation of a drive is feasible. In some cases, schools may be first sighted from land (Bloch *et al.*, 1990a).

Obviously the sighting intensity has, for various reasons (e.g. changes in population size), changed over the almost 300 year-long period. The population of the islands was quite stable in the 18th century at around 5,000, increased through the 19th century to 15,000 in 1890 and further increased in the 20th century to 47,000 in 1990; almost tenfold growth through the whole period.

However, this increase is probably of minor importance compared with the changes in the Faroese community at large, such as fishing activities and improvements in vessel and communication technology. In Bloch *et al.* (1990b) and Hoydal and Lastein (1993), attempts have been made to quantify these community factors as follows: a 1.0 catcheffort index in the stable 18th century increases through the 19th and the beginning of the 20th century to 1.4, reaching 1.5 in periods with increased fishing activities in the Faroe area, (e.g. the period during the Second World War (1940–45) and in the 1970s, when the Faroese high-seas fishing fleet began fishing within the Faroese fisheries zone). The catch effort could have been even higher in the 1980s, if not for the temporary district closures. In Hoydal and Lastein (1993) the ARIMA model was rerun with the grind series corrected for changes in effort. The residuals are lowered and the peak levels are somewhat reduced, but the fit of the model does not improve.

On a smaller scale, both in time and place, weather conditions have a significant influence on sighting possibilities. Broadly speaking, the worse the weather, the poorer are the chances of seeing a school of pilot whales, and in the more extreme (and not uncommon) conditions of stormy weather, heavy rain or thick fog, the possibility of seeing schools of pilot whales is in practice non-existent. Hoydal and Lastein (1993) report on sightings of pilot whales during 12 trips (July-September 1978) in the Faroese area, where on 29 days with good sighting conditions there were 27 sightings (an average of almost one per day) and on 12 days with bad sighting conditions there were three sightings (an average of one every fourth day). The catch rate seems to be correlated with certain weather and main current conditions on the whaling day (Bloch and Joensen, In prep; Jákupsstova, In prep).

The catch effort also depends on the success of the drive and the killing of a sighted school. In this regard, improved communications in the first quarter of this century, and the introduction of motorised boats in the same period, are of great importance. Despite improved technology, however, there may still be situations in which the whales themselves cannot be controlled, or when weather conditions hinder the effective herding of the school.

Groups of whaling bays

The schools are usually seen quite close to the shore. In a study (Bloch *et al.*, 1990a) which examines 43 drives (from July 1986 to July 1988), the distance from shore at which the schools were found was on average 0.9 n.miles; only one school was seen more than 3 n.miles from land. The total distance schools were driven ranged from 0.5 to 16.2 n.miles, with an average of 5.1 n.miles. These observations suggest the need for a closer study of the distribution of whaling bays. Even though the closest whaling bay is generally used, this is not always the case (Bloch *et al.*, 1990a), such as when current, tidal and wind conditions made it more suitable to use a more distant whaling bay.

Fluctuations in the distribution relative to whaling bays is obvious, such as in the 4-year period 1920–23 when all 19 catches were in the S-W group, while in the period 1821–24 only 4 of 19 catches were in this group of whaling bays. This raises the question of whether the observed fluctuations in the N-E/S-W grouping (Fig. 4) can also be partly explained by changes in the geographical distribution of the human population. The settlement structure in the Faroes was already established in the Middle Ages, and only a few places have been settled in the last century (Thorsteinsson, 1978). This is confirmed by the fact that the 36 locations which have been used for whaling are scattered around the islands (Fig. 3), and the majority of these locations have been accessible throughout the period 1709–1992. This holds for all the whaling bays situated in different regional groups (N, E, S, W), amounting to about 50% of the catches (numbered 1–4 in Fig. 3). Three of these (1–3) were also the most frequently-used whaling bays in the oldest pilot whale statistics from the period 1584–1664 (not included in this analysis), with 31 of the total 41 catches in this period.

Thus the changes in the N-E/S-W grouping percentages (from 61%/39% in 1710–1740 to 15%/85% in 1890–1930) cannot only be explained by changes in the settlement structure. Although some of the large S-W proportion in the latter period may be due to an increased population concentration on Suduroy (which experienced an economic boom around the turn of this century) other periods show comparable S-W proportions (Fig. 4), such as in the early 1840s, 1850s and 1970s, when no obvious demographic or community factors can be discerned.

Size distribution of the grinds

The number of whales in a grind varies greatly (from 1 to over 1,000) and the total grindsize distribution is markedly skewed to the left (Fig. 7) with a median value of 110 whales per grind. This distribution can be approximated by a 'geometric' distribution where success probability (p) equals the reciprocal of 148, the average value of whales per grind and where the variance equals $(1-p)/p^2$ (=148²). With a sample size of 14, the 95% confidence interval of the average is [70; 227]. The observed variation of the yearly averages in the period 1979–1992 (Table 1) could be explained as random samples within this model, since only one value (66 in 1991) falls outside the confidence interval (note that the sample size varies between 11 and 21). However, the pattern in this period is quite unlikely (in the first seven years the numbers are above 90 and in the following six years under 90).

The shape of the Faroese distribution resembles that for the 92 drives conducted at Newfoundland from 1952–54 (Sergeant, 1962), but at a lower level. The mean size of these drives is 85 which is not significantly lower than the January mean size of 96 in the grind statistics (Table 4). The Newfoundland catching season was in the summer months, however, when the mean sizes at the Faroes were at their highest (around 160 animals).

Sergeant (1962) also reports offshore observations of 30 pilot whale schools with a mean size of 20. Small schools of pilot whales in the open sea were also seen in the NASS-studies (Buckland *et al.*, 1993), where 90 sightings from Icelandic vessels showed a mean size of 26. However, estimating the school sizes of pilot whales at sea is notoriously difficult with a tendency to underestimate the true size. Sergeant (1962) commented that pilot whales form large, dense schools when they are in danger and probably also when they are migrating, but disperse into scattered groups on the feeding grounds. However, interpretation of such data is difficult, and requires considerably more information on the schooling behaviour of pilot whales, their migratory patterns and whether or not there are specific feeding grounds.

	Grind frequency		Whales per grind	
	No.	%	Average	Median
January	41	2.6	93.6	79
February	34	2.2	119.1	96
March	26	1.7	115.3	66
April	38	2.4	165.3	143
May	52	3.3	123.9	106
June	142	9.1	138.1	102
July	328	21.0	158.3	115
August	431	27.6	163.3	131
September	238	15.2	129.6	98
October	110	7.0	149.0	96
November	70	4.5	134.7	104
December	54	3.5	125.7	97
Jan-July	661	42.3	144.1	109
Aug-Dec	903	57.7	148.4	111

Table 4

Grind statistics according to months and the two seasons: Jan-July and Aug-Dec. Information on month is missing in 65 grinds.

Seasonal variations

At 62°N, the latitude of the Faroes, there are about four times more hours of daylight in mid-summer than in mid-winter. This would suggest a seasonal variation in sighting rate, if all other factors are equal. In fact the seasonal variation is amplified by a variation in weather conditions; in winter, stormy and showery weather is more common and both fishing and the sighting possibilities are diminished.

The distribution of catches by month has one valley in late winter (February-March) and one clear peak in late summer (July-August) (Table 4). There is thus a 1–2 month shift compared to expectations based solely on daylight, so other factors, such as hydrographical and biological conditions, must contribute to the observed variation. It is not possible from these statistics to assess the importance of all relevant factors, but one may guess that the rate of probability of encountering a school is twice as high in midsummer compared with mid-winter due to seasonal daylight and weather conditions.

August is the record month for the number of grinds (421/28%), with the second-highest average number of whales (164). A closer look at the August statistics through the centuries reveals that the period 1887–1923 has a more than twofold frequency of 58% (78 of 135 grinds), and also a high average number, i.e. 203 whales, per grind. This period almost coincides with a period which shows low proportions of both N-E bays and January-July grinds (see the discussion below on the bays and seasonal correlation). The high August numbers can partly be ascribed to this period and some other August-intensive years such as 1840 (7 of 11), 1963–66 (22 of 48), and 1979 (11 of 13).

The grind-size distribution by month (Fig. 9) confirms the high number of whales per grind in August and April and the low numbers in December and January (Table 4). Assuming the geometric model, these monthly differences are significant, as is the difference between August and September averages. The yearly distribution of grind size corresponds with the mating and conception pattern of the long-finned pilot whale (Amos, 1993; Amos *et al.*, 1993; Martin and Rothery, 1993).

Clustering

In addition to large scale (decade/century) temporal trends and seasonal variation in the catch statistics, varied clustering on a time scale of weeks and days is also obvious. As an example let us consider in more detail the grinds from 1979 and 1991 (Table 5). Of the 13 grinds in 1979, 8 occur within an eleven-day period (August 21–31), while the 11 catches in 1991 are spread over seven months and the closest gap between two catches is seven days. The two years also show different patterns in occurrence of bays, such as the distribution in the eastern/western groups, which is 5/0 and 2/6 in 1979 and 1991 respectively. Eleven different bays were used in 1979, and 7 bays in 1991, of which 4 bays were used both years. The pattern of school size was also different; five grinds in 1979 had more than 150 whales, opposed to none in 1991.

In the last 180 years (in the 18th century no catch date is recorded), there have been 62 multiple-grind days i.e. days with two or more grinds, of which 40 were in July and August. Assuming, to simplify, that the 180 years relative to number of grinds in July-August can be divided into three groups 75/65/40 with, respectively, 2/4/6 multiple grinds per year in July-August, then the expected number of multiple-grind days for the total period in a random model is 18. When compared with the 40 days observed, this also indicates a clustering phenomena.

The clustering of catches indicates that in general one cannot assume catches to be independent events in the statistical sense. Any attempt to use the catch data to provide information on putative migration patterns must take this clustering into account. In addition it should be noted that for the first time in the recorded catches, four grinds were

Table 5

Pilot whale catches in 1979 and 1991.	Bay number and group label (N/E/S/W) according to Table	2
	and Table 3.	

	1979			1991	
Date	Whales	Whaling bay	Date	Whales	Whaling bay
03 Feb.	33	N/10	15 Jan.	1	W/5
09 Aug.	208	E/15	23 Feb.	116	N/2
10 Aug.	135	N/8	13 May	138	S/4
17 Aug.	338	S/9	11 June	67	N/2
21 Aug.	27	W/5	25 June	33	W /1
22 Aug.	78	S/6	10 Aug.	70	W /1
23 Aug.	11	W/1	02 Sept.	40	S/23
25 Aug.	233	S/13	10 Sept.	49	W/1
28 Aug.	121	E/ 7	18 Sept.	10	N/8
28 Aug.	1	E/12	30 Sept.	69	W /11
30 Aug.	182	E/15	14 Oct.	127	W /1
31 Aug.	27	E/12			
22 Oct.	279	N/2			

caught on the same day, 16 July 1992, and they were all beached at the four western-most bays of Miðvágur, Bøur, Vestmanna and Leynar (1, 27, 5, 26 in Fig. 3).

Bays and seasonal correlation

Fig. 10 shows a positive correlation between the proportion of grinds in January-July and that in the N-E bays. The line connecting the points chronologically is short given all possible routes between the points. This indicates that the proportions in one period are influenced by the proportions in the preceeding period (in a statistical time series analysis the low order auto-correlations would be positive).

This time-dependent distribution suggests a fluctuation of the proportions in a wider time scale than the 4-year period used here. This is underlined by the fact that nine of eleven points in the lower left-hand corner of Fig. 10 belong to one connected period 1884–1927, which is also characterised by a relatively low grind rate, i.e. with annual means lower than five. Ten of twelve points representing 10 grinds per year or higher lie in the rectangle [30%-62%]x[40%-62%], so a high grind rate tends to give high January-July and N-E bay proportions.

It should be mentioned that for the entire period, almost half of the grinds in August-December (58%) occurred in August (28%) (Table 4). A similar relationship is seen with January-July (42%) and July (21%). So significant changes in January-July proportions are in many cases due to a shift of grind concentration between July and August. The high grind frequency in August was noted above in connection with the discussion of seasonal variations and the clustering phenomenon.

Climatic change and biological variability

Long term trends in sea-surface temperature (SST) are to some extent correlated with the level of pilot whale catches. For instance, the general warming of the North Atlantic between 1900–1940, which can also be seen in measurements from the Faroes (Smed, 1978), corresponds with the increase in the number of grinds caught in the period (Joensen and Zachariassen, 1982).

Joensen and Zachariassen (1982) also found a correlation between the number of grinds in July-September each year and the available data on SST during the same months in the regions west and southwest of the Faroes in the period 1957–76, taken from Stougaard-Nielsen (1978). They found a stronger relationship between the number of grinds and SST in the region 57–59°N, 16–32°W, with correlation coefficients between 0.68–0.74, than close to the Faroes (correlation coefficient 0.57). In this 20-year period the SST near the Faroes was between 11–12.7°C while in the region 57–59°N, 16–32°W it was 7.2–12.8°C. In other words, the SST south-west of the Faroes seems to be a more sensitive measure of the pilot whale catch rate than the SST near the Faroes.

The occurrence of the long-finned pilot whale seems to be positively correlated with the occurrence of its main prey, pelagic squid (Mercer, 1975; Joensen and Zachariassen, 1982; Bloch, 1992; Desportes and Mouritsen, 1993; Hoydal and Lastein, 1993). For instance, the cluster of grinds in August 1979 coincided with large squid catches in the Faroes. In some places such squid abundance has not been recorded for 15 years, although this period has been good for pilot whaling (Joensen and Zachariassen, 1982; Jákupsstova, In prep).

From 1966–69 to 1970–1974 there was a marked change in the climatic conditions of the North Atlantic Ocean, indicated by, amongst other factors, the atmospheric pressure



Fig. 11. Grind incidence each month in the period 1966-1974.

Period	Grinds	Grinds per year	Whales per grind	Jan-July	Western bays	
1966-69	58	14.5	112	30 52%	17 29%	
1970-74	29	5.8	125	7 24%	13 45%	

Table 6Grind statistics from 1966-69 and 1970-74

anomaly for the winter quarter, which showed a N-W gradient in the first period and a S/S-E gradient in latter period (Garrod and Colebrook, 1978). Contemporary changes in ocean biology, such as in planktonic and fish communities, were also observed. The so-called 'Great Salinity Anomaly', i.e. the widespread freshening of the upper 500–800m-layer of the Northern North Atlantic in the 1970s (Dickson *et al.*, 1988), also marks an extreme change in the ocean climate.

Some main grind statistics in the periods 1966–69 and 1970–74 are set out in Table 6, where some interesting changes from the first to the latter period can be observed: a 60% reduction in the grind rate, a 50% reduction of the January-July proportion and a smaller increase in the western bay proportion. Also, a small (non-significant) increase in the number of whales per grind was observed. Fig. 11 shows the monthly grind incidence in the period 1966–1974, and supports some of these observations. The simultaneous changes in (a) the seasonal distribution of the grinds, (b) the whaling bay distribution and (c) the catch rate level, corresponds well with the observations made in the analysis concerning the bays and seasonal correlation (Fig. 10). This suggests that the above climatic and biological parameters in the North Atlantic may be of importance to the abundance of pilot whales in the Faroe area.

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Analysis of Faroese Catches of Pilot Whales (1709–1992), in Relation to Environmental Variations

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ABSTRACT

This paper reviews information on the long-finned pilot whale (*Globicephala melas*) in the waters around the Faroes. In particular, the long term series of catches of pilot whales (1709–1992) are examined in the light of possible relationships between variations in landings of whales and environmental variations. A shift in the pattern of catches around 1920 was noted, which coincides with a general shift in the climatic conditions in the North Atlantic. Long term variations in the time series were observed. Observations of bottlenose whales (*Hyperoodon ampullatus*) show similar variations to the catches of pilot whales, indicating that a common environmental factor (or factors) may be responsible for the variations observed in the time series for both species. Annual variations in both number of schools and mean number of whales per school, appear to be related to changes in sea temperature although the mechanism is unclear. It may reflect changes in the food availability as indicated by investigations of blue whiting and squid in the area. Changes in the current system in the North Atlantic are suggested to be one cause of variability in the catches of pilot whales in the Faroes.

KEYWORDS: PILOT WHALES-LONG-FINNED; NORTH ATLANTIC; STOCK IDENTITY; BOTTLENOSE WHALES; SQUID; FISH; OCEANOGRAPHY; MIGRATIONS

INTRODUCTION

The stock identity of pilot whales (*Globicephala melas*) observed in Faroese waters is uncertain but it is assumed that they are part of larger populations in the North Atlantic (IWC, 1992, pp.197–200). Several studies investigating this are underway (e.g. Amos *et al.*, 1993; Andersen, 1993), and morphometric analysis of samples from the Faroes and Newfoundland waters has suggested that animals from these areas are from separate stocks (Bloch and Lastein, 1993).

Hunting of the pilot whale in the Faroes has been recorded since 1584, but there is reason to believe that the hunting goes further back than that (see review by Zachariassen, 1993). Only pilot whales found within 10 n.miles of the Islands are hunted and it is clear that the area exploited by the Faroese is small compared to the total range of the species in the North Atlantic, a picture confirmed by the extensive NASS-surveys in 1987 and 1989 (Buckland *et al.*, 1993). Weather conditions play an important role in the number of schools landed in the Faroes (Table 1); poor sighting conditions reduce the number of schools sighted and thus potentially captured. Variations in sighting conditions are, therefore, assumed to seasonally affect the number of pilot whales landed at the Faroes (Hoydal, 1985). This paper attempts to examine the long term variations observed in the catches of pilot whales in the Faroes, in particular, with respect to environmental factors.

		Good sighting conditions		Bad sighting conditions	
Trip	Days at sea	No. days	Sightings	No. days	Sightings
1	7	4	8	3	1
2	2	2			
3	1	1	3		
4	2	2	4		
5	3	3	1		
-	_	-	(Big schools)		
6	4	1	(8),	3	
7	1	_		1	
8	4	2	1	2	1
9	6	6	3		
-	Ū	· · ·	(Big schools)		
10	4	2	(2	1
11	2	-	3	1	
12	6	5	4		
Total	41	29	27	12	3

Sighting conditions and sightings of pilot whales during 12 trips in the Faroe area 18 July to 2 October, 1978.

MATERIAL

Cetacean catch data

Written records of landings of pilot whales in the Faroes have been kept since 1584, and the only gap in the series is the period 1641–1708. The full set of data on catches by month, year and whaling bay have been analysed by Müller (1882; 1883a; b) for the time period 1709–1883, Joensen (1962) for the time period 1884–1962 and Joensen and Zachariassen (1982) for the time period 1709–1978. Zachariassen (1993) has updated and reviewed the data for the period 1709–1992. All the catch data journals and other relevant sources for both pilot and bottlenose whales (*Hyperoodon ampullatus*) taken from the Faroes have been examined and compiled by D. Bloch and R. Mouritsen and made available for this study.

Joensen and Zachariassen (1982) examined several non-biological factors that might affect catch numbers, particularly the number of inhabitants, socio-economic changes and technical improvements in catching and communication methods. This was discussed further by Hoydal (1985). In an attempt to try and correct the catch series for these factors, we have assigned the tentative 'correction' values shown in Table 2. We recognise that these values may be imprecise although they are qualitatively appropriate for the purposes of our analysis (see Discussion).

Four time series of catches are used in this study:

- (1) annual number of schools of pilot whales caught in the Faroes in the years 1709–1992;
- (2) annual number of pilot whales caught in the Faroes in the years 1709-1992;
- (3) annual number of schools of bottlenose whales landed in the years 1709–1992;
- (4) annual number of bottlenose whales landed in the years 1709–1992.

It is assumed that the catch series reflect the true catches of whales in the Faroes and that the rare incidences of the number of whales being so great that the recording may have been problematic do not seriously affect the reliability of the data. Possible biases in the series have been reviewed by Bloch *et al.* (1990).

Table 1

Table 2

Correction for effort in the Faroese catch series. Note that the reason for assuming a 50% increase over the whole period is based on the inherent conservatism in pilot whale hunting. It is still a strictly non profit business, with little investment in equipment or facilities that might increase the hunting efficiency.

Period	Effort correction factor	Comments
1700-1800	1	Static community in the Faroes.
1800-1900	1-1.4	Increase in population and economic developments start. End of period, introduction of motor vessels and improved communication.
1900-1940	1.4	No drastic changes. Apart from the war years 1914-1918 the Faroes fishing activity in the Faroe area very limited.
1941-1945	1.5	Increased fishing activity in the Faroe area during the war.
1945-1970	1.4	Back to pre-war situation.
1971-1981	1.5	Increased fishing activity in the Faroe area.
1982-1984	1.3	Restrictions in catches introduced. Drives not allowed in whaling districts if catches have reached certain levels.

Zachariassen (1993) discusses the distribution of the catches by month and locality in different years and periods. Although he does not present a strict statistical analysis, some differences in catch distribution by months and locality among time periods are observed. A more quantitative analysis of the effect of these two factors may explain some of the variation in the data, but as a first step we have chosen to consider the series as a univariate time series of annual numbers of whales and annual numbers of schools.

Other data

One difficulty with examining a series of catch data as long as that for Faroese pilot whales is that rarely are their similar time series available for other factors. One of the few examples is the time series of estimated air temperatures given by Dansgaard (1985) based on measurements of isotopes in Greenland ice cores. The smoothed curve shown in Fig. 1(a) was estimated by use of a 10° polynonium.

The following, more recent oceanographic data were also used:

- (1) sea surface temperature at Mykines, 1914–1962;
- (2) sea surface temperature and salinity in the Faroe Bank Channel, 1978–1992 (Gaard et al., 1993);
- (3) CTD data north of the Faroes, August and September 1982–1991 (Jacobsen and Lastein, In press).

The few published records on prey distribution and abundance (the squid, *Todarodes sagittatus* and the blue whiting, *Micromesistius poutassou*) are also considered.

ANALYSIS

The time series of catches of pilot whales and bottlenose whales

The four time series of catches by species are given in Fig. 1(b-e).

The time series of catches of pilot whales (Fig. 1b-c) show three maxima: around 1725, around 1840 and around 1960. Before 1920 these coincide (Fig. 1a) with minimum temperatures in Dansgaard's (1985) Greenland series with a lag time of around 10 years. After 1920 the correlation is reversed with high catches of pilot whales associated with



Fig. 1 (a) Dansgaard temperature series from Greenland covering the time period 1709–1992. (b) Annual catches of number of pilot whales in the time period 1709–1992. (c) Annual catches of number of schools of pilot whales in the time period 1709–1992. (d) Annual number of bottlenose whales landed in the time period 1709–1992. (e) Annual number of schools of bottlenose whales in the time period 1709–1992.



Fig. 2. Observations of catches of number of pilot whales (×), estimated number of pilot whales (—) and estimated trend covering the time period 1710–1983.

high temperatures in the Greenland series. This suggests that while catches (and by inference, abundance) of pilot whales appears to be correlated in some way with air temperature, this correlation is not straightforward.

Fig. 1(b-c) also indicates that the number of whales is correlated with the number of schools, as supported by a variance analysis of the two time series (correlation coefficient, R, 0.83, F = 737.976 and p=0.000).

Spectral analysis of the periodicities observed in the catch series in Fig. 1(b-c) revealed two periods between 1709–1920 of 73 and 128 years. This is similar to the periods estimated for the Greenland temperature series of 85 and 132 years. This again suggests that the time series of catches is related in some way to the temperature series.

The periodicities observed in the time of series of numbers of pilot whales caught in the Faroes (Fig. 1(b)) were further used to estimate a possible trend in the series. The model used was

Number of pilot whales(year) = const. + $\Sigma ancos (2\pi x year/N) + bnsin (2\pi x year/N) + \epsilon$

where n=1; N= number of years analysed and ϵ is an error term.

Fig. 2, using this model, shows the same three main periods of good catches as observed in the original data and shows that some external factors are affecting the number of pilot whales caught in the Faroes.

The bottlenose time series (Fig. 1d-e) comprises a much smaller number of schools and whales per school. The series shows a remarkable decline after 1920 and it is thought this may reflect poorer recording for this less valued species and also overfishing (Christensen, 1993). For the purpose of comparing the catch time series of pilot and bottlenose whales, it was therefore decided only to analyse the time period 1709–1920. Variance analysis for both number of whales and schools showed a maximum correlation at R=0.53, p=0.00 and R=0.48, p=0.00 respectively.

Abundance of pilot whale prey

From studies in Newfoundland, Sergeant (1962) reported that the pilot whales fed almost exclusively on squid. Desportes and Mouritsen (1993) reported that Faroese pilot whales fed mainly on the squid species *Todarodes sagittatus* and *Gonatus sp.*. However, blue whiting (*Micromesistius poutassou*) and greater argentine (*Argentina silus*) were also



Fig. 3. (a) Stations with catches of *T. sagittatus* in bottom and pelagic trawls with R/V G.O. Sars in April-May 1980 (filled circles) and with R/V Michael Sars in March-April 1981 (open circles). (b) Stations with catches of *T. sagittatus* in August-September 1981 (1), October-November (2) and March-April 1982 (3). Recapture of tagged squid (4).

relatively common in stomachs sampled between 1984 and 1987. In particular, they found that in years when the squid fishery was poor, presumably reflecting the availability of squid, the diet of the pilot whale showed great diversity, with blue whiting being the most common fish species observed (25% of the total fish species observed).

Squid

In recent years, the biology of *Todarodes sagittatus* has been investigated by Norwegian scientists (Wiborg and Gjøsaeter, 1981; Wiborg *et al.*, 1982; 1983; Wiborg and Beck, 1984). Fig. 3 reproduces two charts from Wiborg *et al.* (1981; 1983) that show the seasonal distribution of the squid. Fig. 4 shows the length distributions of the squid caught at certain selected stations. These figures suggest that squid migration patterns are related to the shelf edge, where both the number of squid caught and their length were greatest. The squid feed on fish species such as blue whiting, perlsides (*Maurolicus muelleri*) and other species usually found over the shelf edge.



Fig. 4. Length distribution of T. sagittatus from selected stations in Fig. 3 (continued overleaf).



Fig. 4. (cont.) Length distribution of T. sagittatus from selected stations in Fig. 3.

Gaard (1988) reported that catches of T. sagittatus have been small since 1984, perhaps due to changes in the migration route of the squid. Shimko (1989) reported that the spawning area for this species is in the North Azores area (Fig. 5), from where it migrates to the Norwegian Sea with the North Atlantic Current; several different migration routes are possible and not all of them pass through the Faroese area.

Jákupsstova (In press) has examined Faroese squid catch data since 1950. He found certain 'squid years' with a relatively large bait fishery. There was a general correspondence between numbers of pilot whales caught and 'squid years', although the relationship did not hold for every year. For example, in 1985 no squid were caught although a large number of pilot whales was caught; at the same time squid were abundant in Norwegian waters. This may reflect changes in the migration pattern of both pilot whales and *Todarodes*. Shimko (1989) suggested that in the years with lower pilot whale catches (1986–1988), larvae were observed to the southeast of the Azores, whereas in years with higher catches, they were northwest of the Azores (Fig. 5).


Fig. 5. Scheme of the squid migrations in the Northeast Atlantic (winter grouping). 1 – reproductive part of the range; 2 – direction of larvae drift and adults migration; 3 – places of larvae catch; 4 – places of juvenile molluses catch, age – 82–175 days; 5 – places of immature squids catch, age – 190–200 days; 6 – places of squids catch, age – 240–270 days. (From Shimko, 1989).



Fig. 6. Chart summarising the migration pattern and areas of concentration of adult blue whiting. (From Bailey, 1982).

Blue whiting

The northern stock of blue whiting spawns along the shelf-edge west of the British Isles in March-April (Fig. 6) and then migrates north through the Faroe Shetland Channel/Faroe Bank Channel to its feeding area in the Norwegian Sea (Hansen and Jákupsstova, 1991).



Fig. 7. Number of pilot whales and biomass of blue whiting (Monstad, 1989) estimated for the spawning and feeding area (Fig. 6) covering the time period 1980–1992. — = pilot whales; ---- = blue whiting.

Monstad (1989) has estimated the biomass of blue whiting for the spawning and feeding area, covering the time period 1980–1992. These data are shown in Fig. 7 together with the catches of pilot whales in the Faroes. The correspondence between number of whales landed and biomass of blue whiting seems clear (R=0.876, F=36.16, p=0.000), with respect to blue whiting in the feeding area (Fig. 7), but not with respect to the spawning area (R=0.177, F=0.227, p=0.648). As the investigations of blue whiting were carried out in July-September, in Fig. 8 we have separated the pilot whale catches by month. This shows that pilot whale catches in the Faroes are highest from July-September, connected with the only significant correlation coefficient between the time series of whales and blue whiting in this time period (R=0.73, F=12.554, p=0.005).



Fig. 8. Number of pilot whales and biomass of blue whiting in the feeding area in four different seasons. Key: — = pilot whale; ----= blue whiting. Results from variance analyses: (a) R=0.185; F=0.388; P=0.546; (b) R=0.230; F=0.612; P=0.451; (c) R=0.730; F=12.554; P=0.005; (d) R=0.185; F=0.390; P=0.545.



Fig. 9. (a) Mean annual surface temperature obtained at Mykines (Fig. 10). (b) Number of pilot whales. (c) Number of schools of pilot whales. (d) Number of bottlenose whales. (e) Number of schools of bottlenose whales.

Analysis of temperature observations obtained in Faroese waters

Fig. 9 shows measurements of surface temperature observed at Mykines (Fig. 10), together with observations of whale species, between 1914 and 1962. This suggests that the increase in numbers of schools and whales around 1920 is connected to a mean annual increase in the surface water temperature (R=0.67, F=18.11 and p=0.00).



Fig. 10. Surface currents in the area around the Faroe Islands. MNAW: Modified North Atlantic Water. NI/AI: North Icelandic/Arctic Intermediate Water. NAW: North Atlantic Water.

Gaard *et al.* (1993) calculated the mean annual temperature and salinity in the Faroe Bank Channel (Fig. 10) for the time period 1978–1992. The period 1980–1985 was characterised by low stable temperature and salinity values. After this, both temperature and salinity were generally higher but more variable (Fig. 11). A comparison with the pilot whale time series of catches (Fig. 7) suggests a relationship between the changes in pilot whale abundance around 1985 and the changes in these oceanographic variables.

To examine if the variability in the water temperature north of the Faroes might be connected with the observed variations in the time series presented in Fig. 8, these temperatures were analysed for those years when it was available. Fig. 12 shows the position of the 5°C isotherm at 100m depth north of the Faroes, based on CTD observations obtained during surveys of blue whiting in August-September carried out between 1982 and 1991 (Jacobsen and Lastein, In press). The 5° isotherm extends much further south in 1982 than in the other years. This would force the Atlantic water arriving from the south (Fig. 10) into a narrower area close to the Islands. If the pilot whale migrates with the North Atlantic Current, this would cause the whales also to be concentrated in a narrower area close to the Islands. This is consistent with the fact that a peak in catches was observed in 1982.



Fig. 11. (a) Average temperature of the 100-300m layer in the homogeneous water over the deep part of the Faroe Bank Channel plotted against the time of observation. (b) Average salinity of the 100-300m layer in the homogeneous water over the deep part of the Faroe Bank Channel plotted against the time of observation. (From Gaard *et al.*, 1993).

DISCUSSION

This paper presents a first attempt at examining the long time series of Faroese pilot whale catches in the light of environmental factors. We believe this is an important approach, notwithstanding the number of difficulties inherent in any such approach. Perhaps the most obvious of these is the quantity and quality of associated environmental data available. While it is relatively easy to obtain a reasonably accurate time series of catch data for the Faroese pilot whale fishery stretching back several centuries, it is difficult to obtain such a long time series of oceanographic data (only the estimated air temperature from the Greenland data even approximates this) or data on prey species availability. The latter is particularly significant.

For example, while the Greenland temperature data appear to be correlated with variability in numbers of pilot whale schools and individuals around the Faroes, the mechanism for this is unclear, particularly given the change in direction of the relationship



Fig. 12. Position of the 5° isotherm at 100m depth north of the Faroes in August-September covering the years 1982–1991.

around 1920. Intuitively, the most likely mechanism is via an effect on the distribution and abundance of prey species.

However, the time series of prey data are very short and the data themselves are somewhat equivocal. For example the number of whales appeared to be related to the amount of squid present in the area, but not exclusively. This may be a result of variability in the migration routes of the squid but these migrations are themselves not well understood. There also appears to be some relationship between the distribution of blue whiting and pilot whales, which could be related to variations in the current system in the North Atlantic, which remain to be further investigated. In fact, the migration patterns of the pilot whales in the North Atlantic, as well as their prey species, are still unknown. However, our analysis of the limited hydrographical and biological information available for Faroese waters suggests that the migration route may be related to the North Atlantic Current. This warrants further attention.

We feel that this study has highlighted the importance of examining the catch series in the light of more than simple assumptions about trends in abundance of North Atlantic pilot whales. The question of stock identity is particularly important here. In terms of modelling work, a sensitivity analysis of the effect of our assumptions concerning 'effort modifiers' is required. However, while statistical analysis can provide information on periodicity and correlations, the value of these only becomes apparent if the mechanics of the relationships are identified. Effort must be put into examining further the ecology of both pilot whales and their prey species, in terms of developing hypotheses of the relationship between environmental variables and their distribution, migration and abundance. This will require focussed collection of both oceanographic and biological data.

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Pilot Whales Incidentally Taken During the Distant Water Fleet Atlantic Mackerel Fishery in the Mid-Atlantic Bight, 1984–88

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ABSTRACT

Pilot whales, *Globicephala* sp., have been reported as incidental takes during the Distant Water Fleet (DWF) Atlantic mackerel fishery since 1977. The number of takes reported was anomalously high in 1988 (142 whales) in comparison with those for 1984–87 (12, 42, 17 and 26 whales). Comparison of the general areas where incidental pilot whale takes occurred during 1988 relative to 1984–87 revealed no substantial difference. The area of conflict is principally concentrated from Baltimore Canyon north to Welker Canyon, extending from the 200m isobath shoreward approximately 45 n.miles. The anomalously high take rate may be explained by DWF mackerel fishing operations for January-April 1988. During this period, the fishery was concentrated in the area where past mackerel-marine mammal interactions have been highest. Fishing effort was distributed over a wider area of shelf waters during 1984–87.

KEYWORDS: PILOT WHALES – LONG FINNED; PILOT WHALES – SHORT FINNED; NORTH ATLANTIC; INCIDENTAL CAPTURE; FISHERIES.

INTRODUCTION

Atlantic mackerel, *Scomber scombrus*, have been harvested off the northeastern US coast since the seventeenth century (Anderson and Paciorkowski, 1980). It was not until the arrival of the Distant Water Fleets (DWF) in the 1960s, however, that an intensive trawl fishery developed in the offshore waters between Cape Hatteras and Georges Bank. Catches in the mid-Atlantic Bight increased from less than 400 metric tonnes per year in 1960–65 to 232,300 tonnes in 1971 then dropped to 66,000–142,900 tonnes between 1973–76 (Anderson and Paciorkowski, 1980). Implementation of the Magnusson Fisheries Conservation and Management Act on March 1 1977 extended US jurisdiction over all living marine resources within the 200 mile Exclusive Economic Zone (EEZ), which resulted in a dramatic reduction in DWF mackerel fishing off the northeastern US coast.

¹ Present address: Minerals Management Service, MS 4310, 381 Elden Street, Herndon, VA 22070, USA ² Present address: Ocean Surveys, Inc., 91 Sheffield St., Old Saybrook, CT 06475, USA DWF Atlantic mackerel catches in 1977 were 49,200 tonnes, dropping to less than 1,000 tonnes per year from 1978–81 when they were taken principally as a by-catch in the offshore squid fishery. The DWF fishery eventually increased again from a catch of 6,000 tonnes in 1982 to 43,000 tonnes in 1988. Subsequently, catches rapidly declined to 5,000 tonnes in 1991. The trends in foreign catches during the past decade were due primarily to management decisions by the Mid-Atlantic Fishery Management Council, in response to changing stock sizes (National Marine Fisheries Service, 1991).

The incidental takes of marine mammals in commercial fishing activities have received widespread attention in recent years (e.g. Loughlin *et al.*, 1983; Waring *et al.*, 1990). Incidental takes of pilot whales, *Globicephala* sp., have been reported in the east coast DWF fisheries for squid, hake, Atlantic mackerel and tuna since 1977 (Waring *et al.*, 1990). The majority (84%, n=249) of the pilot whale takes have occurred since 1984 in the Atlantic mackerel fishery, with 12 to 142 whales taken per year.

The sudden increase in the incidental take to 142 pilot whales by the DWF Atlantic mackerel fishery off the northeastern US coast during 1988 prompted the analysis presented in this paper. Here we review the distributions of: (1) pilot whale sightings (1961–88); (2) the DWF Atlantic mackerel fishery (1984–88); and (3) incidental pilot whale takes during the DWF Atlantic mackerel fishing operations (1988 relative to 1984–87).

MATERIALS AND METHODS

Pilot whale sightings along the northeastern US coast were obtained from a variety of sources. The distribution of the long-finned pilot whale *Globicephala melas*, the northern species, overlaps with the short-finned pilot whale *G. macrorhynchus*, mainly a southern species, between $35^{\circ}30'$ N and $38^{\circ}00'$ N (Leatherwood *et al.*, 1976). Although *G. melas* is the most common and the most likely taken in the DWF fisheries, there is a possibility that the southern species might also be occasionally taken. Positive identification to the species level is often difficult. Therefore, in this paper we use *Globicephala* sp.

(1) The Cetacean and Turtle Assessment Program (CETAP) at the University of Rhode Island (URI) conducted dedicated aerial surveys from November 1978-January 1982 and collected opportunistic and historic data made by reliable sources from the mid-1900s to 1982 (Winn, 1982).

(2) Manomet Bird Observatory (MBO) conducted standardized sighting surveys aboard NOAA fishery research vessels operating between Nova Scotia and Cape Hatteras from 1980–88 (Smith *et al.*, 1988).

(3) Observers aboard DWF Atlantic mackerel fishing vessels collected opportunistic marine mammal sightings and incidental take data from 1984–88 (Smith *et al.*, 1988).

Monthly plots, encompassing the DWF Atlantic mackerel fishing season from January to May, were generated to illustrate the following: (1) positions where pilot whales were sighted by CETAP, MBO and observers on the DWF Atlantic mackerel fishing vessels from 1961–87; (2) distribution of DWF Atlantic mackerel fishing activity derived from a random sample of the 1985–88 trawl data; and (3) positions where pilot whales were incidentally taken during DWF Atlantic mackerel fishing operations from 1984–88. Comparisons of the plots between calendar years were performed to identify anomalous conditions. The study area map represented in Fig. 1 illustrates the geographic features that are referenced in the distributional analyses.



Fig. 1. Map of the study area illustrating geographic features.

RESULTS

Pilot whale sightings

Fig. 2 illustrates the monthly distributions of pilot whale sightings made along the northeastern US coast from January through May 1961–87. The sightings available for 1988 were collected onboard the DWF fishing vessels (which were concentrated in a fairly localized area) and on a limited number of US National Oceanic and Atmospheric Administration (NOAA) fisheries vessels. These may not be representative of the overall distribution of pilot whales during 1988, and thus have not been included in these figures.

January and February sightings were concentrated in the shelf waters from the Delmarva Peninsula to the southern edge of Georges Bank (Fig. 2a), primarily along the bathymetric shelf-slope (SH/SL) front. During March, sightings were concentrated in roughly the same area along the SH/SL break, with scattered sightings in the slope waters (Fig. 2b). During April, the majority of the sightings were made from southern New Jersey to Georges Bank (Fig. 2c). Sightings occurred throughout the shelf waters, as well as along the bathymetric SH/SL front, and extended northward along the eastern edge of Georges Bank. May sightings were concentrated along the mid-shelf and SH/SL edge waters from New York Bight to Georges Bank, and into the Gulf of Maine (Fig. 2d). Scattered sightings were made south of this area. Based on these figures, pilot whale distribution was generally fairly extensive throughout this region.



Fig. 2. Distribution of pilot whale sightings (CETAP, MBO, DWF fishery observers) during: (a) January-February 1968-87; (b) March 1961-87; (c) April 1964-87; and (d) May 1966-87.

Distribution of incidental takes relative to DWF fishery

Comparisons of the locations where the incidental takes occurred relative to the area where the DWF Atlantic mackerel fishery was distributed revealed that the takes were generally concentrated from Hudson to Atlantis Canyons, although the fishery was more widespread. A monthly summary of the historic distributions compared to the 1988 data is given below.

During January-February 1985–87, although the DWF fishery extended from the New York Bight southward to Cape Hatteras, throughout the shelf waters (Fig. 3a), the incidental takes occurred primarily in the New York Bight waters and near Washington and Block Canyons just shoreward to the 200m isobath (Fig. 3c). In January-February 1988, the fishery was concentrated in the mid-shelf waters of New York Bight, with scattered fishing south to the Delmarva Peninsula (Fig. 3b), although the takes occurred in mid-shelf waters northwest of Wilmington Canyon and near the 200m isobath near Hudson Canyon (Fig. 3d).









Fig. 5. Distribution of DWF Atlantic mackerel fishery positions during: (a) April 1985–1987 and (b) April 1988; and distribution of incidental pilot whale takes during DWF Atlantic mackerel fishery during: (c) April 1984–87 and (d) April 1988.

Fig. 6. Distribution of DWF Atlantic mackerel fishery positions during: (a) May 1985–1987 and (b) May 1988; and distribution of incidental pilot whale takes during DWF Atlantic mackerel fishery during: (c) May 1984–86 and (d) May 1988.

In March 1985–87, the fishery ranged from Cape Hatteras to New Jersey in the mid– to outer-shelf waters (Fig. 4a), while the incidental takes were concentrated near the 200m isobath from Baltimore to Hudson Canyons (Fig. 4c). In March 1988, the incidental pilot whale takes were concentrated along the 200m isobath from Hudson to Block Canyons (Fig. 4d), although the fishery was distributed from the middle of the Delmarva Peninsula to Block Canyon, in the outer-shelf waters (Fig. 4d).

During April 1985–87, fishing progressed northward and was concentrated throughout the shelf from southern New Jersey to Block Canyon (Fig. 5a), while the incidental takes occurred along the 200m isobath from Hudson to Block Canyons (Fig. 5c). In April 1988, both the fishery and the incidental takes were concentrated near the 200m isobath, extending from Hudson to Atlantis Canyons (Fig. 5b and d).

During May 1985–86, the fishery was located in the shelf waters from southern Long Island to Welker Canyon, with the effort from Veatch to Welker Canyons concentrated close to the 200m isobath (Fig. 6a). Incidental takes in May 1984–86 were concentrated between Block and Welker Canyons, with the majority of takes occurring along the 200m isobath (Fig. 6c). The May 1988 fishing effort was located along the 200m isobath near Block Canyon, though it was curtailed early in May (Fig. 6b). Only one pilot whale was taken near Block Canyon, which is likely an artifact of the suspension of fishing operations (Fig. 6d).

The geographic areas in which incidental takes occurred during 1984–87 were very little different to the areas in 1988 (Fig. 7). The total area in which incidental takes occurred from 1984–87 extended from Oceanographer to Washington Canyons along or shoreward of the 200m isobath, though 81% of the instances occurred in a more confined area



Fig. 7. Areas where pilot whales were taken incidental to DWF Atlantic mackerel fishing.

extending from Baltimore to Welker Canyons. Similarly, in 1988 all incidental pilot whale takes occurred in an area ranging from Wilmington to Welker Canyons, near or shoreward of the 200m isobath.

The number of pilot whales taken in each month from 1984 through 1988 is presented in Fig. 8. The number of incidental takes during DWF Atlantic mackerel fishing operations were anomalously high in 1988, and to a lesser but notable extent in 1985. These anomalies can be summarised in the following context.

The number of pilot whales taken by the DWF Atlantic mackerel fishing fleet totalled 12 whales in 1984, 42 in 1985, 17 in 1986, 26 in 1987 and 142 in 1988. The total number taken during a given month exceeded ten whales on six occasions: 15 in February 1988; 17 in March 1985; 45 in March 1988; 64 in April 1988; 25 in May 1985; and 13 in May 1988. The number of whales taken during one given tow exceeded five whales on nine occasions: six whales three times in April 1988; seven whales once each in February 1988, March 1987, March 1988 and May 1985; eight whales once in May 1985; and 12 whales once in May 1988.

Correspondingly, the total number of tows in which pilot whales were taken was highest in 1985 (16) and 1988 (49). Pilot whales were taken in five or more tows during a given month on five occasions: five instances occurred in April 1987; nine in March 1985; 17 in March 1988; 25 in April 1988; and seven in May 1985.



Fig. 8. Total number of pilot whales incidentally taken during DWF Atlantic mackerel fishing operations off the northeastern US coast from 1984–88.

DISCUSSION

The distribution of the 1988 DWF Atlantic mackerel fishery was anomalous in comparison to the 1984–87 fishery. In January-March 1988, the fishery was concentrated further north (between Wilmington and Hudson Canyons) and generally in mid-shelf to shelf edge waters, as opposed to being distributed throughout the mid-shelf waters from Cape Hatteras to Hudson Canyon as in 1985–87. April fishing effort was similar for all years. The May 1988 effort was so limited that a comparison with historic data was not warranted. Based on the location of fishing effort, it appeared that Atlantic mackerel did not move south to Cape Hatteras during February and March 1988, but instead remained near the Hudson Canyon area. An event that may have contributed to concentrating the Atlantic mackerel near Hudson Canyon during the winter of 1988 was the presence of a large volume of cool, low salinity, shelf water that was detected on the southern New England to mid-Atlantic shelf in the summer and autumn of 1987 (D. Mountain, NOAA, NMFS, NEFC, pers. comm.). This 'cool pool' affected the distribution of several species of finfish and *Loligo* squid (unpublished NMFS, NEFC data), and its influence may have continued into the winter of 1988.

The incidental take of pilot whales during DWF Atlantic mackerel fishing operations was anomalously high in 1988, compared to 1984–87. Similarly, the 1988 kill per day fished rate (0.19) was the highest observed, as compared to 0.05, 0.15, 0.05 and 0.08, for the years 1984–87, respectively (Waring *et al.*, 1990). The DWF Atlantic mackerel fishery was suspended in early May, partly in response to these large increases in kill rates in 1988.

The years 1988 and (to a lesser but still substantial extent) 1985, were also anomalous in that these were the only years in which the number of whales taken in a month exceeded 10 whales, that more than five instances of incidental take of pilot whales occurred in a given month and that more than 10 incidents occurred in one year. These anomalous events occurred in March and May of 1985 and from February through May of 1988.

The high 1988 level of incidental takes of pilot whales appears to be due largely to the fact that the fishery remained in the geographic area where these takes commonly occur, as opposed to being more southerly distributed, especially during February and March, as in past years. As Fig. 7 illustrates, this area is limited to the region from Baltimore Canyon north to Welker Canyon extending from the 200m isobath shoreward approximately 45nm, regardless of the time of year. The reason for the high take rates in April and May 1988 in comparison to previous years is not clear. Furthermore, there are no data indicating that technological changes in fishing trawls are responsible for the high 1988 incidental take.

The seasonality of the historic DWF Atlantic mackerel fishery extended from December to April (Anderson and Paciorkowski, 1980), which corresponds to the present pattern. In addition, international fishing effort, expressed as standardised US days fished per year, during the period of large scale DWF fishing activity increased from approximately 21,000 to 1,735,000 days fished between 1964–74 and declined rapidly thereafter as a result of declining stock abundance and management measures (Anderson, 1976; Anderson and Paciorkowski, 1980). During the period 1985–88, non-standardized DWF effort ranged between 300 and 750 days fished, which is a small fraction of the effort, regardless of standardization, reported during the earlier time period. Extrapolation of current take rates of the historical fishery is, however, not appropriate for several reasons, including technological advances in vessels, trawls and improved electronic fish finding equipment, and the lack of detailed data on the seasonal/spatial distribution of the fishing fleets.

These data suggest that mitigation of incidental pilot whale takes may be accomplished by closure of some or all of the area identified in Fig. 7. Furthermore, under the requirements of the 1988 amendments of the US Marine Mammal Protection Act, the DWF Atlantic mackerel fishery has been designated as a Category I fishery (i.e. with frequent incidental taking of marine mammals). This will require fishery observers to collect detailed information on interactions between vessels and marine mammals, and analyses of these data may lead to mitigation methods other than areal closures. The pilot whale by-catch since 1988 has declined sharply. This is likely attributable to reductions in foreign catch quotas by the US for Atlantic mackerel, which translates into greatly reduced fishing effort.

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Some External Characters of the Long-Finned Pilot Whale off the Faroe Islands and a Comparison with the Short-Finned Pilot Whale

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ABSTRACT

This paper examines the morphological characteristics and colour patterns of the long-finned pilot whales taken between July 1986 and July 1988 off the Faroe Islands. The colour patterns of whales in two complete schools were examined. Two distinct patterns were found: a post-dorsal fin saddle and a postorbital eye blaze. The presence of a dorsal saddle was more common (43%) than the eye blaze (22%). Both patterns became more common with increasing body length and age. The saddle pattern was equally common in males and females, while the occurrence of the eye blaze was significantly more frequent in males (31%) than in females (15%) and not so strongly related to body length or age. There was no indication of any differences between the two schools examined. Length measurements of dorsal fins, flippers and flukes were taken from whales in 29 different schools, including some complete schools and throughout the year. The dorsal fin, the flippers and the fluke show a linear correlation with body length and thus an isometric growth pattern. The linear growth of dorsal fin height and length relative to body length shows a zero trend for the fin height, but a small significantly positive trend for the fin length. This material reveals no evidence of sexual dimorphism.

The relative increase in flipper length and width was linearly related to body length, but for the former there was a negative trend for whales smaller than 250cm, and above that a positive trend. The relative increase in fluke length and span to body length showed a zero trend for the latter and a slight, but significantly negative slope for the former, indicating that the fluke shape changes with the age of the individual; the longer the whale, the shorter the fluke length in proportion to body length. The ratio of flipper length to body length of 510 postnatals was 14.4–30.3%, more than has been previously found. 2.7% of the individuals overlapped with the range given for the short-finned pilot whale, *G. macrorhynchus*. Both the dorsal fin length and the fluke shape were linearly correlated to blubber thickness, and this explains previously found differences in these patterns between the pods as a yearly synchronous variation related to blubber thickness.

Sexual dimorphism was apparent for characteristics of both flippers and flukes; males have longer flippers and longer and wider flukes than females of the same body length. Both immature males and females had significantly smaller flippers and flukes in proportion to body length than mature animals of both sexes.

KEYWORDS: PILOT WHALES-LONG-FINNED; NORTH ATLANTIC; COLOURATION; MORPHOLOGY/ANATOMY; SEXUAL DIMORPHISM; PILOT WHALES-SHORT-FINNED; GROWTH/LENGTH DISTRIBUTIONS.

INTRODUCTION

The value of using naturally occurring marks, including pigmentation characters or the distribution of spots is well known for studies of many animal species. It has proven useful in studies of distribution, migration, stock identification and behaviour for many cetacean species (e.g. see IWC, 1990).

Although differences in the colouration of long-finned pilot whales, *Globicephala melas* Traill, including the long anchor-shaped ventral patch, the dorsal saddle and the eye blaze have been noted (Ritchie, 1924; Sergeant and Fisher, 1957; Sergeant, 1962; Aguayo, 1975; Crespo *et al.*, 1985; Goodall and Galeazzi, 1987), this study is the first time that entire schools have been examined for the frequency of these patterns and particularly with a view to their possible use in connection with other studies.

It is believed that the long-finned pilot whale has been driven ashore and killed for its meat and blubber for as long as the Faroe Islands have been permanently settled (Thorsteinsson, 1986). Two 'types' of pilot whales are mentioned in early sources, one with a broad, curved dorsal fin, and the other with a smaller and more pointed one. It was said that the whales with pointed dorsal fins were more difficult to beach, and that the whales with broad fins were generally fatter. It was also reported that the whales were fattest during winter and spring, and that whales with a broad dorsal fin also had a more heart-shaped fluke, in contrast to the whales with more pointed dorsal fins that had more triangular flukes (Høst, 1875, p.314; Müller, 1882, p.5; Müller, 1883, p.19; Williamson, 1947, pp.70–71, fig. 2; Ryggi, 1960, p.15).

From July 1986 to July 1988, all landed schools of pilot whales were examined to study as many aspects of their biology as possible (Bloch *et al.*, 1993b). Before this extensive sampling period, material from pilot whales was sampled from 1976 to 1986 by Bloch (1992) and historical records contain some details of the occurrence of albino or 'discoloured' whales. Between 1986 and 1988, schools were systematically examined for external characteristics of the individuals. The colour pattern, particularly the frequency of whitish/grayish dorsal patches, was examined to ascertain the possibility of using this as an aid to recognising individual specimens/schools offshore. In addition, the dorsal fin, flippers and flukes were measured for three reasons: (i) to examine the historical suggestions of two 'types'; (ii) to study the possibility of using these measurements in population studies; and (iii) to examine the possible overlap of these measurements with those of the short-finned pilot whale, *G. macrorhynchus*.

MATERIALS AND METHODS

General

A total of 40 schools (3,488 whales) was investigated for external characters. The dorsal fin, flippers and flukes of each whale were measured and basic data on length, weight, age, sex and reproductive status were collected following the procedures outlined in Bloch *et al.* (1993a). Because of Müller's observation (1882; 1883) of fatter broad-finned whales in winter, blubber thickness was also measured.

For some of the analyses, whales have been divided into immature and mature individuals, the males being on average sexually mature at 12.8 years of age, 480.1cm length and 1,210–1,356kg weight (Desportes *et al.*, 1993) and the females at 8.0 years of age, 382.4cm length and 600–650kg weight (Bloch *et al.*, 1993b).

The results are expressed as mean \pm standard error (SE) and the term 'significant' is used solely in the statistical sense of differences significant at the 5% level.

Colouration

Colour pattern was examined in two complete schools in March and June 1988, consisting of 57 and 64 animals, respectively. Presence/absence of dorsal saddle and eye blaze was noted. Of these, 54 (45%) were males and 67 (55%) were females, which corresponds to the average for all schools examined (see Bloch *et al.*, 1993a).

Dorsal fin

The length of the dorsal fin was measured to the nearest centimetre along the base. The height of the fin was taken posteriorly, where the fin is highest (see Fig. 1, no. 1). The dorsal fins of 737 animals from 29 different schools were measured, including all animals from eight schools.

Flippers

Flippers were also measured to the nearest centimetre, the length from the anterior insertion to the tip and the width proximally at its maximum (see Fig. 1, no. 2). Only one flipper from each whale was measured, because once landed, the whales are always laid on one side. A total of 526 whales from 22 schools was measured including all animals from five schools.

Flukes

The flukes were also measured to the nearest centimetre, from the backbone to the notch of the fluke and the half-span of the fluke (Fig. 1, no. 3). In total, 526 whales from 21 schools were measured, including all animals from five schools.

Blubber thickness

Blubber thickness was measured to the nearest millimetre on several places on the body for energetic purposes (Lockyer, 1993). In this study, the average thickness (in mm) at three places taken laterally (Fig. 1, no. 4) was used: (1) anterior to the dorsal fin; (2) posterior to the dorsal fin; and (3) at the level of the anus. Measurements were taken from 487 whales from 27 schools, including all animals from six schools.



Fig. 1. Drawing of pilot whale (*Globicephala melas*) showing the measurements of: (1) dorsal fin length and height; (2) flipper length and width; and (3) fluke length and half-span; (4) places where blubber thickness is measured.



Fig. 2. Dorsal fin saddle of long-finned pilot whale in the Faroe Islands. Photo: Ole Wich.

Reliability of measurements

All measurements were taken according to Norris (1961), except for the flukes, where it was found easier to measure only half the span and the length rather than the width of the flukes (compare Fig. 1 with Norris, 1961, measurement 35). The reliability of the different length measurements is discussed in Bloch *et al.* (1989). The most accurately measured were the dorsal fin height, flippers and flukes, where 89–96% of the measurements varied less than 4cm, or 52–85% varied $\leq 5\%$ of the length (n=27 whales) according to either blind tests among persons taking the same measurements or repeated readings by the same person. The length of the dorsal fin showed, not surprisingly, more variation, as this dimension is not as well defined on the body as the other measurements. Here, 42% of the readings varied less than 5cm or 42% varied $\leq 5\%$, while 77% varied $\leq 10\%$ of the dorsal fin length.

None of the whole schools examined revealed significant differences in the sex ratio (F=0.62) or length distribution (F=1.2) from the average of all the whales. No monthly or annual significant differences in body length were found (F=1.1).

RESULTS AND DISCUSSION

Colour pattern

Normally pilot whales are almost completely black, but newborn and young immature specimens may be a lighter grey (see Leatherwood *et al.*, 1976; Goodall and Galeazzi, 1987). Younger whales are often slightly spotted with grey.

Yonekura *et al.* (1980) reported on geographical variations in colour pattern for shortfinned pilot whales off Japan. Two forms have since been determined (Kasuya *et al.*, 1988; Kasuya and Tai, 1993). Shane and McSweeney (1990) and Miyashita *et al.* (1990) discuss the potential value of photo-identification studies on short-finned pilot whales in the North



Fig. 3. Postorbital eye blaze from long-finned pilot whale in the Faroe Islands. The eye is in the middle to the left, and the blaze crosses the cutting line in the neck. Photo: Ole Wich.

Pacific, while Heimlich-Boran and Heimlich-Boran (1990) have used this technique on G. *macrorhynchus* in the North Atlantic. Evans *et al.* (1986) examined possible differences in colour patterns between schools from the California Bight. The studies of both ventral and dorsal white to greyish-coloured patterns have shown that G. *macrorhynchus* differs considerably from G. *melas*, especially in the occurrence and variability of the dorsal fin saddle, which extends further on G. *macrorhynchus*.

The present study only considers variation in the dorsal pattern, since the ventral pattern appeared almost constant on all the observed long-finned pilot whales (as is also true for the short-finned pilot whale – Yonekura *et al.*, 1980; Evans *et al.*, 1986).

Saddle

The dorsal fin saddle is found just behind the dorsal fin and on large adults can measure more than 1m in length, extending caudally and medially towards the tail. The saddle is broadest (10–15cm) close to the dorsal fin and tapers off to a point. The border between the saddle and the back is seldom distinct and often blurred by spots. The colour ranges from steel to a lighter shade of grey and the colour and distribution vary greatly from whale to whale (Fig. 2). On the whales where the saddle was present it is well described by the words of Sergeant (1962) as 'a wedge behind the dorsal fin, its apex directed backward'.

The saddle is mentioned for *G. melas* from the southern part of the Atlantic Ocean (Davies, 1960; Aguayo, 1975; Linehan, 1979; Crespo *et al.*, 1985; Evans *et al.*, 1986; Goodall and Galeazzi, 1987) and is shown on drawings from Tasmania and off the Eastern Cape of South Africa (Ross, 1984). It is also well described from Newfoundland by Sergeant and Fisher (1957) and Sergeant (1962). From the Faroe Islands, Svabo (1783,

p.249) remarks that in wintertime the border of the dorsal fin is white. This could be an observation of the saddle misquoted by Svabo.

The dorsal fin saddle is also well described from *G. macrorhynchus*, where distinct differences between northern and southern forms occur (Kasuya *et al.*, 1988; Kasuya and Tai, 1993).

Blaze

The postorbital eye blaze is a narrow elongated patch (up to 20cm long), situated behind and dorso-caudally to the eye. It varies from being nearly indistinct to being a very clear, pale grey crossing the cutting line in the neck (Fig. 3). It has been mentioned in descriptions of whales from Scotland (Ritchie, 1924), Newfoundland (Sergeant, 1962), Chile (with photos of very distinct saddle and eye blaze – Aguayo, 1975), Tasmania and off South Africa (Ross, 1984), but not at all by Faroese sources, which otherwise often provide good descriptions of the whales (Debes, 1673; Svabo, 1783; Landt, 1800; Lyngbye, 1817; Graba, 1830; Høst, 1875; Müller, 1882; 1883; Degerbøl, 1940; Williamson, 1947; Ryggi, 1960).

Yonekura et al. (1980) reported that the eye blaze occurred on all short-finned pilot whales examined.

Occurrence of saddle and/or blaze

From the two complete schools of long-finned pilot whales examined (n=121), the presence of the dorsal saddle was more common (43%) than the eye blaze (22%). There was no significant difference (z=0.82) between the sexes in frequency of the saddle but significantly more (z=2.17) males than females had an eye blaze (Table 1a).

(a)	Saddle	%	Blaze	%	Both	%	Total
Male	21	39	17	31	12	22	54
Female	31	46	10	15	6	96	7
Total	52	43	27	22	18	15	121
		(b)	- Saddle	+ Saddle	Total		
		- Blaze	60	34	94		
		+ Blaze	9	18	27		
		Total	69	52	121		

Table 1

The distribution of dorsal saddle and postorbial eye blaze of long-finned pilot whales from the Faroe Islands. (a) The distribution divided by sex; (b) the blaze-saddle interaction.

A clear correlation was found between the occurrence of saddle and blaze ($\chi^2=6.97$; p<0.01) where 18 (15%) had both patterns, while 43 (35%) had either a saddle or blaze (Table 1b). More males than females displayed both colour patterns (z=2.04). Both patterns seemed to be lacking amongst young and small whales (Table 2), although they may be present but impossible to distinguish from the paler colour of the younger whales.

The smallest whale with a blaze was 303cm long and three years old, and the smallest whale with a saddle was 338cm and five years old. Both the saddle and the blaze occur more frequently with increasing age and body length, but the blaze seems to be more evenly distributed among whales than the saddle (Tables 2 and 3).

Svabo's remark (1783) that the dorsal fin takes on a white edge in wintertime could not be verified from this material. The two schools examined were caught on 13 March and 10 June, i.e. one in late winter and one in summer.

As there was no significant difference in blaze and saddle occurrence between the schools this cannot be used as a means of identifying schools.

Of the two colour patterns, only the saddle will be visible when encountering whales at sea and only from a very short distance. The blaze is too pale and moreover the pilot whale seldom surfaces for long periods. Distinct patterns which can be used for individual identification at a distance occur very rarely. Among the Faroese pilot whales, albinism and discolouration have only been recorded for six whales during the period from 1895 to today, including one seen in connection with this study (Bloch, 1992). Therefore, it must

	Saddle				Eye blaze				Total	
Length, cm	M	%	F	%	M	%	F	%	M	F
200-249	0		0	0	0		0	0	0	1
250-299	0	0	0	0	0	0	0	0	4	2
300-349	1	10	0	0	3	30	2	15	10	13
350-399	1	14	4	40	3	43	3	30	7	10
400-449	3	38	21	64	2	25	2	6	8	33
450-499	1	33	6	75	0	0	3	38	3	8
500-549	5	71	0		3	43	0		7	0
550-599	10	71	0		5	36	0		14	0
600-649	0	0	0		1	100	0		1	0
Total	21	39	31	46	17	31	10	15	54	67

Table 2

Occurrence of dorsal fin saddle and postorbial eye blaze related to body length, sampled from the long-finned pilot whale of the Faroe Islands.

Table 3

Occurrence of dorsal fin saddle and postorbital eye blaze related to age, in long-finned pilot whales from the Faroe Islands.

Age, year	Saddle			Eye blaze				Total		
	<u> </u>	%	F	%	M	%	F	%	M	F
0- 5	1	7	0	0	4	27	2	14	15	14
6-10	3	23	5	36	3	23	3	21	13	14
11-20	5	45	9	60	2	18	1	7	11	15
21-30	7	78	13	68	4	44	4	21	9	19
31-45	3	60	2	40	3	60	0	0	5	5
Total	19	36	29	43	16	30	10	15	53	67

be concluded that the normally occurring colour patterns are not useful for individual identification, particularly given the poor visibility and bad weather conditions so common in the Northeast Atlantic.

Dorsal fin

At birth, the dorsal fin was found to be about 30cm long and 10cm high, growing to about 130cm in length and 50cm in height for large males with a close correlation between the length and height (Fig. 4; r=0.92), as also shown by Sergeant (1962). Both the length and height of the dorsal fin show isometric growth relative to total body length (n=733; r=0.92for dorsal fin length; r=0.91 for dorsal fin height). There are no significant differences between the sexes, except that the females stop growing before the males (Joensen, 1962; Bloch, 1992; Bloch et al., 1993b). The linear growth of dorsal fin length and height relative to body length (Fig. 5) shows a zero trend for height, and a small, but significantly positive trend for length, with no sexual difference (n=724; r=0.21; t=5.85). This differs from Sergeant (1962, fig. 7 upper) who found a steeper ascending slope for the length. Nor does it support the view of Rumage (1983), who reported 'marked sexual dimorphism in the size and shape of the dorsal fin'. The only 'sexual dimorphism' seen on the dorsal fin was caused by the fact that large whales were always males, and the larger the whale, the larger the dorsal fin (Fig. 4). The close relationship found between the total body length and dorsal fin length and height (Fig. 5) gives a growth pattern of dorsal fin at age similar to that for body length at age (Fig. 6; and see Bloch et al., 1993b).

Broad or pointed dorsal fins, a question of fat condition

Both Svabo (1783, p.249) and Müller (1882, p.5; 1883, p.19) mentioned that the whales were fatter in winter and had either broad or pointed dorsal fins, of which those with broad fins were the fattest. Our data reveal that blubber thickness increases by some 5–10% of



Fig. 4. The dorsal fin height at dorsal fin length, divided by sex. N=724; 296 males; 428 females; r=0.92.



Fig. 5. The percentage of dorsal fin length and height to body length, in relation to body length, divided by sex. N=724; 301 males; 432 females; For dorsal fin length, r=0.21; t=5.85. For dorsal fin height, r=0.04; t=0.97.



Fig. 6. The percentage of dorsal fin length and height at age, divided by sex. N=680; 184 immature males; 94 mature males; 128 immature females; 274 mature females.



Fig. 7. The dorsal fin length at blubber thickness, divided by sex and maturity. N=481; 135 immature males; 62 mature males; 84 immature females; 200 mature females. r=0.54; t=13.9.

body weight in winter, resulting in an accumulation of lipids, which comprise 15–23% of the body weight in winter from November onwards (Lockyer, 1993). We have also found differences in fin length (F=25.8) but not fin height between schools. A significant correlation exists between dorsal fin length and blubber thickness (Fig. 7; r=0.54; t=13.9). It was also found that dorsal fins from schools taken in winter/spring were significantly longer (F=13.2). A plot of both dorsal fin and blubber thickness by month gives similar curves (Fig. 8). If the yearly changes in blubber thickness and dorsal fin length are both similarly related to season, this suggests that the differences in dorsal fin length observed between schools can be explained by seasonal differences in fat deposits, which must in some way influence the shape of the dorsal fin. The traditional Faroese discussion of broad or pointed dorsal fins may then be supported if the correlation between dorsal fin length and height were split into groups, but no specific groups of dorsal fins are obvious (Fig. 4), nor were sexual differences found.

Flipper

The flippers show a similar age-growth pattern as the dorsal fins (Fig. 9) and a positive relationship with body length. The relative growth for both the flipper length and width is isometric to total body length, but shows a negative trend in flipper length for whales smaller than 250cm, and a positive trend for longer whales (Fig. 10). This was also found by Sergeant (1962, fig. 6). A similar pattern was found for *G. macrorhynchus* (Yonekura *et al.*, 1980).

G. melas and G. macrorhynchus – a small overlap in relative flipper length

The proportion of the length of the flipper to body length is one of the external morphological characteristics used to distinguish long-finned from short-finned pilot



Fig. 8. The seasonal variation in blubber thickness, dorsal fin length, and the fluke shape, i.e. fluke length as percent of the half-span at body length. The standard error of the mean is included, as well as the number of whales included in the means, the fluke shape at the top, the blubber thickness and dorsal fin length at the bottom. N=482 dorsal fins; N=294 flukes.



Fig. 9. The flipper length and width at age, divided by sex and sexual state. N=495; 210 males; 285 females.

whales (Leatherwood *et al.*, 1976). Flipper length as a percentage of body length (from van Bree, 1971; Yonekura *et al.*, 1980; Nores and Peréz, 1988) is 18–27% for *G. melas* and 14–19% for *G. macrorhynchus*. In this study the percentage for 510 postnatal *G. melas* was 14.7–30.3% (average 22.3 \pm 0.24%; Fig. 11). Thus 98% of the material falls inside a



Fig. 10. The percentage of the flipper length and width to body length, in relation to body length, divided by sex. N=521; 219 males; 302 females.



Fig. 11. The frequency distribution of the ratio of flipper length to body length grouped in immatures and matures for males and females. N=510; 143 immature males; 68 mature males; 101 immature females; 198 mature females.

range of 18–30.3% and 94% inside a range of 19–30.3%. This is a wider range than found previously and the lower end overlaps slightly with the range for G. macrorhynchus, but with only a few individuals (14 whales ca 2.7%). The overlap zone (14.7–18%) contains more females (10) than males (4), but similar numbers of immatures (8) and matures (6). As shown below, females have shorter flippers than males and thus the surplus of females in the overlapping zone is not surprising.



Fig. 12. The fluke length (a) and half-span (b) at age, divided by sex and sexual state. N=472; 128 immature males; 69 mature males; 98 immature females; 177 mature females.



Fig. 13. The fluke length at half-span, divided by sex. N=504; 212 males; 292 females; r=0.93.



Fig. 14. The percentage of the fluke length and half-span to body length, in relation to body length, divided by sex. N=504; 212 males; 292 females. Fluke length: r=0.41; t=10.1.

Fluke

The age-growth pattern for the fluke (half-fluke, see Fig. 1) is the same as for the dorsal fin and the flipper (Fig. 12). Both the length and the half-span show a strong linear growth correlation (r=0.93) from 15cm length and 20cm in half-span at birth up to 50cm length and nearly 80cm in half-span for large whales (Fig. 13). Growth is almost linearly



Fig. 15. The fluke shape, i.e. fluke length as percent of the halfspan at the body length, divided by sex. N=504; 212 males; 292 females; r=0.50; t=12.9.

	Ν	Mean ± SE (%)
Fluke lengths as % of body length:	· · · · · · · · · · · · · · · · · · ·	
Male-immature	139	8.48 ± 0.13
Male-mature	64	7.98 ± 0.18
Female-immature	100	8.56 ± 0.16
Female-mature	187	7.92 ± 0.09
Fluke half-span as % of body length:		
Male-immature	139	11.42 ± 0.13
Male-mature	64	11.65 ± 0.20
Female-immature	100	11.11 ± 0.13
Female-mature	187	11.34 ± 0.11

Table 4The means for fluke length and half-span as % of body length.

correlated with body length, while as a proportion of body length it shows a zero trend for the half-span and a slight, but significantly negative slope for the length (Fig. 14; r=0.41; t=10.1), as also found by Sergeant (1962, fig. 7). This means that the shape of the fluke changes as the whale grows, so the longer the whale, the shorter the fluke length in proportion to body length (Fig. 15; r=0.50; t=12.9).

There is a small but significant difference in frequency distributions of fluke length between immatures and matures for both sexes, showing that the flukes grow more quickly at puberty (Fig. 16a). As shown below, the fluke spans for the females are significantly smaller than for the males (Fig. 16b; Table 4).



Fig. 16. The frequency distribution of the ratio of both the fluke length (a) and half-span (b) of the body length, divided by sex and maturity. N=490; 139 immature males; 64 mature males; 100 immature females; 187 mature females.
The shape of the flukes, a question of fat condition

In some of the historical sources from the Faroes it was stated that those whales with broad dorsal fins (which were also supposed to be fatter – Müller, 1882) had heart-shaped flukes, while those with more pointed fins had more triangular-shaped flukes (Høst, 1875, p.314). If the fluke is heart-shaped then the length/span ratio will be smaller than if the fluke is more triangular. Apart from the linear correlation between the shape and body length (Fig. 15), our data also reveal a significant difference among seasons (F=5.46) and schools (F=4.30). Although no significant correlation was found between fluke shape and dorsal fin length related to body length (r=0.078; t=1.76), the seasonal change in fluke shape (and length of dorsal fin) is synchronous with and follows the seasonal difference in blubber thickness (Fig. 8). The flukes were most clearly heart-shaped at the end of the calendar year, which agrees well with Høst (1875) and would suggest that fat deposition influences not only dorsal fin length but also fluke shape.

Sexual dimorphism

Both flipper length and fluke shape show some signs of sexual dimorphism. Flipper length at a given age (Fig. 9) shows only a small overlap zone between immature and mature whales. Furthermore, it is clear from the frequency distribution of flipper length to body length (Fig. 11), that values are higher for males than females, regardless of sexual state. This means that the flippers grow rapidly at puberty and that females always have shorter flippers than males.

A significantly positive correlation was found between fluke half-span and fluke length (Fig. 13), and furthermore, only a short overlap zone was visible between the immatures and matures of both sexes as regards both fluke length and half-span at a given body length and age (Fig. 12a and b). Therefore, the frequency distributions of fluke length (Fig. 16a) and half-span (Fig. 16b) ratios to body length were compared to see if differences existed between sexes and between sexual states. For fluke length there was a significant difference (P<0.001) between immatures and matures of both sexes, while the span differed significantly (P<0.05) between all males and all females. This means that males have longer and wider flukes than females, regardless of body length (Table 4).

In conclusion it can be stated that males can be distinguished from females of the same length by longer flippers and bigger flukes.

CONCLUSIONS

This study has shown that a dorsal fin saddle as well as an eye blaze are found in at least some of the long-finned pilot whales of the Northeast Atlantic, although they are not as distinct as those found for the same species in the Southern Hemisphere. The eye blaze is found more frequently in males than females, while the saddle is more evenly distributed by sex. No differences in occurrence of blaze and saddle were visible between the two schools examined, so it is doubtful whether these can be used to recognise schools offshore or individuals.

Flipper length proportional to body length of long-finned pilot whales from the Faroe Islands, compared with the short-finned pilot whale, G. macrorchynchus, reveals an overlap of 2.7% of the individuals.

Sexual dimorphism was found with respect to both flukes and flippers: males, regardless of length, have longer flippers and longer and wider flukes than females.

Finally, previously observed differences of both dorsal fin length and fluke shape between schools can be explained by yearly synchronous variation in blubber thickness.

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A Report on Patterns of Deposition of Dentine and Cement in Teeth of Pilot Whales, genus *Globicephala*

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ABSTRACT

The present study reports on two aspects of pilot whale tooth structure: (1) deposition rate of dentinal and cemental laminae, and (2) patterns and possible significance of mineralisation anomalies. (1) Teeth from seven known-history captive northeast Pacific short-finned pilot whales, mostly having received tetracycline treatments, were examined. Numbers of cemental and dentinal growth layer groups (GLGs) were observed to be equivalent in teeth of age <15 yrs. Deposition rate was one GLG per yr, and confirmed the suitability of tooth GLGs for age determination in this species. (2) Mineralisation anomalies, their incidence and biological significance, were investigated in the teeth of the known-age short-finned pilot whales and in the teeth of northeast Atlantic long-finned pilot whales collected from Icelandic strandings in 1982 and 1986, and from a Faroese fishery-caught school in 1986. The following anomalous characters were recorded in the teeth: (a) pulp stones: discrete nodules containing concentric rings in the dentine; (b) marker lines, both in dentine and often cementum: discrete laminae which are regular yet noticeably different in appearance from the usual in morphology and affinity for stain; (c) mineralisation interference: irregularities in the lamina formation engendered by differential inhibition/activation of odontoblasts at the mineralisation front, causing realignment of the dentinal tubules and disrupting regular lamination patterns without preventing continuous formation; (d) dentinal resorption: actual erosion and frequent repair of existing regular laminated dentinal tissue; (e) cemental disturbance: any anomalous appearance of the usual regular laminated cemental tissue. Occurrence of these anomalies was scored by sex, current age, reproductive maturity, age at which the anomaly appeared, and in which calendar year. Comparisons of duplicate teeth from the same individual indicated that mineralisation anomalies must be of systemic origin, because type, pattern and age of occurrence of anomalies were similar. Results showed that appearance of pulp stones in the dentine tend to be associated with age at which puberty usually occurs. Marker lines increased with age after one year; there was also significant association with certain calendar years in Icelandic samples. Mineralisation interference increased with age reaching 60-100% incidence in animals >14 yrs in all samples. The incidence appeared related to age rather than reproductive maturity. Cemental disturbance was low in Icelandic whales, but reached ca 50% incidence in Faroese whales, in which it was both age- and maturity-related. Dentinal resorption was not evident in any immature animals. It reached a peak in old males, yet did not appear to greatly affect females until age >25 yrs. Dentinal resorption was common in the Faroese sample, and occurred in almost 100% of the adult males. In Icelandic animals it was <10% in specimens up to age 25 yrs. In very old animals (30+ yrs) incidence reached 20% to 40%. Observations from the knownhistory captives indicated that likely stressors, directly or indirectly responsible for certain mineralisation anomalies, may include sexual maturation, pregnancy and/or parturition, periods of starvation, as well as changes in health and life style.

KEYWORDS: PILOT WHALES; AGEING; MORPHOLOGY/ANATOMY; REPRODUCTION

INTRODUCTION

There have been several previous studies investigating the use of teeth for determination of age in short-finned pilot whales, *Globicephala macrorhynchus* (Kasuya and Matsui, 1984; Sergeant, 1959) and long-finned pilot whales, *G. melas* (Kasuya *et al.*, 1988; Lockyer *et al.*, 1987; Martin *et al.*, 1987; Sergeant, 1962). A general methodological review of age

determination for odontocetes is given in IWC (1980). The laminations in the dentine and/ or cementum have generally been defined in terms of differing (high or low) mineralisation density and/or quality (Boyde, 1980); contiguous pairs comprising a growth layer group (GLG), as defined in IWC (1980). This is, of course, a simplification of the real situation where accessory laminae of varying mineralisation density and thickness are frequently observed. Myrick (1984) has addressed many of these issues. The main problem is the interpretation of laminae in relation to real time, i.e. what constitutes a daily, lunar and annual growth layer. The true incremental rate of growth of laminae has been investigated and established directly for some marine mammal species, but not pilot whales, by studying teeth from animals of known age or history (Hohn et al., 1989), and the use of tetracycline to 'time-mark' hard tissues, i.e. dentine and cementum in teeth and bone (Yagi et al., 1963; Best, 1976; Domning and Myrick, 1980; Gurevich et al., 1980; Myrick et al., 1984; 1988; Myrick and Cornell, 1990). Klevezal' (1980) concluded that in 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 had already been established for terrestrial mammals (Grue and Jensen, 1979). This theme of 'individuality' has been explored further by Akin (1988) for spinner dolphins (Stenella longirostris), where GLG patterns and general tooth morphology were found to be correlated with stock and geographical location. Klevezal' and Tormosov (1971) had previously used characteristics of the dentinal layers to distinguish between groups of sperm whales (Physeter macrocephalus).

However, an approach which assumes a constant regular growth pattern is oversimplified. Detailed examination of teeth of many mammals reveal that events may occur which appear to create systemically rather than locally caused disturbances in the normal regular deposition rate of laminae in the teeth (Myrick, 1988). In cetaceans such disturbances, which may be termed *mineralisation anomalies*, range from 'foreign' inclusions in the teeth, such as bone – true osteodentine (Best, 1966), to tooth-originating materials such as 'pulp stones', frequently labeled as 'osteodentine' (Boschma, 1938; Nishiwaki *et al.*, 1958). Further complexities include distinct laminae, 'deeply darkstained layers (DSL)' defined by virtue of their unusual appearance and affinity for stain (Klevezal' and Myrick, 1984; Myrick, 1991); and various degrees of interference in mineralisation as well as actual resorption of dentinal and cemental tissue (Boschma, 1950; Myrick, 1988). Akin (1988) tried to use many of these characteristics to discriminate stocks but with equivocal results.

The purpose of this study has been twofold. Firstly, the aim has been to determine the true rate of incremental deposition of dentinal and cemental laminae in the teeth of pilot whales, in order to interpret GLGs correctly for age. Secondly, the aim has been to progress beyond this stage, and compare teeth extracted from (a) the same individual to investigate conformity of GLG patterns, and (b) different individuals derived from various sources and localities to study easily identifiable mineralisation anomalies which might have biological significance.

MATERIAL

One tooth was available for each of seven northeast Pacific short-finned pilot whales captured in California waters, six of which had received tetracycline medication during periods of their captive lives. Teeth were collected from these animals at death. Each animal had been maintained in captivity in Sea World establishments, up to the time of death for periods of up to about seven years. The histories of these animals are given in Table 1 on p. 140.

In addition, teeth were available for each of 235 northeast Atlantic long-finned pilot whales, and duplicate teeth were examined for ten of these. This sample comprised 91 whales captured on 11 September 1986 in the Faroese drive fishery at Sandur on the island of Sandoy ($c.~61^{\circ}30'N$, $0^{\circ}11'E$), 36 whales stranded on 21 August 1982 at Rif in Iceland ($c.~64^{\circ}56'N$, 23°50'W) and 108 whales stranded on 26 October 1986 at Thorlakshofn in Iceland ($c.~63^{\circ}51'N$, $21^{\circ}22'W$).

METHODS

All teeth were supplied cleaned, either dry (Faroes) or in alcohol (Sea World captives and Iceland). To my knowledge, none of the teeth had been boiled or treated in any harsh way. Once received, Sea World teeth excepted, they were transferred to distilled water and then to 10% neutral formalin solution for at least 24 hours for fixing, before then being transferred again to distilled water.

Histological preparation

The teeth were initially dried and mounted with *Lakeside thermoplastic cement (no. 70C) on wood blocks designed to fit in the chuck of an *Isomet low-speed rotary diamond saw machine. The Sea World teeth were oriented in such a way that the cut was made slightly off-centre, through the crown, pulp cavity and root of the tooth, so that the final cut was almost exactly central. The tooth was then realigned relative to the cutting blade, using a micrometer travelling screw gauge, so that the next parallel cut through the tooth would result in a section about 100 μ m thick. This section was then allowed to dry and subsequently mounted on a slide using a clear permanent mounting medium, *Protex.

All other teeth were aligned on the chuck and cut in a similar plane, but about 0.5-1.00mm off-centre. The resulting larger pieces from these and the Sea World teeth, i.e., the portion containing or nearest the central zone, were then freed from the cement and decalcified as follows. Teeth were sorted according to appearance, into approximate age categories of neonate, young, young adult, old and very old, mainly to select for tooth size and volume. The teeth were then placed in perforated plastic histological baskets with labels, and decalcified in **RDO*, a commercially prepared mixture of acids, for 4–32 hrs, depending on the tooth volume and in accordance with manufacturer's recommendations. Decalcified teeth were quite flexible and rubbery in texture, and were rinsed in running water for several hours, whence they were re–immersed in distilled water.

The teeth were sectioned on a CO_2 -freezing stage of a sledge microtome at 30–35µm thickness. Sections selected as most central and complete were then stained in histological baskets in Haematoxylin for approximately 2hrs. The sections were then 'blued' in weak ammonia solution, rinsed in distilled water, and dehydrated in 70% alcohol before mounting on 5% gelatin-coated slides. The sections were then dried on a slide warmer and finally permanently mounted using *Protex*. All *Protex*-mounted sections required several days on a slide warmer to completely harden.

Examination

The sections were all examined using a *Zeiss microscope at x15-x500. The lowest magnification was adequate for dentinal GLG examination, but x125-x500 was essential for cemental examination. Decalcified and stained sections were examined in plain transmitted light. Tetracycline-treated sections were examined using transmitted plain, polarised and reflected ultra-violet (UV) light.

Indicates manufacturers' trade names. Use does not necessarily mean recommendation.

Dates: oral tetra- cycline medication and dosage in g	Date of death	Length at death in cm	Weight at death in kg	Maturity at death and/or history since capture	History of health since capture	Time in captivity in yrs.	Estimated age at death in yrs.
Whale no. 7401, matt 10.26.74; 10g BID 10.28.74; 11.5g 10.31.74; 14.5g 09.24.81; 25g BID	rre pregnant fema 10.05.81	le caught on 10 421	788.6 788.6	at capture, weight 562.7 Aborted foetus on 11.06.74; 160cm calf born on 05.25.81, but died few days later Progesterone study indicated 3-6 oestrous cycles; ovaries senescent!	Ag on 01.07.76 Body weight fluct- uations in last few months of life; 863.6kg on 09.30.81, then stopped eating; cause of death - chronic kidney disease	6.95	Minimum 14; could be quite old i.e. 30+ if reproductive history correct
Whale no. 7501, imma No treatments	ature male caught 04.10.76	on 11.14.75, 3 379	148.1cm at capture 375	e Testes of small size and immature	Generally good; cause of death bronchopneumonia	0.42	Approx. 4-5, from body size
Whale по. 7603, ітп и. 02.20.78; 29.5g BID	ature male caught 05.20.78	on 12.20.76, 3 328	22cm on 01.20.77 522.7	, weight 404.5kg on 01. Testes small and immature	.20.77 Good feeding except anorexia Feb. 1978; weight fluctuating from 536-582kg between 02.20.78 and 04.21.78; loss of weight up to death; kidney infection in Feb. and May 1978; cause of death uremia. senticaemia	1.42	Approx. 3-4 from body size

Data for Sea World captive short-finned pilot whales. Note that all dates are given as month/day/year.

Table 1

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Whale no 7802-H. nrohahlv immature female canoht on 11 20 78 3	Scm at canture			
01.17.80-02.08.80; 10.13.83 396 643 15g BID 04.17.81-04.28.81; 12g BID 02.22.83 continuing 7g BID 03.09.83-04.04.83	One large corpus luteum on left ovary; no pregnancies	Variable feeding habits: stopped eating 09.15.83; rapid weight loss from 718kg on 09.16.83; previous good health; cause of death kidney infection and septicaernia	4.875	Approx. 8-10; probably first ovulation
Whale no. 8001, immature male caught on 01.08.80, 274cm at captu	e			
05.09.80-05.12.80; 05.15.80 283 229 7.5g BID/intra- muscularly 229	No information	No health crises until one week prior to death; weight loss; cause of death pneumonia, kidney and liver disease	0.35	Approx. 2-3 from size and year of birth=1978
Whole no 8003 female coucht on 13 16 80 340 Fem at continue uni	aht 477b.a			
12.22.80; 10g SID 07.05.83 374 682 12.26.80; 5g BID	One large corpus Uneum on left ovary; large follicle; no foetus	Weight loss to 432kg by 04.16.81; health good there- after; cause of death lung disease	2.56	Approx. 7-9 from size; probably first ovulation
Whale no. 8227. immature male caught on 12.10.82. 316cm at captu	ą			
12.16.82; 8g 12.19.82 316 370.5	Immature	Not feeding prior to death; cause of death due to complications of natural parasite overload	0.03	Approx. 3 from size

All known-history teeth were photographed and identifiable GLGs and other structures (fluorescent tetracycline bands, accessory laminae, etc.) were measured in terms of thickness and distance from the neonatal line (NL) and pulp cavity edge, using an eyepiece micrometer, calibrated with a 1mm micrometer slide at each magnification. The position of such features was verified by photographic measurement. For all teeth examined, the total numbers of dentinal and cemental GLGs were recorded, as well as the position and nature of any anomalies in the teeth. The site of measurement was at 90° to the axis of the GLGs on the shoulder of one 'limb' of the tooth, level with, or just below the apex of the pulp cavity (Myrick *et al.*, 1988).

All Icelandic and Faroese teeth were examined without reference to biological data. Total dentinal and cemental GLGs, and the anomalies as specified below were recorded. Many of the teeth were also photographed. The captivity information for the Sea World specimens was required to establish a calibrated model of pilot whale tooth layering. This information was kept to a minimum, i.e. whether or not the animal had been given tetracycline and the length of time in captivity.

A summary of tooth preparation techniques for both UV and plain light examination is provided in Appendix 1.

Criteria used for classifying anomalies

(1) Pulp stones

These are discrete nodules containing concentric rings in the dentine (Fig. 1a).

(2) Marker lines

These are discrete laminae found in dentine and often cementum which are regular yet noticeably different in appearance from the normal boundary layers in morphology and affinity for stain (Fig. 1b). They are equivalent to the DSLs and maturational layers described by Klevezal' and Myrick (1984).

(3) Mineralisation interference

This refers to 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 wavy lines, squirls and asymmetry (Fig. 1c), which disrupt usual patterns yet do not prevent continuous lamina formation (Myrick, 1988).

(4) Dentinal resorption

This refers to erosion and frequent repair of existing regular laminated dentinal tissue, resulting in an amorphous and/or globular appearance (Figs 1d and e), frequently with holes, cutting across and into regular tissue (Myrick, 1988).

(5) Cemental disturbance

This refers to any anomalous appearance of the usual regular laminated cemental tissue (Fig. 1e), including mineralisation interference and resorption (Myrick, 1988).

RESULTS AND DISCUSSION

Incremental studies

Information on the observed GLG counts in dentine and cementum, the positions of tetracycline fluorescence and the various mineralisation anomalies are presented in Table



- c. Mineralisation interference in dentine of 7401, 421cm mature female short-finned from California, age 14+ yr, note also the presence of several marker lines; d. Dentinal resorption in dentine of S-2W, 575cm mature male long-finned from Faroes, age 30 yr;
 - e. Cemental disturbance in comontum of S-184, 462cm mature female long-finned from Faroes, age 24 yr; note also the presence of severe mineralisation

interference, dentinal resorption and pulp stones.

2 for the Sea World short-finned pilot whales. The dentinal GLG thicknesses and the average thickness of serial GLGs counted are given in Table 3. The estimated ages for these animals are based on a consideration of several factors including the period of time in captivity, which provides a 'minimum' age; and the length of the animal, which can be related to known sizes at age and approximate growth parameters, such as lengths at birth, sexual maturity and maximum size (Kasuya and Matsui, 1984) and reproductive cycles (Kasuya and Marsh, 1984; Marsh and Kasuya, 1984; 1986). Some reported values for short-finned pilot whales off Japan and long-finned pilot whales in the North Atlantic are given in Table 4. The estimated ages in Tables 1 and 2 are thus approximate and probably under- rather than over-estimated, because the 'ages' reported for the free-living populations are largely based on unverified GLGs for interpretation of age. In addition, the length of the female reproductive cycle (3-5 yrs, long-finned; 6-7 yrs, short-finned) is irrelevant for captive-held females where pregnancy is unlikely to occur after each ovulation. Interestingly, specimen 7401 had a hybrid calf (cross with Tursiops truncatus) on 25 May 1981, indicating an unusual reproductive history. Presence of corpora lutea and albicantia in the ovaries is only a certain indication of ovulation and not necessarily pregnancy unless actually documented; all pregnancies may not have reached term (e.g. see specimen 7401 in Table 1).

The decalcified stained section and the thin untreated section of specimen 7802-H (a 396cm female at death, 13 October 1983, age 8.5yr) are shown in Fig. 2. The photographic sequences demonstrate the methodology described earlier. Fig. 2a shows the stained section with GLGs indicated. Fig. 2b shows an enlargement of the lefthand limb of the section (Fig. 2a), also with GLGs marked. The positions where tetracycline marks were noted are indicated in Fig. 2b. Fig. 2c shows a thin untreated section of tooth, with GLGs indicated. Figs 2d and 2e show an enlarged (to same scale) portion of the lefthand limb of Fig. 2c; in plain light (Fig. 2d), and the same section in reflected UV light (Fig. 2e). The positions of the GLGs (Fig. 2d) and the tetracycline marks (Fig. 2e), which show as brightly fluorescing yellow lines, are indicated. Fig. 2f shows a portion of the cementum on the lefthand limb of Fig. 2c with the cemental GLGs indicated.

The growth in tooth structure, GLGs and the periods of tetracycline medication for the Sea World short-finned captives are shown in Fig. 3. The data indicate average dentinal growth for each GLG, decreasing from (specimens nos 7401, 7603, 7802H and 8003; Fig. 3) 593-520µm in yrs 1-4, to 368-267µm in yrs 5-8. The annual growth rate from tetracycline history is ca 360µm in ages 3-4 yrs, and ca 343µm from age 5-9 yrs; from yrs 7-14, the average rate is 238-247µm, and ca 333µm in the age range 6-9 yrs. Kasuya and Matsui (1984) reported a progressive decrease in thickness of GLGs, measured on the tooth shoulder as follows: 950µm, 400µm, 330µm and 300µm from first to fourth 'year', until only about 100µm by age 30 GLGs. The most rapid growth rate appeared to be between 0.25 and 0.5 GLG when the teeth erupt and the calf commences taking solid food. These data are compatible with the observed data in Table 3, and the known growth rate from tetracycline history. One important observation is that the neonatal line (16-64µm) does not become apparent until a few weeks or even months after birth (Kasuya and Matsui, 1984). The first GLG appears to be the most complicated in terms of growth, frequently with a pronounced stainable accessory lamination at the mid-zone, which could be misinterpreted as the end of the first GLG. This phenomenon has been reported by Hohn (1980) and Kasuya and Matsui (1984). These characteristics may reflect the rapidly changing growth rates and feeding criteria of the calf, as well as behavioural changes and stresses.

[text continues on p. 148]

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			Total no.	of GLGs	CTC CTC	3 position of tet	tracycline marks a	nd mineralisati	on anomalies	
Whale no.	Time in captivity in yr.	Estimated age in yr.	Dentine	Cementum	Tetra- cycline marks	Pulp stone(s)	Marker line(s)	Mineral- isation inter- ference	Dentinal resorp- tion	Cemental disturb- ance
7401	6.95	>14	14.25- 14.5	14	ca 7.5; 14.1? both in D	None seen	4-5; 7; 12; many clear lines 7 - 12 between in D	4 and on; 7 and on; 12 and on are very distorted	None seen	None seen
7501 7603	0.42 1.42	3-4 3-4	4.5 4	4 % + 4	None ca 4 in D bright line at pulp cav. edge adj. to pre-	None seen None seen	3; also 4 ca 3	None seen None seen	None seen None seen	None seen None seen
7802-H	4.875	8-10	8.5	8 or 7?	tenune 5 and 6.25 in D and C; 8.25 in D	None seen	2? in D; 4 in D; 4-5 in C; 8.15 in D	None seen	None seen	Irregular pattern
8001 8003	0.35 2.56	2-3 7-9	° 3 *	2 or 3 8	2.8 in D ca 5.5 in D	None seen Stone in 5-6 in D	None seen 5 in D	None seen Some in 1-2; very markedly distorted after 5	None seen Possible in D	None seen None especial
8227	0.03	ca 3	3.2 or 2; 3 is very pronounced - is artifact?	ca 2	None seen	None seen	None seen	None seen	None seen	None seen

Age and GLG interpretation of Sea World short-finned pilot whale teeth; D = dentine, C = cementum.

Table 2

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e 3	
Tabl	

Serial measurements of dentinal GLG thickness in μm , measured on the shoulder of the tooth, at 90° to the axis of the GLGs.

Total snan of	dentine	5,007 3,008	2,000 7 767	4 151	7 586	3 671	2,311 2 166	2 ,100		
	GLG 15	391+								
	GLG 14	301						(301)	(TAC)	
edge	GLG 13	241							(147)	
Ip cavity	3LG 12 (150						10217	(ncT)	
line to pu	3LG 11 0	120						1000	(170)	
n neonatal	SLG 10 (211							(112)	
ough fron	GLG 9 (135			143+		211+		(135)	
rially thr	GLG 8	195		I	352		271		273	±79
asured se	GLG 7	195			380		271		282	±93
μm, me	GLG 6	150			380		271		267	±115
f GLG in	GLG 5	316	361+		428		361		368	: ±56
ckness o	GLG 4	271	541	481	523		782	181 +	520	±182
Thi	GLG 3	256	662	722	542	782	571	421	565) ±182
	GLG 2	632	609	571	627	872	301	421	576	±180
	CLG 1	902	534	587	475	451	421	782	593	± 182
Pre-	dentine to nl	541	301	406	301	481	211	361	372	± 114
	Whale No.	7401	7501	7603	7802-H	8001	8003	8227	Average)

Table 4

	N. Pacific	N. Atlantic
	G. Macrorhynchus	G. melas
Length at birth	140cm	178cm
Length at sexual maturity, males	394-525 cm (x=422)	430-490cm
females	316cm	366-378cm
Age at sexual maturity, males	16yrs	12-14.3yrs
females	7.5-11.5 (x=9)yrs	6-8.7yrs
Maximum length, males	525-580cm	630cm
females	405cm	550cm
Maximum age, males	45yrs	46yrs
females	62yrs	59yrs

Reported age and growth parameters for short-finned pilot whales off Japan and long-finned pilot whales in the North Atlantic (Sergeant, 1962; Martin et al., 1987; Martin and Rothery, 1993; Kasuya et al., 1988; Desportes et al., 1993 and Bloch et al., 1993).

Life-history events with age and tooth structure for the short-finned captives are indicated in Fig. 3. In all whales maintained in captivity for about one year or longer, it is clear that some type of anomaly formed in the tooth within ca 9 months after initial capture. In four of five whales (7501, 7603, 7401 and 7802H), a marker line is present. In the remaining whale (8003), a pulp stone appeared within a few months of capture, and mineralisation interference, already present, continued. The pulp stone formation coincided with a period of weight loss. All animals experience a period of nutritional stress shortly after captivity, both due to poor feeding and adaptation to a change in diet. Specimen 7401 aborted a foetus within a few months of captivity, the timing coinciding with the formation of a marker line. Specimen 7802H formed a marker line about the time of probable maturation and first ovulation, marked by a large corpus luteum on the ovary (Table 1). Although marker lines appear both before and after capture, their appearance does not seem to be random. They frequently mark the start of a period, often prolonged, of mineralisation interference or more severe disturbance in GLG formation, e.g. specimens 7401 and 8003. The period of severe mineralisation interference in specimen 7401 commenced just prior to and continued throughout her pregnancy that resulted in the live birth of a hybrid calf. The mother died shortly afterwards from illness.

Thus, it appears that these mineralisation anomalies are not random but are often linked with life-history events. Observations from these known-history captives indicate that likely stressors (directly or indirectly) giving rise to mineralisation anomalies include sexual maturation, pregnancy and/or parturition, and periods of starvation or nutritional stress, as well as changes in health and life style (change from free-living to captive).

Mineralisation anomalies

(1) Comparison of teeth from single individuals

Table 5 details GLG counts and anomalies for 10 individuals for which at least two teeth were examined. These results show not only that different teeth from the same individual have similar GLG counts, but more significantly, that they usually show similar growth anomalies and patterns. This is similar to findings reported by Myrick (1988) for several dolphin species. The most variable character in terms of position and age of occurrence is the pulpstone. However, this may depend on the section of the tooth as their discrete nature and frequent placement in the 'limb' of the tooth may result in them being missed when present. Some marker lines do not appear prominent in a few duplicate teeth when



Fig. 3. Chronological life-history events and related age and tooth morphology for captive short-finned pilot whales.

= Rif, Th = Thorlakshofn.
R
uplicate teeth from long-finned pilot whale individuals. R =
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nomalies observed i
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ge
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Deta

Table 5

						1	resence and position (GL	G) of mineral	isation anoma	ies
		F		Age in G	iLGs/years	Dita I		Mineral- isation inter-	Dentinal resom-	Cemental disturb-
w nale no.	Sex	Lengun in cm.	Maturity	Dentine	Cementum	stones	Marker lines	ference	tion	ance
R-3 R-3	щ	412	+ pregt	17+2 19	19 19	- +	+ 9,11,12 + 8/9,12	+ +		, ,
R-14 R-14	M	516	ć +	19-23 23	23-25 24-25	1 1	+ 3,6 + 3,6			
R-16 R-16	щ	405-407	+ pregt	24 24	23 22+	+ ? + 11	+ 2,11,14,?16,17,19 + 2,11,14,16,17,19	+ +		
R-21 R-21	M	501-505	~: +	11 11	10/11 11	∞ ∞ + +	+ 4,8 + 4,8	+ +		
R-25 R-25 R-25	ц	432-434	+ lactg	16-19 18 17+	19 19-23 19	+ 7/6 - + 10	+ 5,8,16? + 5,8,16/15 + 5,8,??10,16/15		, , ,	
R-26 R-26	н	410-411	+ lactg	11 11	11-13 11-13	L + +	+ 1,2 + 1,2	+ +	1 1	
Th-2 Th-2	ц	419	~· +	22 22	18+ 20	+ 7,17 + 12	+ 5,7 -	+ +	~~~ + +	
Th-3 Th-3 Th-3*	ц	400	; +	12 12 11+?	12 12 10+	+ 6,7 + 9 ?	+ 5,6,10,11 + 1,4/5 + 1,5	~ + + +	1 3 4	, , ,

* Very poor preparation of tooth.

LOCKYER: DEPOSITION OF DENTINE AND CEMENT IN TEETH

anticipated, e.g. nos Th-2 and Th-3. Again, this may be a real phenomenon or perhaps it is more likely to be artifactual. It is clear that the importance of obtaining good central sections well prepared histologically, so that there is no distortion of laminations, cannot be stressed enough (see also Hohn *et al.*, 1989). From the overall similarity between duplicate teeth, we may conclude that, in principle, any tooth taken from an individual pilot whale can be used for age determination.

(2) Age-related characteristics

The sub-sample sizes from Rif, once sorted by age, were so irregular and small, that after a preliminary comparison of analyses with results for Thorlakshofn, and given the geographic proximity, samples from both locations were combined. Fig. 4 shows the comparison by age group of the five different anomaly characteristics defined earlier for the Icelandic and Faroese whales; both sexes are included. The levels of incidence of pulp



Fig. 4. Tooth mineralisation anomalies for sexes combined by age and location: Ice=Iceland; Far=Faroes.
(a) Pulp stones; (b) Marker lines; (c) Mineralisation interference; (d) Dentinal resorption; (e) Cemental disturbance.

stones, marker lines and mineralisation interference are similar in both locations, with an increase with age. The increase in pulp stones and mineralisation interference starts later in the Faroese whales, but the pattern is similar. However, the levels and patterns of incidence of dentinal resorption and cemental disturbance clearly differ between the two locations, with low overall levels for Iceland, but with dentinal resorption increasing steadily for the Faroese whales until there is 100% incidence in old animals. As might be expected, the incidence of all characteristics appear to be age-related, but each type has a different level of incidence: the pulp stones and cemental disturbance only reach ca 50% maximum in the oldest animals, whereas the other anomalies show extreme variations from 40–100% depending on locality.

The types of anomaly may be inter-related, and affected to varying degrees by the same internal and/or external factors. Thus each may represent a measure of the severity of response to such factors. I believe that the available evidence (e.g. see Myrick, 1988), particularly that detailing causes of changes in tooth structure (Johannessen, 1964; Nikiforuk and Fraser, 1979; Jensen et al., 1981) suggests that the resorption and transformation of existing dentinal tissues is a response elicited by a severe long-term or continuing change in physiological state, probably with hormone imbalance, which either exacerbates any pre-existing hereditary-based tendencies or initiates a chronic hypocalcaemic condition. Other anomalies such as pulp stones and 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 which show the effects of suprathreshold and chronic cyclic sub-threshold stressors on calcium ion balance and the mode of calcium ion recruitment into the blood. A recent study by Bengtson (1988) on fur seals (Arctocephalus gazella), has shown the occurrence of periodic starving/suckling laminae in mothers and their pups, which are associated with the nursing pattern. This would appear to be directly related to the periodic calcium and nutrient transfer.

Boschma (1950) investigated the problem of resorption along the lines of Colyer (1936) who believed that resorption was caused by physical external pressure, such as that from adjacent teeth. Such physical pressure can actually create resorption (Boyde, 1984), and the rate of erosion depends on the orientation and density of the mineralised tissue. Boschma stated that resorption could not be caused by pressures from adjacent teeth in sperm whales, but that pressures from opposing teeth in the upper jaw might lead to resportion. However, for one of the teeth he examined, he stated

'the abnormality of this tooth is of a similar kind as that previously described by other authors; the cause of the process is unknown. There is at least not any indication of a contact of this tooth with an antagonist in the upper jaw'.

Boyde *et al.* (1984) demonstrated that resorption resulting in typical 'Howship's lacunae', can 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.

The evidence for a systemic cause of anomalies in pilot whales is strengthened by the appearance of the same anomalies in different teeth from the same animal (Table 5). This is discussed further under 'real time-related characteristics'.

Table 6 shows the mean age \pm SE of occurrence of the first, second and subsequent pulp stones and marker lines for each of the three locations for long-finned pilot whales. The maximum number of 'strikes' for each anomaly (note that for pulp stones, that is not the total number, but the number of times when pulp stones were produced) is usually twice Table 6

Mean age ± SE (GLGs/years) of occurrence of pulp stones and marker lines in long-fin pilot whale teeth.

		Mean position c	of recurrence in te	erms of age ± SE	(GLGs/years) of m	ineralisation anorr	naly in the dentine	
:	Pulp	stones			Marke	r lines		
Geographic location	lst	2nd	lst	2nd	3rd	4th	Sth	6th
Rif, Iceland	9.29±1.27	11.0	5.37±0.76	7.71±0.59	11.50 ± 1.00	14.33±1.40	17.17±0.70	19.80±0.58
Thorlakshofn, Iceland	6.54±0.53	5. 57±1.41	4.91 ±0. 45	8.66±0.67	11.68±0.71	12.25±1.48	18.50±1.94	31.00
Sandur, Faroe Islands	10.04 ± 1.32	9.71±2.39	5.87±0.46	10.68±0.65	15.20±1.09	20.25±2.14	20.00±4.00	17.00

for pulp stones and up to six times for marker lines. Klevezal' and Myrick (1984) noted up to five such marker lines in *Stenella*. The mean age for both first and second pulp stone occurrence is similar regardless of location, although the actual age is lowest for Thorlakshofn. The actual age range of *ca* 5.5–11 yrs suggests a possible link with onset of puberty/sexual maturity. However, it must be emphasised that pulp stones initially form within the pulp where they may remain free for a period of time before becoming incorporated into the dentine itself. Thus it is difficult to determine the precise age when the pulp stone was produced. Certainly the age may be earlier than that reported when first identified in the dentine. Many pulp stones contain what appear to be concentric GLGs. However, the deposition rate, if applicable, is unknown.

Results for the marker lines (Table 6), however, indicate a general recurrence at average intervals of usually around 3–5yrs (range 1–12 yrs), commencing at an earlier age (4–6 yrs) than the pulp stones, and continuing up to age >30 yrs. The irregularity of the mean ages which sometimes appear to decrease with time rather than increase, is caused by progressively decreasing sample sizes. The formation of marker lines may be influenced by a repetitive combination of internally generated 'crises' and/or external environmental ones. Alternatively, marker lines could be created as the result of relatively small changes in concert with normal biological rhythms coinciding chronologically.

Kasuya and Matsui (1984) show photographs of sectioned short-finned teeth illustrating what they define as 'secondary dentine'. This resembles mineralisation interference (Myrick, 1988) and usually began between ages 7–16 yrs for both sexes, coinciding with the usual timing of sexual maturation. Unlike the samples in this study, however, Kasuya and Matsui (1984) found differences in the timing of this character among adjacent teeth from the same individual. This suggests that correlation with maturation may only be general, and may in fact be more closely associated with the hormone changes during puberty which are often prolonged in males. Pulp stones and possible resorption can be seen in the 'secondary dentine'. Kasuya and Matsui (1984) also describe 'cellular dentine', layered tissue accumulating at the root and pulp cavity edge in teeth of older animals (>10 yrs). This appeared to be most extensive in old males. This has not been found in the long-finned pilot whales thus far examined.

(3) Sex-related characteristics

The incidence of the five characteristics by sex, all locations combined. is shown in Fig. 5. The levels and patterns of incidence in the two sexes are similar for pulp stones, mineralisation interference and marker lines, with the incidence generally increasing most in the years up to 10–14 yrs. Dentinal resorption and cemental disturbance are not really apparent until older ages, and then the incidence appears to be greater in males. This suggests that in general, susceptibility to the causative factors of these characters is not sex-specific. By contrast Myrick (1988) found that resorption was highest in female *Stenella longirostris*.

(4) Sexual maturity-related characteristics

Fig. 6 shows the incidence of the various characters by sexual maturity status for all locations combined. Dentinal resorption does not occur in the teeth of any immature animals, regardless of age. The reason for this clear demarcation may be connected with the hormonal changes that take place at the transition to adulthood. It is plausible that such hormonal upheaval and the physiological stresses which may accompany it and continue long afterwards, are capable of bringing about hypocalcaemia under certain conditions, as hypothesised in the review by Myrick (1988). For all other characteristics, age is a more important factor than maturity and, as one might expect, the overall mean



Fig. 5. Tooth mineralisation anomalies for Iceland and Faroes locations combined by age and sex: M=male; F=female. (a) Pulp stones; (b) Marker lines; (c) Mineralisation interference; (d) Dentinal resorption; (c) Cemental disturbance.

level of incidence of all characters is lower for immature (i.e. younger) animals. However, the incidence of marker lines with age is almost identical for both mature and immature animals and appears to increase steadily with age, until nearly all specimens are affected. This suggests that external (environmental) factors may be of relevance and a preliminary examination of this is given below.

(5) Real time-related characteristics

Two characters were selected for this analysis: pulp stones and marker lines. The information on year of stranding, age at death and sequential ages at which pulp stones and marker lines occurred, permitted a calculation of the calendar year in which the character appeared in the tooth. Initially, each anomaly and location was treated separately, with the frequency of occurrences for each year recorded alongside the total number of individuals alive at that time. Plots of actual and proportional frequencies by



Fig. 6. Tooth mineralisation anomalies for Iceland and Faroes locations combined by age and sexual maturity status: Imm=immature; Mat=mature. (a) Pulp stones; (b) Marker lines; (c) Mineralisation interference; (d) Dentinal resorption; (e) Cemental disturbance.

year indicated that the Icelandic samples were similar and could thus be combined, whereas Sandur was more often different. Secondly, even when anomalies appeared in a particular year for several whales, the incidence was rarely high, indicating that in general only a minority were responding to whatever the causative factor might be. In addition an anomaly of some kind occurred almost every year. This might be explained partly by a lack of precision in age determination (e.g. ± 1 or 2 GLGs). Chi-square tests on differences between proportions, showed no significant association between year and occurrence of pulp stones for either Iceland or the Faroes. However a significant association (P<0.0001, Chi-square=73.729, df=32) was found for marker lines for Iceland, although not for the Faroes. In particular, the year 1960 was prominent for Iceland when >40% teeth from whales in the sample (which would have been alive at that time) exhibited a marker line. A similar peak occurred in 1953 (Fig. 7).

Manzanilla (1989) reported correlation in the timing of the appearance of hypocalified layers in the dentine of teeth of Peruvian dusky dolphins (*Lagenorhynchus obscurus*) and



Fig. 7. Percentage frequency of tooth specimens with marker lines for both sexes, all ages and all maturity statuses combined, by year for each location: Thorlakshofn (--), Rif (---), Sandur (....).

the 1982–83 El Niño event. The anomalous layer, described as the 'El Niño mark' (ENM) comprised a pair of hypocalcified incremental layers about 75 μ m wide within the 1983 GLG. The feature appeared predominantly, but not exclusively, in adult females. Because the primary prey of the species 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 not display ENMs, but were feeding on a different prey source. This is the first convincing evidence of a connection between tooth anomalies and environmental factors.

In the case of the Icelandic pilot whales, the 1953 and 1960 peaks (Fig. 7) appear to have no obvious environmental correlate. The diet of pilot whales is primarily squid, although other prey may be taken in times of need (Desportes and Mouritsen, 1993). A major problem is that the locality of the whales during those years may have been anywhere in the North Atlantic. A major climatic reversal in the northeast Atlantic commenced around 1960 (Dickson *et al.*, 1975), but the effects of this were experienced over a protracted period of years (Malmberg, 1985) and not as a sharp change as in the El Niño period.

Further investigation of environmental changes at those times may be worthwhile. It is interesting that none of the Faroese teeth had a marker line in those years suggesting that the Icelandic whales were affected by factor(s) that did not influence the Faroese group. This in turn may indicate that the Icelandic and Faroese whales may have originated in separate regions and perhaps do not mix.

CONCLUSIONS

Examination of teeth from seven known-history captive northeast Pacific short-finned pilot whales, mostly having received tetracycline treatments, determined that in teeth of age <15 yrs, numbers of cemental and dentinal growth layer groups (GLGs) were equal. The incremental rate of deposition is one GLG per yr. Both dentinal and cemental GLGs may therefore be used directly for age determination in years.

Five types of mineralisation anomaly can be recognised in pilot whale teeth, and the incidence of these can vary with age, geographical origin, sex and maturity. Observations from the known-history captives indicate that likely stressors (directly or indirectly) include sexual maturation, pregnancy and/or parturition, and periods of starvation, as well as changes in health and life style, such as the transition from free-living to captive. Pulp stones, when present, tend to be associated with age at which puberty usually occurs, and the incidence does not greatly increase thereafter. Marker lines occur throughout life at all ages, after age one year, regardless of state of maturity, and therefore, as anticipated, incidence increases with age; there is also significant association with calendar year e.g. 1960 stands out in Icelandic samples, but not in the Faroese. Mineralisation interference increases with age reaching 60-100% incidence in animals over 14 yrs in both Icelandic and Faroese animals. The incidence is related to age rather than maturity. Cemental disturbance has a low incidence in Icelandic whales, and reaches ca 50% incidence in Faroese whales. This is also age- and maturity-related. Dentinal resorption has not been recorded in immature animals of either sex. Incidence reaches a peak in old males, yet does not appear to greatly affect females until age >25 yrs. Dentinal resorption occurs frequently in the Faroese animals, reaching almost 100% incidence in males. The incidence in Icelandic animals is <10% until age 25+ yrs when incidence rises from 20% to 40% in very old animals (30 + yrs).

The difference in these levels of incidence by location and sex indicates varying degrees of susceptibility to the causative factors. This may be genetically controlled, or simply a measure of local environmental or behavioural stress factors. These factors revealed in the teeth may explain differential mortality and sex ratios, but this requires further examination. Potential hypotheses include the possibility that the higher levels of resorption in teeth of adult males may be connected with the stresses of inter-male competition in reproduction. Reproductive stresses will, of course, differ between the sexes. The male is destined to compete regularly, probably annually, for procreative status in schools which are female dominated. The female however, may only reproduce every 3-5 yrs. If Klevezal' and Myrick (1984) are correct in their interpretation of 'parturition' laminae (DSLs), reproductive history may, in theory, be deduced from the teeth. Periods of nutritional and environmental hardship may be translated into unusual marks in the dentine, where growth ceases temporarily and mineralisation problems arise. Another possibility is that other stress factors, perhaps manmade, such as fishery conflicts, may lead to identifiable anomalies in teeth. Consideration of such hypotheses help to formulate questions that can be addressed experimentally.

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Appendix 1 HISTOLOGICAL PREPARATION OF TEETH

STEP 1 – **P**reparation for all methods.

1. Extraction of tooth from the mandible after rotting of the jaw.

2. Cleaning of the tooth by physical abrasion or enzyme digestion – definitely no boiling.

3. Mounting of dry tooth on wooden blocks using thermoplastic cement, in a plane to permit cutting through the crown to root axis.

STEP 2 - For examination of tetracycline presence with reflected UV light.

4. Cutting of section through centre line (crown and pulp cavity apices) at approximately $100\mu m$, using an *Isomet* low-speed rotary diamond saw with micrometer travelling screw gauge.

5. Mounting of thin section on acid-cleaned glass slide with clear resin permanent mounting medium, *Protex* or *DPX*, under a glass coverslip and drying on a slide warmer for a few days.

STEP 3 – For examination of 'growth layer groups' (GLGs) in dentine and cement using transmitted plain light.

6. Decalcification of remaining larger portion of the tooth (near half) after detachment from the cement and wood block, in RDO, a commercial acid product for pathological use, for 4–32hr depending on tooth volume (5% nitric acid may also be used, but decalcification may take several days or weeks).

7. Complete rinsing of decalcified tooth portion in water for 24hr, followed by temporary storage in distilled water.

8. Fixation of decalcified material in 10% neutral buffered formalin.

9. Section cutting at a thickness of 30–35 micron, from the decalified tooth portion using a freezing stage on a sledge microtome, using *Tissue-Tek* as a mounting medium.

10. Transfer of selected sections to histological baskets and immersion in water using a paint brush, followed by staining in Haematoxylin stain for 2hr, subsequent water rinsing and 'blueing' in ammonia solution for a few minutes, then water-rinsing and partial dehydration in 50% and 70% alcohol.

Flotation onto and arrangement of stained sections on a 5% gelatin smear-coated glass slide under 70% alcohol and subsequent drying of slide and sections on a slide warmer.
 Mounting of dried stained sections with clear resin permanent mounting medium *Protex* or *DPX* under a glass coverslip, and drying on a slide warmer for a few days.

Age and Growth Parameters of the Long-Finned Pilot Whale off the Faroe Islands

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ABSTRACT

Age related parameters are described for the long-finned pilot whale, based on material from 40 entire schools taken in the year-round Faroese drive-fishery. Age has been determined from dentinal and/or cemental growth layer groups (GLGs) in teeth. Longevity is greater in females which attain up to 59yrs, while males attain 46yrs. Overall mortality rates are higher in males, and mean estimates range from 0.0745-0.0817 in males and 0.0622-0.0737 in females. The mean size at birth is estimated to be 177.6cm and 75kg. Males attain a maximum length of 625cm and a weight of 2,320kg; the values for females are 512cm and 1,320kg respectively. The mean adult length (at age >25yrs) is 570cm for males and 446cm for females. Females reach sexual maturity at an age of 8.7yrs, a length of 378.5cm and a minimum weight of 600kg. For both sexes, sexual maturity is determined by body size and not age. Physical maturity, determined from vertebral epiphyseal fusion, occurs between 25-30yrs in most animals. Growth appears to fall into four phases: early postnatal; juvenile; young adult; pre-physically mature adult. Growth is rapid in the first phase and declines as physical maturity is approached (phase four). Growth rates for different regions of the body vary with developmental age. Both the von Bertalanffy and Laird-Gompertz growth models were fitted to the data using different assumptions. The latter provided the best model for describing both growth in length and weight over time. In both sexes the growth curve appears uncomplex, with no pronounced secondary pre-pubertal growth spurt in males. A few schools appear to be significantly different to the mean growth model, suggesting a possibility of difference in stock origin. Overall, there are many similarities with long-finned pilot whales elsewhere throughout the North Atlantic.

KEYWORDS: PILOT WHALES-LONG-FINNED; NORTH ATLANTIC; AGEING; POPULATION PARAMETERS; REPRODUCTION; GROWTH/LENGTH DISTRIBUTIONS; SEXUAL MATURITY; MORTALITY.

INTRODUCTION

Between July 1986 and July 1988, an international programme of research was conducted on the northeast Atlantic long-finned pilot whale, *Globicephala melas* (Traill), off the Faroe Islands. The pilot whale is the focus of a local year-round drive-fishery (Bloch *et al.*, 1990) and details of the programme are provided in a general paper by Bloch *et al.* (1993a). During the two-year period of sampling, 47 notifications of schools were recorded, of which 43 were followed by actual landings. In total, 3,617 pilot whales were caught and 3,470 were examined from 40 drives taken in all months of the year. In the only other comparable study on North Atlantic pilot whales, Sergeant (1962a) examined animals from a drive fishery off Newfoundland¹. However problems of sampling bias arose in that

¹ This material was re-examined and analysed by Kasuya *et al.* (1988b) by counting both the dentinal and cemental layers following the method of Kasuya and Matsui (1984) for the short-finned pilot whale.

study as not all caught animals were sampled and because catches were not made throughout the year.

Several methods have been used to attempt to determine the age of whales over the years. The present standard for toothed whales is to count growth layer groups (GLGs – see IWC, 1980) in the dentine and cement in the teeth, as introduced by Sergeant (1959) and reviewed by Hohn (1990).

Lockyer (1993a) examined patterns of dentine and cementum deposition in pilot whales. Using teeth from captive, known-history short-finned pilot whales, *Globicephala macrorhynchus*, she demonstrated that age could be determined from any undamaged tooth in the jaw. She also found that numbers of dentinal and cemental GLGs were the same in a tooth that each GLG represented an annual growth increment. GLGs have been translated directly into age in years throughout this paper, on the assumption that tooth formation is comparable in both pilot whale species.

MATERIAL AND METHODS

Sampling techniques and data on sex, length and weight are provided by Bloch *et al.* (1993a). In all, 3,442 whales were sexed, 3,047 were measured for length and 622 weighed whole; 411 foetuses were collected and examined. In addition, this paper includes data from 63 foetuses previously sampled and included in Bloch (1992), and data from 59 foetuses sampled between July 1988 and the end of 1992, bringing the total foetal sample size to 533 of which 485 were of known length and 409 of known weight.

A total of 458 foetuses were sexed by one of three methods: (1) macroscopic examination of the external genitalia or gonads; (2) histological examination of the gonads; or (3) examination of the sex-chromatin as described by Andersen *et al.* (1992).

Age determination

Teeth were collected and examined from each individual for almost all schools (2,627 whales from 39 of 43 schools, of which 2,448 provided acceptable age readings). The sampling and initial laboratory treatment are described by Bloch *et al.* (1993a).

The cleaned teeth were treated in a similar way to that described by Lockyer (1993a), for decalcified thin stained sections, except that 5% hydrochloric acid over a period of up to two weeks was used for decalcification. Afterwards, the half-teeth were kept in water with thymol crystals (to discourage bacterial and fungal growth), after rinsing in tap water. The best half-teeth were sectioned at approximately 25–35m μ on a *Reichert*² sledge microtome equipped with either a *Euromex*² electrical or carbon dioxide freezing stage. The sections were floated onto 5% gelatine-coated acid-cleaned slides, dried on a slide warmer and stained in ripened Erhlich's acid haematoxylin for two hrs (when very ripe) or more. After having been rinsed in 70% alcohol, 'blued' in ammonia vapour, rinsed in 70% alcohol and air-dried on a slide warmer at 30°C, the slides were permanently mounted with *DPX-mountant*², a clear resin medium. The readings of the sections were made with x12 magnification for the dentine and x150 for the cementum.

Teeth from five schools were prepared by Lockyer (Bloch *et al.*, 1993a; grind nos 4, 5, 11, 12 and 24) and the remaining teeth were processed by the laboratory of the Zoological Department of the Faroese Museum. A subsample of these were used in the study by Lockyer (1993a).

Most slides were assessed for quality in terms of both preparation and readability. Four categories were used: (1) very clear, easy to read GLGs in both dentine and cement; (2) clear GLGs in dentine and very clear in cement; (3) GLGs readable with difficulty,

² Reference to trade names does not imply endorsement by the authors' Institutes.

particularly in dentine; (4) unreadable in either dentine or cement, even after using several teeth.

The teeth were examined and read by several readers (as listed in Bloch *et al.*, 1993a) for growth layers groups, although most were examined by one of us (DB) alone. The methodology used was carefully monitored and several random samples of duplicate readings were made by other researchers (CL and Toshio Kasuya) over time.

In the summaries of results it should be noted that each age class ranges from age (n) to age (n+1). When calculations are made the values $(n+\frac{1}{2})$ are used. In all other cases (-) is used to present the age class from (n) to (n+1).

Survivorship

Annual mortality rates (z) were calculated by (a) the method of log linear regression (as used for northwest Atlantic long-finned pilot whales by Kasuya *et al.*, 1988b), and (b) the method of Robson and Chapman (1961). Estimates based on Heincke (1913) were also calculated. Age segments were selected to closely reflect natural phases in the life history: birth to sexual maturation, early to middle adult life, old age, and birth to old age. The actual age groups in each segment vary by sex to accomodate different developmental rates. Apart from the overall mortality rates, the segmental analyses were performed using log linear regression only. Other methods did not appear to be appropriate, because an assumption of constant mortality was required. In addition, Siler's (1979) competing risk model was used to examine female survivorship as described by Barlow and Boveng (1991).

Length data

The length of the whales was measured to the nearest cm in a straight line from the tip of the snout to the notch in the fluke, following Norris (1961). In addition to routine measurement of total length, more detailed measurements were taken for one school containing 59 whales (no. 37, table 1 in Bloch *et al.*, 1993a): tip of snout to eye, eye to anus; and anus to notch in fluke. This was partly to study the growth of different parts of the body, partly to compare the official assessment with biological data (Bloch and Zachariassen, 1989) and partly to compare these measurements with corresponding measurements of pilot whales from Newfoundland (Sergeant, 1962b; Bloch and Lastein, 1993).

Growth curves

The most frequently used growth model for cetaceans has been the Bertalanffy model (von Bertalanffy, 1938). It has been used on large baleen whales (Lockyer, 1981) and some dolphin species *Stenella coeruleoalba, Berardius bairdii* and *Phocoena phocoena* (Kasuya, 1972; 1977; Bjørge and Kaarstad, 1990). Another model, the Laird/Gompertz model (Laird, 1969), has been used for *S. attenuata* and *S. longirostris* (Perrin *et al.*, 1976; 1977; Hohn and Hammond, 1985), and both models have been used on the harbour seal, *Phoca vitulina* (Markussen *et al.*, 1989). In this paper we use both models.

The two models have the following characteristics:

	Bertalanffy	Laird/Gompertz
Growth equation $L(t)$	$L_{\infty} (1 - e^{-k(t+t_0)})$	$L_0 e^{A_0/\alpha(1-e^{-\alpha t})}$
Initial length	$L_{\infty} (1-e^{-kt_0})$	L_0
Asymptotic length	L_{∞}	$L_0 e^{A_0/\alpha}$
Growth rate $dL(t)/dt$	$k \ (L_{\infty} - L(t))$	$A_0 e^{-\alpha t} L(t)$
Initial growth rate	$k \ (L_{\infty} - L(0))$	$A_0 L(0)$

. The main difference between them is the assumption made concerning the growth rate: in the Bertalanffy model it is assumed to be a linearly decreasing function of the length, while the Laird/Gompertz model assumes it to be fundamentally linear with increasing length (implied by the division of cells), but with an exponentially decreasing factor. Thus the Bertalanffy function increases progressively more slowly as the asymptotic length L_{∞} , is reached, while the Laird/Gompertz function does not necessarily have its maximum growth rate at t=0, but at $t = \ln(A_0/\alpha)/\alpha$ (which can be >0). The latter can therefore approximate more sigmoid growth patterns. It can also be used to model both length and weight as a function of age, with the traditional relationship between length and weight assumed to be a power function.

Examination of physical maturity

Physical maturity was assessed from the degree of fusion of sutures between the epiphysis and the main part of the vertebral centrum following Mitchell and Kozicki (1984) for sperm whales (*Physeter catodon*), Mead and Potter (1987) for short-finned pilot whales, Aguilar and Lockyer (1987) for fin whales (*Balaenoptera physalus*) and Kato (1987) for southern minke whales (*Balaenoptera acutorostrata*). Only vertebra no. 6 was examined in the southern minke whale (Kato, 1987), as opposed to the whole column in the fin whale (Aguilar and Lockyer, 1987). Mead and Potter (1987) examined short-finned pilot whale vertebrae in the field and in the laboratory.

In this study a chainsaw was used to halve the entire vertebral column from head to tail. After cleaning the halved column in running water, the degree of fusion was noted in the field. Three categories were used, based on those of Mead and Potter (1987): immature (condition 1) – unfused epiphyses, completely separated by cartilage from the vertebral body; intermediate (conditions 1.5 and 2) – a clear fusion line but the epiphyseal plate cannot be separated by force from the vertebral body; mature (conditions 2.5 and 3) – totally fused epiphyses with the line between the epiphysis and centrum almost or completely invisible. This was carried out for up to eight whales from seven schools, totalling 13 females and 23 males.

Female attainment of sexual maturity

Females were classified as sexually mature if at least one ovary contained at least one corpus (luteum or albicans); sexual maturity is considered to have been reached at first ovulation (Perrin and Donovan, 1984).

Hohn (1989) reviewed a number of methods for estimating the mean age at attainment of sexual maturity (ASM). Three methods are used here to estimate mean age, length and weight at attainment of sexual maturity (ASM, LSM and WSM respectively).

Method I

Known age, length and/or weight females with only a corpus luteum on their ovaries and foetuses of known length and weight are considered (n=26 for age, n=31 for length and n=11 for weight). Attainment of sexual maturity is back-extrapolated from the length/ weight of the foetus using the estimates of gestation time (326 days) and foetal growth (0.5335 cm/day between 20–163cm) provided by Martin and Rothery (1993) to obtain the conception date. Estimates of female growth given in Table 9 are used to obtain LSM and WSM.

Method 2

ASM can be considered to be the age at which 50% of the females are mature, as predicted from a logistic curve weighted by sample size. The same is true for LSM and WSM. The

following groupings are used: age classes, 1yr; length classes, 5cm; and weight classes, 25kg.

Method 3

ASM, LSM and WSM can be estimated using the sum of fraction immature method (used earlier for mean body length at birth) favoured by Hohn (1989). Age, length and weight classes are as for method (2).

Neonatal length

Four methods were used to estimate mean body length at birth:

(1) mean length of foetuses and calves between the length of the smallest calf and the largest foetus;

(2) the length at which 50% of births are estimated to have occurred after fitting a logistic curve to the proportion of animals born in 5cm length classes weighted by sample size;

(3) the sum of fraction method described by Hohn (1989) to determine ASM (see below);
(4) the mean length of calves for which no neonatal line is present in the teeth, i.e. recently born (Kasuya and Marsh, 1984).

Only method 3 requires further explanation.

Length at birth can be expressed as follows (5cm length classes are used):

Birth length =
$$j + \sum_{i=j}^{k} p_i x_i$$
 variance = $s^2 = \sum((p_i q_i) x_i)/(n_i - 1)$ (1)

where:

j is the first indeterminate length class;

k is the last indeterminate length class;

 p_i is the fraction of foetuses in length class *i*;

 q_i is the fraction of born animals in length class $i (p_i + q_i = 1)$;

 x_i is the number of length classes combined to obtain a sample size >2 in length class *i*; I_i is the number of foetuses in length class *i*;

 M_i is the number of born animals in length class *i*; and

 n_i is the number of specimens in length class i ($n_i = I_i + M_i$).

The conditions are if:

$$I_i \# n_i$$
, then $p_i = I_i/n_i$ and $q_i = M_i/n_i$

if:

$$I_i = n_i$$
, then $p_i = (I_i - \frac{1}{2})/n_i$ and $q_i = (M_i + \frac{1}{2})/n_i$

if:

 $M_i = n_i$, then $p_i = (I_i + \frac{1}{2})/n_i$ and $q_i = (M_i - \frac{1}{2})/n_i$.

RESULTS AND DISCUSSION

Age determination

Quality of tooth preparation

The assessments of preparation for quality and readability are given in Table 1. Out of 2,243 teeth, 83% were of acceptable preparation quality (values 1, 57.6% and 2, 25.7%) and >95% provided acceptable values 1 (70.5%) and 2 (24.7%) in readability; 2.4% were of unacceptable preparation quality (value 4) and 4.8% (value 3) were unreadable even

	Total	ð?	ð Imm.	ð Mat.	88	¥?	♀Imm.	♀ Mat.	\$ 2	??
Readability		· · ·=								
1	I,581	9	467	165	641	6	400	531	937	3
(%)	(70.5)	(75.0)	(81.8)	(55.4)	(40.5)	(100.0)	(88.I)	(59.1)	(69.0)	(75.0)
2	554	3	91	116	210		45	298	343	1
(%)	(24.7)	(25.0)	(15.9)	(38.9)	(37.9)		(9.9)	(33.2)	(25.3)	(25.0)
3	108		13	17	30		9	69	78	
(%)	(4.8)		(2.3)	(5.7)	(27.8)		(2.0)	(7.7)	(5.7)	
Preparation										
1	1,291	4	410	119	533	3	360	393	756	2
(%)	(57.6)	(33.3)	(71.8)	(39.9)	(60.5)	(50.0)	(79.3)	(43.8)	(55.7)	(50.0)
2	` <i>577</i> ´	<u>َح</u>	Ì117	`105 ´	`227 ´	` 3´	6 7	`279 ´	`349 ´	<u> </u>
(%)	(25.7)	(41.7)	(20.5)	(35.2)	(25.8)	(50.0)	(14.8)	(31.1)	(25.7)	(25.0)
3	321	<u>`</u> 3´	38	<u>65</u>	106	· · ·	21	193	214	<u> </u>
(%)	(14.3)	(25.0)	(6.7)	(21.8)	(12.0)		(4.6)	(21.5)	(15.8)	(25.0)
4	` 54	` '	<u>`</u> 6́	<u></u> 9	15		6	33	39	(*)
(%)	(2.4)		(1.1)	(3.0)	(1.7)		(1.3)	(3.7)	(2.9)	
Total	2,243	12	571	298	881	6	454	898	1,358	4

 Table 1

 Readability and quality of preparation of teeth from G. melas off the Faroe Islands.

after sectioning new teeth, because of inherent problems in the interpretation of the layering pattern.

Readability of teeth appeared to be uniform within a grind, teeth of all animals in some schools being difficult to read (Bloch *et al.*, 1993a: table 1: nos 3, 13, 14, 20, 23 and 34), and easy in others (Bloch *et al.*, 1993a: table 1: nos 4, 5 and 12). Whether this was the result of genetic similarity, post-mortem changes in tissues, predisposition to disease and/or exposure to environmental stresses such as malnutrition, is unclear. However, if the first of these factors is true, this may be a useful characteristic to explore further in relation to stock identity, (the question of genetic relatedness has been examined by Amos *et al.* (1991; 1993) and Andersen (1993) using standard genetic techniques). As an aside, it can be mentioned that only a single whale was found to be affected by paradentosis.

Reliability of age readings

Lockyer *et al.* (1987) found in a subsample from this material that cemental layers tend to outnumber those seen in the dentine (Figs 1a and b) for older (>13yrs) animals. In a few teeth, either the dentine or the cementum was destroyed in some way making it unusable for age purposes. Frequently, mineralisation interference (or secondary dentine as described by Kasuya and Matsui, 1984) totally disturbed the layering in the more recent layers of old whales (Lockyer, 1993a) with nearly all >30yrs having some GLG pattern disruption. More seldom, formation of secondary cementum (Kasuya and Matsui, 1984) rendered the cemental layers unreadable. Disturbances in structure such as pulp stones and mineralisation interference also reduce readability; these appeared to be more related to age than maturation state (Lockyer, 1993a). For determining age, both dentinal and cemental GLGs were read in all teeth; dentinal counts were clearer and more acceptable in juveniles and young adults, while cemental counts were usually used for older animals especially if the count greatly outnumbered the dentinal one.

Generally, there is a highly significant correlation between the readings of the dentinal and cemental GLGs in both sexes (Table 2; r=0.910; n=2,315), which shows however, a decreasing correlation as the age increases beyond 13yrs (Table 2). Disturbances in cementum, and dentinal resorption for the male Faroese whales are related to maturity


Fig. 1. Plot comparison of ages determined from dentinal and cemental GLGs in the long-finned pilot whale off the Faroe Islands: (a) 966 males; (b) 1,483 females.
Symbols: Empty square = immatures; × = matures; filled triangle = unknown maturity.

			age and re	productive	status off		sianus.						
	0-59	years	0-12	years	13-59) years	Imma	ture	Mature				
	r	n	r	n	r	n	r	n	r	n			
Male Female All	0.929 0.897 0.910	917 1,398 2,315	0.955 0.967 0.962	574 656 1,230	0.647 0.627 0.633	343 742 1,085	0.903 0.858	613 495 1,108	0.657 0.655	337 974 1,311			

Correlation of dentinal and cemental GLG readings of pilot whale teeth with sex, age and reproductive status off the Faroe Islands.

more than age (Lockyer, 1993a) and so rather than simply stratify by age (0-12yrs, 13+yrs) which would result in both groups including some immature and some mature individuals, it seems more reasonable to stratify into matures and immatures. As shown in Table 2 and Fig. 1, for immatures the correlation is significantly better for males (z = 3.34), while there is no significant difference between the sexes for the matures (z = 0.06).

Ages

The oldest male aged was 46yrs (n=967, Table 3); 125 (15.1%) males were over 25yrs and 4 whales (0.4%) were over 40yrs (Fig 2a). Of the 1,482 females, the oldest was 59yrs; 323 (24.2%) were over 25yrs while 5 (0.3%) were over 50yrs (Fig. 2b). These are older than previously found for the long-finned pilot whale (Sergeant, 1962a; Crespo *et al.*, 1985; Martin *et al.*, 1987; Kasuya *et al.*, 1988b; Bloch, 1992; Sigurjónsson *et al.*, 1993), but similar to the short-finned pilot whale (Kasuya and Matsui, 1984; Kasuya and Tai, 1993). This may reflect the fact that fewer animals were aged using cemental layers in previous studies of the long-finned pilot whale.

Thus the maximum age of females exceeds that of the males by 13yrs, and the mean age of the female population is 3.8yrs greater (Table 3). This is similar to the pattern found in previous studies (Sergeant, 1962a; Martin *et al.*, 1987; Kasuya *et al.*, 1988b; Sigurjónsson *et al.*, 1993). This has also been found in the short-finned pilot whale off Japan, where the maximum age of the females is some 20yrs greater than that of males (Kasuya and Marsh, 1984; Kasuya and Matsui, 1984; Kasuya *et al.*, 1988a; Kasuya and Tai, 1993).

Although female longevity exceeds that of males, the mean age of both immatures and matures is greater for males (Table 4), due to the earlier age at maturity of females (see below).

Range and average of length (in cm), weight (in kg) and age (in yrs) of G. melas off
the Faroe Islands in the period July 1986 - July 1988,

Table 3

		Length (c	cm)	W	leight (kg))	Age (year)						
	ර්	Ŷ	Both	ਣ	Ŷ	Both	3	Ŷ	Both				
Min Max	174 625	163 512		92 2,320	100 1,320		0.0 46.0	0.0 59.0					
Mean SE N	420 3.3 1,190	387 1.8 1,635	401 1.8 2,825	879 38.0 236	721 14.9 370	783 17.7 606	12.3 0.3 967	16.1 0.3 1,482	14.6 0.2 2,449				



Fig. 2. Age frequency distribution histogram for (a) 967 males, and (b) 1,482 females, all months and years in the long-finned pilot whale off the Faroe Islands. Symbols: Striped bar = immatures; filled bar = matures; hatch bar = unknown maturity.

		Lengt	h (cm)			Wei	ight (kg)	Age (yrs)								
	Imm	ature	M	lature	Imm	ature	Mat	ure	Imm	ature	Mature					
	రే	Ŷ	δ	Ŷ	ੋ	Ŷ	♂	ç	ð	Ŷ	ð	Ŷ				
Min	174	163	458	350	92	100	1,040	524	0	0	11	5				
Max	532	429	625	512	1,300	86 0	2,320	1,320	15	22	46	59				
Mean	353	299	552	432	563	381	1,694	893	5.9	3.7	23.9	22.3				
SE	2.6	2.3	1.7	0.8	21.2	13.2	39.1	9.9	0.2	0.1	0.4	0.3				
Ν	7 88	556	402	1,0 79	170	124	66	246	618	490	337	979				

Range and average of length (in cm), weight (in kg) and age (in yrs) of immature and mature long-finned pilot whales off the Faroe Islands in the period July 1986 - July 1988.

Table 4

Age distribution, mortality and survivorship

Age distribution

Most of the aged animals were collected between July 1986 and June 1987, reflecting the period when most of the collecting effort was expended; subsequent sampling, especially after December 1987, was mainly opportunistic. However, Kolmogorov-Smirnov goodness of fit (K/S) tests (Zar, 1984) on age frequencies showed no significant differences by time period for either sex. Therefore, because samples were believed largely to be representative of entire schools, all months and years of age data were subsequently combined into two data sets: male and female.

The resultant age frequency distributions are shown in Fig. 2. The male and female distributions are somewhat different. In females there is a relatively stable period after about 10yrs until about 30yrs, preceded by a steep mortality in the juvenile years, and again followed by a steeper mortality in the older age classes. In males, there appears to be a more continuous decline in age classes with time, although the decline appears steeper in the juvenile phase than subsequently. Curiously, there appears to be a dearth of males in the 0–2yrs classes, as had been found by Kasuya *et al.* (1988b) for Newfoundland. Between 0–2yrs, there are nearly 40% more females than males but by age 3yrs the number of males and females is similar. Indeed the number of males is actually greater in year class 3. The foetal sex ratio found by Desportes *et al.* (In press-a) would give rise to such a difference between males and females in the neonate and yearling classes from the decreasing proportion of males recovered *in utero* with increasing foetal age. Examination of cohorts by year reveals no consistently strongly or weakly represented year classes, thus the observed frequencies and 'noise' are probably due to chance.

Mortality and survivorship

Estimates of mortality rates (z) are given in Table 5. The estimates for both males and females are highest in the juvenile phase (Table 5), but unlike females, the males do not exhibit a pronounced period of relative stability and low mortality during mid-life, but rather decline steadily with age as noted above (Figs 2a and b). The two methods in Table 5 show similar overall estimates of 0.0745-0.0817 in males and 0.0622-0.0737 in females. Annual overall mortality rates based on Heinke estimates are 0.0586 (age 0-46yr) for males and 0.0605 (age 0-59yr) for females. Estimates for individual age segments (Table 5) are very different. The estimates are similar to those reported -0.0985 for females, using the same method. Sergeant (1962a) obtained 0.0445 for females and 0.058 for males in the age range 1-8yrs, using the log linear regression method. Estimates for short-finned pilot whales range from 0.0393-0.1064 with an overall value 0.0827 for males, and 0.0251-0

		Method of regr (N) = sa	linear loge ession; ample size		Method of Robson and Chapman (1961); (N) = sample size									
	М	ales	Fema	iles	M	ales	Fema	les						
(years)	-z	±0.95CI		±0.95CI	Z	±0.95CI	-Z	±0.95CI						
Juvenile: 0-10			0.0915 (N=608)	0.0186										
0-15	0.0722 (N=677)	0.0127	(11 000)											
3-15	0.1007 (N = 525)	0.0148												
Adult: 11-30	·		0.0104	0.0088										
16-35	0.0548 (N = 270)	0.0128	(N = 700)											
31-45	(((-270)		0.1273 (N=161)	0.0243										
Life:														
0-46	0.0745 (N = 966)	0.0047			0.0817 (N=966)	0.0048								
3-46	0.0778 (N = 814)	0.0052			0.0889 (N=814)	0.0057								
0-59			0.0737 (N=1,482)	0.0050			0.0622 (N=1,482)	0. 003 0						

Table 5
Estimates of mortality rate, z, for males and females long-finned pilot whales off the
Faroe Islands, for the period July 1986 - July 1988.

0.0708 (46.5–70yrs group excluded) with an overall value 0.0449 for females (Kasuya and Marsh, 1984). The current findings for the Faroese pilot whales are therefore within previously reported ranges of mortality rate for both species.

To examine the female age distribution further, the data in Table 6 were fitted using the Siler (1979) model described by Barlow and Boveng (1991) and the actual and predicted curves plotted in Fig. 3. The fitted curve reveals high juvenile mortality followed by a relatively stable period of lower mortality during prime reproductive years, culminating in a higher rate in the post-reproductive or senescent years. This is characteristic of a long-lived mammal investing heavily in each offspring (Barlow and Boveng, 1991). The K/S statistic (Fig. 3) shows no obvious selectivity for particular age classes, i.e. no significant rounding of ages occurred and no strong and weak cohorts were detected.

The age specific survival rates, s, in Table 6, can be converted to estimates of z using z = -lns, and are thus based on the fitted curve rather than the actual data. For females these age-specific estimates of z range as follows: 0.1485-0.243 (0-10yr); 0.0212-0.598 (11-30yr); 0.0661-0.3065 (31-45yr); 0.3425-0.5310 (46-50yr). These estimates generally encompass the mean rates calculated using the log linear regression method. However, it is impossible to determine which estimates of mortality are the most reliable for each age segment, if indeed any. All estimates are likely to reflect natural mortality. Exploitation is unlikely to affect mortality rate greatly, if at all, because entire schools are normally taken.

Observed and predicted frequencies at each age for female long-finned pilot whales off the Faroe Islands, with estimates of age-specific survival rate (s) calculated by the method of Barlow and Boveng (1991).

Age	Observed	Predicted	Lx	Px
in years	frequency	frequency	Proportion surviving	Age-specific surviva
0	87	85.65	1.000	0.862
1	60	73.82	0.862	0.886
2	64	65.42	0.764	0.906
3	80	59.28	0.692	0.923
4	64	54.69	0.639	0.936
5	41	51.20	0.598	0.947
6	66	48.48	0.566	0.956
7	37	46.34	0.541	0.963
8	44	44.61	0.521	0.968
9	34	43.20	0.504	0.973
10	31	42.02	0.491	0.976
11	39	41.02	0.479	0.979
12	41	40.15	0.469	0.980
13	34	39.36	0.460	0.982
14	33	38.64	0.451	0.982
15	50	37.97	0.443	0.983
16	28	37.31	0.436	0.983
17	21	36.65	0.428	0.982
18	40	35.99	0.420	0.981
19	33	35.31	0.412	0.980
20	44	34.60	0.404	0.978
21	32	33.86	0.395	0.977
22	49	33.06	0.386	0.974
23	32	32.21	0.376	0.972
24	41	31.31	0.366	0.969
25	35	30.33	0.354	0.966
26	33	29.29	0.342	0.962
27	22	28.18	0.329	0.958
28	30	26.99	0.315	0.953
29	27	25.73	0.300	0.948
30	36	24.39	0.285	0.942
31	14	22.98	0.268	0.936
32	19	21.51	0.251	0.929
33	18	19.98	0.233	0.921
34	19	18.40	0.215	0.912
35	8	16.78	0.196	0.903
36	15	15.14	0.177	0.892
37	14	13.51	0.158	0.880
38	16	11.89	0.139	0.867
39	6	10.31	0.120	0.853
40	9	8.79	0.103	0.837
41	8	7.36	0.086	0.820
42	4	6.04	0.071	0.802
43	2	4.84	0.057	0.781
44	4	3.78	0.044	0.759
45	5	2.87	0.034	0.736
46	5	2.11	0.025	0.710
47	1	1.50	0.018	0.682
48	1	1.02	0.012	0.652
49	1	0.67	0.008	0.621
50	0	0.41	0.005	0.588
N	1,477			



Fig. 3. Age frequency plot, all months and years, for female long-finned pilot whales off the Faroe Islands with fitted survivorship curve. n=1,482; K/S=0.0215; p=0.254. Symbols: Empty square = observed frequency.

Growth, growth rates and growth-related parameters

Length and weight

The length and sex distributions and ratios for the summed data collected under the international programme, as well as the length and sex distributions and ratios for each school are presented in Bloch *et al.* (1993a). As the length and sex distributions by school were not significantly different from the mean (Bloch *et al.*, 1993a), data for all schools can be pooled. The range and average values of length, weight and age are shown in Table 3.

Lengths

Males in the sample ranged from 174cm to 625cm (n=1,190) and the frequency distribution (Table 4; Fig. 4) shows two clear peaks, one for immatures (mean = 353cm ± 2.6) and one for matures (mean = 552cm ± 1.7). Equivalent values for females (n=1,635) are: range 163cm - 512cm (Table 3); immatures mean 299cm ± 2.3 ; and matures mean 432cm ± 0.8 .

The maximum length of males was 113cm (\times 1.22) greater than females; the peaks in immatures (54cm) and matures (120cm) were also longer. This pattern had been observed in previous studies of this species (Joensen, 1962; Martin *et al.*, 1987; Bloch, 1992; Sigurjónsson *et al.*, 1993). The maximum length of males in this study exceeds that of those from the western North Atlantic (Sergeant, 1962a; Moore *et al.*, 1978; 1979; Crespo *et al.*, 1985; Kasuya *et al.*, 1988b), and the southern form of the short-finned pilot whale (Kasuya *et al.*, 1988a); the northern form however has a greater observed maximum length (720cm, Kasuya and Tai, 1993).



Fig. 4. Length frequency distribution histogram for (a) 1,188 males, and (b) 1,639 females, all months and years, in the long-finned pilot whale off the Faroe Islands. *Symbols*: Striped bar = immatures; filled bar = matures.

Weights

Few weights of complete pilot whales have been reported (long-finned – Sergeant, 1962a; Bloch, 1992; and short-finned – Kasuya and Matsui, 1984; Mead and Potter, 1987).

The range in weights of the 236 males we examined was 92kg to 2,320kg (Table 3) with means for immatures of 563kg ± 21 and for matures of 1,694kg ± 39 (Table 4); in females the range was 100kg to 1,320kg (n=370) with means for immatures of 381kg ± 13 and for matures of 893kg ± 10 (Table 4). Thus males reach a maximum weight of about 1 tonne more than that of females (Figs 5a and b); the mean values for immatures and matures exceeds that of females by 182kg and 801kg, respectively (Table 4).

Body growth

Bloch *et al.* (1993b) examined growth in dorsal fin length and height, fluke length and half span, and flipper width and found that it is proportional to body length. Flipper length increases more slowly than body length for whales <250cm but faster for whales >250cm. Sexual dimorphism in flipper length and fluke width was also found.

In this study we examined growth in (1) skull length, (2) torso (eye to anus) and (3) tail. Linear trends were found with total body length (Figs 6a-c). Skull length decreases relative to body length (r=0.83; n=59; Fig. 6a), as does torso length to a lesser degree (r=0.55; n=59; Fig. 6b). The tail, however increases as a proportion of body length (r=0.79; n=59; Fig. 6c). Thus body proportions change as body length increases. The growth in the tail may be an adaptation to the high speed needed for catching their prey, which comprises mostly gregarious squid species (Mercer, 1975; Desportes and Mouritsen, 1993).

The growth pattern observed is similar to that seen in Newfoundland (Sergeant, 1962b: Figs 1-4), as well as the short-finned pilot whale (Yonekura *et al.*, 1980: Figs 6 and 12) and the harbour porpoise, *Phocoena phocoena* (van Utrecht, 1978), although not all the measurements are directly comparable. These species of toothed whales show a different pattern to the large baleen whales where the head has the greatest growth expansion relative to body length (Lockyer, 1981).

Weight-length relations

PRENATAL

The relationship between body weight (W in kg) and length (L in cm) for foetuses can be expressed by the equation in Lockyer (1993b) with a steeper correlation than after birth (see below):

$$W = 0.00006 \times L^{2.677} \tag{2}$$

POSTNATAL

The weight-length relationship has been examined by Bloch and Zachariassen (1989) and Lockyer (1993b). Briefly, a close relationship was observed between weight and length, and a single equation was found to be satisfactory for both sexes of all ages and throughout all months of the year (Lockyer, 1993b):

$$W = 0.00023 \times L^{2.501} \tag{3}$$

Length and weight at age

The length and weight of all males and females have been plotted at age to give a picture of the dispersion within each age class (males: Fig. 7; females: Fig. 8). Mean growth curves are also shown. The range in weight within each age class is greater than that of length due to the seasonal changes in body fat condition that may constitute 15–23% of body weight (Lockyer, 1993b).

[Text continues on p. 185]



Fig. 5. Weight frequency distribution histogram for (a) 236 males, and (b) 370 females, all months and years, in the long-finned pilot whale off the Faroe Islands. *Symbols*: Striped bar = immatures; filled bar = matures.



Fig. 6(a) and (b). Relative growth in length (a) of skull, and (b) torso. Symbols: Empty square = 24 males; \times = 35 females. (a) r=0.83; (b) r=0.55.



Fig. 6. (c) tail, of the long-finned pilot whale off the Faroe Islands. Symbols: Empty square = 24 males; $\times = 35$ females; r=0.79.



Fig. 7. (a) Length, and (b) weight at age; and (c) the average length ±standard deviation, and (d) the average weight ±standard deviation at each age class, determined from tooth GLGs, in the long-finned pilot whale males off the Faroc Islands. The fitted curves on (c) and (d) are calculated after Laird/ Gompertz 1. Each age class (n) on the graphs is placed at year n, but contains all animals from age n to age n+1, so that each year class in fact represents the mean age $(n+\frac{1}{2})yrs$. Symbols: Empty square = immatures; × = matures; filled triangle = unknown maturity; filled square =

symbols. Empty square = immatures; x = matures; filled triangle = unknown maturity; filled square = mean ±SD; (a) and (c) n=965 males; (b) and (d) n=222 males.



Fig. 7b. For legend see p. 180.



Fig. 7c. For legend see p. 180.



Fig. 8. (a) Length, and (b) weight at age; and (c) the average length \pm standard deviation, and (d) the average weight \pm standard deviation at each age class, determined from tooth GLGs, in the long-finned pilot whale females off the Faroe Islands. The fitted curves on (c) and (d) are calculated after Laird/ Gompertz I. Each age class (n) on the graphs is placed at year n, but contains all animals from age n to age n+1, so that each year class in fact represents the mean age $(n+\frac{1}{2})$ yrs. Symbols: Empty square = immatures; × = matures; filled triangle = unknown maturity; filled square = mean \pm SD; (a) and (c) n=1,478 females; (b) and (d) n=332 females.



Fig. 8b. For legend see p. 182.



Fig. 8c. For legend see p. 182.



Fig. 9. The logistic curve for the length at birth of long-finned pilot whales in the Faroe Islands. Symbols: Empty square == % born animals.

Length and weight at birth

NEONATAL LENGTH

The smallest female calf measured 163cm and the largest female foetus 191cm with 26 calves and 23 foetuses between these lengths. For males the values were 174cm and 185cm with 8 calves and 10 foetuses in between. For both sexes combined, 49 foetuses (26 males) and 39 calves (13 males) occurred between 163 and 191cm.

The results for each of the four methods used to estimate the mean body length at birth are summarised in Table 7.

Using method (1), no significant difference is found between the averaged neonatal length by sex (t=0.27; p>0.50). The pooled estimate is 177.1cm ± 0.9 (n=88). This method was also used by Sergeant (1962a) for this species off Newfoundland. His results (178cm males and 174cm females) are not significantly different to those for the Faroes. Using method (2):

% born =
$$100/(1 + e^{32.974} - 0.186 L)(155 \le L \le 205; r=0.98)$$
 (4)

and from this 50% of births will have occured at 177.3cm (Fig. 9).

Method (3) results in a length at birth of 178.4cm ± 0.6 (n=108) for both sexes combined.

For method (4) there were 25 newborn males and 36 newborn females with no neonatal line. No significant difference was found by sex (t=0.29; p>0.50). The pooled estimate of birthlength of 199.8cm ± 2.4 (n=61) in Table 7 is an overestimate compared to methods (1) – (2) since only born animals are included. This may indicate the neonatal line is not formed exactly at birth, but within the first 2–3 months of life.

The results from methods (1) - (3) are close, with the sum of fraction method giving a slightly higher value. The weighted mean of these, 177.6cm can be considered as the best estimate of the length at birth.

Male foetuses, cm	Female foetuses, cm	Both sexes, cm										
179.4 ± 1.0 N=18 (174-185)	178.1 ± 1.2 N=49 (163-191)	177.1 ± 0.9 N=88 (163-191)										
		177.3 N=143 (155-205)										
		178.4 ± 0.6 N=108 (163-191)										
204.2 ± 3.6 N=25 (174-245)	197.5 ± 3.3 N=36 (163-248)	199.8 ± 2.4 N=61 (163-248)										
		177.6										
Male foetuses, kg	Female foetuses, kg	Both sexes, kg										
		64										
143.6 ± 9.1 N=5 (92-175)	121.6 ± 8.2 N=5 (100-150)	132.6 ± 7.0 N=10 (92-175)										
		75										
	Male foetuses, cm 179.4 ± 1.0 N=18 (174-185) 204.2 ± 3.6 N=25 (174-245) Male foetuses, kg 143.6 ± 9.1 N=5 (92-175)	Male foetuses, cm Female foetuses, cm 179.4 ± 1.0 178.1 ± 1.2 $N=18 (174-185)$ $N=49 (163-191)$ 204.2 ± 3.6 197.5 ± 3.3 $N=25 (174-245)$ $N=36 (163-248)$ Male foetuses, kg Female foetuses, kg 143.6 ± 9.1 121.6 ± 8.2 $N=5 (92-175)$ $N=5 (100-150)$										

Table 7

Different methods used to calculate the length (cm) and weight (kg) of birth of long-finned pilot whales off the Faroe Islands.

The overlap in lengths between the longest foetus (191cm) and the smallest newborn (163cm), is similar to that found for Newfoundland (165–190cm, Sergeant, 1962a). Such overlaps are seen in other species such as the short-finned pilot whale (Kasuya and Marsh, 1984), striped dolphin, *Stenella coeruleoalba* (Kasuya, 1972), and in Dall's porpoise, *Phocoenoides dalli* (Kasuya, 1978).

NEONATAL WEIGHT

Between 1986 and 1988, the largest foetuses found weighed 83kg (female) and 84kg (male), while the smallest newborn found was a 92kg male. In 1990 an 81kg (male) newborn and an 82kg (female) newborn were found. If newborns are considered to be those calves with no neonatal line in the teeth, the mean weight for males was 143.6kg ± 9.1 (n=5, range=92-175kg); and for females 121.6kg ± 8.2 (n=5, range=100-150kg). The combined mean birth weight was 132.6 ± 7.0 (n=10). However given the small sample size, especially of truly 'newborn' calves (where the umbilicus is still unhealed) and the fact that newborns will probably gain weight rapidly, these estimates are likely to be both unreliable and overestimates. If the body weight of newborns is estimated from the mean length of birth calculated above using equation (2), a value of only 63kg is obtained. From this and the weights of the smallest newborns and largest foetuses found, a value of about 75kg is probably a reasonable estimate of mean weight at birth.

Unlike the case for length, there is no overlap between the weights of the largest foetus and the smallest newborn, although this may simply reflect the small sample size. However, if this is a real phenomenon it may be due to the rapid change in body proportions after birth and the deposition of fat and blubber stores (Lockyer, 1993b).

Postnatal growth

Males grow rapidly until they reach a length of 550cm (Figs 7a and c) and a weight of 1.7 tonnes (Figs 7b and d) at about 20yrs of age, after which the rate of growth slows considerably. Females grow rapidly until a length of 425cm (Figs 8a and c) and a weight of 1 tonne (Figs 8b and d) at about 13yrs, after which the growth rate declines.

Age, length and weight at sexual maturation

MALES

Male attainment of sexual maturity is examined in Desportes (In press) and Desportes *et al.* (In press-b) who reported attainment at 14.3yrs + 0.5, 493.8cm \pm 4.6 and 1,277kg \pm 32 and is not discussed further here.

ASM

The youngest sexually mature female observed was 5yrs of age while the oldest immature was 15yrs. A total of 31 females (between 5–15yrs) had their first corpus luteum. From method (1) the mean age was 8.4yrs ± 0.3 . This standard error, however, grossly underestimates the true variation in method 1, as it does not consider the error associated with each parameter used.

The least-squares regression of age and proportion of mature females using a logistic model (method 2) is given below:

% mature =
$$100/(1 + e^{10.070 - 1.249 t})$$
 (5 $\le t \le 12; r=0.98$) (5)

This equation gives a mean age (t) of 8.1yr (n=283; r=0.98) at a proportion of mature females of 50% (Fig. 11a). Method (3), the sum of fraction immature, uses data for 443 females ranging from 5–15yrs. The resultant ASM estimate is 8.7yrs ±0.2.







Fig. 11. The attainment of sexual maturity in long-finned pilot whale females off the Faroe Islands at (a) age (ASM), (b) length (LSM), and (c) weight (WSM). Symbols: Empty square = % mature females; arrow = 50% mature females.



Fig. 11b. For legend see p. 187.



Fig. 11c. For legend see p. 187.

All three methods give similar results. For the reasons given in Hohn (1989) the estimate from method (3), which has the largest sample size and the fewest assumptions, should be regarded as the best.

LSM

Method (1), using data for only the 31 females in their first pregnancy, gives an estimate of $378.8 \text{cm} \pm 2.5$. The size ranges from 349--407 cm after adjustment for conception date (see Materials and Methods section). The shortest mature female was 350 cm and the longest immature female was 418 cm.

Using method (2):

% mature =
$$100/(1 + e^{46.434 - 0.124 L})$$
 (350 $\leq L \leq 420$; $r=0.98$) (6)

gives an LSM of 374.5cm (r=0.98; n=492).

For the same 492 individuals, method (3) estimates an average LSM of 378.5cm ± 0.61 . For the reasons given above, this can be considered the best estimate of LSM.

Body weight at sexual maturity

From method (1) the range in weight of 11 females in their first pregnancy was 507–830kg (mean = 676kg ± 25), again after adjusting data for date of conception (see Materials and Methods section). The smallest mature and largest immature females were 524kg and 620kg, respectively. Using method (2):

% mature =
$$100/(1 + e^{21.863 - 0.036} W)$$
 (500 $\leq W \leq 700; r=0.98$) (7)

This gives an estimated WSM of 607.3kg (n=60; Fig. 11c). Using method (3) gives an average WSM of 627kg ± 2.7 (n=60; weight classes 525-725kg).

The range in estimates in ASM probably reflects the small sample size and the large variation among individuals. In general, WSM seems to occur around at least 600kg.

The values for LSM and WSM estimated here are not inconsistent with those obtained from the Laird/Gompertz growth formula (388.1cm and 638kg) and the length-weight relationship derived in equation 3 (WSM=645kg).

To summarise, a 'typical' female long-finned pilot whale will reach sexual maturity at about 8–9yrs, 380cm and 600kg. The corresponding values from the Newfoundland material are 6–7yrs and 366cm in length (Sergeant, 1962a; Kasuya *et al.*, 1988b).

Laws (1956) estimated length at sexual maturation as a proportion of asymptotic length for several species of marine mammals and obtained a range of 80.0–88.5% for whales. Using our data and the Laird/Gompertz model gives an estimate of 83.7–86.0%.

Sexual maturity – a question of body size more than age

Although the age overlap between immature and mature whales is wide, for both length and weight it is relatively narrow and includes only a few whales (Fig. 12). For males, it is from 11–16yrs; all males less than 480cm and 1,200 kg, regardless of age, are immature (Figs 12a and b). For females, it is 5–15yrs, but with only a single whale in some age classes; all females less than 375cm and lighter than 600kg (Figs 12c and d) are immature. Sexual maturation thus seems to relate more to body size than age. The strong weight/ length relationship found for the Faroese long-finned pilot whale (Lockyer, 1993b), makes it impossible to determine whether length or weight is more important.

This is supported later where it shown that there are differences in the growth pattern between some of the schools, and also differences between whales from the Faroes and Newfoundland (Sergeant, 1962a; b; Bloch and Lastein, 1993). This indicates that while the onset of sexual maturity is correlated with the body size of the whales, other factors appear also to be involved.

[Text continues on p. 194]



Fig. 12. The overlapping zone for males (a and b) and females (c and d) between immature and mature pilot whales off the Faroe Islands by length and weight at age. The number of whales per year class is included.
Symbols: Filled square = matures; filled triangle = immatures.







Fig. 13. The state of physical maturity at length and weight for males (a and c), and females (b and d) in the long-finned pilot whale off the Faroe Islands. Symbols: Empty square = observed means, the same as Figs 7c and d; 8c and d; $\times =$ stage 1 = immature; filled triangle = stage 1.5 = intermediate; plus = stage 2 = intermediate; hourglass = 2.5 = mature; plus with X = stage 3 = mature; (a) n=23 males; (b) n=12 females; (c) n=6 males; (d) n=3 females.



Fig. 13c. For legend see p. 192.



Fig. 13d. For legend see p. 192.

Physical maturity

In other whale species (e.g. sperm, Aguilar and Lockyer, 1987) vertebral fusion begins at both ends of the spinal column simultaneously, but caudal fusion is quicker, so that the last part to ossify is in the anterior half of the column. This pattern was also found in the present study. The pilot whale vertebral column consists of about 55 vertebrae, including the atlas and epistropheus; the last to ossify were nos 16–21 counted from the skull, differing from whale to whale as nos 16–17 or 19–21 as the last vertebrae in the intermediate state. As the last ribs are connected to vertebra no. 16, continued growth in length thus takes place in the lumbar region, the thoracic region remaining fixed.

Males reach physical maturity at an age of 25–30yrs and a length of about 570cm; none of the few males weighed were physically mature, even at a weight of 2,320kg (Figs 13a and c). Females are physically mature from about 30yrs at a length of 450cm and weight of 1,000kg (Figs 13b and d). The growth curves (Figs 7 and 8) show that growth rate declines for both sexes up to the ages of 25–30yrs, length of 450cm (females) and 570cm (males). However, while some whales are found to be physically mature, others are still growing, resulting in an apparent slow continuing growth with age (see later).

Growth increment

Foetal growth is treated by Martin and Rothery (1993) and changes in the foetal sex ratio through pregnancy by Desportes *et al.* (In press-a).

Neonates

The observed, but not significant, difference in neonatal length between the sexes increases in the first age classes. This pattern has been found in the material from Newfoundland, Iceland and Britain (Sergeant, 1962a; Martin *et al.*, 1987; Sigurjónsson *et al.*, 1993). It is not found in the southern form of the short-finned pilot whale and there are insufficient data for the northern form (Kasuya and Matsui, 1984; Kasuya and Tai, 1993).

Postnates

Postnatal growth in the short-finned pilot whale can be divided into four phases, each characterized by a declining growth rate compared with the preceding phase (Kasuya and Matsui, 1984). Four growth phases are evident in our data, but are less marked. These phases are: (1) suckling (the first 2 year classes – Desportes, 1990; Desportes and

Method	ASM, yr	LSM, cm	WSM, kg
Only 1 corpus luteum	8.4 ± 0.3	378.8 ± 2.5	676 ± 25
N (range)	N=26 (5-15)	N=31 (349-407)	N=11 (507-830)
Logistic curve	8.1	374.5	607.3
	N=283 (5-12)	N=492 (350-420)	N=60 (525-725)
Sum of fraction method	8.7 ± 0.2	378.5 ± 0.6	627 ± 2.7
	N=443 (5.15)	N=492 (350-420)	N=60 (525-725)
Best estimate	8.7	378.5	600

Table 8

Different methods used to calculate the age (yr), ASM, the length (cm), LSM, and the weight (kg), WSM, at the attainment of sexual maturity of G. melas off the Faroe Islands.

Phase	Age group	ੇ Length	ර Weight	♀ Length	♀ Weight	Calculation source
	1yr age class	6.8	16.6	5.9	12.8	
0	2yr age class	3.7	6.2	4.2	9.3	Observed means
	1+2yr age class	4.7	9.7	4.8	10.5	
2	Youth	1.46	6.45	1.54	4.38	
3	Adult	0.45	3.58	0.44	2.39	Laird/Gompertz I
4	Old adult	0.09	0.56	0.04	0.22	-

Growth increment in cm and kg per month for age groups of long-finned pilot whales off the Faroe Islands distributed on sexes.

Mouritsen, 1993; Desportes *et al.*, 1993a); (2) juvenile, up until the attainment of sexual maturity at 2–16yrs (males), and 2–8yrs (females) (Martin and Rothery, 1993); (3) first adult (until growth in length nearly ceases, at about 25yrs in males, and 20yrs in females); (4) second adult period with almost no further growth up to the fitted asymptote, L_{∞} (Table 9).

PHASE I

The increase in mean body length and weight is calculated from the observed means and using the estimated neonatal values of 177.6cm and 75kg obtained earlier for the first two age classes. Fitted curves are used for the later stages (Laird/Gompertz 1, see later and Tables 9, 10 and 11). In the first two years there is less agreement between the observed and theoretical values, largely as a result of the small sample sizes in the different age classes. The observed growth in the first year after birth is 6.8cm and 16.6kg/month for males, 5.9cm and 12.8kg/month for the females, which is an average increase of 20–23% of the birth length, and 103–133% increase in weight.

The observed increase in length in the first year is lower than the 55–70% increase found for several other odontocetes (e.g. Kasuya and Matsui, 1984; Hohn and Hammond, 1985). Growth in weight is high in the first year, when the whales more than double their weight. In the second year, growth in both length and weight is slower for both sexes, particularly in males with an average of about 4cm and 6–9kg/month (Table 9).

The overall growth rates for both sexes in the first two years are very similar so that at the end of the first phase, males and females are about the same size.

PHASE 2

This includes the period of juvenile and pubertal growth until the onset of sexual maturity at about 8yrs in females and until past maturity in males at 16yrs. It is characterized by high growth rates (although considerably less than in phase (1)) of 1.46–1.54cm/month and 6.45–4.38kg/month for males and females, respectively (Table 9).

PHASE 3

This covers the period of high reproductive activity for females (Martin and Rothery, 1993) and ends at an age of 20yrs where growth is approaching the asymptotic length L_{∞} . For the males this period ends at an age of 25yrs when they have been histologically, but not socially, mature for about 9yrs (Desportes *et al.*, 1993b; In press-b). Growth rates are considerably lower than in the previous phase, at 0.45–0.44cm/month and 3.58–2.39kg/ month for males and females, respectively (Table 9).

	2	558	563	567	571	575	578	581	584	587	590	592	594	596	598	600	602	603	605	606	608	609	610	611		625
	III	551	554	556	558	560	561	563	564	565	566	567	568	568	569	570	570	570	571	571	572	572	572	572		574
	II	560	563	566	569	571	574	575	577	579	580	581	582	583	584	585	585	586	586	587	587	587	588	588		590
	I	557	560	562	564	566	568	569	571	572	573	574	575	575	576	576	577	577	578	578	578	578	579	579		580
	₫ -S E	4.8	5.3	3.8	5.2	5.9	10.2	5.8	6.6	5.7	7.4	7.3	2.6	0.6	9.0	9.3	8.3					10.0				
	ð-Mean	552	571	562	571	576	586	570	579	579	567	576	589	574	576	585	572			600		590		607		
	N- گ	15	20	14	14	10	×	16	×	15	6	×	ę	4	4	4	m			1		7		1		
ly (IV).	Age	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46		ീ
Bertalant	5	257	282	305	327	348	367	384	401	416	431	444	456	468	479	489	498	507	515	522	529	536	542	548	553	
	III	209	249	284	316	344	370	392	412	430	445	460	472	483	493	502	510	517	523	529	534	538	542	546	549	
	п	232	258	283	308	331	354	375	394	413	430	446	460	473	485	496	506	515	523	530	536	542	548	552	556	
	I	229	256	283	309	334	357	379	399	418	435	450	464	477	489	499	508	517	524	530	536	541	546	550	554	
	ð -SE	3.1	2.8	3.1	2.6	3.4	4.4	3.1	4.7	5.6	5.4	5.1	6.0	7.5	6.0	6.6	8.0	7.4	5.9	6.9	4.9	5.9	6.1	6.0	6.4	
	♂-Mean	218	263	293	317	343	360	378	388	418	425	438	466	460	473	499	508	508	518	555	528	548	550	569	552	
	N- ₽	55	45	51	76	65	54	68	36	38	34	29	25	28	21	21	31	18	21	17	13	20	16	11	13	
	Age	0	-	7	ę	4	Ś	9	L	~	6	10	11	12	13	14	15	16	17	18	19	20	21	22	23	

Table 10

Average and fitted lengths at age for G. metas off the Faroe Islands following the models of Laird/Gompertz (I), Laird/Gompertz (II), Bertalanffy (III) and

2	452	454	456	459	461	463	465	466	468	470	472	473	475	476	478	479	480	481	483	484	485	486	487	488	489	490	101	164	74 74	764	493	512
III	438	439	439	440	440	441	441	442	442	442	442	443	443	443	443	444	444	444	444	444	444	444	444	444	444	444	346	C##	0 1 1		445	445
Π	447	448	448	448	448	448	449	449	449	449	449	449	449	449	449	449	449	449	449	449	449	449	449	449	440	440	ţ,	449	644	447	449	440
I	444	444	445	445	445	445	445	445	445	445	445	445	445	445	445	445	445	445	445	445	445	445	445	445	245			5 5	644 C	440	445	445
ð -S E	2.7	5.5	3.6	3.1	3.6	4.5	4.4	5.7	3.3	6.2	6.3	6.3	8.6	1.0	8.3	6.7	9.1									2 2	c.0					
ð-Mean	445	441	446	442	448	456	449	452	452	444	450	460	458	451	461	458	455	437	448	469	2	440			~~~		404				475	
N- δ	36	14	19	18	20	×	15	14	16	9	. 6	. oc	4	. ~	4	• •	, v	• —	. –	- •	4	-	4		-	- (7				1	
Age	30	31	32	33	34	35	36	37	38	39	404	, 1	4	5 64	44	45	46	47	48	40	f S) 2 2	5	10	50	40	55	56	57	58	59	۔
N	312	320	327	335	342	348	355	361	367	372	378	383	388	303	308	402	101	411	115			774	120	474	432	435	438	441	444	447	449	
III	291	306	320	332	343	353	362	370	175	384	300	395	400 100	405	400	412	715	418	101	124	140	629	124	474	431	432	433	434	435	436	437	
I	224	249	273	295	315	333	348	362	375	385	395	403	D OA	415		2024	120	437	40F		104	439	044	442	443	444	445	445	446	447	447	
-	220	250	777	302	324	343	360	374	386	396	405	412	717	417	17F	130		70 1		401	400	439	440 1	441	442	442	443	443	444	444	444	
δ-SE	7.7	. r i c	10	6	2.5		. r	1		0 7	, r ; c	- 0 - i c	, c , c		- v i c	, c 4 6	7.0	, 4 1 1	<u>,</u> t	- 7	2.7	2.6	2.9	2.7	3.5	3.1	3.1	2.6	3.3	"	4.7 4.7	
ở-Mean	213	243	284	300	306	340	355	358	202		305	000	411	411	410	124	441	450	470	432	434	440	438	445	444	443	443	440	440	141	447	
\$-N	8	3 9	3 3		64	5 =	F 7	00	5	1	70	10	9	‡	n 7	2 2 2	4 6 7 0	57 5	17	41	33	43	32	50	31	41	34		20		27	
Age			- c	4 6	Ω, ∠	t 4	` '	0 r	~ 0	• •	л с	2	= :	2 :	<u>.</u>	4 v	<u>c</u> 1 ;	<u>0</u>	11	18	19	20	21	22	23	24	25	36	27	à c	70 70	

Table 10-continued

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Table 11	Table 11
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Average and fitted weights at age for G. melas off the Faroe Islands following the models of Laird/Gompertz.

Age	ੈ-N	ਰੋ-Mean	ै-SE	8-Laird	♀-N	♀-Mean	♀-SE	♀-Laird
0	15	174	12.7	190	16	152	12.0	173
1	11	249	16.4	247	11	263	18.1	227
2	14	344	21.3	312	11	313	29.2	285
3	22	411	23.7	384	20	373	12.5	345
4	11	501	39.0	462	19	434	18.6	406
5	15	610	18.6	544	8	507	23.7	466
6	18	648	21.1	629	20	545	27.7	524
7	11	688	46.1	/15	11	496	43.5	578
8	8	812	66.2	801	16	690	32.4	628
9	7	837	40.5	88/	8	691	14.0	6/4
10	8	1029	38.0	970	10	/00	23.0	710
11	/	1000	07.2	1050	10	831	40.8	152
12	0	1012	40.0	1127	0	841 805	30.4	/65
13	4	1013	57.4 129.1	1200	10	805	20.0	814 820
14	3	1377	130.1	1200	12	01/ 779	10.3	861
15	2	11/3	133.3	1332	15	//0	19.3	801
17	2	1190	130.0	1391	2	930	104.9	000 806
19	3	1411	120.2	1440	3	921	104.8	010
10	7	1400	25.0	1497	8 0	022	41.9	910
20	2	1608	187.5	1585	11	922	36.4	032
20	2 4	1569	79.6	1624	7	972	38.3	932
22	3	1785	59.6	1659	7	951	35.1	949
23	3	1593	38.3	1690	8	969	53.2	955
24	5	1679	181.6	1719	13	900	31.0	960
25	3	1880	109.1	1744	9	959	35.5	965
26	5	1804	87.8	1767	5	972	64.6	969
27	3	1959	95.8	1788	8	961	42.4	972
28				1807	4	998	36.8	975
29	1	1596		1823	2	889	79.0	977
30	2	1890	390.0	1838	6	1083	68.7	979
31	2	1963	62.5	1852	6	1000	74.0	981
32	2	2079	21.0	1863	3	1049	26.2	983
33	1	1754		1874	2	1030	100.0	984
34				1883	7	953	59.7	985
35	1	2098		1892	1	1110		98 6
36	1	2060		1899	3	1053	52.0	98 6
37	1	2020		1906	2	973	63.0	987
38	1	1820		1912	2	1150	50.0	988
39	2	1930	24 0. 0	1917	2	900	40.0	988
40				1922				988
41				1926	2	1100	100.0	989
42				1930	1	1070		989
43				1933	1	1020		989
44				1936				989
45				1939	2	1088	192.0	990
46				1941				99 0
47				1943				990
48				1945				990
49				1947				990
50				1948				9 90
51				1949				990
52				1950				990
53				1951				9 9 0
54				1952				990
55				1953	1	1275		990
L				1959				990

PHASE 4

In this last phase the males become socially mature (Desportes *et al.*, 1993b; In press-b), while the females are at the middle and end of their reproductive period (Martin and Rothery, 1993). Both sexes reach physical maturity during this period (Fig. 13). There appears to still be a very slight increase in length and weight, of 0.09cm/month and 0.56kg/ month for the males, 0.04cm/month and 0.22kg/month for the females.

The observed growth rates found for the four different periods are similar to those found for G. macrorhynchus, except for the first year, when G. melas shows a slower growth rate (Kasuya and Matsui, 1984).

Growth curves

The length-age and weight-age relationships were estimated for both sexes. Only the Laird/Gompertz model was used to fit the weight-age relationship, while four different models based on the Bertalanffy and Laird/Gompertz equations were used for the length-age relationship shown below. Data from all 40 grinds were used for these calculations. The results are given in Tables 10 and 11 from these equations and the mean length/weight at age from the actual data. Fig. 14 plots the results for females. Equations I and II give the best fit and are not significantly different from each other. Equation II only uses data sets where the weight of the whale is known and was used to examine the level of agreement between the weight-age and length-age relationships obtained from the Laird/Gompertz model to the estimated length-weight power function. Equation I is used in all figures and subsequent comparisons because of the low number of weighed animals.

I. Laird/Gompertz calculated from iterative least-square analyses.

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.

For the weight at age:

$\delta \delta$: W = 189.68 e $^{0.2802/0.120(1-e)}$)	$W_{\infty} = 1959 kg$
$QQ: W = 173.05 e^{0.2931/0.168(1-e^{-0.168t})}$)	$W_{\infty} = 990 kg$
For the length at age:		
$\delta \delta: L = 228.92 e^{0.1209/0.13(1-e^{-0.13t})}$)	$L_{\infty} = 580$ cm
$\Im \Im: L = 219.80 e^{0.1411/0.20(1-e^{-0.20t})}$)	L = 445 cm

II. Laird/Gompertz obtained from the estimated weight-age function (Laird/Gompertz) and the weight-length power function.

$d d: L = 232.04 e^{0.1120/0.120(1-e^{0.1120})}$)	$L_{\infty} = 590$ cm
$\varphi \varphi: L = 223.69 e^{0.1172/0.168(1-e^{-0.168t})}$)	$L_{\infty} = 440$ cm

III. Bertalanffy with L_{∞} as the mean of whales older than 20 and 25 for females and males respectively.

 $\delta \delta: L = 574(1-e^{-0.116(t+3.9)})$ $Q Q: L = 445(1-e^{-0.103(t+10.3)})$ $L_{\infty} = 574 \text{ cm}$ $L_{\infty} = 445 \text{ cm}$

IV. Bertalanffy with L_{\perp} as the longest whale in each group.

$\delta \delta: \mathbf{L} = 625(1 - e^{-0.071(t+7.45)})$	$L_{\infty} = 625 \text{cm}$
$QQ: L = 512(1-e^{-0.040(t+23.5)})$	$L_{\infty} = 512$ cm



Fig. 14. The average length \pm standard deviation, determined from tooth GLGs, in the long-finned pilot whale females off the Faroe Islands. The 4 different fitted curves are calculated after Laird/Gompertz I and II, Bertalanffy III and IV, following Table 10. Each age class (n) on the graphs is placed at year n, but contains all animals from age n to age n+1, so that each year class in fact represents the mean age $(n+\frac{1}{2})$ yrs. Symbols: Empty square = observed means \pm SD, the same as Fig. 8c; 1 = Laird/Gompertz I; 2 = Laird/Gompertz II; 3 = Bertalanffy III; 4 = Bertalanffy IV.

For the Newfoundland animals (Sergeant, 1962a; Kasuya *et al.*, 1988b), growth was divided into 3–4 phases: the first from 0–2.5yrs; the second from 2.5yrs until sexual maturity; and after that a rapidly decreasing growth rate until physical maturity, with a clear female L_{∞} , but not one for males because of the small number of large animals. In this study no clear asymptotic value for length or weight was found but rather a very slow, but significant increase in length with age (Tables 9 and 10). Growth rates in length for males over 25yrs and females over 20yrs are significantly different from zero (t=2.619 for males; t=5.804 for females). The same is true for weight for animals older than 20yrs for both sexes (t=3.336 for males; t=4.228 for females). The correlation for the weight of males older than 25yrs is not significant (t=1.054) but the sample size is small.

This pattern of protracted growth seems to be present in the pilot whales stranded in Iceland (Sigurjónsson *et al.*, 1993). However the British (Martin *et al.*, 1987) or Newfoundland (Kasuya *et al.*, 1988b) material and the material for the short-finned pilot whale (Kasuya and Matsui, 1984; Kasuya and Tai, 1993) all show a clear asymptotic value. However, comparisons should be made with caution because few whales from Newfoundland, Iceland or the British Isles were aged using cementum.

Maximum immature and minimum mature lengths and ages for long-finned pilot whales taken in grinds off the Faroe Islands on 11 September 1986, 22 and 23 January 1987. \underline{L} = length in cm, \underline{A} = age in yrs and (N) = number of individuals within the overlapping zone.

Date	11 September 1986		22 January 1987		23 January 1987	
Parameters	Length (N)	Age (N)	Length (N)	Age (N)	Length (N)	Age (N)
Males Females	532-500 (4) 368-370 (0)	9-11 (0) 9 (0)	487 (0) 369-350 (22)	15 (0) 15-11 (22)	462-460 (1) 390-369 (8)	12-13 (0) 8- 7 (1)

Table 13

Observed mean lengths ± standard error and sample size (N), of male and female long-finned pilot whales larger than 460cm and 360cm respectively, from Newfoundland and Faroe Islands.

Source	Males, cm	Females, cm	
Newfoundland, 1962	$538.0 \pm 0.7(n=454)$	$421.1 \pm 0.8(n=1,364)$	
Faroe Islands, 1978	$540.8 \pm 4.2 (n = 103)$	$441.0 \pm 1.9 (n = 249)$	
Faroe Islands, 1986-88	$540.4 \pm 1.9(n=476)$	$429.2 \pm 0.8(n=1,296)$	

A number of possible explanations for this continued growth can be put forward. For example, systematic overestimation of length, weight and age could result in the lack of an asymptote to the growth curves. However, such problems, at least with respect to length, seem to be unlikely, as shown by Bloch *et al.* (1993a). Errors in individual measurements would probably be swamped by the natural variation in the population, although the smaller sample sizes in the older age classes may give such errors greater importance.

A second possibility is that the observed growth pattern might reflect density-dependent changes in L_{∞} over time, perhaps as a result in the cyclic occurrence of prey (and thus whales) in the Faroese waters (e.g. Joensen and Zachariassen, 1982; Bloch *et al.*, 1990; Hoydal and Lastein, 1993). Some support for this theory is given by the fact that, for females at least, the mean length of larger animals (females >360cm) in the Faroes was higher in 1978 (about 440cm; Moore *et al.*, 1978; 1979) than in 1986–88 (about 430cm) as shown in Table 13, although this also may reflect population/sub-population differences (see below).

Despite the variation in sample sizes, it appears that Faroese and British Isles pilot whales reach greater lengths than those of Newfoundland and Iceland. If true, this may reflect the greater productivity of the northeastern Atlantic (e.g. see Sergeant, 1977) and the Faroes Bank is well known as a highly productive area (e.g. Hansen *et al.*, 1990) frequented by pilot whales (Buckland *et al.*, 1993).

Another possible explanation is that more than one sub-population is found in the Faroese sample, with different values of L_{∞} and age compositions. To consider this further we compared the estimated Laird/Gompertz growth curve with the actual length measurements for each grind. Three grinds differed significantly from the average.

The first grind, containing 220 whales, was landed at Sandoy on 11 September 1986 (see Bloch *et al.*, 1993a: fig. 1, no. 4). It had a higher growth rate and greater L_{∞} reached at an earlier age for both sexes than the mean. The overall life span (Fig. 15a) was shorter and the grind differed significantly in growth pattern from the average of all 40 pods (t_4 =8.87).

Parameter	Newfoundland ¹	Faroes, this study	Faroes, 1978 ²
Mean L, $\delta > 460$ cm	538.0 ± 0.7 (n = 454)	$540.4 \pm 4.9 (n = 476)$	540.8 ± 4.2 (n=103)
Mean L, $\Im > 360$ cm	421.1 ± 0.8 (n=1,364)	429.2 ± 0.8 (n=1,296)	$441.0 \pm 1.9 (n=249)$
Mean L, $\delta > 25$ yrs	557.0 ± 8.9 (n = 5)	570.0 ± 4.9 (n = 125)	-
Mean L, $\Im > 25$ yrs	448.8 ± 2.6 (n= 53)	$446.4 \pm 0.9 (n = 323)$	-

 Table 14

 Mean lengths of adult pilot whales from Newfoundland and the Faroe Islands.

¹Sergeant, 1962a; Kasuya et al., 1988; ²Moore et al., 1978; 1979.

The other two grinds were landed on 22 and 23 January 1987 almost as far away as possible from each other (see Bloch *et al.*, 1993a: fig. 1). The first (no. 17) had 152 whales and the second (no. 18) had 156 whales. Both had lower growth rates than the mean (t_{17} = -5.58; t_{18} =-4.07), but had the same L_{∞} as generally observed (Figs 15b and c).

Males from school no. 4 matured at an earlier age than those from nos 17 and 18. This pattern was not consistent for the females. Certain characteristics of these grinds are given in Table 12.

Bloch *et al.* (1993b) and Bloch and Lastein (1993) have shown significant differences in certain morphometric characters between Faroese and Newfoundland animals. A number of other studies have suggested that different stocks might occur. They include evidence from morphometry (Lockyer, 1993a), genetics (e.g. Andersen, 1988) and pollution burdens (Andersen, 1993; Caurant *et al.*, 1993; Aguilar *et al.*, 1993), although none of the evidence is equivocal. Further work on pilot whales from several North Atlantic locations is necessary before the stock structure can be elucidated.



Fig. 15. The growth pattern for grinds (a) no. 4 (11 September 1986; n=165), (b) no. 7 (22 January 1987; n=145), and (c) no. 18 (23 January 1987; n=154) off the Faroe Islands, the numbers according to Bloch, *et al* (1993a). The fitted growth lines for all 40 pods are included. Each age class (n) on the graphs is placed at year n, but contains all animals from age n to age n+1, so that each year class in fact represents the mean age $(n+\frac{1}{2})yrs$. Symbols: Empty square = males; plus = females; the solid lines as on Figs 7c and 8c.







Fig. 15c. For legend see p. 202.

Summary comparison with the long-finned pilot whale around Newfoundland

Mean body lengths for pilot whales at the Faroes and Newfoundland are summarised in Table 14. The length differences for animals >25yrs old are not significant for either males or females. Previously, Moore *et al.* (1978; 1979) had found that the Faroese pilot whales were longer (on average 1.9% in males, 4.8% in females) than those around Newfoundland for males >460cm and females >360cm. The observed mean lengths for the males are not significantly different (t=1.0). The mean length of the Faroese females from 1986–88 are significantly longer (1.9%) than those from Newfoundland (t=7.4), and the 1978 mean length of Moore *et al.* (1978; 1979) is even greater. Only a more thorough investigation will show if this may be caused by different growth patterns or survival rates in the adult female group.

The growth pattern found in this study, with males having a larger body size (x1.22) and a higher natural mortality rate and shorter life span (by 13yrs) than the females agrees not only with the findings for the long-finned pilot whale off Newfoundland (Sergeant, 1962a) but also the short-finned pilot whale (Kasuya and Matsui, 1984) and the sperm whale (Ralls *et al.*, 1980). However the Faroese pattern did not show the clear secondary burst of growth found in Newfoundland (Sergeant, 1962a) and the sperm whale (Best, 1970; Lockyer, 1981). The mean lengths at age (Fig. 8c) are mostly below the estimated growth curve between ages 7–17yrs, especially between 11–14yrs. There may be a slowing of growth up to age 12yrs followed by a spurt towards adulthood, but the validity of the detailed growth curve has not been tested.

The mortality and survivorship rates are similar in the Faroese and Newfoundland samples although longevity is greater in the former. The considerably greater ages found in the Faroese schools compared with Iceland and the British Isles, may reflect the fact that stranded schools may only represent sub-groups of the original schools. The pilot whales taken off Newfoundland, although driven as entire schools, were not always systematically and thoroughly sampled which may lead to error and/or bias. The observed morphometric differences between Newfoundland and the Faroes regions and the many similarities throughout the whole North Atlantic make the question of stock identity extremely important. Information on distribution, movements and molecular biology are required to resolve this.

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A Review of Molecular Evidence Relating to Social Organisation and Breeding System in the Long-Finned Pilot Whale

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ABSTRACT

Several studies have recently applied molecular methods to questions concerning pod structure and mating system in the long-finned pilot whale, using material sampled from the Faroese drive fishery. The methods include DNA fingerprinting, protein electrophoresis and microsatellite polymorphisms. There is now firm evidence that pods contain related individuals and that the adult males in a pod are rarely the fathers of the unborn foetuses they accompany. Based on two pods that were studied in detail, it was concluded that there is little or no dispersal of either sex from the natal group, even by mature males. This situation parallells observations made on killer whales. Mating appears to occur reciprocally between pods and there is no evidence of strong male reproductive dominance. These findings can be explained in terms of inclusive fitness, but require work in order to establish generality.

INTRODUCTION

This volume contains papers concerning many aspects of pilot whale biology, making it the most extensive study since Sergeant's seminal work published three decades ago (Sergeant, 1962). As such, it would be incomplete without a description of recent work using molecular genetic techniques to elucidate aspects of pilot whale social organisation. However, in contrast to the majority of papers in this volume, the work described in this review has all been published recently elsewhere. We would therefore like to stress at the beginning that this paper contains no new data and has been included primarily for completeness in the context of the volume.

The long-finned pilot whale, *Globicephala melas*, is a medium-sized whale, relatively abundant in the North Atlantic (Klinowska, 1991). Individuals swim in large groups or pods, usually containing between 50 and 200 animals. The species is pelagic, apparently following shoals of squid, its principal food. There is currently no evidence to suggest the existence of local resident populations.

Pilot whales are extremely social and show strong herding behaviour (e.g. Joensen, 1976). This characteristic presumably accounts, in part, for the high frequency at which pilot whales mass-strand. For centuries, the ease with which pilot whales may be herded has been exploited by coastal peoples to capture entire pods for food. Today, only the Faroe Islanders retain a traditional drive fishery, harvesting some 1,700 whales annually. Between 1986 and 1988, this catch has formed the focus of an international programme of research to examine many aspects of pilot whale biology including genetic analysis (Bloch *et al.*, 1993).

Observations concerning social organisation

Observations relating to social organisation are limited because of two factors. First, individual pilot whales are difficult to identify in the field. Second, pods are wide-ranging

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and contain many individuals. Nonetheless, inferences can be drawn from circumstantial evidence relating to both the pilot whale itself, and to two of its closest relatives, the short-finned pilot whale (*G. macrorhynchus*) and the killer whale (*Orcinus orca*).

There are several lines of evidence to suggest that pilot whale pods are matrifocal. Both of the related species mentioned above show a high degree of group stability over time. A resident population of individually recognised killer whales in Puget Sound in the Pacific Northwest, has shown no dispersal from natal groups in more than fifteen years of study (for example Bigg *et al.*, 1990). Over a shorter period, photo-identification has been used to study a resident population of short-finned pilot whales in waters of the Canary Islands (Heimlich-Boran and Heimlich-Boran, 1990). Relatively stable subgroups were identified, although group membership does not appear to be as rigidly defined as it is in *O. orca*. Further support for the long-term association of relatives is given by a study of the reproductive physiology in *G. macrorhynchus* harvested in Japan. Kasuya and Marsh (1984) found evidence of extended suckling, some older females still giving small amounts of milk to their offspring up to 13 years after birth. Such a phenomenon is presumably social in function since the calf's nutritional needs are probably satisfied after a year (Brodie, 1969). Extended suckling may also prove to be a characteristic of *G. melas* (Brodie, 1969).

Most authors assume that *G. melas* is polygynous, drawing attention to sexual dimorphism and evidence of male:male competition (e.g. Sergeant, 1962; Evans, 1987; Martin, 1990). Mature males are up to a metre or so longer than mature females and almost double their maximal weight. Despite sex ratio parity at birth, mature individuals show a pronounced sex-bias towards females (Sergeant, 1962). This is thought to result from a greater longevity among the females. Surface scarring on adult males is most likely caused by intraspecific fighting (Sergeant, 1962). Head-butting fights, where males swim towards each other and collide deliberately, melon to melon, have also been noted (Reilly and Shane, 1986). Finally, anecdotal evidence also suggests the existence of a 'leader' or dominant individual (their 'pilot'), although such an animal could be of either sex.

Field observations of mating are unavailable. However, by extrapolating back from foetal size to conception date, Martin and Rothery (1993) have concluded that mating is broadly seasonal, with a diffuse peak in early summer, in agreement with Sergeant (1962). In the polygynous mating system favoured by most authors, mature males are expected to move between pods in search of receptive females. Such a system implies seasonal changes in the mean pod size and composition. Again, observational evidence is sparse. Both Faeroese records and Sergeant (1962), indicate that sightings of all-male pods are extremely rare. Sergeant (1962) comments further that 'bachelor herds' (small groups containing only mature males and 'senile' females) are more likely to be seen in late summer. However, in view of the paucity of data concerning the behaviour of these groups, it is perhaps unwise to leap immediately to the 'obvious' conclusion that they represent mature males moving between pods.

Very large groups of pilot whales, numbering a thousand or more whales, are also seen occasionally (e.g. P.G.H. Evans, pers. comm.). These gatherings appear to be fusions between several pods and thus parallel observations made on the killer whale. Killer whale pods are numerically much smaller, but are sometimes seen to merge for short periods (Heimlich-Boran, 1988). At such times, observers have noted much surface activity, such as breaching and tail-lobbing, and sexual arousal among the males. Presumably these events provide potential mating opportunities.

In summary, sufficient information is available to speculate about several aspects of pilot whale social organisation. The consensus view is that pilot whale pods are basically matrifocal and that adult males move from pod to pod in search of mates. However, there

are two important cautionary notes. First, there is a strong temptation to use terrestrial parallells as a basis for interpreting patterns of behaviour. Given the unique marine ecology of cetaceans, there may be occasions when this approach is misleading. Second, for the study of many aspects of social organisation the ability to determine age and sex is critical. For *G. melas* these parameters are usually only available when dealing with stranded or harvested material. Given the convenience of working with the latter, it is not surprising that most of our knowledge about pod composition derives from the Newfoundland and Faeroese fisheries. Most of these whales were caught during the summer months and all ventured close to shore. Sergeant himself (1962) notes that there is a difference in the size of pods seen close to land compared with those found further out to sea. Therefore, the possibility that the whales in these two studies are not representative of the population as a whole must not be ignored.

Genetic analysis

Genetic analysis allows us to examine the relationships between pod members and to test some of the predictions that have been made about social organisation in the pilot whale. Data have been gathered using three principal techniques: DNA fingerprinting; microsatellite polymorphisms; and protein polymorphisms.

(a) DNA fingerprinting

DNA fingerprinting is a method which involves the detection of polymorphism amongst some of the most variable DNA sequences yet discovered, known as minisatellites (Jeffreys *et al.*, 1985). These sequences show sufficient variability for positive paternity analysis and the unique identification of individuals. Furthermore, although minisatellites were originally studied in humans, the methodology has since been found widely applicable to other species (for a review, see Burke, 1989).

(b) Microsatellite polymorphisms

Microsatellites are short stretches of di- or trinucleotide repeats (e.g. the dinucleotide repeat AGAGAGAGAG) which vary in the number of repeats they contain (Litt and Luty, 1989; Tautz, 1989; Weber and May, 1989). The resultant variation in length may be screened using the polymerase chain reaction (PCR; Sakai *et al.*, 1988) and yields intermediate levels of genetic variability (Schlötterer *et al.*, 1991).

(c) Protein polymorphisms

Many proteins are polymorphic for amino acids which are not directly involved in the catalytic process. These differences may be resolved by electrophoresis. The levels of genetic variability uncovered are lower than either of the other methods but have the advantage that they can be screened extremely rapidly and easily.

Detailed descriptions of these methodologies are available elsewhere and are not being considered here more than is necessary. The genetic analysis of pilot whale social organisation falls into two broad categories; that dealing with relatedness between pod members and that concerning the pattern of mating. In the latter case, since females are constrained in behaviour by the demands of gestation and lactation, this has concentrated entirely on male mating behaviour.

Relatedness within groups

(i) Genetic differentiation of pods

All available evidence supports the idea that pilot whale pods comprise related individuals. If pods were random assemblages of unrelated individuals, drawn from a

panmictic population, we would expect to find few or no genetic differences between pods. The presence of relatives will change this. Any genes which are shared between relatives will tend to be at a higher frequency in the pod compared with the population at large, and will, therefore, tend to establish inter-pod differences. The greater the average degree of relatedness, the larger will be the differences found between pods. Strong genetic differentiation of pods has been observed at protein loci (Andersen, 1988; 1993), a minisatellite locus (the sequence on which DNA fingerprinting depends) (Amos *et al.*, 1991), and at several microsatellite loci (Schlötterer *et al.*, 1991; Amos, 1993). As an example, at the highly variable HMW locus (Amos *et al.*, 1991) the difference between two pods of about 100 animals each was significant at the 0.1% level (χ^2 =43.506, 9df. 0.001>>p; allelic classes pooled to provide expected values greater than 5).

(ii) Testing for the presence of mother: offspring pairs

If pilot whale pods are indeed matrifocal, each should contain a large number of mother:offspring pairs. To examine how many such relationships exist using DNA fingerprinting would involve a great number of comparisons, making the process prohibitively time consuming. Highly variable single locus systems, for example microsatellites, could be used to eliminate many possible combinations, but are unlikely to identify the true mother with confidence. Instead, individual whales are likely to be genetically compatible with zero, one, two or more females, any or none of which may be the true mother. In order to use single locus genetic information to estimate the number of whales in a pod which are accompanied by their mothers, a novel analytical approach was used (Amos, 1993; Amos *et al.*, 1993).

For each individual in a pod, the actual number of females which are both of sufficient age and compatible genetically (O) is compared with the number that would be expected to be present by chance alone (E). E is calculated assuming random assortment of alleles amongst mature females in the pod. When the true mother is absent, O and E should be equal, and $\{O-E\}$ is distributed about zero. If the mother is present, however, $\{O-E\}$ is no longer zero, but is distributed about some value V. It can be shown that, using highly polymorphic genetic markers, or if the number of possible mothers is large, V tends towards 1. Thus, in a sample of individuals, some accompanied by their mothers and some not, $\{O-E\}$ will be distributed bimodally, with peaks at 0 and around 1. In such samples, the mean value of $\{O-E\}$ becomes an estimator for the proportion of individuals which are with their true mothers. Fig. 1 shows how this analysis was applied to a pod containing 100 pilot whales. The estimated proportion of individuals accompanied by their mothers declines from about 95% among younger whales to 30% among adults. The internal control, a parallel analysis looking for paternity, yields values which do not differ significantly from zero. Summed over all age classes and both study pods, the estimated proportions of individuals with their mothers is 46% $\pm 10\%$ (95% confidence limits) and with their fathers is $3\% \pm 7\%$ (95% confidence limits). These values are consistent with the hypothesis that the majority of pilot whales remain for many years in their natal pod.

(ii) Relatedness between mothers

In order to eliminate the possibility that a pod comprises many unrelated mother/offspring pairs, a second analysis was designed. In the absence of dispersal, a group of animals will become enriched for those alleles carried by successful parents. Greatest enrichment will usually be associated with the oldest females, that is, those with most descendants. In such a group, the age of an animal should correlate with the probability of observing its genotype, calculated on the basis of random assortment of the pod's alleles. This



Fig. 1. Estimated proportion of individuals in the pilot whale pod, Midvagur 240787, accompanied by their mothers (hatched bars) and fathers (plain bars), based on mean $\{O-E\}$ values (see text). Data are partitioned into four age classes. All females older by at least x years are considered potential mothers. Five years is taken as the absolute minimum breeding age, but x was varied to allow for less accurate aging of older animals: age<10, x=5; 11 to 15, x=4; 16 to 20, x=3; 21 to 25, x=2; >25, x=0. When testing for fathers x was modified appropriately: age<10, x=13; 11 to 15, x=12; 16 to 20, x=11; 21 to 25, x=10; >25, x=8. Error bars show 95% confidence limits (modified from Amos, 1993).

correlation will be strongest in highly variable systems where allelic identity within a pod is approximated by the probability of identity through descent.

Fig. 2 shows an example of age plotted against a pod-specific genotype frequency index for the pod Leynar 220787. Positive correlations (p<0.001) were found for both this pod, and a second Miðvágur 240787 (Amos *et al.*, 1993). Computer simulations were used to investigate the meaning of this result by reassigning the pod's alleles back to the original whales according to different rules (Amos, 1993). Neither random reallocation nor the creation of artificial, unrelated families (each comprising a mother and up to nine offspring) resulted in correlations as large as the empirical values. Since no change was made to the original allele frequencies, this implies that, in the pilot whale pods, the breeding system favours strongly the commoner alleles being associated with older individuals. Indeed, correlations very similar to the empirical values were produced readily in model pods in which neither sex dispersed. It was concluded that a high proportion of whales in a pod are related to each other, and that older pod members are particularly strongly linked to the rest of the pod. The most parsimonious explanation is that, as in killer whales, there is little or no dispersal from natal groups.



Fig. 2. Regression of age against pod-specific genotype frequency index for the pilot whale pod Leynar 220787 (n=87, r=0.41, p<0.001). Males are indicated by solid diamonds and females by open squares. Age was determined from dental growth rings. Indices of genotype frequency were calculated as in Amos (1993). Three individuals (all subadult) were not typed for all loci due either to degraded DNA or PCR amplification problems.

(iv) Relatedness of adult male to other pod members

In mammalian social organisation, inbreeding is usually avoided by dispersal of one or other sex, usually the males. The finding that a high proportion of pod members are related maternally is therefore to be expected. However, in Fig. 2, the data points corresponding to adult males appear to be distributed in a very similar fashion to equivalently aged females. If the adult males were born in another pod, their genotype indices would be expected to be much lower. This suggests that the adult males were caught in their natal pods.

For the two study pods, likelihood calculations were made to assess more rigorously whether the adult males were with their natal pods. In both cases, the hypothesis that the adult males are related to the pod in which they were caught is favoured strongly over the alternative hypothesis that they are related to the other pod. Although only two pods were considered, Miðvágur (240787) and Leynar (220787), this evidence is nonetheless persuasive. The microsatellite locus on which the likelihood calculations were performed is extremely variable, with a total of 54 alleles recorded between the two pods. Since the males themselves carried many different alleles (12 alleles in 7 individuals and 15 alleles in 11 individuals in pods Miðvágur and Leynar respectively) and each pod has a highly complex allele frequency distribution, the fit of a group of individuals to a pod is highly significant. Examined by simulation, the estimated probability of a group of males from another pod fitting as well as, or better than, the adult males caught with the pod was <0.001 and ~0.002 for Miðvágur and Leynar respectively (Amos, unpublished; based on

the following assumptions: that there are a total of 60 alleles in the population and that males from another pod have the same allelic distribution as those in the 'home' pod).

Patterns of male mating

(i) Mating within pods

DNA fingerprinting and, subsequently, microsatellite analysis, have shown that adult males are rarely, if ever, the fathers of the unborn foetuses they accompany (Amos *et al.*, 1991; 1993). To date, in thirty three or thirty four cases, spread over five pods, all adult males in the pod could be excluded from being the father. The remaining case is equivocal, paternity being probable, but by no means certain. In addition, an analysis designed to estimate the proportion of offspring accompanied by either their mother or their father (see above) confirmed that the proportion accompanied by their father was not significantly different from zero. Results from the isozyme work are consistent with this conclusion (Andersen, 1993).

(ii) Mating between pods

From the evidence presented above, it appears that pilot whale pods comprise high fidelity extended families. Since the adult males do not mate with their female relatives, presumably so as to avoid inbreeding, mating must occur between pods. However, it is unclear whether few or many males are involved and whether the father(s) of each foetal cohort derive from one or from several different pods.

Although the fathers of sampled foetuses are not known and hence not sampled, their genotypes may be reconstructed by comparing foetal and maternal genotypes. At highly polymorphic loci, the deduced paternal alleles can be very informative. Paternal alleles were derived for two highly variable loci. At the less variable HMW locus (Amos *et al.*, 1991), the paternal alleles within a cohort appear to be more similar to each other than to those in different cohorts. Precise probability calculations of the more extreme examples (Amos *et al.*, 1991), showed that it was unlikely that every foetus had a different, unrelated father. This implies either that some foetuses within a cohort share the same father, or that the males which father a cohort are related.

In contrast, the paternal alleles at locus 468/469, which is even more variable, are predominantly unique within a cohort (Amos *et al.*, 1993). Precise probability calculations yield an estimate that each male, on average, mated with a maximum of 1.2 females within a cohort (assuming conservatively that, in both instances in which mother and foetus have the same genotype, the paternal allele is the one present in another foetus). This apparent contradiction is best resolved by proposing that, in any one year, receptive females are fertilised by a group of related males. This would result automatically if mating occurs reciprocally between pods, the males of one pod fertilising the females from the other and *vice versa*.

DISCUSSION

Molecular methods have allowed a tentative picture of social organisation in the longfinned pilot whale to be constructed. It appears that pods are highly stable extended families from which neither sex tends to disperse. At present, it is very difficult to rule out limited dispersal, although there is no evidence of 'foreign' whales in the pods studied. If dispersal does occur, we have to ask the question 'where do the emigrants go?'. Mating appears to occur reciprocally between pods. Surprisingly, there is no evidence of strong reproductive dominance, although the sample sizes on which this assertion is based are still small. This pattern of behaviour is unusual for mammals. Normally, adult males living in social groups are expected to maximise their reproductive success by competing for access to females. This may lead to harem polygyny, with one or a few dominant breeding male(s) who either force subordinate males to disperse or prevent them from breeding (Emlen and Oring, 1977; Clutton-Brock, 1989). Male pilot whales apparently show neither strong reproductive dominance nor dispersal from their natal pod.

The particular ecology of the pilot whale provides possible explanations for this behaviour. To begin with, there are three possible reasons why strong reproductive dominance may be reduced or absent. First, the relative benefit of being dominant will be decreased when competing males are related to each, as they would be if they were born in the same pod. Second, the size of each pod, coupled with the three-dimensional marine environment, may confound behaviour aimed at establishing control over access to several females simultaneously. Third, if mating events do occur during brief inter-pod encounters, the restricted time frame could itself limit individual mating success.

With respect to dispersal, theoretical considerations suggest that males may remain with their natal pods as a consequence of the absence of reproductive dominance. If the number of direct progeny a male obtains is likely to be small, he may do better by ensuring that any benefits his presence can afford are accrued by the large number of known relatives in his natal pod (Wittenberger, 1979). However, it is unclear in what way adult males can help their relatives. Defence and assistance in a communal feeding strategy are both possibilities, but they are not supported by direct observations. Indeed, in lions, the greater burden of hunting falls on the females (Schaller, 1972), the males effectively existing as social parasites. This raises an interesting alternative possibility; that male pilot whales gain benefit from participating in group feeding strategies, but their presence is tolerated only by close relatives. In either case, inbreeding is avoided by means of an apparent incest taboo.

The picture which emerges from these molecular studies is thus plausible and internally consistent, although necessarily somewhat circular. Pilot whales live in extended families in which the adult males stay at home because the indirect benefits accrued from inclusive fitness potentially outweigh direct strategies such as paternal care and increased mating opportunities that might become available if they moved to another pod. However, this does not explain the rare sightings of all-male groups. These might indicate an alternative mating strategy, or perhaps represent either the beginning or end of a pod's life. In any case, the generality of the findings summarised here will need to be tested further by examining a larger number of pods.

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Further Studies on the Population Structure of the Long-Finned Pilot Whale, *Globicephala melas*, off the Faroe Islands

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ABSTRACT

A genetic investigation of 31 schools of *Globicephala melas* off the Faroe Islands, comprising a total of 1,948 individuals, was performed using isozyme electrophoresis to test the hypothesis of the existence of one or more stocks in the northeastern Atlantic. Three polymorphic allozyme loci, Est-1, Sod-1 and Mpi were used for the analysis of the effect of age-structure and sex on the genotypic composition. It was revealed that males showed significant deviations from the Hardy-Weinberg expectations in some schools, and this could be explained either by a migration of males between the schools or by selection. The 31 schools were pooled together, irrespective of age-classes and sex, and submitted to a hierarchical contingency table analysis performed on gene count data to test the combined effect of school and age/sex division. This revealed that the overall observed heterogeneity was caused by the schools, which implied that it was appropriate to use the allele frequencies from the individual schools to test the stock identity question in a pairwise multilocus G-test. Before this test was performed, all mature males and the foetuses were removed from the schools because of the expected migratory behaviour of the males. One school differed significantly from 16 schools out of 31 schools, but no geographical trend could explain this observation. Another hypothesis, that of the existence of two stocks off the Faroes, one being stationary and the other coming inshore during summer or winter, was tested by dividing and pooling the schools according to the season they were taken; no indication of the existence of two stocks was detected. The presence of linkage disequilibrium further supported the hypothesis of migrating males, although this could also be maintained by other forces such as selection and random genetic drift. Allele frequency differences between identical age-classes between the schools were analysed using the multilocus G-test. The test showed that the allele frequency differences found between the schools were mainly due to mature females, indicating that mature females comprise the core in the school. These observations led to the hypothesis that the overall heterogeneity found between the schools could be due to a combination of a regular pattern of school fusions and fissions, migration of mature males between the schools and a strong maternal family structure within the schools.

KEYWORDS: PILOT WHALE-LONG-FINNED; NORTH ATLANTIC; GENETICS; SOCIAL BEHAVIOUR; STOCK IDENTITY; MIGRATION.

INTRODUCTION

Andersen (1988) described a genetic study of local schools of long-finned pilot whales (*Globicephala melas*) off the Faroe Islands; heterogeneity was detected among the nine schools examined. One school (no. 7 at Viðvik) was found to be distinct from the others. This was the northernmost school considered and the morphology of the individuals within it seemed to be different from other schools. This study extends the previous one and uses isozyme electrophoresis of 22 subsequent schools in order to examine hypotheses on the existence of one or more stocks of long-finned pilot whales in the Northeast Atlantic. A hierarchical analysis of the effects of school and age/sex combinations is included in the study to further elucidate the hitherto observed heterogeneity in the long-finned pilot whale population(s), as well as an analysis of the degree of linkage disequilibrium (D) between the possible two loci-combinations of the three polymorphic

loci based on school totals. The nine schools already examined are included, as they expand the analysis incorporating age and maturity.

MATERIALS

Liver and muscle samples were collected as described by Andersen (1988). The total sample comprised 31 schools caught in the Faroes during the years 1986, 1987 and 1988. Liver samples were only collected from 24 schools. Fig. 1 illustrates the locations of the whaling bays where the whales were caught, and the numbers in brackets indicate the number of schools taken in the particular bay. The schools are numbered following Bloch *et al.* (1993a), throughout this paper (see Table 1 on pp. 223–4).

METHODS

Isozyme electrophoresis was used to study the population structure as described by Andersen (1988). The three previously described polymorphic enzymes, liver esterase (EST, EC 3.1.1.1), mannose phosphate isomerase (MPI, EC 5.3.1.8) and superoxide dismutase (SOD, EC 1.15.1.1) were analysed using horizontal starch gel electrophoresis. The schools where no liver samples were available were only examined for the *Mpi* and *Sod* loci. The zymograms obtained were similar to those observed in the former study even when material had been stored in the freezer at -20° C for a longer period.

Age was determined by counting the numbers of yearly growth zones in the teeth (Bloch *et al.*, 1993b). The females were divided into the three age-classes: 0-5yrs; 6-11yrs and 12+yrs. The first class is expected to contain immature females, the second a mixture of sexually immature and mature females, and the last mature females. Males were divided into two age-classes, 0-11yrs and 12+yrs; the first will contain immature and mature males, and the latter mature males only. These classes were chosen as the sample size was too small to use a finer division by age.

For the hierarchical contingency table analysis, the age-classes in females were reduced to two classes, 0-11yrs and 12+yrs, as for males. This is discussed later, along with the age-class division of males when examining the age/sex combination.

Sexual maturity in females was determined by looking for the presence of corpora in the ovaries (Martin and Rothery, 1993), and sexual maturity in males was examined by looking at the testis weight and smears of sperm (Desportes *et al.*, 1993). Mature males were excluded from the samples for some of the analyses as they are thought to migrate between schools (e.g. Amos *et al.*, 1993) thereby influencing a possible difference in allele frequencies.

For each locus, the goodness of fit to the Hardy-Weinberg expectations was tested. The genotypic proportions for the three loci were compared to Hardy-Weinberg proportions for each of the 31 schools, after the known mature males, foetuses and undetermined individuals had been excluded (the justification for this exclusion is discussed further later). Likewise, the genotypic distribution for each age-class in the 16 largest schools was compared with Hardy-Weinberg expectations, as were the genotypic distributions by sex in all 31 schools. $F\sqrt{N}$ is used as a test for the goodness of fit to the Hardy-Weinberg proportions (Brown, 1970), where F is the maximum likelihood estimator of Wright's inbreeding coefficient. A negative $F\sqrt{N}$ indicates a deficit of heterozygotes, whilst a positive $F\sqrt{N}$ indicates an excess of heterozygotes when the observed genotype distributions are compared to the Hardy-Weinberg proportions. $F\sqrt{N}$ approximates a normal distribution with zero mean and unit variance when the hypothesis of Hardy-Weinberg Weinberg proportions is true. F^2N is equal to the chi²-test.



Fig. 1 Locations of the whaling bays where the whales were caught. Numbers in brackets indicate number of schools taken.

The hierarchical contingency table analysis was performed on gene count data, conditioned on school and age/sex divisions, and using a log-linear model (Christiansen et al., 1984). This was done by testing the effect in hierarchically ordered hypotheses,

starting with H_0 being no effect of the combined school and age/sex division on the common allele frequency, and H_1 , to test the hypothesis of no effect of school coordinated with the hypothesis (H_1^*) of no effect of age/sex combination on the allele frequency. The analysis was performed using a logit model and linear regression to test the additive fitted model. The analyses were divided into three cases describing the *Est-1*, *Mpi* and *Sod-1* loci, respectively. First, school plus age/sex combination were fitted into the additive logit model to test the H_0 hypothesis. Second, the model was fitted with school only, to test the H_1 and H_1^* hypotheses. This procedure is based on the assumptions that the genotypic distributions are in Hardy-Weinberg proportions and the gamete frequencies are in Robbins' proportions.

Deviations from Robbins' proportions (D) were tested in a two-locus analysis of the three different combinations of the polymorphic loci using the gene-counting procedure under the assumption of random union of gametes as described by Hill (1974) and Weir and Cockerham (1979). If this assumption is violated, D cannot be estimated by the gene counting method, and Burrow's estimator should be used to estimate linkage disequilibrium. Burrow's estimator is composed of the contribution of gametes from within individuals and between individuals to the total linkage disequilibrium (Weir and Cockerham, 1979). In this study it is evaluated using a chi²-test and one degree of freedom. The test statistics used in the cases where random union of gametes were accepted, were the chi²-approximation of the -2log (likelihood-ratio), abbreviated LogLik. The test for the hypothesis of random union of gametes has five degrees of freedom since the total number of observations for a pair of loci are 9-1=8 and the number of free parameters estimated is three, p, q and D. The hypothesis of D=0 is also tested by the likelihood ratio test with one degree of freedom. The hypotheses were first tested within each school and thereafter the LogLik estimates were added to give the appropriate totals.

Wright's F-statistic (1951) was used to obtain a measure of F_{st} for the total sample of schools, which is a measure of genetic differentiation due to population subdivision. Furthermore, as $F_{st} \approx 1 / (1 + Nm)$ in Wright's infinite Island model, if $m \ll 1$ (m, the probability that each gamete is an immigrant; N, the effective population size) it is possible to use F_{st} to get a rough estimate of Nm. This is one way of quantifying the amount of gene flow between subpopulations in terms of the numbers of individuals or gametes that move between the subpopulations per generation. F_{st} over the three polymorphic loci was estimated using Weir and Cockerham's (1984) unbiased estimator, θ , for F_{st} . According to Slatkin and Barton (1989), who compared F_{st} , rare alleles and maximum likelihood methods for estimating average levels of gene flow and reasonably large sample sizes. They found that all were useful methods for indicating current or recent importance of gene flow relative to genetic drift, and were all in general equally sensitive to both variation in population structure and selection.

The genetic differences between the 31 schools were also analysed using a G-test for independence (Sokal and Rohlf, 1981) and pooling the three polymorphic enzyme systems by adding the separate G-values. For this procedure the computer program accompanying Biometry (1981) was used.

RESULTS

The hypothesis that the observed all-round heterogeneity could be ascribed to differences between different age-classes divided into the two sexes within the schools was first examined at the single locus level by looking at the genotypic distribution and the deviation from Hardy-Weinberg expectations. Only the 16 largest schools were chosen and even then the division into the combination of sex and age-class had to be coarse and the resultant sample sizes were likewise small (results not shown). Deviations from Hardy-Weinberg proportions at the *Est-1* locus, *Sod-1* locus and *Mpi* locus were observed in a few cases and distributed randomly among the age-classes and schools. As a whole, no deviations were observed at the *Est-1* locus, while for *Mpi* and *Sod-1*, deviations were observed in 9.3% of the cases. This was found in both old mature females and males, foetuses and young immature females and males.

The second hypothesis tested was that the heterogeneity could be due to differences between the genotypic distribution by sex alone. The results of the goodness of fit to the Hardy-Weinberg expectations in females and males and the sample sizes for the 31 schools are given in Table 1. Both immature and mature individuals are included. Significant deviations were observed in only a very few cases at the *Est-1* and *Sod-1* loci, each time in males. At the *Mpi* locus males displayed significant deviations in 13% of the schools, showing a uniform distribution of an excess and deficit of heterozygotes, while in females no significant deviation was observed.

Table 1

Sample size (N), test for the goodness of fit to the Hardy-Weinberg proportions, $(F\sqrt{N})$, and allele frequencies (q) of the fastest allele for the two sexes at the *Est-1*, *Sod-1* and *Mpi* loci. School numbers are as allocated in Bloch *et al.* (1993). Dates are in the form year, month, day. No mature male samples were available from Tórshavn (22) 870410.

T 1.				Est-1 Sod-1					Mpi			
Locality (school no.)	Date	Sex	$\overline{F\sqrt{N}}$	9	N	$\overline{F\sqrt{N}}$	q	N	$\overline{F\sqrt{N}}$	9	N	
Gøta (1)	860710	f m	-0.44 0.37	0.650 0.594	20 16	-0.72 -0.43	0.348 0.400	23 15	-1.65 -2.10*	0.413 0.344	23 16	
Leynar (2)	860712	f m	-1.41 0.55	0.641 0.725	39 20	-0.15 -0.86	0.575 0.458	40 24	-0.92 -1.89	0.400 0.283	40 23	
Bøur (3)	860730	f m	-0.66 0.44	0.635 0.525	37 20	0.14 -1.46	0.355 0.500	38 23	1.67 -0.43	0.361 0.500	36 22	
Sandur (4)	860911	f m	-0.74 -0.52	0.879 0.620	29 25	0.50 -1.00	0.470 0.500	33 25	-1.28 2.32*	0.546 0.442	33 26	
Øravík (5)	860915	f m	-0.84 0.72	0.765 0.688	34 32	-1.65 -0.21	0.4 93 0.451	72 51	0.92 -0.44	0.500 0.426	76 54	
Gøta (6)	860925	f m	0.04 -0.30	0.605 0.692	19 13	1.68 -1.13	0.400 0.367	20 15	0.89 -1.08	0.500 0.563	20 16	
Viðvík (7)	860927	f m	undef. -0.38	1.000 0.889	9 9	-1.67 0.00	0.500 0.333	9 9	-0.33 0.30	0.500 0.44	9 49	
Funningsfjørður (8)	861025	f m	-0.19 -0.91	0.600 0.643	20 14	0.54 -0.52	0.350 0.531	20 16	-0.19 -0.27	0.400 0.375	20 16	
Miðvágur (9)	8611 01	f m	-1.18 -1.18	0.632 0.767	34 15	-1.13 0.97	0.373 0.394	106 71	0.00 0.28	0.495 0.451	106 71	
Fuglafjørður (10)	861111	f m	-0.37 -0.24	0.921 0.735	19 17	0.13 1.28	0.455 0.535	33 29	0.46 2.57*	0.397 0.362	34 29	
Hvalvík (11)	861114	f m				0.00 -1.08	0.500 0.231	20 13	-1.43 0.76	0.650 0.577	20 13	

Table 1 (cont.)

				Est-1			Sod-1		Мрі		
Locality (school no.)	Date	Sex	F√N	<i>q</i>	N	F√N	9	N	F√N	q	N
Vestmanna (12)	861115	f m	-0.29 0.36	0.929 0.688	14 8	0.69 -0.80	0.407 0.391	70 55	-0.35 1.00	0.443 0.409	70 55
Hvalvík (13)	861124	f m	0.68 -2.10*	0.474 0.563	19 16	1.81 1.46	0.412 0.483	57 30	-0.70 -0.54	0.404 0.500	57 31
Fuglafjørður (14)	861128	f m	1.52 -0.49	0.786 0.833	7 6	-0.37 -0.34	0.410 0.500	39 34	-1.30 -0.05	0.423 0.456	39 34
Tórshavn (16)	861223	f m	-0.72 undef.	0.786 1.000	7 2	0.36 1.15	0.313 0.500	8 12	0.67 0.56	0.563 0.542	8 12
Hvannasund (17)	870122	f m				-0.13 1.18	0.439 0.441	74 51	1.39 -0.61	0.493 0.421	74 51
Vágur (18)	870123	f m				-0.02 -1.88	0.464 0.395	14 19	0.25 1.17	0.357 0.316	14 19
Leynar (19)	870131	f m				1.20 0.90	0.529 0.389	17 9	-0.12 0.90	0.353 0.611	17 9
Hvalvík (20)	87 020 7	f m				0.84 0.18	0.386 0.483	57 29	0.89 0.03	0.535 0.414	57 29
Leynar (21)	870323	f m				-1.15 -0.47	0.351 0.500	47 18	0.41 -2.12*	0.531 0.333	47 18
Vágur (24)	870516	f m				-1.30 2.03*	0.405 0.300	21 15	-0.22 -0.43	0.500 0.400	21 15
Leynar (25)	870722	f m	0.12 0.07	0.773 0.694	55 31	-1.33 0.35	0.350 0.484	60 32	1.14 1.73	0.425 0.453	60 32
Míðvágur (26)	870724	f m	1.27 -0.02	0.759 0.775	56 40	-1.19 -0.46	0.377 0.500	57 43	0.81 -0.86	0.316 0.384	57 43
Miðvágur (28)	870802	f m	0.96 0.85	0.732 0.833	28 18	- 0.56 2.12*	0.411 0.333	28 18	1.89 0.42	0.482 0.556	28 18
Vágur (29)	870819	f m	-0.61 1.33	0.667 0.750	24 16	-0.16 -0.65	0.289 0.313	26 16	-0.86 0.49	0.442 0.469	26 16
Klaksvík (31)	870829	f m	-1.50 undef.	0.667 1.000	9 2	-0.16 1.17	0.318 0.700	11 5	-1.90 -0.07	0.364 0.417	11 6
Vágur (32)	8 7091 8	f m	-0.79 -0.56	0.800 0.800	10 5	0.53 0.37	0.600 0.400	10 5	-1.05 0.37	0.250 0.400	10 5
Tórshavn (33)	871008	f m	-0.49 0.15	0.776 0.700	29 10	0.24 -0.33	0.370 0.455	27 11	1.83 -1.51	0.679 0.600	28 15
Vágur (34)	871020	f m	0.21 0.63	0.700 0.750	20 10	0.86 -1.36	0.450 0.300	20 10	0.35 -1.90	0.425 0.500	20 10
Leynar (43)	880610	f m	-1.25 -1.18	0.761 0.815	44 27	-0.60 -0.88	0.422 0.429	45 28	-0.37 -0.76	0.589 0.500	45 28

* Significant at the 5% level.

As no overall deviation from the Hardy-Weinberg proportions was observed in the genotypical distribution of each age-class and sex combination in the 16 largest schools, and no overall sex difference was found, all schools were pooled and submitted to the

System	H ₀ School + age-sex	H ₁ Age-sex	H ₁ * School
EST	0.001*	27.7	0.001*
MPI	0.027*	28.7	0.023*
SOD	8.21	0.7*	41.5

Results from the hierarchical contingency table analysis of the gene count data, showing o	only te	est
probabilities for the given hypothesis (p-values given in $\%$).		

Table 2

* p < < 5%.

hierarchical contingency table analysis. The results are shown in Table 2. There seemed to be an effect of schools+age/sex combination at the *Est-1* and *Mpi* loci on the allele frequencies, as the H_0 hypothesis was rejected. This effect can be described by schools and not by the age/sex combination as seen from the table. At the *Sod-1* locus, H_0 was accepted, indicating no effect of schools+age/sex combination on the *Sod-1* allele frequencies. Instead, there appeared to be an effect with age/sex combination. If this is excluded, the effect of schools may also be excluded.

Table 3 compares the genotypic distribution to the Hardy-Weinberg proportions $(F\sqrt{N})$, allele frequencies of the fastest migrating allele (q) and the sample sizes for the 31 schools when the known mature males, foetuses and undetermined individuals in the three polymorphic enzyme systems are excluded. No significant deviation was observed at *Est-1* and *Sod-1*. At the *Mpi* locus significant deviations from the Hardy-Weinberg proportions were seen in 6.5% of the schools, which is more than expected. This deviation is observed at the *Mpi* locus in schools 1 and 31.

The results of the analyses of allele frequencies between identical age-classes between the 16 schools are shown in a reduced form in Fig. 2. Four age-classes 0-5 and 12+yrs for females, and 0-11 and 12+yrs for males revealed, not surprisingly, deviations significantly more frequent than expected.

The results of Wright's *F*-statistic showed $F_{st} = 0.010$, Nm = 25 for the total sample of 30 schools including mature males and foetuses (school 22 contains only females and young individuals), $F_{st} = 0.009$, Nm = 28 for the total sample of 31 schools excluding mature males and foetuses, and $F_{st} = 0.017$, Nm = 14 for the total sample of 31 schools only containing mature females.



Fig. 2. The frequency of significant deviations found for each age-class when comparing them pairwise in the multilocus G-test between the 16 schools.

			Est-1		Sod-1			Mpi		
Locality	school no.	F√N	q	N	F√N	q	N	F√N	q	N
Gota	1	-0.14	0.621	29	-0.20	0.371	31	-2.68*	0.422	32
Leynar	2	-0.94	0.698	48	-0.29	0.510	48	-1.28	0.354	48
Bour	3	-0.17	0.606	47	0.19	0.404	47	0.86	0.411	45
Sandur	4	-0.07	0.769	39	0.00	0.500	44	0.14	0.477	43
Øravík	5	0.76	0.720	50	-1.07	0.495	105	0.76	0.476	106
Gøta	6	-0.13	0.630	23	1.53	0.360	25	0.57	0.540	25
Viðvík	7	-0.14	0.962	13	-0.86	0.462	13	-1.08	0.385	13
Funningsfiørður	8	-0.53	0.577	26	0.05	0.375	28	-0.47	0.357	28
Míðvágur	9	-1.45	0.638	29	0.54	0.378	123	0.45	0.492	123
Fuglafiørður	10	-0.81	0.860	25	1.11	0.446	46	1.72	0.370	46
Hvalvík	11				-0.11	0.429	28	-1.05	0.607	28
Vestmanna	12	1.29	0.861	18	0.62	0.398	98	-0.18	0.434	98
Hvalvík	13	-0.22	0.500	21	1.90	0.417	60	-0.67	0.433	60
Fuglafiørdur	14	1.52	0.786	7	-0.83	0.430	57	-1.24	0.465	57
Tórshavn	16	-0.49	0.833	6	0.90	0.389	9	0.30	0.556	9
Hvannasund	17				0.17	0.420	94	1.03	0.489	94
Vágur	18				0.12	0.412	17	-0.12	0.353	17
Leynar	19				1.28	0.500	22	0.28	0.409	22
Hvalvík	20				-0.25	0.379	66	0.00	0.492	66
Leynar	21				-0.86	0.400	60	-0.01	0.483	60
Tórshavn	22				0.40	0.342	38	-0.04	0.461	38
Vágur	24				0.16	0.362	29	-0.19	0.500	29
Levnar	25	0.61	0.761	71	-0.15	0.383	77	1.38	0.442	77
Míðvágur	26	1.52	0.775	89	-1.06	0.428	90	0.47	0.333	90
Míðvágur	28	1.56	0.803	38	0.05	0.395	38	1.94	0.513	38
Vágur	29	-0.49	0.729	35	-1.00	0.297	37	0.13	0.460	37
Klaksvík	31	-1.36	0.700	10	-0.43	0.333	12	-2.08*	0.375	12
Vágur	32	-1.02	0.786	14	1.06	0.536	14	-0.55	0.321	14
Tórshavn	33	-0.01	0.764	36	-0.26	0.397	34	1.41	0.657	35
Vágur	34	0.80	0.712	26	0.28	0.423	26	-0.42	0.462	26
Leynar	43	-0.88	0.800	50	1.27	0.392	51	-1.53	0.588	51
Total		0.99	0.730	750	0.88	0.413	1467	0.96	0.458	1467

Sample size (N), test for the goodness of fit to the Hardy-Weinberg proportions, $(F\sqrt{N})$, and allele frequencies (q) of the fastest allele for the two sexes at the *Est-1*, *Sod-1* and *Mpi* loci. Mature males, foetuses and undetermined individuals were excluded.

Table 3

* Significant at the 5% level.

The test for sex differences in allele frequencies in the three polymorphic systems was performed by a G-test for independence. The data are not shown, but significant differences were only observed in schools 4 and 31, which are not significantly frequent in comparison to the total number of schools.

Results of the tests for linkage disequilibrium and random union of gametes in the twolocus analyses are shown in Table 4. The hypothesis of random union of gametes was accepted in the *Mpi/Sod-1* and *Mpi/Est-1* combinations and Hill's estimate of D can be used here. For the *Sod-1/Est-1* combination, deviation from random union of gametes was observed in two cases. These two schools, therefore, were excluded in the test for linkage disequilibrium, D = 0, and Burrow's estimator, $\Delta = 0$, is used instead. Linkage

	Log-like	lihood			
	Loci	LogLik	р	df	
	Mpi/Sod-1	154.26	0.389	150	
Random union of gametes	Sod-1/Est-1	130.09*	0.049	105	
	Mpi/Est-1	127.70	0.197	115	
	Total	412.04	0.065	370	
	Mpi/Sod-1	49.51*	0.014	30	

31.26

33.06

113.83*

0.069

0.080

0.002

Sod-1/Est-1

Mpi/Est-1

Total

Test for random	union of gametes,	and linkage	disequilibrium	(D) between	combinations	of the
	three polymorphic	c loci Mpi, So	d-1 and Est-1 fo	r the 31 school	ols.	

Table 4

* p < 0.05.

D = 0



Fig. 3. Histogram depicting the frequency of significant deviations found for each school, when comparing them pairwise in the multilocus G-test. Figures from Table 1.

disequilibrium was detected in the *Mpi/Sod-1* and *Sod-1/Est-1* combinations and retained when adding across the three possible combinations of polymorphic loci.

Fig. 3 shows the results of the pairwise multilocus G-tests after pooling the immature females and males and mature females. Only the significance is indicated. It is assumed that the results from the age-structure analysis for the 16 schools can be extrapolated to the 31 schools. Here school 33 diverges from the others by being significantly different in 51.6% of the cases.

DISCUSSION AND CONCLUSION

Pilot whale schools are known to have an 'excess' of mature females to mature males, the males probably being polygynous (Sergeant, 1962; Martin *et al.*, 1987). They are probably composed of several family entities, which is why the age-structure within the schools might influence the allele frequencies by either differential migratory behaviour of the

21

23

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different age-classes or zygotic selection. This is one possible hypothesis for explaining the heterogeneity found so far off the Faroe Islands (Andersen, 1988).

In the present study, analysis by individual age-classes for each sex within the 16 largest schools revealed no significant deviations in genotypic distribution from Hardy-Weinberg expectations. The age-classes were therefore pooled and the whales were divided by sex alone within the 31 schools and tested in the single locus analysis. The female and male samples both comprised a mixture of immature and mature animals.

Although the Hardy-Weinberg expectations were fulfilled for females, significant deviations were found for males at the *Mpi* locus (Table 1). This might be due to migration of males between schools or selection giving higher mortality to certain genotypes. If males migrate between schools regularly then we would not expect mature males or males close to maturity present within a school at any time to accord with the Hardy-Weinberg proportions. If uniform selection is working on one of the alleles at the *Mpi* locus and there is no migration between schools, then we would expect the selection to work in the same direction in all schools, causing identical effects on the genotypes in relation to the Hardy-Weinberg expectations. This possibility cannot be excluded as there is some tendency towards disparity in the distribution of the two alleles at the *Mpi* locus towards allele 2, the slower migrating allele.

When dividing the genotypes of the different schools by age and maturity, in one of the schools, school 11, none of the genotypes of possible fathers represented in the *Sod-1* locus corresponded to the genotype for a one-year-old animal. This supports the theory of migratory behaviour of mature, long-finned pilot whale males. This has been suggested and confirmed in the study of Amos *et al.* (1991) who examined five pilot whale schools with a total of 34 mother-offspring pairs using DNA-fingerprinting. For 88% of the foetuses, the accompanying mature males could be excluded as fathers, indicating a high degree of gene flow between the schools. They also found that in one school, four out of five foetuses in one length-class had an identical paternal allele. This allele was only present in 11% of the examined whales and rather rare. This suggests that only one or two males fathered these foetuses. Furthermore, the remainder of the older foetuses in the same school could not have had these fathers. This agrees well with our observations.

The hierarchical contingency table analysis shows that the age/sex combination has no effect on the allele frequencies of *Est-1* and *Mpi*, but that the observed heterogeneity is due to the social structure within the schools. The *Sod-1* locus does not display the same effect of schools+age/sex combination on allele frequency, but indicates an effect of age/ sex combination and not of schools (Table 2). It seems likely that the foetuses cause this effect on the allele frequency of *Sod-1*.

These observations led to the pooling of young animals and old mature females in the 31 schools (i.e. excluding mature males, foetuses and undetermined individuals) to consider the stock identification question by examining the allele frequency differences (see below). No significant deviations from Hardy-Weinberg proportions at the *Est-1* and *Sod-1* loci were found (Table 3). The significant deviation at the *Mpi* locus (Table 3) for both schools 1 and 31 might be because these whales belonged to larger schools, where the rest of the whales had been seen to escape.

Wright's F-statistics suggest high gene flow rates between schools, irrespective of which of the total samples are used, and consequently suggest a rather homogeneous population of pilot whales off the Faroes. However, the significant deviations frequently found when testing the allele frequencies of identical age-classes pairwise between schools (Fig. 2) contradict this expectation, as does the analysis of genetic differences between the 31 schools (Fig. 3) if only young animals and mature females are considered. The result of this pairwise comparison between the 31 schools using the multilocus G-test confirms the view of Andersen (1988) that there is a heterogeneous population of pilot whales off the Faroe Islands. As in the former study, one school (no. 33) diverges from the others by being significantly different in 51.6% of the cases.

Gene flow or migration is generally regarded as inhibiting genetic differentiation between a local population and an infinite population in equilibrium, although this depends on how migration is defined (Fix, 1978). In the present study we assume that pilot whales comprise either several definite populations or sub-populations or schools of several families. In such circumstances migration might be kin-structured. If the migrating individuals are related to some extent this would not have the 'expected' stabilising effect on allele frequencies.

Most of the observed allele frequency deviations between identical age-classes amongst schools are due to old mature females (Fig. 2), confirming earlier suggestions that mature females comprise the 'core' of the school (Sergeant, 1962; Martin *et al.*, 1987). This was also found by Amos *et al.* (1991). However, results for mature males suggest that they form a rather homogeneous total population.

Significant differences in allele frequencies for young males and females may reflect the significant differences in allele frequencies between the mature females and suggest that different males have fathered the young in different schools.

The hypothesis of migrating males is supported by the results of the linkage disequilibrium test shown in Table 4. Other factors such as selection and random genetic drift may also cause or influence linkage disequilibrium. For example, in small populations, gamete frequencies fluctuate from generation to generation, causing variation in D, while selection in a large, randomly mating population may favour certain combinations of alleles, thereby producing linkage disequilibria. Continuous migration of mature males between schools may also maintain the detected level of linkage disequilibrium, especially in combination with selection and random genetic drift (Hartl, 1980).

There are five factors which imply that selection might operate on males after conception and influence the allele frequencies: (1) the skewed sex-distribution within the schools; (2) the lack of confirmed observations of bachelor groups; (3) the homogeneity in the mature male population; (4) the higher male mortality rate (Sergeant, 1962; Kasuya *et al.*, 1988) and (5) the absence of a skewed sex-ratio immediately after conception (Andersen *et al.*, 1992).

In a study of heavy metal loads in the Faroese pilot whale, Caurant *et al.* (1993) found higher mean levels of cadmium per $\mu g/g$ wet weight compared to other marine mammal species. They examined four schools (numbers 5, 22, 25 and 33) and detected a significantly lower level of cadmium in the liver in school 33. This suggests that the cadmium levels could be used as tracers of school history and may indicate the existence of sub-populations. The fact that school 33 was significantly different in both our study and that of Caurant *et al.* (1993) suggests that this school had been feeding in another area and may represent a different sub-population. This hypothesis awaits further investigation.

In an earlier study, Andersen (1988) found school 7 to be different from the other schools. Because it was also the northernmost school, one hypothesis was that it represented a hitherto unknown stock of G. melas in the Northeast Atlantic. The present study shows a southern school (no. 33) as being different and the two schools (nos. 1 and 7) still diverge clearly from the additional schools considered here. However, no obvious geographical distribution is detected when pooling presumed northern, southern, eastern and western localities. This is perhaps not surprising since the localities are whaling bays selected by the Faroese Government as being suitable for catching whales, and do not reflect exactly where the whales were first seen.

One hypothesis is that two stocks of pilot whales are found in Faroese waters, one that is present year-round and one that comes inshore seasonally. This was examined by seperating schools by season, pooling the summer and winter schools, and carrying out a homogeneity test at each locus. The results of the test (not shown) did not support the hypothesis based on these two seasons. Similarly no annual trend was detected.

The observed differences in allele frequencies between the schools in spite of the indications of migratory males are also seen between groups of Cayo Santiago rhesus monkeys (Melnick and Kidd, 1983) and Japanese macaques (Nozawa *et al.*, 1982). The social structure of these cercopithecines is well understood. As in pilot whales, the adult sex ratio is skewed towards females. This is partly due to their earlier maturation and partly due to the emigration of the males from their natal group which exposes them more than females to predation and disease (Melnick and Pearl, 1987). The females usually stay in their natal group thus forming matrilines within the groups. On some occasions, such as in the case of the Cayo Santiago rhesus monkeys, the groups split up according to their maternal relatedness, causing an increase in the relatedness within the groups and an increase of genetic difference between the groups, which gives rise to significant differences in allele frequencies (Cheverud *et al.*, 1978). Given the similarities in social structure, the different factors influencing the allele frequencies in the monkeys might well be those that influence the pilot whale as well.

Consequently, one hypothesis to explain the population structure of the long-finned pilot whale off the Faroe Islands based on the observed heterogeneity found in the species, is that it could be generated by a regular pattern of fusions and fissions of schools, combined with the migration of mature males between schools and a strong maternal family-structure within schools, possibly consisting of several female-lineages. This hypothesis is supported in the present study by the results of the test for allele frequency differences between identical age-classes in different schools, by the estimate and test for linkage disequilibrium, and by deviations from Hardy-Weinberg proportions in the total male sample from some schools.

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Reproductive Maturity and Seasonality of Male Long-Finned Pilot Whales, off the Faroe Islands

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ABSTRACT

Reproductive activity and seasonality of male long-finned pilot whales is described, based on material collected from 39 schools landed in the Faroe Islands in the period July 1986-December 1989. Determination of sexual maturity and activity is based on morphological and histological examination of testis, density of spermatozoa on smears, plasma testosterone titration, and social factors correlated with life-history data such as body length, body weight and age. Puberty begins at an average age of 13.4yrs and histological maturity is reached at an average age of 17yrs; social maturity seems to be delayed for several years. Most parameters examined showed a substantial overlap between maturity stages. Age, body length and weight are unreliable indicators of maturity; testis length appears to be the best. Testicular activity is diffusely seasonal and peaks between March and September. No cessation of activity is observed and a non-negligible proportion of males is capable of reproducing outside the main breeding season. Testis weight increases 1.5 times during the period March-September. Testosterone concentrations increased by about 2.5 times in the period March-September minus July, showing a bimodal pattern with a dip in July. School structure indicates that males may move away from their natal school after puberty and join other schools or segregate, at least temporarily.

KEYWORDS: PILOT WHALE—LONG-FINNED; REPRODUCTION; SEXUAL MATURITY; SEASONALITY; NORTH ATLANTIC; BEHAVIOUR; SOCIAL; WHALING-MODERN.

INTRODUCTION

Until recently, little was known about the reproductive biology of male long-finned pilot whales, *Globicephala melas*. The only available information for the northeastern Atlantic concerned estimates of length and age at sexual maturity based on small sample sizes (Morton, 1963; Cowan, 1966; Desportes, 1982; 1983; Collet, 1987; Martin et al., 1987; Bloch, 1992; Sigurjónsson et al., 1993). Sergeant (1962) carried out a more thorough investigation of animals taken in the fishery off Newfoundland, but the limitations of the data and the narrow seasonal spread of the sampling only allowed him to give approximate estimates of age and length at sexual maturity and to report an apparent decline in spermatogenetic activity in late summer. Moreover, problems in age estimation had rendered the estimated life history parameters inaccurate (Kasuya et al., 1988). Male reproduction in the related short-finned pilot whale, *Globicephala macrorhynchus*, has been more comprehensively studied (Kasuya and Marsh, 1984; Kasuya and Tai, 1993). Although Kasuya and Marsh (1984) detected signs of seasonality in sperm production, the seasonally-limited sampling period again prevented a complete investigation.

Estimates of age and size at sexual maturity and knowledge of reproductive cycles are essential to our understanding of the reproductive strategy and ecology of a species and may provide valuable information for the rational management of exploited populations.

A unique opportunity to carry out detailed studies of the reproductive biology of male long-finned pilot whales arose from the initiation of a two-year international programme on the ecology and status of the species focusing on the Faroese pilot whale drive fishery (Desportes, 1990; Desportes *et al.*, 1993b). The catch is non-commercial, opportunistic and non-selective (see for review: Bloch *et al.*, 1990; Sanderson, 1991). In particular, the programme provided an opportunity to examine seasonality, as complete schools were sampled throughout the year. Access to a large number of animals compensated partly for the impossibility of conducting longitudinal studies, as is usually the case when investigating the reproductive seasonality of land mammals. Changes in testis weight and plasma testosterone concentrations throughout life have been previously examined (Desportes *et al.*, In press). The present study correlates these changes with histological examination and investigates the question of seasonality. It also attempts to evaluate the best criteria for routinely assessing sexual maturity in pilot whales and to determine the actual age at which males reached breeding status, taking into account physiological and social factors.

MATERIALS AND METHODS

Data were collected from 1,148 males from 39 schools of long-finned pilot whales caught in the Faroese drive fishery over a three-year period, July 1986-December 1989. Testes and blood samples were obtained from 672 and 214 specimens respectively. Other sample sizes are given in the following section or in tables and figures. For logistical reasons, complete data and sample sets were not obtained from all the whales. This explains discrepancies in sample sizes which may exist between tables when dealing with combined parameters.

Field procedures

Field procedures for the general programme are described by Bloch *et al.* (1993a) and only those specific to the present study are mentioned here.

Blood samples were taken immediately after the animal was killed. They were collected from the neck vessels in 50ml heparinized tubes and kept on ice until laboratory processing. On a few occasions samples were taken directly from the heart, but these were heavily haemolysed. Plasma samples were divided into aliquots and stored at -25° C until assays.

Desportes (In press) found that the asymmetry in weight and tissue maturation within a testis and within a pair of testes was sufficiently small to allow a single testis and a single histological sample to be used to routinely assess sexual maturity in long-finned pilot whales. Thus a single testis from whichever side was the most accessible for sampling was collected and histological examinations were performed on a single sample from the mid-length cross section of the testis taken from the side opposite to the epididymis.

Fresh testes and epididymis were weighed separately to the nearest gram. Testis length, width and height were recorded to the nearest millimetre.

Histological samples were fixed and preserved in 10% buffered formalin. Initially they were taken and fixed within 24 hours of the death of the whales. This procedure did not give satisfactory results for any more detailed histological diagnosis than the presence or absence of mature seminiferous tubules. Thereafter, histological samples were taken and fixed in formalin as soon as a testis was removed. Even so, there were still noticeable differences in tissue degradation between whales of the same school according to how quickly after death the sample had been collected.

When the testes were removed, smears were taken with a cotton stick from the midlength cross section of the testis and the epididymis, and the beginning of the ductus deferens, and air-dried.

Microscopic examination

Samples for histology and cytology were processed using standard techniques in the laboratory of Anatomo-cyto-pathology of the Faroese Central Hospital. Histology slides were stained with Hematoxylin-Eosin and smears with Papanicolaou stain.

Testicular slides from 478 individuals were examined at a magnification of 100–400x. Maturity of testicular tissues was assessed by observing an entire section of about 1cm² and following criteria used for other mammals (e.g. Courot *et al.*, 1970). The stages of histological maturity used for the short-finned pilot whale (Kasuya and Marsh, 1984; Kasuya and Tai, 1993) were followed for comparative purposes. They were defined according to the proportion of seminiferous tubules being mature, i.e., containing spermatocytes, spermatids and spermatozoa, among at least 100 tubules circular in outline and randomly selected:

immature: 100% of the tubules are immature;

maturing: both mature and immature tubules are found, subdivided into *early maturing* when less than 50% of tubules are mature and *late-maturing* when between 50% and 100% of tubules are mature;

mature: 100% of the tubules are mature.

Testicular tissue was also examined for relative quantity of interstitial tissue, lumen size, tubule elongation and abundance of spermatozoa.

Tubule diameters were measured with an ocular micrometer. Mean diameters were taken as the average of at least six randomly chosen round tubules, each one measured on two diameters at right angles. When both mature and immature tubules were present, six tubules of each category were measured. Each resulting mean was weighted by the corresponding proportion of mature/immature tubules, thus taking into account the varying distribution of mature and immature tubules. The overall mean diameter was taken as the sum of these two weighted values.

The sample of smears comprised 133 testicular smears, 325 epididymal smears and 83 ductus deferens smears. They were scanned at a magnification of 10–40x using a field diameter of 1.82mm. The relative density of spermatozoa was classified as follows:

none: no spermatozoa present;

low: less than 10 spermatozoa per field;

intermediate: above low with no fields showing packed spermatozoa;

high: at least some fields exhibited layers of densely packed spermatozoa.

Estimation of sexual maturity

Techniques used to estimate the average age at attainment of sexual maturity (ASM) have been reviewed by Cooke (1984), DeMaster (1984) and Hohn (1989). Two different methods are used here to estimate both ASM and LSM (the average length at attainment of sexual maturity) and estimates from both are presented in the Results section.

(a) The non-parametric method of the sum of fraction immature, Hohn (1989)

ASM is estimated as the sum of the fraction of animals immature in each indeterminate age class added to the age of the first indeterminate age class. The method was applied to the proportion immature within 1-year age class and 5cm length class, and for the LSM the

sum of fraction immature and the variance were multiplied by five, i.e. the number of cm per length-class.

(b) The age at which 50% of the specimens are sexually mature

This is predicted from a two parameter logistic curve fitted to the fraction-mature-at-age/ length (midpoint of classes from – and including – the highest class for which all individuals were sexually immature up to the lowest class for which all individuals were mature).

Hohn (1989) noted that variations in curve-fitting techniques will lead to changes in estimates. Values obtained from the sum of fraction immature method are more suitable for comparative purposes, and we preferred them as 'best' estimates. Since different criteria are used to assess male sexual maturity in various studies, the age and length at the attainment of each of the three stages of sexual maturity were estimated.

Index of testis development

An index of testis development was calculated as the testis weight in grams (excluding the epididymis) divided by the testis length in millimetres, thus defining maturity in terms of unit of testis weight per unit of testis length.

Testosterone assay

Plasma testosterone concentrations were measured in duplicate by radio-immunoassay and intra- and inter-assay; coefficients of variation were 6 and 13% respectively. Details of the procedure are given in Desportes *et al.* (In press).

Age estimation

Age estimation was performed by counting growth layer groups (GLGs) in both dentine and cement on thin stained sections of decalcified teeth as described and presented in Bloch *et al.* (1993b).

School structure

The structure of 39 schools landed during the study period was examined in terms of male sexual maturity in an attempt to determine when males reach social maturity, i.e. obtain access to females for breeding. Of these, 19 were selected, for which no escapees were reported and all males were of known age and sexual maturity. These schools were landed in January (2), February (2), March (2), May (1), June (1), July (3), September (1), October (2), and November (5). One of the schools was the male-only school described in Desportes *et al.* (1993a). Females were considered mature when they had ovulated at least once (Perrin and Donovan, 1984). Females probably close to ovulation were those with a corpus luteum but no detectable foetus, i.e., probably a corpus luteum of ovulation (CLO).

Four factors were considered: (a) the proportion of males at each stage of maturity; (b) the age structure of mature males; (c) the relative proportion of males and females capable of reproducing; and (d) the seasonal changes of these parameters in relation to the two periods of sexual activity defined from testis weight and testosterone concentration.

Statistical analysis

The results are expressed as mean \pm standard error (SE). One way ANOVA, t and chi² tests were performed for statistical comparisons, following Sokal and Rohlf (1981). Pearson's correlations and regressions were used except in analyses related to social structure where Spearman's rank correlations were used. Sample sizes are not mentioned

in the text when they are given in tables or figures. The commercial software package SYSTAT (Wilkinson, 1988) was used for statistical analyses and curve fitting.

Presentation of results

For ease of legibility, data from immature animals are only partly presented since the full set is shown in Desportes *et al.* (In press). Data for mature males are shown by periods of testicular activity (described below) to illustrate the effect of seasonality.

RESULTS

Histological examination

Immature testes (n=187; Fig. 1a)

The tubules were tightly packed with no lumen and embedded in abundant interstitial tissue. Tubule diameters ranged from 40 to 80μ (Table 1). A single layer of undifferentiated cells, similar in appearance, lined the periphery of the tubules. As the testis developed, the space between tubules decreased from >1 to <0.25 of a tubule diameter and the proportion of 'circular' tubules decreased from 50% to only a few per histological field. The number of peripheral undifferentiated cells also decreased; Sertoli cells were found in testes heavier than 240g. Gonocytes could be observed central to the peripheral layer, their number increasing with the size of the testis from <1 to 4–6 in circular sections of tubules. In some testes heavier than 150g, spermatogonia showed major mitotic activity and spermatocytes could be observed, mainly in the zygotene or pachytene stages. Leydig cells were present singly or in clusters of a few cells in the interstitial tissue of small testes. They seemed to regress or dedifferentiate as the testis grew and were rarely observed in testes heavier than 200g.

Fully mature testes (n=241; Fig. 1f)

Testes classified as mature had very little interstitium, large elongated seminiferous tubules with open lumen and a complex germinal epithelium consisting of spermatogonia, Sertoli cells and other cells in various stage of spermatogenesis. Tubule diameter ranged from 113 to 299 μ m (Table 1). The interstitium was less cellular than in immature testes. Leydig cells were not numerous and appeared usually in a perivascular position in small clusters of 4–10 cells. The extensive elongation of the tubules made 'circular' tubules appear rare, making the sections appear different from those observed for example in rats, hedgehogs, bulls or humans. It was difficult to observe any cellular association issued from a regular and coordinated development of new germ cell generation, and the area covered by groups of similar cells was small. The spermatogenetic pattern was more similar to that in humans with presumably a helical movement of spermatogenesis along the long axis of the tubule.

Maturing testes (n=50, Fig. 1b-e)

Maturing testes contained various proportions of both immature and mature tubules; areas of typically immature tubules were observed near areas of fully mature tubules producing spermatozoa (Fig. 1b, e). Although the appearances of the immature and mature areas were similar to those in immature and mature testes, the size of the tubules differed (Fig. 1c, d). In 31 maturing testes the mean diameter was $76.2\mu m \pm 2.4$ for immature tubules (range:48.3-112.1) and $148.2\mu m \pm 3.7$ for mature tubules (range: 111.3-199.5) as opposed to $58.0\mu m$ in immature testes and $219.7\mu m$ in fully mature testes (Table 1). The immature tubules were on average half the size of the mature ones of the same



Fig. 1. Testis of *Globicephala melas*, hacmatoxylin and cosins stained. In all photographs, the scale bar represents 0.05mm. A: Immature (19 August 1987, 9yrs old, 450cm, weight of single testis 115g).x200. B: Early maturing (13 March 1988, 13yrs old, 480cm, weight of single testis 341g).x100. C: Late maturing, immature zone (19 August 1987, 17yrs old, 560cm, weight of single testis 1,136g).x200. D: Early maturing, mature zone (13 March 1988, 13yrs old, 480cm, weight of single testis 341g).x200. E: Late maturing (24 July 1987, unknown age, 565cm, weight of single testis 1,646g).x100. F: Mature (10 June 1988, 27yrs old, 560cm, weight of single testis 1,646g).x100. F: Mature (10 June 1988, 27yrs old, 560cm, weight of single testis 1,980g).x200. Active germinal epithelium. H: Mature (22 January 1987, 23yrs old, 551cm of body length, weight of single testis 1,683g).x200. Regressed germinal epithelium. Note the lack of intermediate cells between A and B spermatogonics and the few spermatozoa.

testis (51.8% \pm 1.9, range: 29.6–75.5%). Leydig cells were more easily observable in immature zones.

Given the clear zonation of mature and immature seminiferous tubules, the mean tubule diameter of maturing testes was calculated as described earlier and ranged from 89 to 184µm (Table 1).

Characteristic and maturity stage	Mean (sem)	Range	Sample size	T-tests. P
		Tungo		
Testis weight (g)				
Immature	88.3 (88.4)	9 - 346	187	0.000
Early maturing	525.1 (30.7)	248 - 760	20	0.000
Late maturing	1027.5 (60.7)	575 - 1922	30	0.000
Mature	2840.7 (69.7)	807 - 6150	241	
Epididymis weight (g)			
Immature	28.0 (2.1)	6 - 115	79	0.000
Early maturing	110.9 (12.0)	76 - 161	6	0.008
Late maturing	193.6 (20.4)	131 - 297	8	0.000
Mature	414.5 (14.7)	166 - 658	5 1	
Testis length (mm)				
Immature	126.4 (3.3)	55 - 195	89	0.000
Early maturing	228.5 (7.9)	195 - 245	6	0.002
Late maturing	28 0.0 (9.7)	258 - 312	6	0.000
Mature	407.5 (5.3)	347 - 500	53	
Index of testis develo	pment (g/mm)			
Immature	0.6 (0.0)	0.1 - 1.4	89	0.000
Early maturing	2.1 (0.3)	1.2 - 3.1	6	0.012
Late maturing	4.2 (0.6)	2.3 - 6.7	6	0.000
Mature	7.2 (0.3)	3.0 - 11.9	53	
Seminiferous tubule d	liameter (µm)			
Immature	58.0 (0.9)	40 - 80	98	0.000
Early maturing	105.1 (4.0)	89 - 133	12	0.000
Late maturing	137.0 (5.2)	101 - 184	19	0.000
Mature	219.7 (2.7)	113 - 299	166	
Age (year class)		-,	<u>, , , , , , , , , , , , , , , , , , , </u>	
Immature	58 (0.3)	0 - 15	158	0.000
Farly maturing	143(05)	11 - 18	18	0.004
Larry maturing	16.4 (0.5)	11 - 22	26	0.000
Mature	25.4 (0.4)	14 - 46	225	
Rody length (cm)	. ,			
Immature	361.5 (5.8)	174 - 506	187	0.000
Farly maturing	493.8 (4.6)	458 - 545	20	0.001
Larry maturing	519.5 (4.8)	464 - 565	30	0.000
Mature	561.0 (1.8)	475 - 625	240	
Body weight (kg)				
Immature	703.5 (60.7)	92 - 1300	34	0.001
Farly maturing	1277.2 (32.3)	1210 - 1356	5	0.275
Late maturing	1426.6 (105.4)	1100 - 198 0	7	0.002
Mature	1794.7 (39.6)	1175 - 2320	49	_

Mature

Table 1

Gonadal characteristics, age, body length and body weight by maturation stage as determined by histological examination of testis tissue; t-test values compare means from one stage to the next.

Gonadal and individual characteristics for each stage of histological maturity

Table 1 gives the arithmetic means and ranges of certain gonadal and individual measurements for each stage of histological maturity. Although mean values for one stage were significantly smaller than for the following one for all criteria (t-tests, p < 0.02; Table 1), except for mean body weight, there was a substantial overlap between stages for most criteria, particularly for age, body length and body weight. All criteria except testis length, showed considerable overlap between early maturing and late maturing specimens making these two stages difficult to separate by other than histological methods. Although testis length appeared to be a good indicator of sexual maturity, this may be an artifact of the small number of maturing specimens.



Fig. 2. Logistic curve fitted to the fraction-mature in successive age classes for early and late maturing and mature stages in *G. melas*. Numbers of males in each class are given at the top of the figures. Symbols: solid triangle, early and late maturing and mature males; solid square, mature males (dots for late maturing stages have been omitted for clarity).

Average age (ASM) and length (LSM) at the attainment of sexual maturity

Sexual maturity for the 178 animals for which no tissue samples were available was deduced from the combination of the available criteria (gonad measurements, age, body length and weight) and the ranges defined for each stage of histological maturity given in Table 1.

Estimates of ASM and LSM are given in Table 2. Fig. 2 shows the logistic curve fitted to the fraction-mature-at-age relationship for early and late maturing and mature stages.
		Stages of sexual maturity			
	Methods	Early maturing	Late maturing	Mature	
ASM (years)	sum of fraction immature	13.8 (0.2)	15.0 (0.2)	17.0(0.3)	
	50% of fraction mature	13.9 (0.1)	15.0 (0.1)	16.8(0.1)	
LSM (cm)	sum of fraction immature	485.9 (1.2)	499.2 (1.3)	516.2(1.3)	

Estimates of the average age (ASM) and length (LSM) of male pilot whales at the attainment of the three stages of sexual maturity. Standard errors are in parentheses.

Testis growth

A sharp increase in testis weight (from 0.25 - >1.5kg) occurred between about 460-520cm in body length (Fig. 3a), 1,000-1,500kg (Fig. 3b) in body weight and 11-18yrs of age (Fig. 3c). Most of these animals were classified as maturing, confirming the view that this growth spurt corresponds to puberty. Beyond this period, testis weight continued to increase with body length and body weight (r=0.43, n=236, r=0.618, n=45 respectively, p<0.001), but was no longer correlated with age in males older than 21yrs (n=153,



Fig. 3a. Weight of testis as function of body length (n=382), in *G. melas.* Symbols: cross, immature male; solid triangle, early maturing male; X, late maturing male; solid square, mature male caught between March and September; square with X, mature male caught between October and February. The lines connect the arithmetic means of testis weight for each class.



Figs. 3b and 3c. Testis weight as a function of body weight (n=142) and age (n=397). Symbols as in Fig. 3a.



Fig. 4. Testis length (4a) and index of testis development (4b) as a function of body length in G. melas (n=154). Symbols as in Fig. 3.

p=0.07). Individual variation in testis weight with age, body length and weight became important from puberty onwards, and could only partly be explained by seasonality.

The testis length (Fig. 4a) and index values (Fig. 4b) showed the same sharp increase as testis weight. Testis length and index values were not significantly correlated with body length in males longer than 520cm (p=0.052, n=48).



Fig. 5. Mean diameter of seminiferous tubules as a function of testis weight (n=295) in G. melas. Symbols as in Fig. 3.

The diameter of seminiferous tubules increased as the testis matured (Fig. 5). It was correlated with testis weight in immature males (p < 0.001, n=98, r=0.70), maturing males (p < 0.001, n=31, r=0.71) and mature males with testis weighing less than 2.5kg (p=0.001, n=60, r=0.43). The enlargement in tubule diameter made only a limited contribution to the increase in testis weight in immature males. In testis weighing more than 2.5kg, tubule diameters and testis weight were no longer correlated (p=0.076, n=104).

Sperm production

The density of spermatozoa increased from testicular to epididymal to ductus deferens smears. Sperm density on epididymal smears increased as the testis matured (Table 3).

Correspondence between histological maturity of testis and abundance of spermatozoa on epididymal smears. The numbers represent the percentage of testes in each category.

Table 3

	Epididymal sperm density				
Histological maturity	None	Low	Intermed.	High	Sample size
Immature (%)	82	18	_	-	22
Early maturing (%)	-	81	19	-	21
Late maturing (%)	-	33	49	18	33
Mature (%)	-	18	43	39	249



Fig. 6. Proportion of mature males showing a high density of spermatozoa on epididymal smear as a function of age and season in mature males of G. melas (n=232). Symbols are as follows: square with X, mature male caught between March and September; solid square, mature male caught between October and February. Sample sizes are given above symbol.

Only for immature testes was the density 'none' recorded of the 22 males identified as immature from histological examination and for which epididymal smears were also available; four (all \geq 8yrs old) showed low densities of spermatozoa on epididymal smears. High densities were found only in late maturing (18% of smears) and mature testes (39% of smears).

As would be expected, the increase in sperm density with testis maturation was reflected in an increase with increasing age. The density 'none' was observed in males between 0 and 15yrs. Smears showing low sperm density were observed from the age of 8yrs and their proportion decreased dramatically between 12 and 18yrs of age. Smears showing intermediate sperm density were observed from the age of 12yrs, and smears with high sperm density from the age of 14yrs with one exception, an 11yr old late maturing male.

The influence of age on sperm density in mature males was examined for the epididymal smears. The sample was arbitrarily stratified into 3-year age classes and divided into two seasons, October-February and March-September, to remove any seasonal (see below) bias (Fig. 6). In both periods, the age classes 29–31 and 32–34 combined showed significantly higher sperm density than the younger classes combined (chi² tests, p<0.01). Sperm density seemed to decrease from the age class 35–37 in the winter period (no data available for the summer period) but sample sizes were too limited to test whether this decrease was significant.

Table 4

Plasma testosterone concentrations by stage of sexual maturity. The periods take into account the seasonality shown in Fig. 6 (no data available in May and June); t-test values compare arithmetic means between one stage and the next.

Maturity stage and season	Mean (sem) ng/ml	Range ng/ml	Sample size	T-tests P
October - February, plus Ju	ıly			
Immature	0.4 (0.5)	0.0 - 2.8	82	0.000
Early maturing	1.4 (0.3)	0.5 - 2.7	8	0.094
Late maturing	2.6 (0.6)	1.1 - 6.2	9	0.035
Mature	4.4 (0.3)	1.2 - 13.4	51	
March - September, minus	July			
Immature	2.5 (0.9)	0.1 - 29.4	40	0.201*
Early maturing		2.5	1	
Late maturing	7.3 (2.7)	2.2 - 11.2	3	0.283
Mature	10.7 (1.1)	2.7 - 22.1	20	

* In this case the t-test compares means between immature and late maturing stages.

Endocrine testicular function: testosterone concentration

Plasma testosterone concentrations ranged from 0.01 to 29.4 ng/ml (Fig. 7). They became significantly correlated with age in males older than 10yrs (p=0.049, n=104, r=0.194). Most immature males younger than 8yrs showed low (<1ng/ml) concentrations. After



Fig. 7. Plasma testosterone concentrations as a function of age (n=195) in G. melas. Symbols: cross, immature male; solid triangle, carly maturing male; X, late maturing male; square with X, mature male caught between March and September (except July); solid square, mature male caught between October and February plus July. The line connects the arithmetic means of testis weight for each class.

8yrs levels began to increase with a sharp increase between 12 and 20, i.e. simultaneously with that in testis weight. Plasma concentrations >10ng/ml were observed only in males 15–32yrs old, except for two immature males (5yrs and 6yrs) showing concentrations higher than 28ng/ml. With one exception these high concentrations were observed in the period March-September minus July (see below).

Individual variation was a major factor with considerable overlap between all stages, even immature and mature, year round (Fig. 7, Table 4). In the period October-February plus July, the mean concentration was significantly smaller for immature whales than for any other stages. Means differed also between early maturing whales and mature ones (t-tests, p < 0.001) and late maturing whales and mature ones, but not between early and late maturing stages. In the period March-September minus July, individual variation increased and mean concentrations differed significantly only between immature and mature males (t-test, p < 0.001).

Seasonality of sexual activity in mature males

Reproductive seasonality was investigated by analysing changes in testis weight, testosterone level, histological appearance of testicular tissue and sperm density on epididymal smears. Testis weight showed a clear seasonal pattern in mature pilot whales (Fig. 8a), although there was some individual overlap even between January and June. Testis weights were low in January and February and increased in March (March > February: t-test, p < 0.001). They were high from March to September, with no significant differences between months although they peaked in June. Testis weights began decreasing in September (August > October, t-test, p=0.014), and from October to



Fig. 8a. Monthly variation of mean testis weight (8a, n=247) in mature male G. melas. Sample sizes are below the error bars, which represent one standard error from the mean.



Fig. 8b and c. Monthly variation of mean plasma testosterone concentrations (n=71), and mean diameter of seminiferous tubules (n=166) in mature male G. melas. Sample sizes are below the error bars, which represent one standard error from the mean.

February values were low and not significantly different. Mean testis weight increased about 1.5 times (t-test, p < 0.001) between the periods of low (October – February) and high (March to September) testicular activity.

Testis length (TL) and index of testis development (ITD) data were only available in February (8), March (11), April (2), June (9), October (18) and November (5). Mean values of both parameters differed significantly between the periods of low and high testicular activity (p=0.009 and p<0.001 for TL and ITD respectively).

Despite the absence of data for May and June, testosterone concentrations showed a clear bimodal pattern (Fig. 8b). Ranges overlapped substantially between most months, but not between April and August, and December. Testosterone concentrations were low from October-December, with no significant differences between means. They began increasing in January (February > December: t-test, p=0.007) and rose steadily to April (March > January: t-test, p=0.007). In July concentrations dipped to January-February levels (April > July: t-test, p=0.003). They rose again in August (August > July: t-test, p=0.035), remained at a similar level in September then declined in October (August-September > October: t-test, p=0.031). Mean concentrations did not differ significantly in the period of low activity, (October to February plus July) or in the period of high activity (March to September minus July) and concentrations increased about 2.5 times between these two periods (t-test, p<0.001).

Testis weights were correlated with body length in mature males and with age in young mature males; testosterone concentrations were correlated with age. Any seasonal variation in the length or age composition of the mature male sample could, therefore, have accounted for some or even all of the seasonal variation observed. There was, however, no significant monthly variation in mean age or body length for the male sample related to testosterone concentration nor any significant difference between means for the high and low periods of endocrine activity. There were significant monthly variations in body length and age for the male sample related to testos of testos of endocrine activity. There were significant monthly variations in body length and age for the male sample related to testis weight (ANOVAs, p < 0.010), but no seasonal trend, and there was no significant variation between periods of testicular activity as defined above.

Testis histology also showed a seasonal pattern although the general picture was somewhat blurred by significant individual variation. A decrease in spermatogenesis was noticeable from September until January, with low levels of spermatogonia and spermatocyte density, a lack of 'intermediate' stages between spermatogonia A-B and spermatozoa (Fig. 1h). A reduced lumen persisted, even in December and January, in involuted tubules containing only a few spermatogonia and degenerating primary spermatocytes. The cells were often clumped together and the lumen of the tubules contained their degenerating remains. The lowest densities of germ cells and spermatozoa were observed in January. In February 'intermediate' cells and spermatozoa reappeared, announcing the onset of a new wave of spermatogenesis. Greatest activity was observed in May and June with numerous deeply stained and condensed chromatins lining the periphery of the tubules (Fig. 1f). All males showed intense spermatogenic activity in May and June. However, in autumn and winter, males with and without involuted tubules could be observed within the same pod (Fig. 1g-h), involuted and non-involuted tubules were seen on the same slide and, in a few cases, one testis of a pair could show signs of involution while the other did not. This individual variation may partly explain the unclear seasonal pattern of tubule diameters (Fig. 8c).

Monthly differences were significant (ANOVA, p=0.001); means differed significantly between February and March, March and April, June and July, November and December (t-tests, p<0.001, p=0.005, p=0.031, p=0.050 respectively), and between the periods March-September and October-February (t-tests, p=0.049). When data were pooled over two-month periods, means increased significantly from January-February to March-April (t-test, p=0.031) and decreased significantly from May-June to September-October (t-test, p=0.010).

Seasonal changes in sperm density were also observed on epididymal smears. For the same age class, a higher percentage of smears showed high sperm density in the period March-September than in the period October-February (Fig. 6). The proportion of epididymal smears of mature males showing low, intermediate or high sperm densities varied significantly between months (chi², p < 0.001; Fig. 9) with the prevalence of smears with high sperm density peaking in March and in July-August. Cellular debris increased noticeably on smears from October to February. The seasonal decline in spermatogenic activity was simultaneous with the decreasing proportion of smears showing high densities of spermatozoa, but spermatozoa were present on smears all year round.



Fig. 9. Monthly variations in the proportion of mature males showing a high (filled), intermediate (crosshatched) and low (empty) density of spermatozoa on epididymal smear in G. melas (n=249). Numbers above bars are sample size.

In months with low activity (October to February), testis weight, testosterone level, histological features and sperm density did not decrease to the level found in either immature or maturing individuals, and involuted mature tubules did not have the same appearance as immature tubules. No period with complete testicular inactivity was identified and spermatogenesis never completely ceased.

School structure in terms of male sexual maturity

As all 38 mixed schools examined contained, in various proportions, immature and mature males and immature, pregnant (except one), lactating and resting females, they can be considered breeding schools.

The average composition of the 19 schools selected for this analysis is given in Table 5. There were more females than males in all mixed schools except one (average, 1.6 females per male) and more mature females than mature males (average, 6.1 mature females per mature male). Four schools (22%) landed in March, May and June (2) contained no maturing males, while all schools contained at least one mature male.

The number of individuals in each of the social categories listed in Table 5 was correlated with school size, except the number of early maturing males (p>0.50). All the parameters examined in Table 5 were independent of school size. The number of mature males and mature males 22yrs old and older was weakly correlated with the number of ovulating (CLO) females (p<0.05, Fig. 10).

Between-school variation was important for all parameters considered, but only the proportion of CLO females, mature males and maturing males + mature males < 22yrs differed significantly between schools (chi², p<0.001, p<0.050, p<0.025 respectively). Consequently the number of CLO females per mature male and per mature males 22yrs old and older also differed significantly between schools (chi², p<0.005). Possible differences between the periods of high and low activity defined earlier were examined.

Table 5

Compositions of 18 mixed and one male-only schools of long-finned pilot whales landed in the Faroes between July 1986 and December 1989. CLO females are those possessing a *corpus luteum* but no detectable foetus, i.e. probably a *corpus luteum* of ovulation. Other abbreviations are explained in the Table.

		Mixed scho	Male-only school	
School composition		Mean (sem)		Range
School size		69.4 (7.8)	26 - 156	8
Females	Total	61.1% (1.3)	49.1 - 70.3	-
(% lotal)	CLO (CLO)*	41.3% (1.2) 7.5% (1.7)	0.0 - 41.3	-
Males	Total	38.9% (1.3)	29.7 - 50.9	100%
(% Total)	Immature	25.5% (1.3)	15.6 - 36.6	25.0%
	Early maturing	1.6% (0.5)	0.0 - 7.7	-
	Late maturing	1.4% (0.4)	0.0 - 4.4	12.5%
	Mature (MM)	10.5% (1.2)	1.6 - 19.3	62.5%
	Mature < 22yrs(MM21)	3.2% (0.6)	0.0 - 10.2	37.5%
	Maturing + MM21	6.1% (0.9)	0.0 - 15.3	50.0%
	Mature = > 22yrs(MM22)	7.3% (1.0)	1.6 - 15.8	25.0%
Sex ratios	Female/Male	1.6 (0.1)	0.9 - 2.3	-
	MF/MM	6.1 (1.5)	1.8 - 26.0	-
	MF/MM22	8.3 (1.5)	2.2 - 26 .0	-
	CLO/MM*	1.0 (0.3)	0.0 - 6.0	-
	CLO/MM22*	1.2 (0.4)	0.0 - 6.0	-

* In this case the sample size is only 17 schools.



Fig. 10. Number of mature males 22yrs or older as a function of the number of ovulating females in 17 schools of *G. melas.* Symbols: solid square, mature male caught between March and September; square with cross, mature male caught between October and February.

No seasonal pattern was detectable for any of the parameters, except for the proportion of late maturing males. This decreased significantly from 2.2% (SE=0.5, range 0-4.4%, n=9) in the period October-February to 0.3% (SE=0.2, range 0-1.5%, n=8) in the period March-September (t-test, p=0.006).

In the two schools that contained only one mature male, the males were 25 and 26yrs old. The youngest mature male was 14yrs old in a school containing two mature males, 17yrs old in a school containing three mature males, and 17 and 20yrs old in two schools containing four mature males. Thus, single mature males were several years older than the youngest mature males in schools containing two mature males or more.

The age structure of the mature males in the 18 mixed schools was as follows:

- 16 schools contained mature males in the age class 14–21 (i.e., all except the two schools with a single mature male),

-17 schools (94%) contained mature males in the age class 22-26,

-5 schools (28%) had mature males between 22 and 26yrs of age as the oldest male,

- 13 schools (72%) contained mature males in the age-class 27–34, and all these schools contained males in the age class 31–34,

- 7 schools (39%) contained mature males 35yrs old or older.

The five mature males from the male-only pod were 16, 16, 18, 22 and 24yrs old. Thus, mature males <22yrs were always in the company of older mature males, and the age-class 31-34 was represented in all schools containing animals older than 26yrs.

DISCUSSION

Criteria for assessing sexual maturity

If the sexual maturity of a large sample of males is to be assessed, it is important to try and identify criteria with the least possible overlap between stages and for which the necessary data/samples can be collected and processed easily and rapidly.

Histological examination for spermatogenesis is usually considered as the only positive identification of maturity, but is time-consuming. In addition, in species with comparatively large testes, such as cetaceans, histological sections correspond to only a small area of testis. This may lead to inaccurate assessment of maturity for individual whales. In our sample, for example, 18% of males classified as immature from histology alone had spermatozoa in the epididymal smears and had thus already reached the early maturing stage. Examination of epididymal smears is more like sampling an entire testis and might be more accurate, but it is also time-consuming and may pose problems if the production of spermatozoa is cyclical.

Although data on body length, weight and age are relatively easily and routinely collected, the large overlap in values between all maturity stages makes them inaccurate single indicators of maturity in most cetacean species. This is particularly true for pilot whales where overlap was found even between immature and fully mature males.

The physical characteristics examined in this study overlap considerably between maturation stages. The best indicator (i.e., with the smallest overlap) was the length of the testis. The reduced overlap may reflect less sensitivity to seasonal variations or simply be an artifact of the small sample size. Given its ease of collection, however, further effort should be applied to assessing its value as an indicator of sexual maturity in pilot whales, and indeed other cetacean species.

For land mammals, testosterone concentrations are usually used to determine sexual maturity. In pilot whales, however, the degree of overlap between maturation stages renders this approach unreliable. Desportes *et al.* (In press) discussed the reasons for this level of variation and listed several factors known to affect testosterone secretion in other mammalian species. Seasonality only accounted for part of the variation in pilot whales since data overlapped in both seasons of activity even between immature and mature stages. A high degree of individual variation was also reported in fin whales (Ølafsson and Kjeld, 1986; Kjeld and Arnason, 1989), in minke whales (Yoshioka and Fujise, 1992) and in three longitudinal studies of dolphins (Harrison and Ridgway, 1971; Judd and Ridgway, 1977; Wells, 1984). Although testosterone concentrations provide a good tool for following the sexual activity of male cetaceans over time, they cannot be used as a single indicator of sexual maturity. In addition, the highest levels of testosterone observed in mature males were found in males younger than 20 years which we do not consider as being socially mature (see below). Thus high testosterone levels may not be an indicator of social status and successful mating.

The age and length at attainment of sexual maturity cannot be compared directly on the basis of testis weight or testosterone levels among species or even stocks of the same species (Desportes *et al.*, In press; Perrin and Henderson, 1984; Perrin and Reilly, 1984; Brownell and Ralls, 1986; Aguilar and Monzon, 1992). Hohn *et al.* (1985) suggested that an index of testis development normalising testes weight by testes length, thereby removing the variability in testis weight due to differences in body length, may provide a tool for comparison of maturity between stocks or species. They found, as an example, that the spotted dolphins in their study and the common dolphins studied by Collet and St. Girons (1984) had similar values for immature and mature stages despite the relatively heavier testes of common dolphins. The index values in our study, however, are more than

three times those given for spotted dolphins although Hohn et al. (1985) use combined testicular and epididymis weight.

Studies of primates (e.g. Harcourt *et al.*, 1981; Harvey and Harcourt, 1984; Kenagy and Trombulak, 1986; Krebs and Davies, 1987) and more recently cetaceans (e.g. Brownell and Ralls, 1986; Aguilar and Monzon, 1992) have related differences in breeding systems and sperm competition to differences in testis size. Such studies should be continued particularly for small odontocetes since they may provide valuable information on breeding systems of species for which behavioural data are difficult and costly to obtain.

Sexual maturity and breeding longevity

Several definitions of sexual 'maturity' can be considered: (i) physiological (i.e. the ability to produce at least some spermatozoa); (ii) histological (i.e. as defined earlier); (iii) functional (i.e. fertile); and (iv) social (access to ovulating females and successful fertilisation occurs – see Best, 1969). In pilot whales, physiological maturity corresponds to the early maturing stage and is reached at an ASM of 13.8yrs; histological maturity is reached about 3.5yrs later at an ASM of 17.0yrs. The attainment of functional and social maturity are much more difficult to assess without behavioural observations.

Male pilot whales can produce spermatozoa when as small as 438cm and as young as eight years (cf. smears). Most early maturing males had very little or no seminal fluid microscopically detectable in the epididymis, and less than 20% of them exhibited 'intermediate' densities of spermatozoa while 67% of late maturing males exhibited at least intermediate densities of spermatozoa. Sperm density on epididymal smears continued to increase well into the late maturing stage, i.e., until 20–21yrs. Thus, the fertility of early maturing males can be considered lower than that of late maturing and mature males, even though the minimum density of spermatozoa required for 'fertility' is not known. Early maturing males have most likely not reached functional maturity, while most late maturing males are probably functionally mature. Functional maturity thus corresponds roughly to the late maturing and mature stages and is reached at an ASM of about 15yrs.

The available evidence suggests that social maturity is not equivalent to either functional or histological maturity, i.e., that the youngest 'mature' males may not be socially mature. Although the examined pilot whale schools always contained mature males, maturing, in particular late maturing, males were not always represented. This may be because they are unable to substitute for mature males. Body weight (Bloch *et al.*, 1993b), testis weight and tubule diameter continued to increase until about 25yrs, i.e., some seven years after histological maturity was reached. Single mature males were several years older than the youngest mature males in schools containing more than one, and mature males younger than 22yrs always occurred in the company of older ones. It thus seems likely that successful mating may not take place until several years after histological maturity is reached and be delayed to the age of 22yrs or even 25yrs.

It was also found that sperm density was significantly higher in the age class 29–34. The age class 27–34 was represented in all the schools containing males older than 26yrs (72%), suggesting that the age class 29–34 might be the main breeding group in males.

The high values of testosterone and testis weight found in some young mature males do not contradict this view. High levels of plasma testosterone are observed during puberty in several mammalian species (McCann *et al.*, 1974; Ghanadian *et al.*, 1975; Berger *et al.*, 1976; Saboureau and Dutourné, 1981). In the case of wolves, although only one pair reproduces in a pack, endocrinal and behavioural data show that all mature animals appear physiologically capable of reproduction and during the reproductive season subordinate females ovulate and subordinate males show testicular development (Packard et al., 1985). Spermatogenesis occurs in non-breeding male naked mole-rats, although the testosterone levels are lower than in breeding males (Faulkes et al., 1991).

In Newfoundland pilot whales, Sergeant (1962) took the macroscopical presence of seminal fluid in the epididymis as the criterion for functional maturity (in testes weighing 1.7g or more). He estimated the LSM to be 490cm, i.e., the mean length between the largest immature (510cm) and the smallest mature (465cm). ASM was estimated at 12yrs based on the *histological* detection of seminal fluid. If the macroscopical detection of seminal fluid and the smallest male with seminal fluid had testes weighing about 1.7kg, which corresponds roughly to the age of 15yrs on Sergeant's plot of testis weight against age. In the Faroes, most late maturing and mature males had seminal fluid in the epididymis while early maturing males usually did not, and the attainment of the functional maturity as defined by Sergeant thus corresponds approximately to the attainment of the late maturing stage (ASM = about 15yrs and LSM about 500cm).

The values of ASM and LSM for Faroese and Newfoundland males are not incompatible, given the disparity in the methods used, the small Newfoundland sample size and the fact that Sergeant (1962) sometimes used estimated and not direct values.

Comparison with other studies dealing with North Atlantic male pilot whale reproduction is difficult, since they are based on very limited samples and did not estimate ASM and LSM (Cowan, 1966: 27 males; Desportes, 1982: 8 males; Martin *et al.*, 1987: 11 males; Bloch, 1992: 41 males; Collet, 1987: 11 males; Sigurjónsson *et al.*, 1993: 12 males). The pattern of testis growth they presented, however, was not inconsistent with the Faroese data, and testicular growth spurts took place within the same range of body length and age data (Desportes *et al.*, In press).

Comparison is possible, however, with studies of the southern and northern forms of the related short-finned pilot whale (Kasuya and Marsh, 1984; Kasuya and Tai, 1993) since sample sizes were large and similar or related methods and criteria were used. Many results were similar, including the correlation of age and body length with maturity, the tendency of larger males to mature at a younger age and the cessation of testis growth at about 25yrs, with larger mature males having heavier testes than smaller ones. The attainment of the late maturing stage was also considered as the attainment of functional maturity in short-finned pilot whales, and histological maturity occurred later at an ASM of 17.0yrs for both forms. A major difference is that we considered that long-finned pilot whales reached social maturity some five years after histological maturity, whereas Kasuya and Marsh (1984) and Kasuya and Tai (1993) considered that histological maturity and social maturity were equivalent in short-finned pilot whales, as has been described for striped dolphins (Miyazaki, 1984) and sperm whales (Best, 1969; Best *et al.*, 1984).

Although the maturing stage included males between 11 and 22yrs of age, the low percentage of maturing males in schools suggests that either testicular maturation occurs rapidly or that animals in this stage are under-represented in the harvested schools. Humans progress through the pubertal stage at a rapid rate, and not in synchrony with their chronological peers (Sinclair, 1973). This is likely to be the case in long-finned pilot whales and it has also been suggested for short-finned pilot whales (Goebel-Diaz, 1986). This implies that the overall group information will underestimate the rate of changes and overestimate the period over which they take place.

In our sample, sperm density appeared lower in males over 34yrs, possibly reflecting a decline in potential reproductive success. No evidence for such a decline was observed in short-finned pilot whales (Kasuya and Marsh, 1984; Kasuya and Tai, 1993). However, the oldest male long-finned pilot whales did undergo spermatogenesis and testis weight did not appear to decline with age, thus the decline in density may not mean that older males

could no longer successfully reproduce. Further examination with a larger sample size is required. Harman and Talbert (1985) point out in their review of reproductive ageing, that although there is considerable evidence that males in many species do show an overall reduced reproductive capacity with age, there is a high degree of individual variation and some males retain their full reproductive function into old age.

Seasonality

Testicular activity clearly has a strong seasonal component in Faroese pilot whales. It is highest between March and September with an overall 1.5 fold increase in testis weight and an overall 2.5 fold increase in testosterone concentrations. There is, however, no period of complete cessation of activity; high testis weights and testosterone concentrations were found from October-February when 23% of males exhibited high densities of spermatozoa. These results agree with the findings on female reproductive activity where conceptions and births were estimated to occur mainly from spring to early autumn, but also in winter months (Martin and Rothery, 1993). Reproductive activity is thus diffusely seasonal in males and females.

The mean testosterone concentrations showed a clear bimodal pattern (although no data were collected in May and June) with a monotonic increase from January to April, a dip in July and a second peak in August-September. Bimodal patterns in testosterone levels have been reported for bottlenose dolphins (Harrison and Ridgway, 1971) and many avian and mammalian species (e.g. Gulamhusein and Tam, 1974; Boissin *et al.*, 1980; Atkinson and Gilmartin, 1992). The pattern is consistent with the bimodal distribution of breeding events proposed by Martin and Rothery (1993) for the Faroese long-finned pilot whale, with a secondary peak of conceptions in September. Since foetal mortality is important in pilot whales (Brault *et al.*, 1993; Martin and Rothery, 1993; Desportes *et al.*, In press) and particularly at the beginning of pregnancy (Brault *et al.*, 1993), the protracted period of elevated testicular activity of seven months with a bimodal pattern of testosterone concentrations may be an adaptive feature allowing females miscarrying early in pregnancy to reconceive in the same season.

Comparison with the results of Sergeant (1962) for Newfoundland is problematic. He describes a cessation of male sexual activity in late summer and the restriction of nearly all conceptions to a six-month season limited by the period of male reproductive activity. However, his sampling period was limited to the period July-October, and this may explain the apparent difference with the Faroese results.

Similar diffuse seasonality in testicular activity has been reported for the spotted dolphin (Hohn *et al.*, 1985) and suggested for the common dolphin (Harrison *et al.*, 1969; Harrison, 1972; Hui, 1979), the bottlenose dolphin (Harrison and Ridgway, 1971) and the short-finned pilot whale (Kasuya and Marsh, 1984; Kasuya and Tai, 1993).

This diffuse seasonality is interesting because it contrasts with the patterns accepted for land mammals. Mauget *et al.* (1981) believe that the concept of a reproductive 'cycle' requires the existence of a resting period in sexual activity. Boissin *et al.* (1980) and Mauget *et al.* (1986) define two possible patterns: – definite reproductive seasonality with a strict involution of testicular activity in autumn and winter concomitant with a lack of sexual activity; or a continuous or long breeding period or a breeding period controlled by temporal variation in forage availability and temperature, with males remaining physiologically capable of reproduction throughout the year. Definite seasonality with a limited period of testicular activity and a resting period with complete involution of spermatogenesis has been described for harbour porpoises (Sørensen and Kinze, In press; Sørensen, pers. comm.).

The diffuse seasonality observed in Faroese long-finned pilot whales may be a species or

family, adaptative feature, but may also be partly due to the non-geographical homogeneity of the sample. Geographical variations in breeding seasons have been reported for land mammals, and sometimes among populations close geographically, but isolated (Novoa, 1970; Neaves, 1973). Similar variations have also been described in odontocetes (short-finned pilot whales – Kasuya and Tai, 1993; spotted dolphins – Barlow, 1984; Hohn *et al.*, 1985; spinner dolphins – Barlow, 1984; common dolphins – Collet and Saint Girons, 1984; sperm whales — Best *et al.*, 1984; harbour porpoises – Gaskin *et al.*, 1984; killer whales – Matkin and Leatherwood, 1986).

Pilot whales are found throughout the North Atlantic, and it is not yet known whether the Faroese drive fishery operates on one or more populations. Significant differences have been found between pods in organochlorine loads (Aguilar et al., 1993), heavy metal loads (Caurant et al., 1993; In press), parasitic loads (Balbuena, 1991; Desportes et al., 1993a; Raga and Balbuena, 1993) and allele frequencies of electrophoretic markers (Andersen, 1988; 1990; 1993). These differences support the idea of a non-homogeneous population with at least three groups of schools in those landed during the period 1986-1988 (Desportes et al., 1993b). A preliminary comparison also showed that testis weight of mature males varied significantly among the four schools landed in September although there were no significant differences in age or body length (ANOVA, p=0.032; Desportes, unpublished), also supporting the idea of non-homogeneity in Faroese schools. Variations in school geographical history may imply asynchrony in the timing of reproductive events determined by environmental factors, and hence a drift from the main peak of testicular and breeding activities. This would help to explain the high degree of individual variability observed in most parameters studied. Further analysis and comparison of various parameters are clearly needed to verify this hypothesis.

School structure and sexual behaviour

In mammalian species it is usual for maturing offspring of one or both sexes to leave their natal groups (Greenwood, 1980). In numerous species males disperse (Jensen, 1969; Ridgway and Harrison, 1981; Clutton-Brock *et al.*, 1982; Mauget *et al.*, 1986), but they can also become subordinate individuals which do not reproduce (Rasa, 1984; Packard *et al.*, 1985; Trivers, 1985; Mauget *et al.*, 1986; Faulkes and Abbott, 1991; Faulkes *et al.*, 1991). In odontocetes, male dispersal has been found for sperm whales, striped dolphins, hump-backed dolphins and bottlenose dolphins (Best, 1969; Norris and Dohl, 1980; Wells *et al.*, 1980; Best *et al.*, 1984). Kasuya and Marsh (1984) suspected dispersal of maturing short-finned pilot whale males on the basis of the uneven distribution of maturing males among schools and the lack of males in the age-range 10–20yrs. In killer whales, dispersal was observed in 'transient' pods but not in 'resident' pods (Bigg *et al.*, 1990).

Amos *et al.* (1991a; b; 1993) postulate on the basis of genetic analysis that male longfinned pilot whales do not disperse from their natal groups. They neither father offspring within their own pod nor show strong reproductive dominance. Groups of related males (i.e. from one pod) must mate when two or several pods meet or when adult males visit other pods. These events must be transitory since paternity testing has failed to reveal fathers (Amos *et al.*, 1993). These results are, however, based on detailed analysis of only two pods, landed two days apart in close proximity and likely to be related (Amos *et al.*, 1991a) and thus may not be representative of all of the sampled pods. Both schools included, for example, very few maturing (0 and 1) and young mature males (3 and 0<22yrs) among their 90 and 102 individuals, respectively.

In fact, we believe that the structure of Faroese pods suggests that maturing and young mature males move away from their schools and aggregate in others, at least temporally, since the population of maturing males and mature males <22yrs ranged from 0 to 8% and

15% respectively and the proportion of these two groups combined varied significantly among schools. The existence of a male-only group composed of males <25yrs (Desportes *et al.*, 1993a) and the significantly lower proportion of late maturing males in the period March-September also supports this hypothesis.

The proportion of mature males and mature males 22yrs old and older varied between schools from 0 to 19% and 16% respectively. Their numbers were weakly correlated with the number of ovulating females, suggesting that mature males may aggregate in certain schools at certain times and that one of the controlling factors might be the female reproductive cycle. Schools consisting mainly of large males, if not only of males, and without calves, have also been caught in the past by the Faroes drive fishery (Bloch, 1992), and have been observed in other places (e.g. see review in Evans, 1987). Sergeant (1962) also postulated some segregation by mature male long-finned pilot whales off Newfoundland, at least in late summer, citing a school comprising nine mature and one immature male and four probably senile females and two groups of mature males separated from other individuals, one at sea and the other during a drive.

There is, thus, some evidence that male long-finned pilot whales from puberty onwards may, at least temporarily, move away from their natal schools, aggregate in others and/or form non-breeding schools which may include some immature males and old females. This feature may play a role in the bias sex ratio observed from puberty onwards, although probably less importantly than the higher male mortality described by Martin *et al.* (1987) and Bloch *et al.* (1993b).

If some segregation does occur in pilot whales and males move between pods, even for short periods, it is perhaps surprising that non-breeding or male-only groups are not more often identified. Several factors may explain this. The non-breeding schools observed in Newfoundland and the Faroes reveal that they may comprise immature as well as adult males. These schools will not be recognised as having a special composition, unless the sex, age and reproductive status of all the individuals is known, particularly at sea since only large bulls are positively identifiable. Reaction to vessels has been found to vary for different growth stages, sex and reproductive state in the Dall's porpoise (Kasuya and Jones, 1984), and it is possible that this may also occur for pilot whales. Furthermore, solitary pilot whales or small groups are more likely to be missed by observers. Of the 18 mixed schools analysed from the Faroes, 67% contained less than 10 mature males, so any group of related males leaving a school for mating is likely to be small. Thus it is infact not surprising that such individuals and groups are under-represented in fisheries, since opportunistic drive fisheries do not target such small units. In the Faroes, the smallest complete school landed between July 1986 and June 1988 contained 26 animals. The average for 43 schools was 84.7 ± 8.0 , although several of them were known to be part of bigger groups (Bloch et al., 1990). Over the period 1709-1992, the average size of 1,629 schools was 147.8 whales; 2.5% of them were single whales (Zachariassen, 1993). Nonbreeding schools may also be under-represented in catches or strandings because of a geographical or offshore segregation as has been described for the sperm whale and the harbour porpoise (e.g. see review in Evans, 1987).

In conclusion, the social behaviour and mating system of pilot whales has not yet been elucidated and more information is needed from genetic studies, detailed analysis of school structure in fisheries and at sea, and an examination of the behaviour of individuals.

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Reproductive Parameters of Female Long-Finned Pilot Whales (*Globicephala melas*) Around the Faroe Islands

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ABSTRACT

Nearly 2,000 female long-finned pilot whales, *Globicephala melas*, from the Faroese catch were examined, measured and sampled between July 1986 and June 1988. Females of this stock ovulate for the first time at an average age of 8yrs and average body length of 375cm. The attainment of a minimum body length, rather than a minimum age, seems to trigger menarche. The pattern of ovulation varies considerably within and between animals, but the average rate of one ovulation every 4yrs varies little through life. Ovulation and pregnancy may occur in even the oldest animals, but the interval between births increases throughout life, and pregnancy beyond 40yrs of age is rare. The average reproductive cycle is 5.1yrs in duration, but the youngest mature females shorten the lactation and 'resting' phases to the extent that pregnancy often occurs while they are still producing milk for the previous calf. Gestation lasts about 12 months; the calf is born at a mean length of 177cm and mass of 74kg. Conceptions and births are diffusely seasonal, peaking in summer and autumn. There is no evidence of consistent breeding synchrony within pods. Little difference could be found between the reproductive characteristics of this stock and that of the Newfoundland stock which was studied in the late 1950s.

KEYWORDS: PILOT WHALE-LONG-FINNED; NORTH ATLANTIC; REPRODUCTION; SEXUAL MATURITY; SEASONALITY.

INTRODUCTION

The long-finned pilot whale was one of the first odontocete species to be the subject of a quantitative study based on the examination of animals killed in a directed fishery. The results of Sergeant's (1962) study of whales taken off Newfoundland, Canada are still widely quoted and most of the analytical techniques he employed remain in use three decades later. This species occurs in temperate waters throughout the North Atlantic, usually remaining in deep oceanic waters. It is one of the most commonly stranded cetaceans along the Atlantic coast of Europe, and such strandings have offered limited opportunities for investigating its biology in this region (e.g. Martin *et al.*, 1987; Sigurjónsson *et al.*, 1993). Nevertheless, a comprehensive study with large sample size has hitherto been lacking for northeastern Atlantic pilot whales.

The long-established drive fishery of pilot whales by Faroe islanders ($c.62^{\circ}N$, 7°W) differs from that of the now defunct Newfoundland industry, in that it is operative throughout the year and usually takes entire social groups of whales without any selectivity. A collaborative study of nearly all the whales captured in the Faroes between July 1986 and July 1988 (Bloch *et al.*, 1993a), including 1,680 females, thus offered a unique opportunity to derive estimates of population reproductive parameters from detailed carcase examination and sampling. This paper deals with reproduction in

females; males are discussed separately in another paper in this volume (Desportes *et al.*, 1993).

MATERIALS

All primary data analysed in this paper were derived from long-finned pilot whales taken in the Faroese drive fishery between 10 July 1986 and 10 June 1988. A total of 3,061 animals, and a further 331 foetuses, were examined and sampled during this period. Animals from 38 separate kills (grinds in Faroese) are represented (Appendix 1) and in most cases the entire group of whales originally sighted was driven ashore, killed and made available for examination. A few whales from some grinds were known to have escaped or to have been unavailable for sampling for various reasons, but their loss is very unlikely to have a significant impact on the analyses. However, several grinds were known to have been incompletely examined (Bloch et al., 1993a) and the samples of animals from these drives are likely to be biased in some way. Data from these grinds has only been used in analyses where such possible biasses cannot influence the result. For this reason, sample sizes vary between analyses presented below. Because of the nature of the material, the methods used to collect it, and steps taken to avoid possible biasses, we feel justified in assuming the dataset to be largely representative of the population from which these whales were taken. Anomalous results from some of the analyses presented in this paper indicate, however, that some bias probably exists in the representation of adult females at particular stages of the reproductive cycle; this is discussed, where appropriate, in the text.

METHODS

1. Sampling and laboratory protocol

Whales were examined as soon as possible after the drive was completed. On the basis of an initial examination in the field, and later analysis of measurements and samples described below, females were classified as either sexually immature, pregnant, pregnant and lactating, lactating, ovulating, or resting, using the criteria of Perrin and Donovan (1984). Ovulating females were defined as those with a very large follicle or large corpus luteum but without a macroscopic foetus in either uterine horn. Tissue sampling was normally carried out within 12 hours post mortem, but in some large or remote grinds the process was not completed for a further 12 hours. Nevertheless, no relevant changes occurred to tissues used in this study within this period of time. Standard techniques for measuring, sampling and examining whale carcasses were adopted by the Faroese research programme and are described in detail elsewhere in this volume (Bloch *et al.*, 1993a). Here, we will deal only with those observations, measurements and tissues specifically related to the examination of reproduction in females.

Animal age was determined from dentinal and cemental laminae in the teeth, using decalcified thin stained sections (Bloch *et al.*, 1993b; Lockyer, 1993). All were examined by D. Bloch, and a sample of these by C.H. Lockyer and T. Kasuya. Age was recorded as an integer, this being the number of completed years represented in the laminae assuming that a pair of light and dark layers are equivalent to one year. This rate of deposition was inferred from known-age short-finned pilot whales, G. macrorhynchus (Lockyer, 1993). A whale in age class n could therefore be between n and n+1 yrs of age, and we have assumed an average of n + 0.5 in some analyses. Evidence of lactation was looked for internally by sectioning the mammary gland and often externally, by pressing the area around the mammary slits and noting any fluids emanating from the nipples. Pregnant females with colustrum in their mammary glands were identified as such, and the term

'lactating' is used in this paper for mothers judged to be producing milk for a freeswimming calf. Maximum mammary gland depth, and its colour and condition was recorded. Uterine horn diameters, in their collapsed state, were measured at the point where the uterus divides into two and helped identify females that had recently calved.

Both uterine horns were carefully searched for the presence of foetuses, and the condition of the uterine mucosa was noted. The body length and weight of all foetuses was recorded. If the sex of the foetus was not obvious visually, it was preserved for microscopical or biochemical sex determination in the laboratory (Andersen *et al.*, 1992). If the possible presence of a foetus was indicated by the condition of the uterus or a large ovarian corpus, but nothing was found, special care was taken to look for (a) a very small foetus and (b) evidence of a recent birth, e.g. from the condition of the mammaries.

Both ovaries were briefly examined on site, carefully cut from the reproductive tract and preserved in 10% buffered formalin. They were later washed, weighed, examined by eye for the presence of surface scars and hand-sectioned in slices of 0.5–2mm thickness. Corpora lutea were measured on three perpendicular axes and weighed. Corpora albicantia were measured on two axes and graded into one of five age classes on the basis of form, colour and structure (young, medium young, medium, medium old, old). An index of the abundance of macroscopic follicles (5 classes: few, few-moderate, moderate, moderate-many) and the mean diameter of the two or more largest follicles was recorded.

2. Statistical techniques and assumptions

Unless otherwise stated, data were pooled between years and between pods. Variation in the size and structure of pods was considerable (see Appendix 1), but the catch was apparently non-selective and we assume that the grinds examined are representative of the population(s) occurring in Faroese waters. The assumption of a uniform pattern of reproduction between years is made in many analyses, partly on the basis that no differences could be found between the years in which the sample was collected. Some groups of animals were sampled and measured incompletely because of time constraints in the field, so sample sizes vary between analyses presented below.

2.1 Estimating the average age, length and weight at sexual maturity

We define the onset of sexual maturity in females as the time of first ovulation. It was, of course, rare that an animal was captured and examined during the short period that it was ovulating for the first time, so it was necessary to adopt methods of estimating these values indirectly. We used three such methods:

(a) Back-calculation from animals in their first ovulatory cycle

Females with a single corpus luteum and no other corpora in either ovary must be ovulating or pregnant for the first time. If pregnant, we have used the estimation of foetal growth rate (see Results section 2.3) to calculate the length of time prior to death (at which time their age was known) that the animal ovulated.

(b) Sum of fraction immature

Cooke (1984), DeMaster (1984) and Hohn (1989) described an almost unbiased nonparametric method of estimating the average age of attainment of sexual maturity (ASM). This was calculated as the sum of the fraction of animals immature in each age class between that of the youngest mature and that of the oldest immature, added to the age of the first indeterminate age class. Thus,

$$ASM = j + \sum_{i=j}^{k} p_i x_i$$

variance =
$$s^2 = \Sigma \frac{(p_i q_i) x_i}{N_i - 1}$$

where

if
$$I_i \neq N_i$$
, $p_i = \frac{I_i}{N_i}$
 $q_i = \frac{M_i}{N_i}$
if $I_i = N_i$, $p_i = \frac{I_i - \frac{1}{2}}{N_i}$
 $q_i = \frac{M_i + \frac{1}{2}}{N_i}$

j = the first indeterminate age class

k = the last indeterminate age class

if
$$M_i = N_i$$
, $p_i = \frac{I_i + \frac{1}{2}}{N_i}$
 $q_i = \frac{M_i - \frac{1}{2}}{N_i}$

- p_i = fraction of immature specimens in age class *i*
- q_i = fraction of mature specimens in age class $i (p_i + q_i = 1)$
- x_i = number of age classes combined to obtain a sample size of > 2 in age class i
- I_i = number of immature specimens in age class *i*
- M_i = number of mature specimens in age class *i*
- N_i = number of specimens in age class $i (N_i = I_i + M_i)$

This technique is equally applicable to the assessment of length and weight at sexual maturity.

(c) Age/length/weight at which the proportion mature is 0.5

We fitted a logistic curve to a plot of the proportion of animals in each age/length/weight class that had attained sexual maturity and took the point at which the curve predicted 50% maturity.

2.2 Estimating the foetal growth rate: Modelling the distribution of foetal lengths at each sample date

Model formulation

The method uses a mathematical model to describe the distribution of foetal lengths observed on a given sample date. The basic idea is that the variation in foetal length stems mainly from the seasonal variation in the times of conception. The approach involves the following assumptions:

Assumption 1

The growth of the foetus is linear with constant rate, except for the initial period of curvilinear growth. This assumption ignores any random variation in growth both within an individual and between those individuals conceived at the same time. More realistically, we assume that this variation is small relative to the variation in foetal length arising from the seasonal variation in the time of conceptions. The assumption implies that

over the period of linear growth, length at time t_i and the conception time are related by $l_i=b$ $(t_i - t - t_0)$, where b is the linear growth rate and t_0 refers to the initial period of curvilinear growth from the model of Huggett and Widdas (1951) discussed more fully under Results section 2.3 (see Fig. 1). In other words, a foetus of length l_i at time t_i is assumed to have been conceived at time $t=t_i - t_0 - l_i/b$.

Assumption 2

The main source of variation in foetal lengths on a particular sampling occasion is due to the seasonal variation in conception times. We assume that the conception rate has an annual pattern and consider the following two models.

Von Mises distribution

This is a periodic exponential curve of the form

$$c(t) = Ae^{\kappa \cos 2\pi (t-\mu_c)}$$

where the unit time interval corresponds to one year. Peak conception rates occur annually at times $t=\mu_c$, $\mu_c\pm 1$, $\mu_c\pm 2$, etc. The parameter \varkappa measures, inversely, the spread of conception times in one year; $1/\varkappa$ is the variance of the von Mises distribution. A is a scaling factor which depends on \varkappa .

Mixture of two von Mises distributions

Estimation of the times of conception for each individual using the estimated growth rate from the fitted von Mises model suggests two peaks in the seasonal pattern (see Results section 2.3.1). This bimodal effect is apparent with any reasonable value of the foetal growth rate, so the value chosen only influences the position of the peaks and, to a lesser extent, their separation in time. To model this distribution we consider a conception curve comprising a mixture of two von Mises distributions given by



 $c_m(t) = pAe^{\kappa \cos 2\pi (t-\mu_{c1})} + (1-p) Ae^{\kappa \cos 2\pi (t-\mu_{c2})}$

Fig. 1. Model of foetal growth pattern, after Huggett and Widdas (1951). Conception occurs at the x/y intercept. The embryo initially grows slowly and curvilinearly, then reaches a linear rate of body growth which continues throughout the remainder of the foetal period. Birth occurs at time t_g and the period of linear growth is taken to be t_g -t_o.

where μ_{c1} and μ_{c2} are the times of the early and late peaks of conception and p is the proportion of conceptions in the early group. The spread of conception times is assumed to be the same in each group.

Assumption 3

The overall mortality rate (adults + foetuses) is constant, at least during the phase of linear growth. Thus, of the foetuses conceived at time t, the proportion which survive to time t_i is equal to $e^{-\lambda(t_i-t)}$, where λ is the instantaneous mortality rate per unit time.

Assumption 4

The foetuses measured on a particular sampling occasion are a random sample from the population. This assumption implies independence of observations on females in the same pod and may therefore be upset by any synchrony in the times of conception of females in the same pod. This point is discussed further in Results section 2.5 on testing for synchrony within pods.

In the application of the model we restrict foetus lengths to the range 0.2–1.62m. The lower limit is chosen to exclude the effects of the initial period of curvilinear growth and the upper limit is imposed so that few if any foetuses will have been born; the smallest neonate in our sample was 1.63m in body length. Combining the above assumptions gives the distribution of the length of foetuses in the range (0.2m-1.62m) at time t_i for the unimodal von Mises model as

$$f(l_i|t_i,b,\mu,\kappa) = \frac{e^{\kappa\cos 2\pi(t_i-l_i|b-\mu) - \lambda l_i/b}}{\int_{0.20}^{1.62} e^{\kappa\cos 2\pi(t_i-x/b-\mu) - \lambda x/b} dx}, 0.20 < l_i < 1.62$$

Note that t_0 has been absorbed into the parameter $\mu = \mu_c + t_0$, where μ is the modal time of intercept of the linear part of each foetal growth trajectory and the time axis, and μ_c is the time of peak conception rate. The corresponding expression for the mixture model contains a sum of two exponential terms in the numerator and in the integrand of the denominator.

Fitting the models

The above models were fitted to the samples of foetus lengths in the range (0.2-1.62m) by the method of maximum likelihood. This involves finding the values of the parameters which maximise the likelihood

$$L(b,\mu,\kappa) = \prod f(l_i|t_i,b,\mu,\kappa)$$

where f is given above and the product is taken over all the foetus lengths. To maximise the likelihood we used the quasi-Newton iterative search algorithm. The method provides approximate standard errors for the parameter estimates although these are based on the assumption that the model holds and therefore does not allow for possible biases due to failure of one or more of the above assumptions. We ran the iterative process using nine combinations of starting values: growth rate of 1.6, 2.0 and 2.8 my⁻¹, position of first peak 0.4, 0.6 and 0.8y. The second peak was fixed at 0.9y. In each case the iterative search converged on the same solution. We made no attempt to estimate the mortality rate λ because the model is not very sensitive to this parameter. Instead, we fitted the models using a range of values λ =0.0, 0.20 and 0.50 to assess the effect of our uncertainty in the mortality rate.

Method	Age (years)	Length (cm)	Weight (kg)
Back-calculation from state of pregnancy	8.38 SE = 0.253 n = 31		
Sum of fraction immature	8.50 SE = 0.140	375 SE = 1.43	609 SE = 11.3
Proportion mature = 0.5, predicted from fitted curve	8.02 SE = 0.150	374 SE = 1.50	600 SE = 12.6
Weighted mean	8.3	375	605

Estimates of the average age, length and weight of female pilot whales at the attainment of sexual maturity. For details of methods employed, see text.

Table 1

RESULTS

1. Commencement and subsequent patterns of ovulation

1.1 Age at sexual maturity (ASM)

The youngest mature female in our sample was aged 5.5 (± 0.5) yrs, and the oldest immature was aged 15 (± 0.5)yrs, although this was an aberrant animal in that it was 4yrs older than the next oldest immature female. Almost all pilot whales in our sample ovulated for the first time between age classes 6 and 9.

Estimates of the average ASM from the three methods of assessment (see Methods section 2.1) are shown in Table 1; Fig. 2a shows the fitted curve for method (c). Since there is no reason to believe that any of these methods is more or less biased than any other, it is most appropriate to adopt the weighted mean of these three estimates (weighted by the reciprocal of the variance). Our estimate of the mean age at sexual maturity is therefore 8.3yrs.

From the fitted logistic curve, we estimate that 50% of the population matures within 21% of the ASM.



Fig. 2a. Logistic curve fitted to the proportion of females that were sexually mature in successive age classes. Corrected for the fact that animals in age class n can be between n and n+1 yrs of age, the curve predicts that 50% of animals are mature at an age of 8.0yrs (SE =0.15).



Fig. 2b. Logistic curve fitted to the proportion of females that were sexually mature in successive 3cm body length classes. The curve predicts that 50% of animals are mature at a length of 374cm (SE=1.5).



Fig. 2c. Logistic curve fitted to the proportion of females that were sexually mature in successive 25kg body weight classes. The curve predicts that 50% of animals are mature at a weight of 600kg (SE=12.6).

1.2 Body length at sexual maturity

The shortest mature female measured 350cm (pregnant with a 22cm foetus) and the longest immature female was 418cm in body length. Estimates of the average length at sexual maturity from methods (b) and (c) are given in Table 1; the fitted curve for method (c) is shown in Fig. 2b. We believe it reasonable to adopt the weighted mean of 375cm as our best estimate of the body length at attainment of sexual maturity of an average female pilot whale in this population. Fig. 2b indicates that 50% of the population reaches maturity at body lengths within 5% the average length at maturity.

1.3 Body weight at sexual maturity

In our sample, sexual maturity occurred at body weights of between 524 and 715kg. Fig. 2c shows the fitted curve for method (c), which predicts that 50% of animals mature within 13% of the average weight. From Table 1, we estimate the average weight at sexual maturity to be the weighted mean of 605kg.



Fig. 3. Number of corpora on both ovaries, with age, for 1,443 females.



Fig. 4. Mean number of corpora on both ovaries by age class, for all sexually mature females.

1.4 Ovulation rate

Plotting the number of corpora in both ovaries against age for the 1,402 females with 2 sampled ovaries (Fig. 3) demonstrates a great deal of variation within each class on both axes, and it is clear that there must be variation between individuals in the rate at which ovulations occur in addition to the age at which ovulation first occurs (Results section 1.1). The picture becomes a little clearer if we look at the mean number of corpora for each age class of sexually mature females (Fig. 4), for which a straight-line regression predicts an average accumulation rate of 0.25 (SD=0.01) corpora per female per year, or one every four years, for both the entire age range (5-59yrs, n=851 animals) and a restricted age range to avoid small sample sizes (ages 6-40, n=820). This result can be taken as evidence

that, in this species as in other cetaceans, corpora persist throughout the lifetime of the animal as a macroscopic body in the ovary (Marsh and Kasuya, 1984; Perrin and Donovan, 1984).

1.5 Ovulatory senescence

An important question is whether ovulation continues throughout life or ceases many years before death in the oldest animals. We tested this by looking at the relationship between age and corpora number in the oldest animals in our sample. The number of females in the very oldest age classes (>40yrs) is very small and the scatter of points (mean number of corpora against age) commensurably wide. The regression of corpora number on age, where age is >40, did not produce a slope significantly different from zero (p=0.17). The sample size was increased, and any difference from *G. macrorhynchus* explored, by extending the lower limit of age classes included in the regression to that beyond which Kasuya and Marsh (1984) found no ovulating or pregnant females. The straight-line regression of mean corpora number on age, where age >36 and weight is proportional to sample size, is significant and positive (p<0.001) with a slope (0.29, SD=0.06) indicating that a new corpus is added every 3.45yrs on average. This is not significantly different from the figure for all mature females.

Further evidence that ovulation can occur at an advanced age is that, of the 33 females aged more than 40yrs, two (aged 41 and 55) had a corpus luteum and were pregnant, two (aged 43 and 44) had at least one 'young' corpus albicans and a further 6 (aged 40–55) had at least one corpus albicans categorised as 'medium young'.

For comparison, the criteria tentatively put forward by Marsh and Kasuya (1984) to indicate reproductive senescence (i.e. no macroscopic follicles, no corpora lutea and all corpora albicantia classified 'old') were applied to the ovaries in our sample; 54 animals (4.8%) out of the 1,070 mature females for which we have both ovaries were categorised as senescent, i.e. would not ovulate again.

An independent method of checking the validity of this tentative result, providing an upper bound of the number of females in our sample likely to have ovulated for the last time, was devised as follows. We assume for the purposes of this calculation that all females of \geq 40yrs of age have ovulated for the last time. Then, an animal in this category with, say, 15 corpora must have been capable of ovulating again when it had accumulated 14, 13, 12 etc. corpora, and it is simple to combine such information for all of these older females to construct a list of probabilities of an animal being senescent with a given number of corpora. Applying this formula to the current sample of 1,070 mature females, the prediction is that 47 females (4.4%) would not have ovulated again had they lived. Given that we know the original assumption (that all animals of \geq 40yrs of age have ceased to ovulate) is incorrect, we conclude that fewer than 4%, and thus a very small proportion of the mature females alive at any time, have ceased to ovulate.

1.6 Discussion

The age at first ovulation is one of the few parameters in which there would appear to be a difference between the Faroese population of pilot whales in the late 1980s and the Newfoundland population in the 1950s. Albeit from a small sample, Sergeant (1962), later supported by Kasuya *et al.* (1988b), reported a mean age at sexual maturity of 6–7yrs. Using method (a) of the current paper (back-calculation from primiparous females), the mean for the Canadian sample is 6.5yrs (SD=0.87, n=12), compared to our best estimate for the Faroese population of 8.3yrs (SD ≈ 1.4 , n=31). These values are significantly different (p<0.001) but in the absence of accurate estimates of population and the relative

nutrition of the two stocks, it would be hazardous to predict the reasons for Newfoundland pilot whales reaching maturity almost two years earlier than their Faroese counterparts.

Without detailed histological examination of the reproductive tract, it is difficult to determine whether any individual female has definitely ovulated for the last time, and even more difficult to say if any subsequent ovulation would lead to a pregnancy or not. Nevertheless, the evidence presented in this paper is adequate to conclude that fewer than 5% of the mature females alive at any time have ceased ovulation.

Judging by the degree of synchrony with which the population reaches maturity, it appears that the first ovulation is triggered more by the achievement of a critical body length than by either a minimum age or gross body mass. This characteristic has been noted in other cetaceans, e.g. Balaenopterids (Lockyer, 1984).

2. Conception, gestation and parturition

2.1 Body length at birth

The smallest neonate in our sample measured 163cm in body length, and the largest foetus was 191cm long, so there is a considerable range of body size at which birth can occur, amounting to 17% of length and some 60% of mass. A logistic curve fitted to the proportion of animals born in successive 5cm length classes (Fig. 5) predicts that 50% of births have occurred at a body length of 176.8cm (SE=2.1).



Fig. 5. Logistic curve fitted to the proportion of animals in successive 5cm body length classes that had been born. The curve predicts that 50% had been born at a length of 176.8cm, which was adopted as the mean length at birth.

2.2 Body weight at birth

Fig. 6 shows a log-log plot of foetal body weight on length, for 238 foetuses considered to have reached the linear phase of growth ($\geq 0.2m$ in length) and 44 calves of up to 2.5m (approximating to one year of age). The fitted regression line has the equation ln(W)=2.63 + 2.89 ln(L), ($r^2=99.1\%$, p<0.001), and therefore $W=13.87L^{2.89}$, where W=body weight in kg and L=body length in m. The SE of the slope is 0.016.



Fig. 6. Log-log plot of body weight on length for 238 foetuses and 44 calves up to 2.5m in body length. The regression line defines the relationship W=13.87. $L^{2.89}$, where W= body weight in kg, L= length in m. The SE of the slope is 0.016.

Substituting the mean length at birth (1.768m) (see Results section 2.1) into the regression equation gives an estimate of mean body weight at birth of 72.1kg. Adjusting for variance in the length at birth and about the allometric relationship in the back-transformation to a linear measure (2.3%), we arrive at an estimate for the mean weight at birth of 73.8kg. The tight grouping of points around the regression line indicates that the allometric relationship holds good through the latter part of the gestation period. This is confirmed by restricting the dataset to the 61 foetuses and 21 calves of a body length within 0.5m of the mean length at birth. The regression equation on this subset gives a steeper slope (3.6) but also predicts a mean weight at birth rounded to 74kg.

2.3 Foetal growth, the duration of gestation and seasonality of breeding

It is convenient to consider mammalian foetal growth in two stages (Huggett and Widdas, 1951). In the first, the early weeks of development after conception, the embryo/foetus accumulates mass slowly and its length increases non-linearly. The second stage commences when foetal body length begins to increase at an approximately constant rate. This 'linear' phase is thought to continue throughout most or all of the remaining gestation period (Fig. 1). We followed the lead of Huggett and Widdas (1951) and most subsequent studies of cetacean foetal growth in dividing the gestation period (t_g) into an initial non-linear portion (t_0) and a period of linear growth (t_g-t_0) which starts at the point where the slope of body length growth is extrapolated backwards onto the time axis (Fig. 1). We will refer to the absolute time at which this intercept occurs as T. In the analyses below, the value of (t_g-t_0) for this population of pilot whales is calculated by dividing the mean length at birth by the average rate of foetal growth.

Clearly, no foetus could be measured other than at the time of its mother's capture, so the rate of growth in the uterus has to be inferred indirectly. A plot of the body length of each foetus against the date on which its mother was killed is shown in Fig. 7. It is immediately apparent that on many sampling days foetuses ranged from barely



Fig. 7. Length of foetuses (+) and calves of one year old or less (●) plotted against date of capture. Note the wide spread of foetal lengths observed on many sampling days. The horizontal line indicates the estimated mean length at birth (176.8cm). The diagonal lines indicate the foetal growth trajectories fitted by the 'mixture' von Mises model for the main annual peak of conceptions (solid line) and secondary peak (dashed line).

macroscopic to near-term with many of intermediate size, and small foetuses can occur throughout the year, so conceptions and births are not well synchronised within the population.

A clearer picture of the temporal spread of conceptions within an annual 'cohort' and its subsequent growth was gained by plotting all foetal lengths against day of year (Julian day), then concatenating three copies of the pattern to mimic three consecutive 'years' (Fig. 8). The eye immediately picks out diagonally oriented concentrations of points, separated by regions with few points, demonstrating that conceptions and births are



Fig. 8. Three concatenated copies of a plot of foetus length on Julian day of capture. The purpose of this exercise is to show the development of a nominal 'cohort' which, because of poor breeding synchrony, spans a considerable period of time between conception of the earliest foetus and birth of the latest.

seasonal to some extent, and provides a basis for allocating foetuses to one cohort or another for the purposes of estimating the rate of foetal growth using regression analysis (method 2 below). Thus, cohorts were discriminated by lines of slope 1.78 (my⁻¹) with an intercept on the time axis of day 60 in each year for the regression analysis only. No assumption of cohort discrimination is required for the modelling work.

2.3.1 Estimation of (t_g-t_0) , approximating to the duration of the linear phase of growth In order to avoid considering foetuses which have not yet reached the stage of linear growth, we arbitrarily ignored all those smaller than 0.2m in this analysis. Furthermore, to overcome any possible bias related to some foetuses being born at shorter body lengths than others, we included only those with a body length less than that of the shortest neonate (1.63m). Excluding the longest foetuses in this way should also help to overcome bias caused by any possible flattening of the growth trajectory in near-term foetuses. We employed two analytical methods to estimate the foetal growth rate:

Method 1. Modelling the distribution of foetal lengths at each sample date (see Methods 2.2 for a description of the technique.)

Using a mortality rate of λ =0.20, the parameter estimates for the single von Mises model were as follows: \hat{b} =2.13 my⁻¹ (SE=0.31); $\hat{\mu}$ =0.641 (SE=0.06) κ =0.94 (SE=0.12). Estimated growth rates using different mortality rates were λ =0, \hat{b} =2.14; λ =0.50, \hat{b} =2.16. So, the estimates are not particularly sensitive to the precise choice of the mortality rate. Note, however, the relatively large standard error for the estimated growth rate. This model predicts the peak birth rate to occur on Julian day 172 (21 June) and, using a mean length at birth of 1.768m (Results section 2.1), that $(t_g - t_0)$ =300 days if foetal mortality is as high as 50%, which seems likely (Desportes *et al.*, In press).

To check the assumed form of the seasonal pattern of breeding we estimated the distribution of birth dates (DOB) using the estimated growth rate, i.e. $DOB=t_i + (BL-l_i)/\hat{b}$, where BL=mean length at birth. Fig. 9(a) shows a histogram of the estimates together with the fitted single von Mises curve. This suggests a second later peak in the conception rate, and a likelihood ratio test to compare models shows a statistically significant improvement in fit for the mixture model (deviance $\chi^2_2=33.90$, p<0.001).

Using a mortality rate of λ =0.20, parameter estimates for the mixture model are as follows: \hat{b} =2.44 my⁻¹ (SE=0.16); $\hat{\mu}_1$ =0.601 (SE=0.03); $\hat{\mu}_2$ =0.938 (SE=0.03); κ =2.36 (SE=0.26); p=0.66 (SE=0.05). Using different mortality rates, the estimated growth rates are: λ =0.0, \hat{b} =2.45 my⁻¹; λ =0.50, \hat{b} =2.43 my⁻¹.

Fig. 9(b) shows a histogram of the estimated birth dates using an estimated foetal growth rate of 2.43 my⁻¹ together with the fitted underlying bimodal conception curve and demonstrates a reasonably close agreement between the distribution of estimated times and the model distribution. With a bimodal conception curve, $(t_g - t_0) = 266$ days and peaks of the birth rate are predicted on Julian days 119 (29 April) and 243 (31 August).

Although the assumption of a temporally bimodal pattern of breeding gives a better fit to the data, we cannot completely exclude the possibility that this is the result of a sampling artefact. We therefore consider both options in parallel in the analyses below.

Method 2. Linear regression analysis

The standard method of estimating the foetal growth trajectory, and thus both the rate and duration of linear growth, is to apply a least squares linear regression to either the raw plot of foetus length on sampling date or mean lengths of, say, monthly samples (e.g. Sergeant,


Fig. 9a. Frequency distribution of births predicted by the single von Mises model (see text for details). Each vertical bar represents one week.



Fig. 9b. Frequency distribution of births predicted by the 'mixture' von Mises model (see text for details). Each vertical bar represents one week.

1962; Kasuya and Marsh, 1984; Perrin and Reilly, 1984). Unfortunately, this method will always underestimate the rate of growth in species with a low degree of breeding synchrony, and thus lead to an overestimate of gestation time, because in both early and late gestation one tail of the distribution is necessarily missing (late conceptions and early births). Both these omissions act to depress the estimated rate of growth. When conceptions are highly synchronized it may be possible to apply a correction factor to allow for the bias (Philo *et al.*, 1992) but this approach does not apply to the pilot whale data for which the seasonal variation in conception times is large.

Much of the bias can be removed by recognising that sampling date is actually an estimator of foetal age (albeit one with large error), and regressing sampling date on body

length. This theoretically removes any sensitivity to the (necessarily almost arbitrary) body lengths chosen to delimit the foetal sample used. Using a reconstructed single 'cohort', regression of date on length gives an estimated daily growth rate of 0.5335 cm/ day (SE=0.085) or 1.947 my⁻¹ (r²=0.52, p<0.001), giving (t_e - t_0)=331.4 days.

To examine the properties of the method we applied it to simulated data using the same sampling occasions as in the Faroese fieldwork. First, we used a model in which the conception times followed a Normal distribution with mean 0.64 and standard deviation 0.2 (these values are suggested by the fitted von Mises model described above). Simulated conception times were transformed to length measurements using a growth rate of 1.947 my⁻¹ and constrained to lie in the range 0.2–1.62m. For each set of simulated data the regression method was used to estimate the growth rate. From 1,000 such estimated growth rates the mean was 1.859 my⁻¹, showing that the regression method underestimated in this case by an average of 1.947-1.859=0.088 my⁻¹. In a second set of simulations, using a growth rate of 2.15 my⁻¹, the mean of 1,000 estimates was 1.92 my⁻¹, so the method underestimated by 0.23 my⁻¹ (equivalent to an increase in gestation time of 36 days). We then modified the model to mimic the effect of a second peak in the conception curve by sampling from a mixture of two Normal distributions with means 0.60 and 0.94, standard deviation 0.1, with a proportion 0.66 in the first group, and using a growth rate of 2.43 my⁻¹ (these values were based on the fitted von Mises mixture model). From 1,000 sets of simulated data the mean estimated growth rate was 1.892 my⁻¹, equivalent to an overestimate of 76 days in gestation time. Lowering the modelled growth rate to 1.947 my⁻¹ produced a mean estimated growth rate of 1.774 my⁻¹, i.e. an underestimate of 0.173 my⁻¹ or 32 days of gestation. Because of the bias in the method and its insensitivity to changes in the growth rate of the sampled population, we conclude that regression is not, in general, a satisfactory method for estimating foetal growth rate in this and similar mammal populations. Nevertheless, it provides a useful lower bound to the range of possible values.

2.3.2 Estimation of the duration of the initial non-linear phase of growth (t_0)

It is not possible to directly determine the date of conception for any foetuses in our sample, and no doubt some tiny embryos were missed, so we cannot accurately describe either the shape or the duration of early foetal growth from the current data. We are dependent, therefore, on published estimates of the relationship of t_0 to t_g , $(t_g - t_0)$, or some other parameter and there is no universally accepted formula to adopt. Strict adherence to the guidance of Huggett and Widdas (1951) would give $t_0=0.2t_g$, i.e. $t_0=0.25$ $(t_g - t_0)$, but Laws (1959) suggested a correction for length rather than weight data which would yield

$$t_0 = 0.22 \ (t_g - t_0). \tag{1}$$

Calder (1982) proposed:

$$t_0 = 7.25 \ . \ m_{neo} \ ^{0.19}, \tag{2}$$

where m_{neo} is the body weight at birth in g.

Substituting a value for $(t_g - t_0)$ in equation (1) of: 300 days (unimodal model), t_0 =66.0 days; 266 days (bimodal model), t_0 =58.5 days.

Substituting a value for m_{neo} of 74kg (see Results section 2.2), into equation (2) gives $t_0=61$ days. It seems reasonable to adopt a round figure of 60 days as a working value for t_0 , but to bear in mind that this rather arbitrary value is subject to error.

2.3.3 Estimation of the total gestation period based on the foetal growth model Total gestation period $(t_g) = (t_g - t_0) + t_0$ = 300 + 60 = 360 days (11.8 months, 0.99yrs) unimodal model = 266 + 60 = 326 days (10.7 months, 0.89yrs) bimodal

model

2.3.4 Seasonality of conceptions based on the foetal growth model

Evaluation of the pattern and timing of conceptions is critically linked to the estimate of gestation length. If breeding in the population as a whole has only one peak, then our adopted model predicts that the highest rate of conceptions occurs on Julian day 175 (24 June, Fig. 10a). If breeding is bimodally distributed, then it predicts peaks on day 159 (8 June) and day 283 (10 October, Fig. 10b). In both cases, the lowest rates of conception occur in January and February.



Fig. 10. Frequency distribution of conceptions predicted by the single von Mises model (a) and the 'mixture' von Mises model (b), assuming that the initial non-linear portion of growth (t_0) lasts for 60 days (see text for details). Each vertical bar represents one week.



Fig. 11. Approximate frequency distribution of conceptions, by month, based on direct examination of the pilot whale catch. (a) Percent of mature females ovulating or very near ovulation, (b) Percent of non-pregnant mature females with a large (≥10mm) follicle, (c) Percent of pregnant females carrying a tiny (≤5cm) foctus. Note that distribution (c) should be moved to the left by, perhaps, 1–3 months (representing the time since ovulation to achieve this foetal size) to become comparable with (a) and (b) (offset estimated by reference to Snow, 1986).

2.3.5 Seasonality of conceptions based on biological sampling data (a) Timing of ovulations

A total of 147 females were considered to have been examined at, or near, ovulation based on examination of the reproductive tract. Expressed as a percentage of the total number of mature females examined in each month, the prevalence of ovulation is shown in Fig. 11(a), in which a main season of June-September and a peak in June are clear.

(b) Follicle sizes

Follicle development, as indicated by the proportion of non-pregnant mature females which had a large (≥ 10 mm diameter) follicle on either ovary, was greatest in March, April, June and September, with a peak in April (Fig. 11b).

(c) Occurrence of very small foetuses

Taken as a proportion of mature females or pregnant females examined in each month, foetuses of 5cm or less were most common in May, June and July, with a peak in June. Conception preceded the examination date by an unknown time, but an estimate of 1–3 months would seem reasonable (Snow, 1986) putting the conception peak, based on this small sample, around March-May (Fig. 11c).

2.3.6 Seasonality of parturition based on biological sampling data

(a) Using data on neonates

A method of assessing the timing of births is to back-calculate from the length and date of capture of young calves. Doing so for animals of one year of age or less should avoid biasses resulting from non-uniform sampling across the year. In doing so, we assume that pilot whales of this 'stock' are about 2.5m in body length at 1 year of age (Bloch *et al.*, 1993b) and, in the absence of adequate information to the contrary, that the rate of growth is constant over this time at approximately 2.5m-1.77m (length at 1 year – length at birth)= 0.73 my^{-1} . The results of this exercise are shown in Fig. 12, in which the estimated birth dates of 215 animals of 1 year of age or less have been plotted on one nominal 'year'.



Fig. 12. Frequency distribution of birth dates derived by back-calculating to the mean length at birth from the length and date of capture of 215 calves. The animals were estimated to be of one year of age or less and a uniform growth rate of 0.73 my⁻¹ was assumed.

The apparently low frequency of births in September and October may be an artefact since the pattern as a whole does not differ significantly from a uniform distribution throughout the year.

A uniform temporal distribution of births seems unrealistic, so another attempt was made, this time reducing possible bias due to inter-animal differences in growth or error in estimating the average rate of growth. This was done by lowering the length threshold below which neonates were considered, from 2.5m to 2.0m, so reducing the length of time since birth. This produced a pattern of births with a peak in August and a smaller one in January (Fig. 13a).

(b) Using data on large foetuses

Employing the same argument, that the actual growth rate chosen for extrapolation is less critical when animals are near birth, foetuses of 150cm or more in length were chosen to provide a frequency distribution of the dates at which they would have reached the mean length at birth had they lived. A growth rate of 2.15 my⁻¹ (from the unimodal model) was adopted and the distribution shown in Fig. 13b was derived, with peaks in April/May and September. This distribution is significantly different from that of Fig. 13a (χ^2 =42.1, d.f.=11, p<0.01) and is not materially altered by using growth rates of 1.947 my⁻¹ (from the regression analysis) or 2.43 my⁻¹ (from the bimodal model).

2.4 Synchrony of conceptions within pods

Establishing the degree of synchrony of conceptions within pods is important because: (a) it has implications for the genetic structure of the pod; (b) the method for modelling the distribution of foetal lengths assumes that the foetuses sampled on a given day are a random sample from the population of foetuses alive at the time of sampling; this assumption would not hold if there was differential synchrony of conceptions within pods.

We tested for synchrony by comparing the variation in foetus lengths between pods with that within pods. Large variation would result from systematic differences in conception times between pods or from clustering of conception times within pods. The data do not allow this analysis on a day by day basis since each day's catch normally consists of only one pod. An approximate method, which allows for the seasonal pattern of variation in conception times, is to group the catches by month and test for synchrony within each month. A potential problem is that individuals within a pod may belong to different annual cohorts, thereby increasing the variation within pods and decreasing the potential for detecting synchrony effects. To allow for this, data on each sampling occasion were split into 'high' and 'low' groups using a dividing line with an intercept 6 months out of phase from the estimated time of the peak conception rate and a slope equal to the estimated foetal growth rate (using the unimodal breeding pattern model). This affected only the months July-September where there were two fairly distinct groups of data, and the precise position of the line used to separate the groups made little difference. In the remaining months the distribution of lengths appeared to be unimodal. Then for each month we calculated a one-way analysis of variance and used the F-ratio of between pod mean square to within pod mean square to test for synchrony. The magnitude of the effect was measured by estimating the between- and within-pod components of variation. No effect was detected in any given month, possibly because of relatively small sample sizes, so we pooled sums of squares and obtained the following results:

Low group, July-September

 $F_{10,63} = 1.31 \ (p > 0.20), \ V_{\text{between}} = 0.0019, \ V_{\text{within}} = 0.0325$



Fig. 13. Approximate frequency distribution, by month, of parturition based on (a) extrapolation back to the mean length at birth of 49 neonates of ≤ 200 cm body length, using a post-natal growth rate of 0.2 cmd⁻¹ or 0.73 my⁻¹, (b) extrapolation forward to the mean body length at birth of 50 foctuses of ≥ 150 cm body length, using a growth rate of 1.94 my⁻¹. Fig. (c) is the combination of (a) and (b).

High group, July-September $F_{4,22} = 1.75 \ (p > 0.10); V_{between} = 0.0062, V_{within} = 0.0324$ High group, April-October $F_{15,182} = 1.53 \ (p = 0.10); V_{between} = 0.0082, V_{within} = 0.1400$ We conclude that there was no evidence for differential within-pod synchrony. Note that if we pool the data for July-September, where the within pod variation is similar in both groups, then the estimated between-pod component of variation accounts for about 8% of the total. The corresponding figure for April-October is 6%.

2.5 Discussion

Size at birth

The mean body length at birth, 176.8cm, is clearly consistent with the figure of 174–178cm quoted by Sergeant (1962) for Newfoundland pilot whales. However, Sergeant simply took the mid point between the longest foetus and the shortest calf, a method which is very sensitive to the presence of abnormal animals and effectively ignores the majority which are born at intermediate lengths. A more rigorous comparison can be made by finding the length at which 50% of births had occurred in the Canadian study. From Sergeant's table 11 we can see that the answer to this is 180–183cm. Given the error in measurement and the sample sizes involved, the directly comparable values from these two studies must still be considered indistinguishable.

Our estimate of the mean body weight at birth, 74kg, is rather less than that derived for the Newfoundland catch by substituting the mean length at birth into the allometric length/weight relationship given by Sergeant (1962). This yields 79kg, uncorrected for variance about the regression line. Nevertheless the allometric exponent given by Sergeant (1962) is very similar to that we have calculated for Faroese animals (2.895, compared with 2.892) and we conclude that there is no demonstrable difference in birth weight or foetal growth characteristics between these stocks.

Seasonality of reproduction

The various indicators of the timing of conception can be relied upon to different degrees. The presence of a small foetus is clearly proof that conception occurred, but we know so little about the rate of embryonic development in cetaceans that even its size and date of death cannot be used to deduce its conception date more accurately than about ± 1 month. Ovulating females may have conceived very recently, may be about to conceive, or may have failed to conceive in this cycle. There is independent evidence, however, that the great majority of ovulations do result in a successful pregnancy (Results section 3.3), so the occurrence of ovulating females should be a reasonable guide to the timing of conceptions. Follicle development must clearly precede ovulation, but many large follicles do not lead to ovulation and may indeed become atretic (Marsh and Kasuya, 1984). Thus, while the presence of a follicle of ≥ 10 mm in diameter is likely to be an indication of ovulatory activity (Marsh and Kasuya, 1984), it does not necessarily accurately predict the timing of any associated ovulation and conception.

Overall, ovarian activity and the seasonal occurrence of the smallest foetuses are interpreted to indicate a likely peak of conceptions between April and June, perhaps with a secondary peak in September. This is consistent with information presented by Desportes *et al.* (1993) on male pilot whales around the Faroes, which undergo seasonal changes in their reproductive organs. In mature males, testis weights are highest between March and September, peaking in June, while testosterone levels rose steadily to April, were not measured in May or June, were significantly lower in July and climbed to a second peak in August/September.

Information on the timing of births is perhaps rather less clear. The 49 smallest neonates had a distribution of estimated birth dates peaking in August, but this and other studies (Miyazaki, 1977; Barlow, 1984) have raised some doubts about the validity of assuming a

uniform growth rate from birth in small cetaceans and the patterns of parturition which result. Extrapolation from the 50 largest foetuses indicates peak births in April/May and, to a lesser extent, in September. If these two similar-sized samples are combined, May becomes the dominant month, followed by September, and April-September is the peak period with 75% of births (Fig. 13c).

There are several, independent, measures which could be considered as support for the hypothesis of two conception peaks during the year. Firstly, the monthly apparent pregnancy rate (Table 2), which has peaks in June, September and November. Secondly, the proportion of mature females showing signs of recent or imminent ovulation; this peaks in June and August/September (Fig. 11a). Thirdly, the testosterone data for mature males from Desportes *et al.* (1993) mentioned above.

The frequency distribution of parturition dates constructed by back-calculating from young animals of approximately 1 year of age or less (Fig. 12) is less clear-cut than that derived from foetal data. The distribution cannot be distinguished from a uniform distribution statistically, and, since there is clear independent evidence of breeding seasonality, we must suspect that the assumptions are incorrect and that the true parturition pattern is being masked by an inadequate understanding of growth in the first postnatal year. The rate of increase in body length probably diminishes in the year after birth as it does in most mammals, including other small cetaceans (e.g. *Stenella attenuata*; Hohn and Hammond, 1985), but there seems little point in modelling the influence of such non-linear growth on the distribution of birth dates without specific information for pilot whales.

Overall, evidence relating to the shape of the frequency distribution of conception and birth dates is equivocal. The bimodal model is supported by several independent measures, and certainly fits the foetal data better, but there is perhaps sufficient doubt to justify considering the unimodal model in parallel. A second distinct peak of conceptions has rarely been demonstrated for mammals living in a seasonally variable environment where an adaptive advantage accrues to those females giving birth at a particular time. Nevertheless, a multimodal breeding pattern has been proposed for *Stenella coeruleoalba* on the Pacific coast of Japan (Kasuya, 1972; Miyazaki, 1977) and two Stenella species in the eastern tropical Pacific (Barlow, 1984). Interestingly, in each case the multimodal pattern was evident from the length frequency distributions of foetuses but not those of young calves, as here. The Japanese dolphins, at least, live in a region subject to seasonal fluctuations and are therefore arguably comparable to pilot whales off the Faroes.

If it exists, what does a multimodal distribution of breeding events imply? Barlow (1984) argued that such a pattern could be brought about by changes in the length of the reproductive cycle, perhaps as a density-dependent result of hunting pressure. This would certainly make sense in a situation where females were ready to conceive mid-way between single annual breeding seasons and where giving birth outside the normal period did not confer a significant disadvantage to either mother or calf. An alternative explanation, and one which perhaps fits the present situation better where the second peak is smaller and a lot less than 6 months later, is that most of the animals conceiving at the second peak were doing so having already conceived at the main peak and lost the foetus. early in gestation. This is consistent with the fact that the proportion of mature females carrying a foetus reaches one peak in June and another in September, both followed by a fairly prompt slump (Table 2). It would perhaps be advantageous to conceive again in the same season after an early pregnancy termination, in order to avoid wasting a whole year. Both scenarios are consistent with the fact that selective pressures to give birth at a particular time of year must be low (since synchrony at the population level is clearly poor), regardless of whether the pattern is unimodal or bimodal.

An alternative explanation for bimodality could be that the Faroese catch is taken from two pilot whale populations, each of which has a unimodal breeding pattern but with peak frequencies several months apart. This possibility is not supported by any direct evidence as yet, but heterogeneity within the Faroese catch has been reported by authors examining other aspects of the biology of this species (Andersen, 1988; 1993; Caurant *et al.*, 1993; Raga and Balbuena, 1993; Aguilar *et al.*, 1993), and a parallel situation exists for *G. macrorhynchus* in the North Pacific (Kasuya *et al.*, 1988a; Kasuya and Tai, 1993).

Foetal growth rate and the duration of gestation

In this paper we have followed convention and applied the foetal growth model of Huggett and Widdas (1951) to derive an estimate of gestation time from the calculated rate of linear growth. Unfortunately, there is no direct evidence from cetaceans to either support or discredit the applicability of the model to this mammalian order because in no species is both the rate of foetal growth and the gestation length accurately known. There is no apparent reason to suspect that pilot whale embryos undergo delayed implantation, as do seals and some terrestrial mammals, or exhibit some other growth pattern which would not conform to the Huggett and Widdas model. Nevertheless, estimates of cetacean gestation length derived solely by means of the model should be treated with some caution.

The broad spread of conceptions and births across the year, evident from the range of foetal lengths on any one day, complicates estimation of the rate of foetal growth (and therefore the length of gestation). It was a surprise to find that the statistical technique most commonly used in this situation, that of least squares regression of foetal length on time, was inappropriate in these circumstances and had to be disregarded. The alternative approach, of regressing date on length, seemed to overcome some of the difficulties but was also found to give underestimates of the true value with simulated data. We have used it mainly to indicate a lower bound on the real foetal growth rate.

Assuming that the Huggett and Widdas (1951) model is appropriate and that the initial non-linear portion of foetal growth is therefore of about 60 days in extent, the available information on foetal length with date of capture, examined both with modelling procedures and regression analysis, points to a gestation length of a year or less in Faroese pilot whales. The temporal distribution of conceptions and that of births derived largely from analyses of independent data seem similar, thereby also implying a gestation period of about 12 months. This is consistent with the rate of foetal growth (2.15 my⁻¹) predicted by our unimodal breeding pattern model (assuming foetal mortality of 50%) and a value for t_0 (applying Huggett and Widdas) of 60 days. If our bimodal model is correct, and the period of linear foetal growth is 8.7 months rather than 9.9 months, then a 12 month gestation would imply a period of non-linear growth (t_0) of 99 days (or 0.27 y gestation time). This is too long to be consistent with the Huggett and Widdas model.

It is difficult to envisage a way in which the duration of gestation can be determined to any greater degree of accuracy without repeated measurements of a growing foetus or information from captive-held animals. Such data are available for two related Delphinid species, the bottlenose dolphin (*Tursiops*) and killer whale (*Orcinus*). Schroeder (1990) gives 12 ± 0.5 months as the gestation period for *Tursiops*, a smaller species, and Walker *et al.* (1988) assert that it is about 515 days (16.9 months) in *Orcinus*, which is considerably larger than *Globicephala*. In general, adult body size is positively correlated with gestation time within mammalian orders (Millar, 1981), so a pilot whale gestation of much less than a year would appear unlikely, and we consider that a figure of about 12 months gives the best fit to the data available in the present study. This is at the upper end of the 95% confidence interval derived from the bimodal breeding model (9.7–12 months) and near the middle of that for the unimodal model (9.7–16 months), which fits the foetal length data less well.

Although we are unable to give a certain and precise value for the rate of foetal growth and the gestation period in Faroese-captured pilot whales because they cannot be measured directly, none of our estimates are similar to those calculated by Sergeant for this species (growth rate=1.54 my⁻¹, gestation=15.5-16 months) or those given by Kasuya and Marsh (1984) for the closely-related G. macrorhynchus (growth rate= 1.24 my^{-1} , gestation=14.9 months). Other papers have quoted gestation periods of around 15-16 months for G. melas (e.g. Harrison, 1969; Frazer and Huggett, 1973) but all use, indirectly or directly, Sergeant's (1962) figure. The considerable differences in the estimates of this important parameter between the current and earlier papers can at least partially be explained by a brief comparison of the analytical methods and data sets used. Sergeant's calculations were hampered by bias in the catch and lack of data for all but a few months in late summer and autumn, as the author acknowledged. The foetal growth trajectory given in his fig. 18, on which the estimate of gestation length is based, is critically sensitive to the estimate of the mean date of birth, which was almost certainly biased by lack of data earlier in the year. Another factor acting to depress the angle of the growth trajectory in Sergeant's fig. 18 is that the mean length of foetuses during the Newfoundland catching season is biased towards early conceptions and will thus be artificially inflated, resulting in a downward bias in the intercept of the trajectory with the x (time) axis. This bias would only have become obvious from samples taken later in the season when most of the cohort had been conceived, but winter catches were not made off Newfoundland. We conclude that Sergeant's estimate of the linear rate of foetal growth for this species is likely to be a considerable underestimate of the true value. For reasons given in our evaluation of the use of regression analysis to estimate foetal growth rates, we also consider that the foetal growth rate for G. macrorhynchus calculated by Kasuya and Marsh (1984) is likely to be an underestimate. The nature of the data available to both of these studies precludes the possibility of establishing the length of the gestation period other than by extrapolation from the estimated rate of foetal growth. Nevertheless, it is notable that a shorter gestation period than originally estimated, implied by faster foetal growth, would certainly be consistent with the data presented in these benchmark papers.

Breeding synchrony

The lack of any greater synchrony of conceptions within pods than between pods is of fundamental importance to our understanding of the social mechanisms governing mating and paternity in pilot whales. Amos *et al.* (1991a; b; 1993) and Amos (1993) have shown, albeit in a small number of Faroese pods, that fathers do not remain for more than a few months, at most, in the same pods as the foetuses they have sired. Nevertheless, sometimes the fathers of most of the foetuses in a pod, perhaps conceived many months apart, seem to be genetically related to each other, arguing for some kind of longer-term association between two or more pods. Our findings indicate that potentially receptive females in a pod do not all synchronise their ovulations in response to the periodic availability of suitable males. It would therefore be advantageous for males to make repeated visits to other pods in order to find newly-receptive females, whether they visit alone or as part of a pod which merges with another.



Fig. 14. Periodic curve fitted to the proportion of mature females pregnant by Julian day, weighted by sample size. Each point represents one pod. The formula of the curve is

$$p = \frac{\mathrm{c}^{-0.947+0.396\cos 2\pi (t-0.601)}}{1 + \mathrm{e}^{-0.947+0.396\cos 2\pi (t-0.601)}}$$

Table 2	
Apparent pregnancy rate, by month.	

	No. mature females	No. pregnant	% pregnant (SD)
January	137	24	17.5 (3.2)
February	52	12	23.1 (5.8)
March	46	11	23.9 (6.3)
April	123	33	26.8 (4.0)
May	15	5	33.3 (12.2)
June	28	13	46.4 (9.4)
July	176	57	32.4 (3.5)
August	42	12	28.6 (7.0)
September	153	60	39.2 (4.0)
October	77	19	24.7 (4.9)
November	207	63	30.4 (3.2)
December	41	5	12.2 (Š.1)
Σ	1,097	314	

3. Reproductive rates

3.1 Pregnancy rate

The apparent pregnancy rate (APR), i.e. the proportion of all sexually mature females that are pregnant, varied dramatically between grinds and across the year (Table 2). We fitted a periodic curve to the data on a grind-by-grind basis (Fig. 14) which gave a peak of

36.6% in summer and a low point of 20.7% in winter, a ratio of 1.77 between the extremes. A large seasonal fluctuation in the apparent pregnancy rate could be caused by one or more of the following:

(a) A gestation period of other than 12 months. If more than this, the early and late stages of each pregnancy occur at the same time of year and a foetus will effectively 'count double' between the dates of conception and birth. If gestation is less than a year, the APR will be low between the times of peak births and peak conceptions.

(b) Substantial foetal mortality, especially if abortions are not followed by another pregnancy later in the same year.

(c) A biased sample, whereby pregnant females are disproportionately sampled at a particular time of year.

Option (a) is not supported by the balance of evidence (discussed in Results section 2.5) which indicates a gestation length of about 12 months, but in itself a seasonally fluctuating APR could be considered substantial evidence that the gestation period is considerably greater or less than a year. In order to examine the weight of this argument, we modelled the effect on the apparent pregnancy rate of a gestation length of between 10 and 17 months, in increments of 1 month. Assuming no sample bias, a constant annual foetal mortality rate of either 20% or 60% and either a bimodal or unimodal frequency distribution of births, the results shown in Table 3 were obtained. These show that the APR fluctuation observed in the Faroese sample could not be entirely reproduced by any combination of reasonable values for gestation length, foetal growth rate and foetal mortality rate. The ratios of maximum to minimum APR values during the year were almost insensitive to the rate of foetal growth, but the higher foetal mortality rate increased the ratio significantly, especially at gestation lengths of 11-13 months. Gestation lengths of 10 or 11 months seem consistent only with APR patterns very different from those recorded in this study. Gestation periods of 12 months or more often produced APR peaks and troughs roughly consistent with those observed, dependent on the parameter values used, but maximum: minimum ratios of only up to 1.48. This suggests that the Faroese pilot whale catch is not an unbiased sample of the population from which it is taken, and for some reason pregnant females are seasonally disproportionately represented in relation to mature females at other stages of the reproductive cycle.

3.2 Age-specific fecundity

The proportion of mature females that are pregnant by age class (Figs 15 and 16) demonstrates a clear decline in pregnancy rate with increasing age. The relationship is described well by a logistic regression of the formula

$$P(x) = \frac{1}{1 + e^{0.014 + 0.04479x}}$$

where P(x) is the proportion of mature females pregnant at age x (Fig. 15). We also fitted a linear regression (not shown) weighted by sample size with a slope of -0.0083 and an intercept with the x axis (indicating a zero probability of pregnancy) at age 55 years (F=33.9, p<0.001). Nevertheless, the sample included an animal of 55yrs of age that was pregnant, and there is clearly considerable individual variation in reproductive output in older whales (see Results section 3.8). Truncating the data at age 40, to avoid the possibly misleading influence of the very oldest animals in the sample, has no significant effect on the slope of the regression which predicts zero pregnancy at age 56yrs.



Fig. 15(a). Age-specific pregnancy rate with a fitted logistic regression of the formula

$p = \frac{1}{1 + e^{0.014 + 0.04479x}}.$

Table 3

Simulated characteristics of the apparent pregnancy rate (APR) due to variation in gestation length, foetal mortality rate and linear rate of foetal growth. Parallel simulations are shown for a bimodal (a,b) and unimodal (c,d) temporal pattern of breeding. Unrealistic gestation lengths with

given foetal growth rates are marked *.

	Foetal grov	wth rate $= 1$.	96 my ⁻¹	Foetal	growth rate =	$= 2.43 \text{ my}^{-1}$
Duration of gestation in months	Max. APR / Min. APR	Predicted time of max. APR	Predicted time of min. APR	Max. APR / Min. APR	Predicted time of max. APR	Predicted time of min. APR
a. Bimodal bre	eeding distribution	on; annual fo	etal mortality ra	te = 20%		
10	*	*	*	1.55	Early Dec.	Early May
11	*	*	*	1.25	Early Dec.	Mid May
12	1.05	Early Oct.	Mid Mar.	1.06	Early Nov.	Mid Apr.
13	1.18	Early Jun.	Mid Feb.	1.19	End Jun.	Mid Mar.
14	1.31	Mid Jun.	Mid Feb.	1.33	Mid Jul.	Mid Mar.
15	1.40	End Jun.	Late Feb.	1.43	End Jul.	Mid Mar.
16	1.44	Mid July	Early Mar.	*	*	*
17	1.44	End Aug.	Mid Mar.	*	*	*
b. Bimodal bro	eeding distributi	on; annual fo	etal mortality ra	ate = 60%		
10	*	*	*	1.62	Early Dec.	End Apr.
11	*	*	*	1.32	Late Nov.	Early May
12	1.17	End Sep.	Mid Mar.	1.18	End Oct.	Mid Apr.
13	1.24	Mid Jun.	Early Mar.	1.26	Early Jul.	End Mar.
14	1.35	Mid Jun.	Late Feb.	1.39	Mid Jul.	End Mar.
15	1.43	Late Jun.	Early Mar.	1.47	End Jul.	End Mar.
16	1.46	Mid Jul.	Early Mar.	*	*	*
17	1. 4 6	Early Sep.	Mid Mar.	*	*	*

с.	Unimodal breedin	ng distribu	tion; annual fo	petal mortality rate =	20%		
	10	*	*	*	*	*	*
	11	*	*	*	1.19	Late Oct.	Late May
	12	1.06	Early Sep.	End Mar.	1.06	Early Sep.	Early Apr.
	13	1.15	Mid Jul.	Mid Feb.	1.15	Mid Jul.	Mid Feb.
	14	1.27	Late Jul.	Mid Feb.	1.27	Mid Jul.	Mid Feb.
	15	1.36	Mid Aug.	Mid Feb.	1.36	Mid Aug.	Mid Feb.
	16	1.42	Late Aug.	Early Mar.	*	*	*
	17	1.45	Early Sep.	Mid Mar.	*	*	*
d.	Unimodal breeding	ng distribu	tion: annual fo	oetal mortality rate =	60%		
	10	*	*	*	*	*	*
	11	*	*	*	1.26	End Sep.	Early May
	12	1.18	Early Sep.	End Mar.	1.18	Early Sep.	End Mar.
	13	1.23	Mid Aug.	Early Mar.	1.23	Mid Aug.	Mid Mar.
	14	1.33	Mid Aug.	Early Mar.	1.33	Early Aug.	Early Mar.
	15	1.40	Mid Aug.	Early Mar.	1.40	Mid Aug.	Early Mar.
	16	1.46	Late Aug.	Early Mar.	*	*	*
	17	1.48	Early Sep.	Mid Mar.	*	*	*

Table 3 continued



Fig. 15(b). Age-specific inter-pregnancy interval derived from the inverse of the regression.



Fig. 16. Age-specific proportion of mature females of known reproductive status which were determined to be pregnant (P), pregnant and lactating simultaneously (PL), lactating (L) or resting (R) at the time of their death.

3.3 Conception rate

The conception rate is the proportion of mature females which conceive each year. Because of the probability of bias in the apparent pregnancy rate it would not be justifiable to derive this parameter directly from pregnancy data. Clearly, it must be no greater than the ovulation rate, which averages 0.251 across all age classes (see Results section 1.4). An extreme lower bound is the ratio of the number of calves of one year old or less (judged by length):mature females, i.e. 0.176. The difference between these figures is brought about by infertile (including multiple) ovulations, foetal mortality and, on average, mortality of calves in the first 6 months of life. Thus, on average (0.176/0.251) = 70% of all ovulations lead to a calf surviving to age 6 months. If, as we suspect, the proportion of pregnant females in the sample is biased upwards, at least in summer, then the proportion of lactating females is likely to be biased downwards. In this case, the figures of 0.176 and 70% derived above will similarly be biased downwards. Without relevant data to guide us, any estimate of where the conception rate value might lay in this range is necessarily arbitrary. Our appraisal, based partly on independent evidence of significant foetal mortality in this stock (Desportes et al., In press) is that the conception rate is likely to be close to 0.24, which will thus be used as a working value below. It implies that 4.5% of ovulations are infertile and that 73% of conceptions lead to a calf surviving to about 6 months after birth.

3.4 Fecundity rate

We define this as the proportion of mature females giving birth each year. Following the arguments in 3.3 above, the value will be between 0.176 and 0.24. We choose an arbitrary figure of 0.195 on the basis that rather more losses between conception and an average age of 6 months post partum are likely to occur prior to birth than after it. This implies total foetal mortality of 19% and neonatal mortality (up to 6 months of age approximately) of 10%. It is worth noting that the minimum APR from the curve fitted in Fig. 14 is 0.207, which looks to be realistic (and therefore probably unbiased) on the basis of the independent data discussed above.

3.5 Gross birth rate

This is defined as the ratio of number of births per year to number of animals in the population, i.e.

fecundity rate
$$\times \frac{\text{no. mature females}}{\text{no. all animals}} = \frac{0.195}{2,792} \times 1,097 = 0.077$$

3.6 Mean inter-pregnancy interval

The mean interval between conceptions is simply the reciprocal of the conception rate, i.e. (1/0.24)=4.2yrs or 50 months.

3.7 Mean inter-birth interval

This is not affected by the estimate of the gestation period and, similarly, is the reciprocal of the estimated fecundity rate i.e. (1/0.195)=5.1yrs (61.5 months).

3.8 Reproductive senescence

We have shown that, on average, females of this stock apparently continue to ovulate throughout life (see Results section 1.5). Nevertheless, of 41 females of known

reproductive status aged 40yrs or more in our sample, only two (4.9%) were pregnant and it is possible that some animals had ceased to ovulate altogether and/or that only a small percentage of ovulations in these older females lead to a successful fertilization. Twenty one (51.2%) of these oldest whales were 'resting', i.e. were not pregnant, lactating or ovulating and 18 (43.9%) were classed as lactating. The fact that one of the three oldest females in our sample, a 55 year old, was pregnant demonstrates that successful reproduction can potentially continue throughout life.

3.9 Lifetime reproductive output

From the curve of the age-specific inter-pregnancy interval, constructed from the reciprocal of the logistic regression of proportion pregnant against age (Fig. 15b), it is possible to estimate at what ages an average female pilot whale conceives and to construct a curve of the cumulative number of conceptions with age. Assuming first pregnancy at 8.5yrs of age, the curve predicts an average of 5 conceptions by 19.7yrs of age, 8 by 31.4yrs of age, 10 at 42.8yrs of age and 12 at 61.7yrs of age. If foetal mortality is 19% as estimated (see Results sections 3.3 and 3.4), this amounts to an average calf production of 4.1 by 19.7yrs of age, 6.5 by 31.4yrs of age, 8.1 by 42.8yrs of age, and 9.7 by 61.7yrs of age. These figures will be upwardly biased if pregnant females are over-represented in the sample in summer, as we suspect.

An estimate of the average lifetime calf production was derived thus:

$$LCP = \sum_{x=1}^{50} l_x \cdot p(x-1) ,$$

where

LCP = lifetime calf production l_x = probability of survival to age x (from Bloch *et al.*, 1993b) p(x-1) = age specific pregnancy rate at age (x-1) taken from the fitted logistic regression.

The basis for this calculation is that females pregnant at age x-1 will give birth at age x if they survive. The result, 3.85, is an overestimate of the true value because it ignores foetal mortality. Allowing for an annual foetal mortality rate of 20% or 60% applying for half the gestation period (because, on average, pregnant females were probably killed and sampled half way through gestation), the revised figure would be 3.5 or 2.7 calves respectively.

3.10 Discussion

Although Faroese-captured female long-finned pilot whales give birth less frequently as they grow older, few become reproductively senescent before they die and pregnancy can occur in even the very oldest animals. This is consistent with the conclusions of Kasuya *et al.* (1988b) for *G. melas* off Newfoundland. Long-finned pilot whales, at least in the North Atlantic, thus follow what appears to be the normal pattern of reproduction in large mammals, (e.g. northern fur seal *Callorhinus ursinus*, Smith and Polacheck, 1981; walrus *Odobenus rosmarus*, Fay, 1981; elephant *Loxodonta africana*, Lee, 1991) i.e. a period of sustained high fecundity in early/middle adulthood followed by an age-related decline in pregnancy rate. Even if true reproductive senescence does occur in a proportion of the oldest females, so few live long enough to enter this phase (only some 10% of females reach 40yrs of age; Bloch *et al.*, 1993b) that it is unlikely to represent a significant and

functional part of the life history or social ecology of this species. This is in contrast to the situation in southern form G. macrorhynchus of the North Pacific, where 25% of adult females were judged to be post-reproductive (Kasuya and Marsh, 1984), and eastern North Pacific killer whales (Olesiuk *et al.*, 1990).

The results of simulation trials exploring the relationship between the apparent pregnancy rate, foetal mortality rate, gestation length, foetal growth rate and the unimodality or bimodality of the conception curve (Table 3) are enlightening. On the basis that 10 or 11 month gestation periods would produce APR maxima and minima at very different times of year to those observed, they can perhaps be discounted at this stage. These simulations indicate little difference between the APR characteristics generated by unimodal and bimodal breeding patterns with the same parameter values. However, a 60% foetal mortality rate produces seasonal differences in the APR nearer to those observed than a 20% rate at gestation lengths of around a year, and there is clear evidence that similarly high mortality probably does occur in this stock of whales (Desportes *et al.*, In press). None of the scenarios examined produced as high a ratio of maximum:minimum APR as observed in our sample, so some degree of bias in the representation of pregnant females probably does occur off the Faroes, especially in summer. Such bias must be considerable if gestation is of about a year in duration as other evidence indicates, and less so if it is nearer to 15–17 months.

The possible reasons for over-representation of females in any particular phase of reproduction are difficult to imagine in relation to the sample of animals considered in this study, but Kasuya and Marsh (1984) reasoned that a similar bias probably existed in their G. macrorhynchus dataset, so the cause of the problem may be inherent in samples of harvested pilot whales.

The conclusion that about 70% of ovulations result in a calf surviving to 6 months of age seems robust on the basis of the data from which it is derived. Nevertheless, it is inconsistent with the high level of foetal mortality deduced by Desportes *et al.* (In press) and with Sergeant's (1962) estimate that an average of 1.3 ovulations preceded each pregnancy. The present result indicates that almost all ovulations must be fertilised and implies that foetal and neonatal mortality must be less than 43% combined. Realistically, these figures could only be incorrect if the number of calves was upwardly biased in our 38 sampled pods.

Direct comparison with some of the conclusions of Sergeant (1962) and Kasuya et al. (1988b) related to reproductive parameters of long-finned pilot whales off Newfoundland are not meaningful because of the recognised temporal and other biasses in the catch from which their data were derived. Sergeant's estimate of crude birth rate, for example, implicitly assumes that all pregnancies detected would have led to a successful birth, so the fact that it is higher (0.1-0.13) than that presented here (0.077) cannot be taken as evidence of any difference. The same argument applies to crude birth rates presented by Kasuya and Marsh (1984) with regard to G. macrorhynchus. Nevertheless, given that the gross birth rate calculated from the proportion of pregnant females will give an upwardly biased result, the present figure of 0.075 seems consistent with results of work, using the same types of data as here (population cross-section), on other Delphinids (Tursiops truncatus, Delphinus delphis and three Stenella species), and probably higher than that of Orcinus orca (Perrin and Reilly, 1984). Recent long-term observational studies of individually recognisable killer whales (Olesiuk et al., 1990) and bottlenose dolphins (Wells and Scott, 1990) have provided reproductive parameter values from a quite different perspective. The crude birth rate for T. truncatus was 0.055 compared to the 0.077 estimated for G. melas in this study. Olesiuk et al. (1990) estimated a mean birth interval for killer whale pods of 5.32yrs, superficially almost identical to our estimate of 5.1yrs for G. melas, but the killer whale figure did not account for neonatal mortality (i.e. calves that died before they were seen by observers) and is therefore inflated. Their value for killer whale fertility rate (i.e. proportion of mature females giving birth each year) was 0.251, and for reproductively active females it was 0.375. The comparable figure for Faroese pilot whales is considerably lower, at 0.195, and nearer to that for *Tursiops* in Florida (0.18) (Wells and Scott, 1990; from values in their fig. 2A).

Because of large seasonal differences in the apparent pregnancy rate in Faroese pilot whales, it would be misleading to take a single figure as being representative, and comparisons with other species must therefore be made with caution because an overall pregnancy rate is the most commonly quoted measure of the rate of reproduction. A more meaningful comparison can perhaps be made between the current study and that of pilot whales off Newfoundland (Sergeant, 1962) by correcting for seasonal differences in data collection. Thus, Sergeant found that 169 out of 529 mature females in his sample (31.9%) were pregnant, and a comparable figure for the Faroes, during the period July 15-October 14 when the Canadian samples were collected, is 117/323 (36.2%). These values are not significantly different ($\chi_1^2 = 1.64$, p > 0.1).

Our estimate of an average of 6.5 births for females living to 32yrs of age and 8.1 births at 43 is greater than that of Kasuya and Marsh (1984) for *G. macrorhynchus* (4.4 births by 42yrs of age). Olesiuk *et al.* (1990) estimate an average of about 5.4 calves surviving to 6 months of age for female killer whales living to reproductive senescence at about 40yrs of age. Allowing for neonatal mortality, tentatively put at 37%-50% for this stock of killer whales (Olesiuk *et al.*, 1990), the lifetime calf production must be similar to that of northeastern Atlantic pilot whales.

Although undoubtedly subject to some error, the figure of an average lifetime calf production of 2.7 based on age-specific pregnancy and survivorship curves and a high but realistic foetal mortality rate is interesting in the context that each female needs to replace herself if the population is to remain stable. Desportes *et al.* (In press) show that the natal sex ratio is about 2 females:1 male, so the predicted lifetime productivity of female calves would be 1.8. This figure looks superficially healthy, but would be subject to upward bias if pregnant females are disproportionately sampled in summer as we suspect.

4. Lactation and the 'resting' phase of the reproductive cycle

4.1 Duration of lactation

Milk production is assumed to continue until soon after the calf is weaned or dies. Our estimate of the mean duration of lactation by implication encompasses lactations terminated both normally and by the loss of a calf, and so will be somewhat less than that of the mean age of a young pilot whale at weaning.

In most cases lactation seems to be terminated before the next conception, but of 84 females with the smallest foetuses (<30cm body length) in our sample, 32 (38%) were still lactating after the previous pregnancy. Table 4 demonstrates that few females continue lactating into the latter stages of pregnancy, but that a very small minority may not entirely interrupt the production of milk at any stage of the reproductive cycle.

It is usual to estimate the mean duration of lactation in cetaceans from the product of the ratio of lactating:pregnant females in the sample and the duration of pregnancy. In fact, this technique is only valid if there is little or no foetal mortality since the appropriate ratio is actually that of lactating females:births per year. It is also very sensitive to seasonally biased sampling. A more robust estimate of the mean duration of lactation (L) is therefore assumed to be

Foetus length class (cm)	No. PL	No. P only	Proportion PL	SD
≤20	22	38	0.37	0.06
20.1- 40	12	27	0.31	0.07
40.1- 60	9	18	0.33	0.09
60.1- 80	6	20	0.23	0.08
80.1-100	8	22	0.27	0.08
100.1-120	5	14	0.26	0.10
120.1-140	2	12	0.14	0.09
140.1-160	1	30	0.03	0.03
160.1-180	2	21	0.09	0.06
180.1-200	0	4	0.00	0.00

Number and proportion of pregnant females that are simultaneously lactating, by length class of their foetus.

Where:

- RLP =maximum ratio of lactating:pregnant females in any period of the year (from Fig. 17),
- S = best estimate of foetal survival from January to birth (estimated from Results section 3.4 assuming that rather more than half of the estimated foetal mortality occurs in the first half of gestation).

The maximum value of the ratio of lactating:pregnant females is used in this calculation because we know that, especially in summer, the proportion of pregnant females in the sample is greater than the proportion that will give birth that year. There is independent evidence to indicate that in January, when the ratio of lactating:pregnant females is highest, the proportion of mature females in the sample that are pregnant is unbiased (see Results section 3), lending support to the validity of the calculation above.



Fig. 17. Ratio of lactating:pregnant females across the year in consecutive periods of 28 days.



Fig. 18. Ratio of lactating:pregnant females by age. Each point represents females in 3 consecutive age classes; 5-7yrs, 8-10, 11-13 etc.

4.2 Effect of female age on the duration of lactation

Figs 17 and 18 show the ratio of lactating:pregnant females by age. Even if age classes of 10yrs or below are ignored because many of these young animals will not have entered their first period of lactation yet, it is clear that the ratio increases with age. The slope of the regression is 0.13 (SE=0.04, p<0.02). Assuming that the duration of gestation is age-independent, the duration of lactation must be greater in older females. Of those in our sample aged 40yrs or more, 18 were lactating and only 2 were pregnant. This indicates a mean duration of lactation in these older females, ignoring foetal mortality, of approximately

$$\frac{18}{2} \cdot \frac{1}{\text{gestation length}} = 9.1 \text{yrs} \text{ (assuming gestation lasts 1 year)}$$

The comparative figure for animals aged 21–39 was 2.9 or 3.2yrs, indicating that the oldest females lactate for about three times as long, on average, as those in the early or middle stages of their reproductive life. This increase seems to occur quite suddenly from about 40yrs of age onwards and may well be brought about by a few senescent individuals continuing to lactate long after their final pregnancy, rather than a uniform sudden increase in the duration of lactation across all of the oldest animals.

Independent confirmation that lactation continues for longer in older reproductively active females is given by the fact that the mean age of females simultaneously pregnant and lactating is 2.7yrs greater than that of females which are pregnant but not lactating (21.3yrs ± 1.75 (2 SE) compared with 18.6yrs ± 1.27 (2 SE)). This difference is significant (t=2.26, p=0.024) and shows that, on average, older animals are more likely to begin a pregnancy before completing lactation after the previous calf. Taken with evidence that the mean inter-birth interval increases with age (see Results section 3) there seems no doubt that lactation does indeed continue for longer, on average, in older females.

4.3 'Resting' period

We define the resting period as the time between the cessation of lactation and the next conception. This period is missed altogether in at least 38% of reproductive cycles, i.e.

those in which ovulation and conception occurs during lactation (see Results section 4.1). An upper limit of its average duration is

$$\overline{R} = \overline{IBI} - \overline{L} - G$$

= 5.1 - 3.35 - 1.0
= 0.75 yrs (9 months)

where

 \overline{R} = mean duration of resting period, \overline{IBI} = mean inter-birth interval, \overline{L} = mean duration of lactation, G = gestation period (yrs).

Note that \overline{R} is slightly inflated because \overline{IBI} includes a period of time 'lost' to abortive pregnancies in addition to the normal reproductive cycle.

The plot of the ratio of resting:pregnant females by age (Fig. 19) indicates that the length of the resting phase remains fairly constant until females are in their late 30s, when it increases rapidly. This effect may be simply due to the increasing inter-birth interval at this late stage in life (Results section 3.7), but would be enhanced by any animals that are truly reproductively senescent. Resting animals form an increasingly large proportion of all mature females from about age 20 onwards (Fig. 16).

4.4 Discussion

There is clearly so much variation in the duration of the reproductive cycle within and between animals that the concept of a 'mean' duration of any phase except completed pregnancy itself is perhaps misleading. It seems clear that, on average, the reproductive cycle lasts considerably longer in older animals than younger, and much of that extra time



Fig. 19. Ratio of resting:pregnant females by age. Each point represents females in 3 consecutive age classes; 5-7yrs, 8-10, 11-13 etc.

is devoted to an extended lactation period. However, foetal losses (Desportes *et al.*, In press), the ability of many females to ovulate and conceive during the latter stages of lactation, and the probable two discrete peaks of conception each year must increase the range of individual patterns of reproduction within the population as a whole.

The increased duration of lactation in older females may be due to one or more possible factors, e.g.: (1) a higher survival rate of calves; (2) provision of milk to calves other than their own; (3) increased energetic investment in later calves. Of these, (1) and (3) have been demonstrated in longitudinal studies of individually-recognisable terrestrial mammals (e.g. Clutton-Brock *et al.*, 1982; Clutton-Brock, 1984), and (2) could increase the inclusive fitness of the individual because calves in the same pod are likely to be genetically related (Amos, 1993).

SUMMARY AND CONCLUDING REMARKS

The dataset on which this study was based is undoubtedly one of the largest and most comprehensive of its kind hitherto available for any cetacean species. Complete social groups were freshly examined, measured and sampled in every month of the year, yielding a total of over 3,000 whales. Nearly 2,000 of these were females and formed the dataset explored in this paper. It is instructive to review what such a wealth of raw data can reveal about the reproductive characteristics of the population from which the sample was drawn.

Females of this stock ovulate for the first time at a mean age of 8yrs and a range of 5–15yrs. Sexual maturity seems to be triggered by the attainment of a critical body length (median 375cm, range c.350-418cm) than either age or body mass. Only about half of all females live to reach the age at which they give birth for the first time, but by far the majority of those that do will continue to reproduce until death. The reproductive cycle of ovulation, conception, pregnancy, lactation and 'resting' lasts about 5yrs on average, but the interval between births is less than this in early maturity and increases through life. The approximately one animal in 10 that survives to reach 40yrs of age is probably still ovulating, and capable of pregnancy and birth, but the interval between conceptions is now so great that they spend many years 'resting' between weaning one calf and conceiving the next. The duration of lactation also increases with age, extending the interpregnancy interval even more in these older animals. A small minority of whales may become incapable of further ovulations at some stage in their lives, due either to ovarian exhaustion or dysfunction.

Conceptions and parturitions can occur at any time of year, but are more frequent in summer and autumn. Gestation lasts about 12 months. There is a great deal of variation in reproductive history between individuals in the population. Some mature early in life, some much later. Some die young, some live for more than 50yrs. Some ovulate relatively frequently, others slowly. Because of the nature of the data considered in this study we cannot say whether, for example, early maturing females are likely to produce more calves in their lifetime than those that delay ovulation for a few years. Such information has only recently started to become available for cetaceans, and from very different sources of data; long-term observational work in which recognisable animals and their offspring are monitored over many years (e.g. Bigg *et al.*, 1990; Clapham and Mayo, 1990; Olesiuk *et al.*, 1990; Payne *et al.*, 1990). Such longitudinal studies, when carried out for a length of time commensurate with the longevity of the species, are able to provide answers to questions which cannot be addressed by looking at an animal (or even thousands of animals) just once, i.e. at their death. The reverse is also true: observational studies in the

Table f

Summary of reproductive parameters and characteristics of long finned pilot whales off the Faroe Islands, 1986-1988.

Measure	`Best' estimate	Comments
Mean age at sexual maturity	8.3 years old	
Mean length at sexual maturity	375cm	
Mean weight at sexual maturity	605kg	
Gross birth rate	7.7%	
Mean ovulation rate	0.25 year^{-1}	
Conception rate	0.24	
Reproductive lifespan		Ovulation continues throughout life in many females, but inter- pregnancy interval increases with age and pregnancy is rare after 40 years of age
Gestation period	About 12 months	Assumes no delayed implantation and that the foetal growth model of Huggett and Widdas (1951) is appropriate
Mean lactation length	3.4 years (40.2 months)	
Mean inter-birth interval	5.1 years (61.5 months)	Lower limit - sensitive to foetal mortality in 2nd half of gestation
Synchrony of breeding		No evidence of consistent within- pod synchrony
Seasonality of breeding	Conceptions and births are diffusely seasonal. Most are spring to autumn, but some occur in the winter months too. Peak conception and birth rates probably April-June, with a lesser peak in September.	
Mean body length at birth	176.8cm	
Mean body weight at birth	74kg	

field cannot, for example, provide information about ovulatory activity or foetal growth, or provide more than an upper bound on the duration of gestation.

The estimation of when pregnancies began and ended, and how long pregnancy lasts, provided the greatest challenges in the current study. Despite the size of the dataset and the many statistical procedures which were employed to explore and analyse it, there is still uncertainty about these parameters for this population of whales. The fundamental

reason for this is simply that the timing of breeding is immensely variable both within and between pods. The sample, large as it is, is inadequate to allow an accurate characterisation of the population as a whole in this regard.

Perhaps the most striking result of this study is that our best estimate of the gestation length of long-finned pilot whales is considerably shorter than that published previously. Few cetacean gestation lengths are precisely known, but Sergeant's (1962) estimate of 15.5–16 months is well-established in the literature and has been used to help derive generalised mathematical relationships between gestation length or foetal growth rate and body size at birth in Odontocetes (e.g. Perrin *et al.*, 1976; 1977; Kasuya, 1977). With the benefit of a larger sample size, year-round sampling and computer-based simulation techniques we can now see why and how Sergeant arrived at what was probably an overestimate of the gestation length of his study population but, despite the advantages available for the current work, we cannot say by exactly how much; simply that 12 months looks to be the most likely figure. Ironically, a single closely-monitored pregnancy would provide a more precise figure for the duration of gestation than can be gained from the study of nearly 2,000 harvested whales.

Of all the reproductive characteristics compared between Faroese-caught female pilot whales in the 1980s and those taken off Newfoundland in the 1950s, only one, the age at sexual maturity, is demonstrably different. This parameter is recognised as one of the most variable, both within and between populations of mammals, including cetaceans (e.g. Lockyer, 1984; Perrin and Donovan, 1984). Its lower value in the intensively hunted Newfoundland stock than in Faroese animals may have been density-dependent, and the difference certainly cannot be taken as evidence of isolation between pilot whales in the two areas. Reproductive data for this species are scarce from elsewhere in the North Atlantic, but nothing yet published (e.g. Martin *et al.*, 1987; Sigurjónsson *et al.*, 1993) is inconsistent with the results presented in this paper which may, therefore, be applicable to *G. melas* throughout the North Atlantic.

The most salient results from the analyses in this paper, are given in Table 5.

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APPENDIX 1

Information relating to the capture and composition of the 38 pilot whale pods.

An asterisk in column 3 indicates that only part of a larger pod was landed. Parentheses in column 6 indicate that the number given represented only a sub-sample of the whales landed. Percentages given in the final row ignore sub-sampled pods. Of the 1,847 females recorded, 1,680 (91%) were examined and sampled in detail, and provided the data analysed in this study.

Location	Date	Total no. whales examined	No. sexed female	% female	No. mature females	% females mature
Gøta	10/07/86	41	24	58.5	18	75.0
Leynar	12/07/86	137	81	59.1	50	61.7
Bøur	30/07/86	54 *	35	64.8	22	62.9
Sandur	11/09/86	220 *	125	56.8	76	60.8
Øravik	15/09/86	118	72	61.0	49	68 .1
Gøta	25/09/86	29	18	62.1	15	83.3
Viðvík	27/09/86	16	8	50.0	6	75.0
Funningsfjørður	26/10/86	34 *	19	55.9	11	57.9
Miðvágur	01/11/86	174	105	60.3	62	59.0
Fuglafjørður	11/11/86	55	31	56.4	20	64.5
Hvalvik	14/11/86	32	20	62.5	15	75.0
Vestmanna	15/11/86	123	69	56.1	48	69.6
Hvalvik	24/11/86	77	50	64.9	35	70.0
Fuglafjørður	28/11/86	71	40	56.3	27	67.5
Gøta	06/12/86	85	56	65.9	(2)	-
Tórshavn	23/12/86	118	65	55.1	41	63.1
Hvannasund	22/01/87	152	88	57.9	57	64.8
Vágur	23/01/87	156	106	67.9	69	65.1
Leynar	31/01/87	26	17	65.4	11	64.7
Hvalvik	07/02/87	80	52	65.0	30	57.7
Leynar	23/03/87	65 *	46	70.8	26	56.5
Tórshavn	10/04/87	190	118	62.1	8 0	67.8
Fuglafjørður	21/04/87	68	39	57.4		-
Vágur	16/05/87	36	22	61.1	15	68.2
Leynar	22/07/87	90	59	65.6	40	67.8
Miðvágur	24/07/87	103	58	56.3	46	79 3
Miðvágur	02/08/87	47	28	59.6	20	71.4
Vágur	19/08/87	45 *	28	62.2	15	53.6
Klaksvik	29/08/87	15 *	10	66.7	7	70.0
Vágur	18/09/87	17	11	64.7	7	63.6
Tórshavn	08/10/87	45	30	66.7	20	66.7
Vágur	20/10/87	39	23	59.0	16	69.6
Hvalvik	24/10/87	72	42	58.3	30	71 4
Tórshavn	17/02/88	59	35	59.3	22	62 9
Miðvágur	13/03/88	57	28	40 1	20	71 /
Røur	20/04/88	111	66	50 5	43	/1. 4 65.2
Hyannasund	20/04/88	138 *	83	60 1	4 5 (6)	05.2
I evnar	10/06/88	66	40	60.6	28	- 70.0
L~y nai	10/00/00	00	-TU	00.0	20	70.0
Total		3,061	1,847	60.3	(1,105)	65.7

Preliminary Results on the Diet of Long-Finned Pilot Whales off the Faroe Islands

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ABSTRACT

The diet of pilot whales off the Faroes is described, based on 857 stomachs collected from 44 schools of long-finned pilot whales caught by the Faroese drive fishery in the period July 1986-November 1989 and covering all months of the year. 78% of the stomachs contain prey remains but only 5% flesh remains. The average length and age at the onset of weaning is estimated at 215cm for females and 222cm for males corresponding to about 6.5 months for both sexes. The oldest male found with macroscopic traces of milk in the stomach was 7yrs old; the oldest female was 12yrs old. Prey items include 12 genera of cephalopods, 15 genera of fish, as well as crustaceans and miscellaneous other items, all fairly common species around the Faroe Islands. Prey comprises several ecological and behavioural types. Despite the variety of prey items, pilot whales feed mainly on the squid species: *Todarodes sagittatus* and *Gonatus* sp. The diet is almost exclusively *T. sagittatus* when it is available. Pilot whales demonstrate clear preferences when given the choice, but can also diversify their diet according to prey availability. The diet varies between years and according to whale size and reproductive status. Calves shorter than 300cm in length eat smaller prey and also more shrimps and smaller squid species.

KEYWORDS: PILOT WHALES—LONG FINNED; AGE; FEEDING; NORTH ATLANTIC; SQUID; FISH; CRUSTACEA; REPRODUCTION; BEHAVIOUR MOVEMENT; DISTRIBUTION.

INTRODUCTION

The diet of long-finned pilot whales *Globicephala melas* has been reviewed by Mitchell (1975) and Evans (1987) and studies were usually limited to a listing of species found in a few stomachs (Mercer, 1967; Evans, 1980; 1982; Desportes, 1982; Goodall and Galeazzi, 1985; Clarke, 1986a; Martin *et al.*, 1987; Whitehead and Hope, 1991; Bloch, 1992; Sigurjónsson *et al.*, 1993). However, work carried out in Newfoundland (Sergeant, 1960; 1962) and in the Faroe Islands (Desportes, 1985) attempted to evaluate the relative importance of the prey and estimate the daily food intake. All studies revealed that cephalopods form the bulk of the food and seasonal movements of pilot whales towards the coast have been related to inshore movements of squid. Abundance of prey: *Illex illecebrosus* off Newfoundland (Mercer, 1975); *Todarodes sagittatus* off the Faroes (Joensen and Zachariassen, 1982; Hoydal, 1986; Hoydal and Lastein, 1993; Zachariassen, 1993); and *Loligo palei* and *Scomber scombrus* off the northeastern United States (Payne *et al.*, 1993).

As shown by Clarke (1983; 1985; 1986a), a knowledge of a predator's diet combined with a knowledge of the prey biology and behaviour can lead to a much better understanding of the predator itself and the food chain in general. For example, stomach

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examination can provide information on the migration and movements of whales, if some prey can be assigned as markers because of their restricted geographic or bathymetric distribution or their absence in the locality of the catch. The estimation of the biomass of prey required by the predator provides information on its role in the marine ecosystem and may enable quantification of certain species-fisheries interactions. Most squid species are poorly sampled from nets (Clarke, 1983; 1985; 1986a), and pilot whale diet analyses may also improve our knowledge of them. Stomach content data can provide information on the age and size of predators at the beginning of weaning and thus on the duration of lactation (Best, 1979; Best *et al.*, 1984; Kasuya and Marsh, 1984).

Long-finned pilot whales are the subject of an opportunistic, direct hunt in the Faroe Islands (see review by Bloch *et al.*, 1990; Sanderson, 1991). This catch has been the focus of a large scale international programme on the ecology and the status of the species (Desportes, 1990; Bloch *et al.*, 1993a; Desportes *et al.*, 1993). This offered an excellent opportunity to investigate the diet of the species. Whole schools containing animals of both sexes and different age classes and reproductive state were sampled all year round, allowing seasonal, sex, size and reproductive condition comparisons.

MATERIALS AND METHODS

Stomachs of 872 pilot whales from 46 pods of those driven ashore in the Faroes between July 1986 and September 1990 were examined. Within each pod, the stomachs of all whales 3m or smaller, and about ten larger ones were examined (i.e., about 20% of the whales). Details of the material collected are given in Table 1. Data obtained in the Faroes in August and September 1984 (Desportes, 1985) is given for comparison.

The different categories of prey have been identified for all stomachs, but identification to species was only fully carried out for 391 stomachs collected from 25 drives in the period 1986–87. Throughout this paper, therefore, frequency of occurrence of prey classes refers to the 682 stomachs with solid food remains, while quantitative data by category and species refers only to the 391 stomachs sampled in the period 1986–87.

Field procedures for the general programme are described by Bloch *et al.* (1993a) and only those specific to this study are mentioned here.

Searching

As in all delphinids, pilot whale stomachs comprise three compartments: fore, main and pyloric (see Desportes, 1985, for more details). All three were opened and carefully

Details on the material collected. Percentages are given in parenthesis (stomachs with prey remains include stomachs with flesh remains).

Table 1

Years	1986	1 9 87	1988	1989	1990	Total
No. schools sampled Sampling months	16 7,9 - 12	17 1 - 5,7 -10	7 2 - 6, 9	4 9, 11	2 9	46 all
No. of stomachs: examined empty (%) with milk only (%) with prey remains (%) with flesh remains (%)	381 38 (10.0) 66 (17.3) 277 (72.7) 7 (1.8)	340 28 (8.2) 33 (9.7) 279 (82.1) 26 (7.6)	96 10 (10.4) 9 (9.4) 77 (80.2) 12 (12.5)	40 2 (5.0) 2 (5.0) 36 (90.0) 1 (2.5)	15 1 (7.1) 1 (7.1) 13 (86.7) 0	872 79 (9.1) 111 (12.7) 682 (78.3) 46 (5.3)

searched macroscopically at the laboratory for milk, prey, flesh, hard remains of prey (cephalopod beaks, fish otoliths and bones, eye lenses, shells, etc.), miscellaneous items and the presence of parasites.

All three compartments could contain milk and undigested hard remains of prey. Most flesh was found in the forestomach, although partially digested flesh, such as cephalopod crowns or buccal masses was sometimes retrieved from the main stomach. The total intestine was also searched for about one third of the whales but seldom contained any remains.

Flesh remains were kept in 5% formalin, beaks and bones were kept in 70% alcohol and otoliths were dried.

Determination of size and age at weaning

Infestation by many parasites, especially those found in the digestive tract, is the result of food intake and the presence of such parasites is a positive indication of feeding on solid food even in the absence of food remains and can be used to estimate the onset of weaning. The presence of the nematode *Anisakis simplex* and cysts of the cestode *Pholeter gastrophilus* were used to indicate that solid food had been taken.

The data were collected by the authors and Balbuena (Balbuena, 1991; Raga and Balbuena, 1993). The whales were divided into four categories according to presence of milk, food remains and parasites in the digestive tract:

(i) stomach totally empty (no milk traces, no food remains, no parasites);

- (ii) stomach with traces of milk only (no food remains, no parasites);
- (iii) stomach with traces of milk and remains of food and/or parasites;

(iv) stomach with remains of food and/or parasites and no traces of milk.

The average length at the onset of weaning for both sexes was estimated using the fraction immature method described by Hohn (1989), using 5cm length classes. The average age at the onset of weaning was deduced from the average length, following the length/age relationship given in Bloch *et al.* (1993b).

Identification of prey items

Presence of milk was assessed macroscopically, visually and by smell; biochemical tests were not performed.

Undigested prey could sometimes be immediately identified and squid flesh could usually be distinguished from fish flesh. Since the digestive process was usually very advanced in the stomachs, most samples could only be identified to genus or species by closer examination of hard parts, e.g. beaks and otoliths. To overcome to some extent the problem of differential digestion rate of cephalopods, fish and shrimps, their presence in the stomachs was assessed by searching for eye lenses when no larger remains were available.

Size and weight of prey were estimated from the rostral length of squid lower beaks, the hood length of octopod lower beaks and the length or weight of fish otoliths, uncorrected for digestion. The methods used for identification of beaks and otoliths, and the relationships between length and weight of prey and beaks or otoliths are described elsewhere (Clarke, 1962; 1980; 1986b; Desportes, 1985; Hårkønen, 1986).

Crustaceans and gastropods were identified by the international project BIOFAR (Nørrevang, pers. comm.).

Relative importance of prey

The occurrence of shrimps, fish and squid was determined, but only fish and squid were quantified by number and weight. Upper and lower squid beaks and left and right otoliths

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were counted and the highest count of either beaks or otoliths was considered the minimum number of individual squid or fish ingested.

As a preliminary estimate of the relative importance of fish and squid prey species percent frequency of occurrence (F%) and percent number of prey (N%), including both fish and squid was assessed. We used as an index of importance of a given item a frequency number index defined as $FN=F\% \times N\%$.

Age determination

Age determination was performed by counting growth layer groups in both dentine and cement on thin stained sections of decalcified teeth; the results were kindly provided by Bloch *et al.* (1993b). The age in months of calves in the 0-year class was calculated by using the mean length at birth (177.6cm) and the growth rates (6.8cm and 5.9cm per month for male and female respectively) given by Bloch *et al.* (1993b).

Statistical analysis

The results are expressed as mean \pm standard error (SE). Chi² tests were performed for statistical comparison and Shannon's index (1948, *in* Zar, 1984) was used as measure of diversity.

RESULTS

Age and size at the onset of weaning

The fraction at age and length of whales 15yrs old or younger and 415cm long or smaller found for the four categories are given in Fig. 1. Table 2 provides data on the onset of weaning. Weaning appears to begin at around $6\frac{1}{2}$ months in both males and females. Milk was still detected in males up to 7yrs and females up to 12yrs.

All of the animals whose stomachs contained traces of milk were immature, except the oldest one, a 12yr old 391cm pregnant female with a 141cm foetus.

Weight of food in the stomachs

The proportion of whales having empty stomachs did not vary significantly among years (Table 1, chi² test). This was also true for the August/September period (the two months when whales were sampled in 1984 – Desportes, 1985) between 1986 and 1990 (Table 3, chi² test). Only 5% of the stomachs containing prey remains also contained flesh over the period 1986–90 (4.7% for August-September) significantly lower than August-September 1984, when all the stomachs containing food also contained flesh (Table 3, chi² test, p<0.001). The two greatest quantities of flesh retrieved from pilot whale stomachs in the period 1986–90 were 0.2kg and 0.8kg (three partially digested squid mantles, and fish bones and a little partially digested flesh respectively). In comparison, in August-September 1984 (Desportes, unpublished data) the average weight of rinsed and drained squid mantles retrieved from the stomachs of nine young males and females (body length: 310–397cm) was 2.5kg (range: 0.4–4.5kg).

Prey species and their relative importance in the diet

Cephalopods were found in most (F=92.5%) of the 682 stomachs containing remains of solid food during the period 1986–90. Fish and crustaceans were reasonably common (F=24.3% and 9.8%, respectively), while miscellaneous items, including animal and non-animal remains, were occasionally found (F=3.2%).

The items found in 391 stomachs sampled in the period 1986–87 are listed in Table 4, with the frequency of occurrence and percent by number for fish and squid prey. Table 5



Fig. 1. Frequency distribution per age (1a) and length classes (1b) of calves of G. melas, according to stomach contents: , empty stomachs and no parasites; , milk only with no parasites; , milk plus remains of solid food and/or parasites; , remains of food and/or parasites but no traces of milk.

Stomach contents		Males	Females
Milk and food, no parasites	Minimum	200cm, 3.3 months	177cm, <1 month
Milk and parasites, food or not	Minimum	215cm, 5.5 months	213cm, 6.0 months
No milk, food and/or parasites	Minimum	217cm, 5.8 months	232cm, 9.2 months
Parasite and/or food, milk or not	Average	222.2± 2.4cm, 6.6 months	215.2 ± 2.0 cm, 6.4 months
Milk, no food, no parasites	Maximum	322cm, 3 years	237cm, 10 months
Milk and food, no parasites	Maximum	294cm, 1 year	288cm, 1 year
, I		279cm, 2 years	286cm, 4 years
Milk and parasites and/or food	Maximum	346cm, 4 years	317cm, 6 years
		340cm, 7 years	391cm, 12 years

Details on the onset of weaning in pilot whales off the Faroes. The average length at onset of weaning is estimated from the fraction immature method described by Hohn (1989) using 5-cm length classes. Ages less than one year are deducted from lengths.

gives some data on the prey biology, including rarity and habitat. Cephalopods were of prime importance and accounted for 93% of the 7,267 fish and cephalopod prey retrieved from the 381 stomachs containing fish and cephalopod remains.

Cephalopods

At least 15 categories of cephalopod prey were identified, distributed within at least 10 families. Eight were identifiable to species level and a further six were identifiable only to genus. One category could not be identified, but belonged to a very characteristic genus. A few beaks were too damaged to be identified.

Among these 15 categories, Gonatus sp. (including Gonatus fabricii) and Todarodes sagittatus were by far the most dominant, both occurring commonly and of prime importance by number (FN=2,383 and 1,683, respectively). Five other categories each occurred in more than 5% of the stomachs, Brachioteuthis sp., Sepiola sp. (prob. atlantica), Teuthowenia megalops, Histioteuthis A and Eledone cirrhosa, representing altogether 13% of the prey.

The Megalocranchia, Rossia and Mastigoteuthis genera represent new records for the known diet of pilot whales in this area.

Proportion of pilot whale stomachs found to contain flesh remains in August-September in 1984 (Desportes, 1985 and unpublished) and in the period 1986-1990. The number of stomachs containing flesh is given as percent of stomachs containing prey remains. Percentages are given in parenthesis.

Table 3

Years	1984	1986	1987	1988	1989	1990
No. schools sampled Sampling months	3 8,9	4 9	4 8.9	2 9	2	2
No. of stomachs: examined empty (%) with prey remains (%) and flesh (%)	67 3 (4.5) 58 (87.7) 58 (100)	96 4 (4.2) 72 (75.0) 0	69 3 (4.3) 64 (92.8) 8 (12.5)	23 1 (4.3) 19 (82.6) 0	27 0 25 (92.6) 1 (4.0)	14 1 (7.1) 13 (86.7) 0

Items found in 391 stomachs of pilot whales landed in the Faroe Islands in the period 1986-1989. The total number of cephalopod and fish prey is 7,267. Percent frequency of occurrence, F%; Percent number of prey, Cn%. (Percents <0.1 are indicated as <).

Prey species	Family	F%	Cn%	FN1
Cephalopod	······································	93.7	93.0	8,714
Todarodes sagittatus	Ommastrephidae	52.7	31.1	1,639
Gonatus sp. incl. G. fabricii	Gonatidae	48.1	48.3	2,323
Brachioteuthis sp.	Brachioteuthidae	12.0	5.2	62
Sepiola prob. atlantica	Sepiolidae	7.4	3.2	24
Teuthowenia megalops	Cranchiidae	7.2	2.9	21
Histioteuthis A	Histioteuthidae	6.4	1.0	6
Eledone cirrhosa	Octopodidae	6.1	0.5	3
Histioteuthis reversa	Histioteuthidae	2.8	0.3	1
Chiroteuthis imperator	Chiroteuthidae	0.5	0.1	<
Megalocranchia sp.	Cranchiidae	0.3	<	<
Rossia macrosoma	Sepiolidae	0.3	<	<
Mastigoteuthis sp.	Mastigoteuthidae	0.3	<	<
Loligo sp.	Loliginidae	0.3	<	<
Unidentified sp. 1	U	0.3	<	<
Unidentified		3.6	0.2	1
Fish		22.3	7.0	156
Argentina silus (greater Argentine)	Argentinidae	8.4	2. 2	18
Micromesistius poutassou (blue whiting)	Gadidae	7.2	2.4	17
Reinhardtius hippoglossoides (Greenland halibut)	Pleuronectidae	1.8	0.3	1
Gadiculus argenteus (silvery pout)	Gadidae	1.8	0.1	0.2
Trisopterus sp. (pout)	Gadidae	1.5	0.1	0.2
Coryphaenoides sp. (rat tail, grenadier)	Macrouridae	1.3	0.6	0.8
Lycodes sp. (eelpout)	Zoarcidae	1.3	0.4	0.5
Brosme brosme (torsk)	Gadidae	1.0	0.2	0.2
Ammodytes sp. (sandeel)	Ammoditidae	1.0	0.2	0.2
Merlangius merlangus (whiting)	Gadidae	0.5	<	<
Glyptocephalus cynoglossus (witch)	Pleuronectidae	0.5	<	<
Rhinonemus cymbrius (four-beared rockling)	Gadidae	0.5	<	<
Hyppoglossus hyppoglossus (halibut)	Pleuronectidae	0.3	<	<
Melanogrammus aeglefinnus (haddock)	Gadidae	0.3	<	<
Trichiuridae (ceabbard fishes)	Trichiuridae	0.3	<	<
Unidentified		4.9	0.3	1.5
Crustacean		13.8		
Pandalus montagui (shrimps)	(decapod)	13.8	-	-
Munida tenuimana (galathee)	(decapod)	-	-	-
Unidentified		-	-	-
Miscellaneous				
Aphrodite aculeata	polychaete	-	-	-
Nereis sp. (mandibles)	polychaete	-	-	-
Yoldiella sp.	gastropod			
Tyblomangelia nivalis	gastropod			
Shark eggs (Galeus melastomus?)		-	-	-
Feathers		-	-	-
Algae		-	-	-
Stones (size of a walnut or smaller)		-	-	-
Fishing hooks, nylon threads, plastic bags		-	-	-

Some data on the biology of pilot whale prey off the Faroes. Depth and behavioural data on fish are given for the vicinity of the Faroes and based on information from the Faroese Fishery Research Laboratory and Whitehead *et al.* (1984-1986). Data on cephalopods are based on Clarke (pers. comm.). Data on shrimps are given for the vicinity of the Faroe Islands and have

been communicated by the international project BIOFAR (Norrevang, pers. comm.). Rarity (in nets and predators for cephalopods, in trawlers for fish): VC, very common; C, common; F, frequent; R, rare. Habitat: N, neritic; O, oceanic; C, coastal; D, demersal; P, pelagic;

HB, hyper benthos.

Cephalopod families	Rarity			
	Nets	Predators	Habitat	
Ommastrephidae	С	С	NO	DP
Gonatidae	С	С	Ο	DP
Brachioteuthidae	F	R	0	Р
Sepiolidae	С	R	С	DP
Cranchiidae	С	С	0	Р
Histioteuthidae	R	С	0	Р
Octopodidae	С	С	Ν	D
Chiroteuthidae	С	С	0	Р
Mastigoteuthidae	F	R	0	Р
Loliginidae	С	С	Ν	DP

	Rarity	Habitat		Depth(m)	
Fish species					
Argentina silus	С	Ν	DP	150-1,000	
Micromesistius poutassou	VC	NO	DP	100-1,000	
Reinhardtius hippoglossoides	С	NO	DP	400-1,200	
Gadiculus argenteus	С	Ν	DP	60-1,000	
Trisopterus sp.	С	Ν	DP	0- 250	
Coryphaenoides sp	С	NO	DP	600-2.800	
Lycodes sp	С	NO	D	200-1.200	
Brosme brosme	С	Ν	D	20-1.500	
Ammodytes sp.	С	Ν	DP	0- 200	
Merlangius merlangus	VC	С	D	0- 200	
Glyptocephalus cynoglossus	С	Ν	D	0- 500	
Rhinonemus cymbrius	С	Ν	D	50- 550	
Hyppoglossus hyppoglossus	С	NO	DP	50-2.000	
Melanogrammus aeglefinnus	F	Ν	DP	0- 200	
Trichiuridae	С	Ν	D	300-2,000	
Crustacean	·····		, * * ·		
Pandalus montagui	VC	HB			

Fish

Fifteen fish categories were identified, 10 to species level. A further four were identifiable only to genus and one only to family. Fish prey were distributed within at least eight families. Few otoliths could not be identified. Fish flesh was found only occasionally.

No fish species was common, although two species, Argentina silus and Micromesistius poutassou, were far more common than the others (FN=19 and 18, respectively), each contributing to more than 30% of the fish prey.

Three families represented in our sample (Macrouridae, Zoarcidae and Trichiuridae) represent new records for the known diet of pilot whales in this area.
Crustaceans

Crustaceans occurred in nearly 14% of the stomachs and were usually the shrimp species *Pandalus montagui*. Fresh or little digested shrimps were often found alone or in stomachs containing only beaks and fish bones and otoliths, i.e., as the freshest prey, thus indicating that they were not secondary but direct prey of pilot whales. They have not been previously recorded as being direct prey of pilot whales.

Miscellaneous other items

Miscellaneous items occurred occasionally in the stomachs. Some are typically remains of indirect prey (e.g. mandibles of *Nereis* and gastropod shells), but others had more likely been ingested accidentally (e.g. fresh *Aphrodite*, shark eggs).

Small stones were retrieved occasionally from forestomachs, always in small numbers.

Diversity of food items

A large range of items were retrieved from the pilot whale stomachs, with 30 categories of likely direct fish or cephalopod prey. The diversity in each stomach is nonetheless quite low with 48% of them containing the remains of a single species (Table 6). The maximum Shannon diversity index (H'_{max}) for the number of categories was 1.48 while the actual index (H') was only 0.67 (Zar, 1984). The evenness, H'/H'_{max} , is 0.45.

In total, 7,267 fish and cephalopod prey were retrieved from 381 stomachs, with an average number of prey per stomach of 19.1 ± 0.1 . The highest number of prey represented in a single stomach was 380, all *Gonatus*.

Changes in diet according to length and reproductive state of whales

The occurrence of cephalopods in pilot whale stomachs does not change significantly according to whale length or reproductive state, but the occurrence of fish and shrimps does (chi² test, p<0.001, Table 7). The occurrence of shrimps is significantly higher in whales <400cm long, while the occurrence of fish is significantly higher in immature females >300cm, in lactating females and in males >500cm.

Occurrence and percent by number of fish and cephalopod prey varied between whale groups of different length and reproductive state (Table 8). The importance of fish prey varied strikingly between groups. Fish were of very little importance in non-lactating mature females, but appeared in 60% of the stomachs of males >500cm, comprising 22% of the prey. Cephalopods represent the bulk of the diet for all groups, but the relative importance of species varied considerably. Small species such as *Brachioteuthis* sp. and *S*.

		No. s	pecies per omach	No stomacha
Stomach content	No.	Max.	Average	with one sp.
All stomachs	382	8	1.91±0.06	47.9%
Stomachs with cephalopod only	286	6	1.61 ± 0.05	58.4%
Stomachs with fish only	23	5	1.61 ± 0.23	6 9 .6%
Stomachs with fish and cephalopod:				
total	73	8	3.19 ± 0.16	38.4%
cephalopod species	73	5	1.84 ± 0.14	54.8%
fish species	73	4	1.36 ± 0.07	71.2%

Table 6

Prey diversity in stomachs of G. melas off the Faroes over the period July 1986-December 1987.

Table 7

	No.	Cephalopod F%	Fish F%	Shrimps F%
Males and females <=250cm	87	95.4	11.5	24.1
Males and females 250-300cm	125	95.2	16.0	14.4
Immature females >300cm (301-383cm)	94	91.5	30.9	13.8
Males 300-400cm	85	89.4	23.5	9.4
Males 400-500cm	41	95.1	17.1	2.4
Males >500cm	91	82.4	52.7	1.1
Pregnant females (371-495cm)	33	96.7	6.1	3.0
Pregnant and lactating females (398-463cm)	18	94.4	11.1	0
Lactating females (380-483cm)	69	95.7	31.9	2.9
Resting females	31	96.8	19.4	6.5

Frequency of occurrence (F%) of cephalopod, fish and shrimp prey taken by 674 pilot whales off the Faroes in the period 1986-1990, according to length and reproductive state. The actual range size of each group is specified for females.

atlantica occurred respectively in 54% and 22% of the stomachs of pilot whales <250cm, accounting for 25% of the prey. In contrast, *S. atlantica* was not found in the stomachs of males >400cm and mature females. *Brachioteuthis* sp. accounted for less than 1% of the prey in whales >300cm.

Smaller whales ate smaller prey than larger ones: *Todarodes sagittatus* mantle sizes reached up to 25cm in whales <300cm but averaged 16.6 \pm 1.5cm, while they reached up to 50cm and averaged 24 \pm 2.1cm in whales larger than 400cm.

Changes in the diet according to yearly prey availability

From fishery data the months of greatest *Todarodes* abundance around the Faroes are August and September and the diet during *Todarodes* months is compared for three years, 1984, 1986 and 1987 (Table 9). In '*Todarodes* years', *T. sagittatus* migrate in great abundance around the Faroes and in the fjords.

1984 was an exceptional year for the Faroese *Todarodes* fishery with 1,147.3 tons landed. Only cephalopods appeared in the stomachs. Diversity was very low with only three species represented and 57% of the stomachs containing a single species. *T. sagittatus* occurred in all stomachs containing food, and represented 96% of the beaks (FN=9,570). *Gonatus* sp. appeared in 40% of the stomachs but contributed only 4% of the prey (FN=168).

By contrast, no *Todarodes* at all were landed in 1986. Cephalopods still represented the main diet component, but fish occurred in 45% of the stomachs containing food and represented 8% of the prey. Six species of cephalopods were represented and four occurred each in more than 10% of the stomachs. *Gonatus* sp. was the main prey item (FN=6,941) and although *T. sagittatus* still appeared in 30% of the stomachs it represented only 4% of the prey (FN=113). The diet was more diverse with only 33% of the stomachs containing a single species.

1987 was a poor year for the squid fishery, with only 10.7 tons landed. *T. sagittatus* was present in some fjords, but at deeper depths than usual. The diet was, as in 1984, centred upon *T. sagittatus*, which appeared in 94% of the stomachs and contributed 91% of the prey (FN=8,528). Five other cephalopod species were also present, two of which, *Gonatus* sp. and *E. cirrhosa*, appeared in 23% of the stomachs although they totalled only

Frequency of occurrence (F%) and percent number (Cn%) of prey taken by 380 pilot whales off the Faroes during the period 1986-1987, according to length and Table 8

reproductive state (stomachs containing only shrimp remains are not considered here). Other cephalopod species include Megalocranchia sp., R. macrosoma, Mastigoteuthis sp., Loligo sp., unidentified sp. 2; other fish species include H. hyppoglossus, M. aeglefinnus, Trichiuridae. Each of them appeared only in one stomach. Males, M; Females, F. Species no. is the minimal number of species consumed by a whale group. (Whale grouping is the same as in Table 7.)

	A = 2	+F 50cm	M 250-3	+F 00cm	F imr >30	nature 0cm	M 300-41	00cm	M 400-5	00cm	M >50()cm	F Preg	nant	F Preg	+Lact	F Lact	ating	F Res	ting
No.	F% 46	Cn% 1530	F% 68	Cn% 606	F% 59	Cn% 957	F% 47	Cn% 657	F% 22	Cn% 325	F% 47	Cn% 1028	F% 21	Cn% 512	F% 10	Cn% 306	F% 41	Cn% 1111	F% 19	Cn% 240
Cenhalonod	96.7	99.4	95.6	96.7	91.5	95.5	97.9	86.6	6.06	97.2	80.9	78.2	100	9.66	100	100	95.1	8.68	100	9.66
T. sagittatus	28.3	3.8	50.0	45.7	61.0	60.8	74.5	60.2	40.9	40.3	48.9	23.1	57.1	31.6	80.0	13.1	58.5	20.7	63.2	62.2
Gonatus sp.	69.69	57.1	39.7	25.7	35.6	21.7	34.0	17.8	63.6	52.3	53.2	53.3	71.4	66.0	70.0	86.9	48.8	67.5	57.9	35.3
Brachioteuthis sp.	54.4	19.9	13.2	7.9	3.4	0.7	4.3	0.6	ı	ı	2.1	0.2	14.3	0.6	•	•	9.8	0.4	١	ı
S. atlantica	21.7	4.8	14.7	8.9	10.2	7.8	6.4	5.6	ı		ı	ı	ı	,	•	•	•	,	ı	•
T. megalops	21.7	11.4	11.8	2.6	5.1	0.5	4.3	1.1	4.5	0.3	ı	•	4 .8	0.2	·	ı	4.9	0.3	5.3	0.8
Histioteuthis A	4.3	0.4	8.8	2.1	6.8	2.2	6.4	0.5	4.5	4.0	4.3	0.8	14.3	1.0	ı	ı	7.3	0.5	5.3	0.4
Eledone cirrhosa	4.3	0.3	5.9	1.5	10.2	0.9	6.4	0.5	4.5	0.3	6.4	0.3	4.8	0.2	ı	ı	4.9	0.2	10.5	0.8
H. reversa	4.3	0.3	2.9	1.5	1.7	0.3	2.1	0.2	ı	ł	ı	ı	1	ı	ı	•	9.8	0.4	5.3	0.4
C. imperator	4.3	0.7	ı	ı	•	١	·		•	,	ı	ı	t	ı	ı	•	•	ł	•	ı
Others	6.5	0.5	ı	ı	1.7	0.1	ı	ł	ı	•	2.1	0.4	1	ı	ı	•	ı	ı	١	•
Unidentified	6.5	0.2	4.4	0.7	5.1	0.3	4.3	0.3	ı	ŀ	4.3	0.2	ı	ı	ı	ı	2.4	0.1	ł	ı
Fish	8.9	0.6	14.7	3.3	25.4	4.5	25.5	13.4	22.7	2.8	59.6	21.8	4.8	4.0	0	0	22.0	10.2	5.3	0.4
Argentina silus	•	ı	4.4	1.2	5.1	0.7	8.5	2.7	9.1	0.9	25.5	3.3	4.8	0.2	ı	•	19.5	7.8	ı	•
M. poutassou	8.7	0.6	4.4	1.5	10.2	2.1	10.6	6.3	4.5	0.3	17.0	8.1	۰	·	ı	•	2.4	1.4	ı	٠
R hippoglossoides	١	ı	'	ı	,	•	ı	•	4.5	0.3	10.6	1.8	•	ı	ı	,	2.4	0.1	١	٠
G. argenteus	ı	ı	1.5	0.2	•	•	4.3	0.6	ı	ı	4.3	0.2	4.8	0.2	ı	ı	2.4	0.2	ı	ı
Trisopterus sp.	ı	ł	ı	ı	3.4	0.3	2.1	0.2	4.5	0.3	4.3	0.4	ı	·	ı	•	ı	ı	ı	•
Coryphaenoides sp.	,	•	•	•	•	·	ı	,	,	ı	8.5	3.9	ı	•	ı	·	2.4	0.6	•	۰
Lycodes sp.	•	ı	ı	•	1.7	0.4	,	ı	4.5	0.6	6.4	1.9	ı	•	ı	•	ı	•	•	•
Brosme brosme	ı	•	•	ı	ı	۱	2.1	1.7	4.5	0.3	4.3	0.3	•	ı	ı	·	ı	ı	ı	•
Ammodytes sp.	ı	•	·	ı	1.7	0.1	4.3	1.5	ł	ı	2.1	0.1	•	ł	ı	ı	ı	ı	·	•
M. merlangus	,	ı	1.5	0.2	1.7	0.2	ı	,	·	ı	ı	ı	•	·	·	•	ı	•	•	•
G. cynoglossus	ı	1	,	•	1.7	0.1	,	,	ı		2.1	0.2	ı	ı	ı	ı	ı	ı	•	•
E. cymbrius	ı	ı	ı	,	1.7	0.1	ı	ı	·	•	2.1	0.1	·	•	•	٠	•	•	•	٠
Others	•	ı	•	•	1	,	ı	•	ł		6.4	0.8	•	·	۰	•	ı	•	ł	•
Unidentified	•	I	2.9	0.3	6.8	0.4	6.4	0.5	•	I	17.0	0.8	,	١	ı	•	2.4	0.1	5.3	0.4
Species no.	I	1		12	-	2	[14	1	1	1	8		8		5		12		٢

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Table 9

August - September	1	984	1	986	19	87
5 1	F%	Cn%	F%	Cn%	F%	Cn%
Prey species	n=35	n=4080	n=47	m=2268	n=62	n=806
Cephalopod	100	100	91.5	92.4	96.8	99.5
Todarodes sagittatus	100	95.7	29.8	3.8	93.5	91.2
Gonatus sp. incl. G. fabricii	40.0	4.2	87.2	79.6	22.6	5.2
Brachioteuthis sp.	-	-	10.6	0.3	-	-
Sepiola prob. atlantica	-	-	21.3	7.7	1.6	0.1
Teuthowenia megalops	-	-	6.4	0.3	3.2	0.2
Histioteuthis A	-	-	4.3	0.8	1.6	0.1
Eledone cirrhosa	2.9	<	-	-	22.6	2.5
Unidentified	-	-	2.1	<	3.2	0.1
Fish	0	0	44.7	7.6	6.5	0.5
Argentina silus	-	-	17.0	0.5	-	-
Micromesistius poutassou	-	-	25.5	6.4	-	-
Gadiculus argenteus	-	-	8.5	0.2	-	-
Ammodytes sp.	-	-	6.4	0.5	-	-
Unidentified	-	-	2.1	<	6.5	0.5
Crustacean	0	0	29.8	-	9.7	-
Pandalus montagui	-	-	29.8	-	9.7	-

Frequency of occurrence (F%) and percent number (Cn%) of prey taken by 144 pilot whales in August and September off the Faroe Islands in 1984 (Desportes, 1985 and unpublished), 1986 and 1987. Percent <0.1, <. (Stomachs containing only shrimps remains are considered).

8% of the prey. Fish accounted for less than 1% of the prey but was present in more than 6% of the stomachs. A single species was found in 48% of the stomachs.

DISCUSSION

Weaning

The age at the onset of weaning can be estimated from stomach examination. However, although presence of food is a positive indication that weaning has occurred, the lack of solid food remains does not necessarily mean it has not. As noted earlier, the presence of certain parasite species also indicates solid food intake, as parasites persist in stomachs longer than prey. In Faroese long-finned pilot whales, the infestation by stomach parasites can begin during the first year of life and their prevalence was exceptionally high in most schools and close to 100% from the second year of life onwards (Balbuena, 1991; Raga and Balbuena, 1993).

The average age at which pilot whale calves begin weaning was estimated to be close to 6.5 months in both females and males, but with considerable individual variation. Some calves start feeding on solid food when only a few months old, whereas milk with no traces of food or parasites was observed in a 3yr old male from a school in which all non-suckling individuals were infested, suggesting little or no feeding on solid food by this calf. Suckling individuals as old as 4yrs for females and 2yrs for males were also found with prey in their stomachs but no parasites, in schools where the prevalence of infestation was 100% in non-suckling individuals, again showing that a few individuals might have milk as the major nutrient source over a protracted period of time.

Length of lactation can also be estimated on the basis of direct observation of stomach contents (Best, 1979; Kasuya and Marsh, 1984). The detection of small quantities of milk mixed with digested food is difficult and biochemical tests to assess the presence of lactose should be used (Best, 1979; Best *et al.*, 1984). As milk is easily digested it will disappear from the stomach quicker than solid food remains and in particular hard remains. Although the frequency of nursing is not known, it is probably rather low towards the end of the nursing period and thus absence of milk does not necessarily mean completion of weaning. The analysis of stomach contents provides a more reliable information on the onset of weaning than on the completion of suckling, and the detection of milk in the stomach will underestimate the lactation period. More than 25% of pilot whales in the year-classes 3 and 4 had macroscopically detectable milk in their stomachs, suggesting that a high proportion of 3 and 4yr old calves suckle regularly and that the suckling period extends over at least five years in a significant number of calves.

These results concur with the mean lactation period of 3.4yrs given by Martin and Rothery (1993) from the ratio of lactating to pregnant females, given that this figure takes into account lactations terminated both normally and by loss of a calf.

Sergeant (1962) estimated that pilot whale calves off Newfoundland began feeding on solid food at 221cm in length and that the mean length at weaning was close to 239cm, corresponding to a mean age of 6-9 months, similar to the value in this study. The estimate given by Kasuya and Marsh (1984) for *G. macrorhynchus* is also between 0.5 and 1yr of age.

Milk was found in the stomach of a 7yr old male and a 12yr old pregnant female. Kasuya and Marsh (1984) reported that a mature female short-finned pilot whale may have been still suckling, noting that this occurred occasionally in Steller's sea lions (from Pitcher and Calkins, 1981). It is not known whether such older suckling animals nurse from their own mother or/and other females. Communal nursing is difficult to detect in cetaceans and has not yet been positively recorded, but it is known in land mammals (Gubernick, 1981; Clutton-Brock, 1991).

A protracted suckling/lactation period has also been mentioned for other toothed whales. In short-finned pilot whales, some calves suckle for 9 (female) to 15 (male) years, particularly calves of older females (Kasuya and Marsh, 1984; Kasuya, 1989; Kasuya and Tai, 1993). In sperm whales, milk traces were detected biochemically in stomachs of juveniles up to 13 years old (Best, 1979; Best *et al.*, 1984). Extended suckling may be of social rather than nutritional importance for the calf and is consistent with the stable matrilineal school structure described by Andersen (1990; 1993) and Amos *et al.* (1991a; b; 1993a; b).

Methods of diet analysis

Evaluation of the feeding habits of animals from their stomach contents is complicated by several factors, some of them being enhanced further when identification and quantification are based on the use of hard parts of prey. As pointed out in other studies (Hyslop, 1980; Bigg and Perez, 1985; Clarke, 1985; 1986a; Martin and Clarke, 1986; Murie, 1987; Prime and Hammond, 1987; Pierce and Boyle, 1991), a major problem inherent in diet analyses is the differential digestion rate of the various components which can lead to overestimation of the importance of some of them. Soft tissues of cephalopods are, for example, quicker to disintegrate than fish, and small soft prey will disappear before larger, tougher species.

Otoliths and beaks are known to accumulate in toothed whale stomachs for several days, or even weeks in the case of sperm whales (Clarke, 1980). The length of time the remains of different species stay in the stomachs will vary according to their size, fragility

and composition. Cephalopod beaks are retained for a longer period than fish otoliths (Ross, 1984; Bigg and Perez, 1985) and otoliths of different fish families, e.g. gadids and clupeids, are eroded at different rates (Prime and Hammond, 1987). Miller (1978) found that in fur seal stomachs, squid beaks remain several days whereas otoliths pass through rapidly. In addition, some fish species do not have otoliths.

The use of the otoliths to calculate importance by weight brings additional biases. Their erosion during the digestive process leads to a loss in physical size and perhaps density which is difficult to evaluate and depends again on their original shape. A further problem from using only hard parts in prey identification, is that material from the stomachs of the primary prey may be mistaken as food items of the predator.

Looking at the occurrence of cephalopod statoliths which, having the same structure as the otoliths, are more likely to be digested at the same rate, might be one way of overcoming the problem of differential digestion rate between cephalopod and fish prey. Searching for eye lenses, as done in this study, helps reduce the bias, but can only be used to assess the relative occurrence of fish and cephalopods and does not reduce the problem of different sizes of indigestible remains disappearing at different rates.

As these biasses have not been assessed in this preliminary analysis, we have not attempted to estimate the nutritional importance of the various items in the pilot whale diet. In particular, the importance of the fish component is probably underestimated. Nevertheless, we feel confident that the approximate rank order of importance estimated here is correct.

Quantity of food in the stomachs

Some species of whales are known to sometimes vomit stomach contents during driving, chasing or capture, particularly sperm whales (Caldwell *et al.*, 1966; Kawamura, 1971; Clarke, 1980). This has been occasionally observed in pilot whales, e.g. a few specimens shot on the edge of the Faroe Bank had the entire oesophagus full of fresh squid. However, if vomiting was the only explanation for the lack of flesh in the 1986–90 period, why did the stomachs contain (and sometimes were filled with) fresh squid in 1984? Many stomachs full of milk were also recovered in 1986–90. The length of the drive may influence vomiting, but this changes a great deal from hunt to hunt, varying from 15 minutes to several hours. In 1984, the three schools sampled were killed after drives which lasted 15 minutes, 3 and 6 hours respectively, and most whales were found with stomachs containing fresh squid. In the period 1986–90, the drives lasted from 15 minutes to nearly 11 hours with less than 30% of them lasting more than two hours (Bloch *et al.*, 1990; G.D., pers. observation) and yet no stomachs contained any significant fresh remains. The general absence of flesh in the period 1986–90 seems more likely to indicate that the whales fed further offshore during that period than in the summer of 1984.

Diet

As in many North Atlantic areas (Desportes, 1985; Martin *et al.*, 1987; Sergeant, 1960; 1962), pilot whales feed mainly on squid around the Faroes. Although two species, *T. sagittatus* and *Gonatus* sp., dominate, the diet can be supplemented with a large range of items including fish and shrimps. Although the shrimps found in the pilot whale stomachs could have been indirect prey, they would be expected to be digested and disappear rapidly from the stomachs, particularly if they were secondary prey already partially digested. Their occurrence as the freshest prey shows that they can be direct prey of pilot whales, and particularly of young animals.

Pilot whales do not exploit all the available abundant food resources in an area. In our sample, neither cod, herring nor mackerel were found, although they are common species

in the neritic zone and have been reported as pilot whale prey elsewhere (Sergeant, 1962; Evans, 1980; 1987; Desportes, 1985). Thus pilot whales do show preferences in their diet and cephalopods are clearly the favourite prey. In the '*Todarodes* periods' of 1986 no dramatic changes were reported in the availability of fish on the Faroe plateau. Nevertheless, in the absence of *T. sagittatus*, although pilot whales diversified their diet, it was by mainly feeding further north on the deeper water squid species *Gonatus* rather than on the widely available fish species.

Although cephalopods are clearly preferred, common fish species may become dominant when squid are not available. In a pod caught in July 1986, 73% of the whales had fed on greater argentines, *A. silus*, which represented 63% of the prey. In pilot whales off Newfoundland, cod and Greenland halibut were also found to be the main prey at certain times (Sergeant, 1962; Mercer, 1967).

There is also selectivity among cephalopod species. In August-September, in years when *T. sagittatus* is abundant on the Faroe shelf, the diet becomes nearly monospecific. The same pattern is observed on the edge of the Faroe Bank, where specimens were caught with stomachs full of fresh *Loligo forbesi* and beaks of the same with only a few unidentified fish bones (R.M. and E. Gaard, pers. comm.). A monospecific diet is observed also off Newfoundland where stomachs are filled with *Illex illecebrosus* (Sergeant, 1962).

The cause of these preferences is not clear. In several marine predators the basis for food selection is thought to be the energy and nutrient content of the prey (e.g., puffin: Harris and Hislop, 1978; gannets: Nelson, 1978). In pilot whales, the ranking in importance of squid species defined so far, grossly follows the ranking in calorific values given by Croxall and Prince (1982) and Clarke *et al.* (1985). If the energetic value of prey was, however, the only driving factor, then it would be more advantageous for pilot whales to feed upon fish rather than squid. It may be, for example, that the total nitrogen content and the content of different amino acids influences the predator's choice. These vary greatly from species to species within squid showing significantly higher values than fish for some amino acids (Sugimura *et al.*, 1954).

Although pilot whales demonstrate clear preferences when given the possibility, they may diversify their diet according to prey availability. Studies in different areas and at different times may thus yield quite different results on apparent feeding preferences. Waring *et al.* (1990) suggest that fish are not always an 'alternate' prey of pilot whales and that Atlantic mackerel is an important prey in winter and early spring in the mid-Atlantic and southern New England regions. Understanding the driving factors underlying the feeding preferences of pilot whales requires greater knowledge of the pilot whale diet in various geographical areas, especially offshore, and in different seasons.

Feeding behaviour

Apart from some squid species of unknown status, pilot whales feed on prey fairly common around the Faroes. Even though *Gonatus* sp. is not thought to be present on the Faroe shelf, it is very abundant further offshore on the slope of the shelf and in deeper water to the north of the Faroes. Although pilot whales feed mostly either on oceanic or neritic species, they also eat some typically inshore species such as *S. atlantica* and *M. merlangus* (whiting). Many prey species are mid-water species or carry out vertical migration, e.g. *T. sagittatus, A. silus* (greater argentine), *R. hippoglossoides* (Greenland halibut) and *Coryphaenoides sp.* (rat tail), but some are also typically demersal, e.g. *E. cirrhosa, B. brosme* (torsk) and *Lycodes sp.* (eelpout). Pilot whales feed either above rocky or soft bottoms, and mostly on gregarious species and luminous squid species.

From our knowledge of their prey, pilot whales seem able to forage at a wide variety of water depths, most commonly between 100 and 500m. Genera such as *Gonatus, Histioteuthis* and *Coryphaenoides* may be taken at greater depth, but are also found in water shallower than 500m. Prey such as *T. sagittatus* may be taken from near the surface at night and pilot whales have been observed feeding upon squid at the surface on the slope of the Faroe Bank (R.M., pers. obs.).

On the edge of the Faroe Bank, pilot whales are often seen feeding between 08:00 and 15:00hr (R.M., pers. obs.), but no periodicity in feeding activities was evident from our sample. The time for complete digestion given by Sergeant (1962) for pilot whales is less than 8 hours. If this is so, the three pods sampled in 1984 had been feeding at different periods, one during the night and the other two in the afternoon. During the sampling period, the schools were spotted or killed at various times of the day and again no feeding periodicity was observed. Any feeding activity pattern is likely to change according to geographical characteristics and the behaviour of the prey.

Changes in diet according to size and reproductive state

The diet of pilot whales changed with the growth of individuals and their physical ability to feed and hunt. Smaller individuals fed preferentially on smaller prey, which could be either the smaller individuals of a species or a small species.

The diet also appeared to vary according to special energetic requirements; for example lactating females ate more fish and more fish species than any other groups of mature females and larger males ate much more fish than any other group of whales. Lactation is a costly energetic period for the mother, particularly in the first year (Lockyer, 1993). One explanation might be that the extra energetic cost of milk production is met by eating more fish (which have a generally higher calorific value than squid – see particularly table 6.3 in Evans, 1987). A similar phenomenon has been observed in spotted dolphins where lactating females change their diet from mainly squid to mainly fish (Bernard and Hohn, 1989). As suggested by Cockcroft and Ross (1990), time spent in maternal care may reduce the foraging time of mothers and make it beneficial for them to show less preferences and to take any prey presenting itself.

Differences in the diet for individuals of different age, sex, and reproductive classes have also been reported for other odontocetes including the sperm whale (Best *et al.*, 1984), the spotted dolphin (Bernard and Hohn, 1989) and the bottlenose dolphin (Barros and Odell, 1990; Cockcroft and Ross, 1990). More information on the diet, energetic requirements and behaviour of the various classes is needed to evaluate this question further in pilot whales.

CONCLUSION

One interpretation of the data presented is that the feeding pattern of pilot whales in the summer of 1984 was exceptional and more usual from 1986 onwards. However, it is more likely that the 1984 sample, with stomachs full of *T. sagittatus*, is simply characteristic of years with a great abundance of *T. sagittatus*, while the diet in 1986 and onwards reflected the scarcity of this species on the Faroe plateau in those years. In addition to year class strength, the abundance of *T. sagittatus* in this area, and consequently in the fjords, is dependent on hydrographic conditions in the northeast Atlantic, and in particular on the characteristics of the North Atlantic current. The variability of the flow in the region northeast of the Faroes causes years without *Todarodes* (S.H. í Jákupsstova and B. Hansen, Faroese Fishery Laboratory, pers. comm.). Although *T. sagittatus* occurs almost

every year in Faroese waters, at least in small numbers, the most recent 'good' year was 1984.

Stomach content examination provides information on the feeding of predators and, when compared to prey availability, on the choice exerted by the predator. However, it only gives a 'snapshot' for each individual and seldom provides information on where the prey have been ingested if only hard remains are present. In parallel with stomach examinations, it would be useful to conduct analyses for providing longitudinal individual information on diet. Schell *et al.* (1989a; b) and Schell (unpublished manuscript) show, for example, that stable isotope ratios provide a record of feeding and migratory behaviour of whales, since they differ between prey species (Fry, 1988) and geographical areas (Dickson, 1986; Saupe *et al.*, 1989). Such techniques may provide information on the ability of individual whales to change from one main prey species to another and thus whether some of the diet variations observed between areas and seasons represent 'population' differences in feeding strategies, or whether they are only related to prey availability.

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Seasonal Changes in Body Fat Condition of Northeast Atlantic Pilot Whales, and their Biological Significance

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ABSTRACT

The carcase composition of long-finned pilot whales, Globicephala melas, taken in the Faroese drive fishery between July 1986 and June 1988 was routinely examined. Body weights were obtained for 232 foetuses and 622 whales of both sexes from calf to adult bull size, at all times of year throughout the 2-year period. In addition, length, girth and blubber thickness measurements were collected for 693 whales. Samples of blubber, muscle, visceral organs and fats were analysed for biochemical composition. An increase in body fat content during the winter months from November onwards was found. This was observed as an increase in wet weight lipid content from ca 1% to >45% in head and tail muscle, and possibly from 50% to >70% in visceral fat. Actual weight of fat deposits around visceral organs such as intestinal mesenteries and kidneys (which comprised >40% organ weight during January) also increased. These relative and absolute increases in fat deposits were observed in all whales regardless of sex and reproductive status. The lipid content of blubber varied between ca 70-85% wet weight of blubber with the lowest level in summer and highest in mid-winter. Morphometric data indicated that blubber thickness increased in the winter, thus increasing overall body fat reserves. The relationship between body weight (W in kg) and length (L in cm) can be described by the formula $W=0.00006L^{2.677}$ for foetuses >45 cm total length, and by $W=0.00026L^{2.484}$ for males and $W=0.00020L^{2.521}$ for females. For both sexes, incorporation of a mid-girth measurement increased the logarithmic weight/length correlation r² value from 0.951 to 0.964 in males and from 0.927 to 0.935 in females. Using three girth measurements (posterior to flipper insertion, and anterior and posterior to the dorsal fin) and logarithmic weight/length/girth correlation was 0.967 in males and 0.939 in females. Muscle constituted about 26% body weight (increasing from 22.5% to 30.5% with maturity and size), and blubber about 25% body weight (24% in adults and 26% in juveniles). During winter, the absolute lipid increase within the muscle comprised up to about 11.5% body weight, compared with summer. In winter, fat around the viscera comprised about 1.5% body weight, and the blubber weight increases totalled 5-10% body weight. Overall, the winter lipid accumulations constitute 14-23% body weight. Such an energy reserve amounts to about 170-210kg or 1.34-2.16x106 kcal in a 1 tonne whale (e.g. a fully adult female). Virtual depletion of these energy reserves by summer implies that decreased prey availability may coincide with increased demand for energy to devote to reproduction during the period winter to summer. There is no evidence that the energy demands of reproduction on females require any special storage strategy, different from that of adult males and juveniles.

KEYWORDS: PILOT WHALE-LONG-FINNED; ENERGETICS; MORPHOLOGY/ ANATOMY

INTRODUCTION

Aims

This study investigates the relationship between carcase energy and feeding, growth and reproduction of long-finned pilot whales (*Globicephala melas*) taken in the year-round drive fishery in the Faroe Islands in the northeast Atlantic. The study comprises a small part of a comprehensive investigation of the fishery in the Faroes (Bloch *et al.*, 1993a) in

which the whales are caught by local people for domestic consumption. The nature and practice of the fishery are described by Bloch *et al.* (1990). In general entire schools of pilot whales are taken. Hence, all age and reproductive classes are represented in the catches, providing a unique opportunity to collect data on the animals.

Background

Information on the general natural history of the long-finned pilot whale is essential in order to study the species in the context of its environment, and to identify key features in the life cycle which demand high energy. A summary of such information is given below.

The long-finned pilot whale is distributed throughout the waters of the northeast Atlantic from the Barents Sea in the north as far south as northwest Africa (e.g. Evans, 1980; 1982; McBrearty *et al.*, 1986). They are found in European waters year-round, and mass strandings frequently occur in all months of the year (e.g. Sheldrick, 1976). Fraser (1974) believed that the species distribution was directly associated with the North Atlantic current, possibly via the distribution of squid with respect to the current (Gaard, 1988). Evans (1980) discussed the likelihood that the Faroese and southern British Isles pilot whales are from separate populations, the overwintering northern group off Scotland coming from the Faroese summer grounds. Recently, Andersen (1988) has provided evidence from enzymatic allelic frequency studies, that the whales around the Faroes are not a single homogenous stock. This conflicts somewhat with the belief of Sergeant (1986) that pilot whales form a continuous cline across the entire North Atlantic, based largely on the catch histories of the Newfoundland and Faroe Islands fisheries. In summary, the stock identity of North Atlantic pilot whales remains unclear.

Prey abundance is thought to influence distribution and school size. McBrearty *et al.* (1986) and Evans (1980) noted that school size appears to vary seasonally, with frequent summer feeding aggregations of >100 animals (see also Brown, 1961; Severin, 1976). Otherwise, two thirds of schools sighted between 48° - 58° N usually contain <10 whales. The diet of the Atlantic pilot whales is primarily squid (Evans, 1980; Desportes *et al.*, 1988; Desportes and Mouritsen, 1993) and includes the genera *Illex*, *Ommatostrephes*, *Architeuthis* and *Todarodes*. Fish which may be consumed include cod (*Gadus morhua*), turbot (*Scophthalmus maximus*) and horse mackerel (*Scomber scombrus*). Joensen and Zachariasen (1982) and Hoydal (1985; 1986) noted that the appearance of the pilot whales around the Faroes was correlated with the commercial squid catches (and hence squid abundance), and also sea temperature. A similar pattern was noted for the Newfoundland area (Mercer, 1975). In addition to this direct predator prey relationship, Reinert (*in* Evans, 1980), found a correlation between herring (*Clupea harengus*) and pilot whale abundance around the British Isles, over a 300-year period; the whales were not feeding directly on the fish.

A new analysis of female reproductive parameters based on data collected under the international programme at the Faroe Islands (Martin and Rothery, 1993) has suggested some quite different values to those previously assumed. The old and new values are summarised in Table 1. According to Martin and Rothery (1993), conception peaks around mid-July and calving in early July.

The long-finned pilot whale has been the subject of exploitation on both sides of the North Atlantic, whaling effort being concentrated around Newfoundland (e.g. Mercer, 1975) in the west and the Faroes (e.g. Zachariassen, 1993), Shetland Isles (e.g. Venables and Venables, 1955) and Ireland (e.g. O'Riordan, 1975) in the east. Accurate fishery records for the Faroes exist from 1584, with only one gap from 1641-1709 until the present and the fishery probably dates from the 'middle ages' (Zachariassen, 1959; Müller, 1882; Joensen, 1962; Bloch *et al.*, 1993a; Zachariassen, 1993).

	Martin 8-		Previous studies
Parameter	Rothery	Value	Source
Breeding cycle	5 years	3-4years	(Sergeant, 1962; Martin <i>et al.</i> , 1987; Kasuya <i>et al.</i> , 1988)
Gestation	12 months	14.5 months	(Kasuya <i>et al.</i> , 1988)
Ovulation rate	4 years	2.9 years	(Kasuya et al., 1988)
Lactation	44 months	21 months	(Kasuya et al., 1988)
Age at sexual maturity	8-8.5 years		

 Table 1

 Female reproductive parameters for the long-finned pilot whale.

MATERIAL AND METHODS

Data collection

Between 10 July 1986 and 10 June 1988, 41 schools of pilot whales taken in the drive fishery were examined biologically (Bloch *et al.*, 1993b). Data and samples relevant to energetics were collected for the majority of these schools. The general sampling methodology is described by Bloch *et al.* (1993b) and is not repeated here. Once the animals were at the designated butchering site, they were sexed and measured. At this time the animals were usually manoeuvred about the quay or taken from the water by means of a crane and whole animals were sometimes weighed by using a scale attached to the crane strops (see below).

The carcases can not be tampered with in any other manner until the sysselmand (sheriff) and grindforeman have completed their inventory of the whales. When this is complete, dismemberment could begin and samples were collected. Whether whales could be weighed 'piecemeal' largely depended on being able to acquire or purchase carcases from the locals, at the sysselmand's discretion, in order to allow ample time to dissect and weigh each organ and tissue, either on-site or, for small whales and foetuses, at the Natural History Museum site in Torshavn. For this weighing procedure, a tripod, lever hoist and various weighing scales ranging from 10–500kg with hooks/buckets, etc. were used.

Sampling procedure

Measurements of total body weight, piecemeal weight, total length, girths and blubber thickness were made. The sites of measurement used for the present analysis are shown in Fig. 1. Length was measured from snout tip to tail notch in a straight line. Girth was estimated by doubling half-girths, measured as the whale lay on one side. Blubber thickness was measured dorsally behind the blowhole, at three mid-lateral and three midventral body positions. The whales were generally weighed whole using a 2 tonne *Miniweigh* tensile link accurate to ± 1 kg, linked to a remote digital readout, and suspended from a quayside crane. Whales exceeding 2 tonnes were weighed using the same system but halving the effective load by means of two blocks above the suspension point. Whales less than 1 tonne and which were also weighed in pieces were weighed using a *Ropod* portable tripod with a lever-hoist and suspended tensile link or 1 tonne *Salter* dynamometer. During weighing the whales were suspended by means of a noose around the tail stock or, more usually, by inserting a lanyard through a slit made at the base of the dorsal fin. This latter method resulted in most whales hanging almost horizontally when lifted, the fin being close to the centre of gravity. Samples of about 100g tissue were



Total body length (L)

Fig. 1. Positions of sampling and measurement on the pilot whale body: L=total length, D_1 =dorsal, L_3, L_4, L_5 =lateral and V_3, V_4, V_5 =ventral blubber thicknesses, G_2, G_3, G_4 =girths; encircled coded sites (D_1, L_4 and V_4) represent regions where blubber and underlying muscle have been sampled; other tissues sampled include subcutaneous and visceral fats, liver, kidney, heart and vertebral bone; stomach contents and milk also when available.

collected from blubber, muscle, liver, kidney and other miscellaneous tissues (Fig. 1). These were frozen and maintained at -25°C within about 24hr of the kill.

Biochemical analysis and collation of data

The individual morphometric data were collated on computer with relevant biological information (maturity, reproductive status, age). The tissue samples were analysed for lipid content (% of wet weight of tissue) as described for fin and sei whales (Lockyer *et al.*, 1984; 1985; Lockyer, 1987a; b) by gravimetric lipid extraction using a double extraction technique with chloroform/methanol (Bligh and Dyer, 1959) and about 1g of coarsely chopped or minced tissue. The tissues were sub-sampled centrally from the original 100g of frozen tissue. Blubber samples were cut in a uniform strip, about 1cm² in cross section, through from skin to underlying connective tissue; the skin was removed before analysis. All lipid extracts were stored in airtight glass tubes in a freezer at -50° C. The dry residue from the lipid extraction comprised virtually all protein, and was used as an approximate estimator of protein content of tissues. Data resulting from these tissue analyses were also coded on computer.

Additional data

A few previously unpublished morphometric and biochemical data, collected, processed and analysed in a similar manner, were available from pilot whales stranded on Humberside (east coast England) on the 17 January 1985. These data were not added to the Faroese data base, but were used for comparison.

RESULTS AND DISCUSSION

Morphometric data

Body weight

A total of 622 whales were weighed, 593 whole and 29 piecemeal. Of these, 373 were identified as females and 248 as males. In addition, girth and/or blubber thickness

measurements were obtained for 693 whales. Body weights (weighed whole) of 232 foetuses from 45cm up to near-term were also obtained; girth measurements were obtained for ten of these. Nine foetuses were weighed piecemeal. The relationship between total body weight and length by sex is shown in Fig. 2. There is considerable sexual dimorphism in this species, the males attaining a greater body length and weight.

Stepwise multiple linear regression analyses incorporating different factors indicated logarithmic relationships between weight (W), length (L) and all girth (G_x) measurements. It was found that girth correlates strongly with body weight, and thus one



Fig. 2. Total body weight at length for male and female pilot whales, and foetuses.

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Body weight/girth correlation in pilot whales. W = body weight, kg; $G_3 = mid-girth$ anterior to dorsal fin, cm.

Category of whale	Weight/girth relationship, $W = aG^{b}$ where weight is in kg, girth in cm	SE of b	r ²
Foetus	$W = 0.00009 G_2^{2.905}$	0.497	0.830
Male	$W = 0.00009 G_{2}^{2.962}$	0.091	0.914
Female	$W = 0.00009G_3^{2.953}$	0.089	0.898

measurement can be used to predict the other (Table 2). Length also correlates strongly with body weight (Table 3). The correlation between W and L is increased slightly by incorporating a mid-girth factor, G_3 , as observed for baleen whales (Lockyer and Waters, 1986; 1987), but use of additional girth factors does not greatly increase the correlation in pilot whales, again as in baleen whales (Víkingsson *et al.*, 1988). For estimating weight therefore, length should be adequate, although incorporation of a mid-girth factor improves the prediction slightly. The weight/length relationships (Table 3) are not significantly different by sex. Analysis by reproductive category revealed the following tendencies, although none are statistically significant: (1) juvenile females are consistently lightest for length; (2) juvenile males are similar to adult females in weight/length relationships; (3) adult bulls are the heaviest for length; (4) pregnant females may be heavier for length than lactating ones. Furthermore, weight/length relationships did not appear to change significantly with changing seasons. In terms of weight prediction from length therefore, pooling all data, regardless of sex, reproductive status and season, is acceptable. The resultant weight/length and weight/length/girth formulae are:

$$0.00023L^{2.501} \tag{1}$$

where SE of the exponent=0.025, r²=0.940, sample size=620;

$$0.000104L^{1.451}G_3^{1.316} \tag{2}$$

where SE of the exponents=0.097 and 0.118 respectively, $r^2=0.954$, sample size=230.

A total of 38 piecemeal weighings were made. These animals were all initially weighed whole. Table 4 presents the percentage carcase composition of muscle, blubber and visceral organ weights for various categories of animals. The blubber and muscle weights are generally underestimated as remnants of both usually adhered to the tail and head with some muscle also adhering to the skeleton. These remnants usually amounted to only a few (<10)kg, or about 0.5–3.5% of total body weight, depending on the size of whale (300–2,500kg range). This percentage is less than the observed overall seasonal weight changes reported later. Another source of weight error is blood and fluid loss during both kill and butchering. However, as all whales were flensed in a similar manner, these losses are assumed to be constant. Table 4 shows that adults had the greatest proportion of muscle and foetuses the least. Blubber proportions are similar for all groups, although slightly less for foetuses (late-term). The viscera weighed the most in foetuses, by as much as 5% body weight more than in adults. The remaining part of the body (54–65%, not shown in Table 4) included head, tail, skeleton and adhering tissue remnants as well as body fluids lost during flensing.

During the summer, no visceral fat was seen around the heart, intestine or kidneys, unlike in winter when they were surrounded by fat and the kidneys had a high fat content. For example, in two animals weighed piecemeal from a drive at Hvannasund on 22

les. W = total body weight, kg;	posterior to dorsal fin, cm.
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Table 3

-	Formulae for predicting body weight fi L = total body length, cm; $G_2 =$	from length, and length and girth measurements in male anterior girth at axilla, cm; $G_3 = mid-girth$ anterior to	$\frac{1}{2}$, female and foctal pilot whales. W = total body weig o dorsal fin, cm; $G_4 = girth$ posterior to dorsal fin, cm	ıt, kg;
Relationship	Foetuses	Males	Female	
W=	Formula, W=	SE r ² Formula, W=	SE r^2 Formula, W=	SE r ²
aL ^b	0.00006L ^{2.677}	$b = 0.035 \ 0.963 \ 0.00026L^{2.484}$	$b = 0.36 0.951 0.00020L^{2.521}$	b=0.037 0.927
aL ^b G [°]	0.00007L ^{2.551} G ₃ ^{0.101}	$b = 0.301 0.987 0.00021L^{1.600}G_3^{1.123}$ c = 0.363	$b=0.137 \ 0.964 \ 0.0008 L^{1.203} G_3^{1.636}$ c=0.168	b=0.142 0.935 c=0.171
aL ^b G ₃ G ₄	$^{\circ}$ 0.00012L ^{2.663} G ₃ $^{-0.259}$ G ₂ $^{-1.347}$ G ₄ $^{0.960}$	$b=0.263 0.996 0.00005 L^{1.776} G_3^{1.795} G_3^{0.266} G_4^{0.971}$ c=0.318	$b=0.144 0.967 0.00005L^{1.169}G_{3}^{1.417}G_{2}^{0.597}G_{4}^{-0.261}$ c=0.372	b=0.150 0.939 c=0.292
		d=0.518	d=0.266	d=0.268
		e=0.322	e=0.287	e= 0.186

		Perc	entage body weigh	$t \pm SE$
Sex	Reproductive class	Muscle	Blubber	Viscera
Male and Female	Foetus	17.57 ± 1.31	21.97 ± 1.60	14.54±0.64
Male	Immature	24.35 ± 2.25	23.25 ± 2.14	10.70 ± 1.32
Female	Immature	22.34 ± 1.20	24.05 ± 1.13	8.60 ± 1.16
Male	Mature	29.62 ± 1.39	23.01 ± 1.91	10.97 ± 0.89
Female	Mature	30.49 ± 1.76	23.48 ± 1.20	11.16 ± 0.68

 Table 4

 Muscle and blubber components of the pilot whale body as percentages of total body weight.

January 1987, the dissected renal fat which was packed between and around the renculi, comprised 21–46% of the total weight of the kidneys. Table 5 shows the dissected weights of fats from these January-caught whales of 1987.

 Table 5

 Distribution of visceral fat within the pilot whale body as determined by dissection.

	Longth	Waight		Weight	t of visceral f	at type in kg	
Date	cm	kg	Renal	Cardiac	Thoracic	Abdominal	Total
22.01.87	441	1,022	1.36	0.35	no obs.	5.13	25.00
	Date 22.01.87 22.01.87	Date Length cm 22.01.87 441 22.01.87 545	Length Weight Date cm kg 22.01.87 441 1,022 22.01.87 545 1.755	Length Weight Date cm kg Renal 22.01.87 441 1,022 1.36 22.01.87 545 1.755 7.44	Length Weight Weight Date cm kg Renal Cardiac 22.01.87 441 1,022 1.36 0.35 22.01.87 545 1.755 7.44 1.29	Length Weight Weight<	Length DateWeight cmWeight kgWeight of visceral fat type in kg22.01.874411,0221.360.35no obs.5.1322.01.875451.7557.441.296.889.48

Seasonal patterns in percentage of total body wet weight devoted to blubber, muscle and viscera were similar in both juveniles and adults (sexes combined), with lower fat tissue weights in summer than in winter and spring (Fig. 3). The percentage of muscle appeared to remain fairly stable throughout the year. Although visceral tissues weighed more in winter and spring than in summer, the differences were small and probably a result of lower accuracy in weighing which was much more variable than in other tissues because of loss of parts. The general pattern is one of fattening in winter and spring. As no significant change in body weight associated with season was found, the observed seasonal differences in proportions of body weight devoted to various tissues must indicate a reduction or biochemical alteration in weight of other structures, for example weights may diminish through replacement of tissue water by lipid.

Girth and blubber thickness: effects of season and body length

Girth at any given length is greatest in spring and winter and least in summer (Fig. 4). Midgirths of juvenile males and females are similar and considerably smaller than adults. Adult males have the greatest girth at any given length of all reproductive classes. There appears to be no difference in mid-girth between adult females of differing reproductive status. It can be concluded that, despite differences between different classes in girth at a given length, all whales increase in girth seasonally. Mean mid-lateral blubber thickness is









Fig. 3(c). Seasonal changes in distribution of weight of body tissues for all whales.

greatest in spring and winter and least in summer (Fig. 5). The blubber in juveniles is relatively thinner than in adults, on a length basis. However, it increases markedly with length whereas the converse appears to be the case in adult females where the largest females have thinner blubber than the smallest. In adult bulls, blubber thickness remains stable regardless of size. In view of the relatively large muscle mass in adults (Table 4), where heat dissipation may be a problem with overly thick blubber providing too efficient an insulation, it is perhaps not surprising that blubber thickness does not increase with length. The surface area:body weight ratio is much less in adults than in juveniles. Blubber thickness may decrease with size increase in order to prevent overheating.



Fig. 5. Mean mid-lateral blubber thickness $(L_3+L_4+L_5)/3$ at length (L) by season for pilot whales.

The morphometric data described above demonstrate a pattern of seasonal changes, mainly in fat tissue, with increases during winter and spring. Measurable weight changes are not always apparent. Seasonal changes in tissue biochemistry and density (i.e. tissue volume and lipid content) may explain how these observed differences in body composition could occur without changing weight.



Fig. 6. Seasonal lipid content of blubber and visceral fat with attached 0.95 CI.



Fig. 7. Seasonal lipid content of muscle with attached 0.95 CI.



Fig. 8. Seasonal lipid content of visceral organs (liver, kidney and heart) with attached 0.95 CI.

Biochemical data

Lipid content of tissues

The lipid content of the blubber was similar in both the ventral and head regions (Fig. 6). A peak was present in December and a low in August in the ventral samples, although the 95% confidence intervals are wide (Fig. 6). No significant differences were found among reproductive classes (immature, mature, and for females – pregnant, lactating, pregnant+lactating, anoestrous). Blubber lipid content of British stranded pilot whales during January 1985 was 77.48+1.02%, very similar to that of the Faroese whales.

Visceral fat also shows a difference in lipid content between winter (high) and summer (low) although again the means fall within the 0.95 CI of each other (Fig. 6).

The lipid content of muscle increased dramatically during the winter months (Fig. 7), from about 2% in July to 40–50% in January, rather similar to the case of baleen whale muscle described by Lockyer (1987a; b). The overall seasonal pattern is similar to that of the fat tissues just described.

Some of the visceral organs also varied seasonally in lipid content (Fig. 8): in the kidneys it increased from about 5% during June and July, to about 35% in December to January; in the liver and heart it remained relatively stable with low levels of between 1.5% and 4.5% of tissue wet weight (although there was some hint of slight seasonal variation in the liver).



Fig. 9. Seasonal lipid content of bone, milk and sub-cutaneous fat with attached 0.95 CI.

Some values for other tissues collected opportunistically were obtained: bone had a high lipid content of about 15% wet weight tissue during late summer (Fig. 9); subcutaneous fat, present as a subdermal fat layer beneath the blubber only during winter, was also high in lipid at about 43% wet weight tissue (Fig. 9). The milk, like that of other cetaceans (e.g. Tomilin, 1946; Berzin, 1972; Lockyer, 1987a) was high in lipid at about 22% wet weight.

The lipid content of all foetal tissues tended to increase with size of foetus. The blubber lipid level increased steadily with growth and development of the foetus, measured in terms of length (Fig. 10) and weight (Fig. 11) until at birth, it was similar to that of a calf and adult, within the range 70–85% (see Fig. 6). Lipid content of muscle also increased with growth (Fig. 12). It reached about 6% by birth, and a level close to that of the adult in early winter; however, the values for the neonate (Fig. 12) appear to be highly variable. Lipid contents of foetal kidney, liver and heart varied in the ranges 0.4-2.3% and 0.3-3.1%, and *ca* 1.6% respectively, the higher levels usually being associated with older foetuses.

Some tissues show marked seasonal changes in tissue lipid content, notably muscle and kidney. The less pronounced seasonal variations in the blubber lipid, however, were





Fig. 12. Lipid content of foetal muscle with growth and development in terms of body length.

nevertheless consistent with the hypothesis of blubber being a dynamic fat store as discussed with respect to the morphometric analyses. Body weight is probably not a useful indicator of seasonal changes in body fat condition because increases in lipid levels reduce tissue density, so that weight does not vary even if tissue bulk alters. Thus girth, blubber thickness and biochemical analyses are better indicators of fat condition.

Protein residue in tissues

Protein residues averaged about 6% in blubber, 25% in muscle, 14–15% in kidney and 21% in liver. Protein residues were lower in early foetuses, but close to post-natal levels in near-term foetuses.

Energetics

This section attempts to explain the findings of the morphometric and biochemical analyses in terms of the overall energy budget of the animal. An obvious recurrent and apparently seasonal drain on energy reserves is that of reproduction.

Seasonal variations in carcase energy density

The morphometric data and biochemical analyses indicate seasonal variation in body fat condition, both with respect to actual tissue (blubber and fat tissue) and lipid content

(blubber and visceral fats, muscle and kidney). These findings are by no means novel. Müller (1882) stated that it was well known locally in the Faroes that whales were 'lean' in summer and 'fat' in winter.¹ Faroese waters form only a small part of the Atlantic Ocean, and the theory of seasonal fattening assumes that local whales follow similar behavioural patterns simultaneously. Despite the uncertainty, this assumption is not unreasonable given the reported seasonal correlations between whale fatness and local food supply. Precise levels of change cannot be given as the data are not for a single school year-round, but for different schools at different times of the year, but the analyses do support the view that seasonal fattening occurs, as it has reportedly done regularly each year, for several decades.

The relatively small change in the lipid content of the blubber, with either season or age, suggests that blubber does not function primarily as an energy store, but probably serves other functions of a thermoregulatory, buoyancy, physiological or structural nature. In this context it is significant that the blubber lipid content is similar from near-term foetus to adult. Perhaps of even more significance is the similarity in percentage body weight that blubber comprises in these groups. From the early stages of development, blubber has a well-defined higher protein-fibre matrix (6%) than muscle (<1%), suggesting some specialised function other than energy store.

Estimation of the energy reserves in the body requires calculation of tissue weight increases and lipid content changes. Muscle comprises about 22.5–30.5% body weight (most in adults) and blubber about 25% body weight. During winter, the muscle lipid increases to about 40–45% of wet weight of tissue, amounting to about 9.0–13.7% body weight of lipid. Around the viscera, there is an increase of about 1.5% body weight of fat, which at 75–80% lipid content, constitutes 1.2% body weight of lipid. The blubber weight increases comprise about 5–10% body weight, of which 70–85% is lipid. Overall this represents about 4–8% body weight of lipid, if lipid content of blubber is 80% or more. In total, such an energy reserve amounts to about 14.2–22.9% body weight of lipid. For an adult female of body weight 1,000kg, using a conversion of 9,450kCal.kg⁻¹ for lipid (Brody, 1968), this amounts to between 1.34–2.16x10⁶ kCal and, because of virtual depletion in summer, must be assumed to be associated with seasonal changes in prey availability.

The above analyses reveal that muscle provides the largest energy reserve. Pond and Mattacks (1987) proposed that lipid stores in muscle were used up before visceral deposits and other superficial fat reserves (e.g. blubber in whales), from an investigation of enzyme activity in fat cells in these locations. They proposed that muscle lipid provided a local source of energy for high energy-consuming locomotory muscles (e.g. tail muscles in whales). This is probably the case in the pilot whales, where the lipid level of muscle is already greatly depleted by April, although that of the blubber is almost intact.

Dietary energetics

The main and preferred diet of pilot whales is squid. Desportes *et al.* (1988) and Desportes and Mouritssen (1993) found that for Faroese whales examined during the study period, 77% of stomachs contained food, of which 91.7% contained squid, 24.7% fish and 12.9% shrimp. It is uncertain how frequently feeding takes place, but presumably feeding follows the diurnal migrations of the squid, and consumption would be maximal depending on

opportunity. A weak estimator of food intake has been given by Sergeant (1969) in a relationship where heart weight:body weight ratio approximates a tenth of the feeding rate. This formula has been widely used in the marine mammal literature and would indicate a daily consumption of about 40kg for a 1,000kg whale. However, more recently, Innes *et al.* (1986) have discredited this theory. Innes *et al.* (1987) estimate ingestion rate as an allometric function of body weight for cetaceans,

$$IB = 0.123 M^{0.80}, \tag{3}$$

where M=body weight in kg, and IB=ingestion rate in kg day⁻¹. The correlation coefficient, r^2 , was 0.85. From this, an adult 1,000kg whale would daily consume about 31kg food, rather less than the Sergeant estimate. Clarke *et al.* (1985) give an average calorific content of wet weight of *Todarodes sagittatus* tissue as 4.27kJ.g⁻¹(1.02kCal.g⁻¹). Thus the predicted daily intake for a 1,000kg adult whale amounts to 3.16x10⁴kCal. Annually this totals about 11.54x10⁶kCal from about 11.3 tonnes of squid.

Metabolic expenditure

Lavigne *et al.* (1986) have shown that observed metabolic rates for marine mammals do not differ from the known relationship between basal metabolic rate (Q) and body weight (M) for terrestrial mammals (Kleiber, 1975). This equation predicts

$$Q=70M^{0.75},$$
 (4)

where Q is in kCal.day⁻¹, and M is in kg. On this basis, Q for an adult 1,000kg whale would be 1.24×10^4 kCal.day⁻¹. The actual daily expenditure is likely to be at least 1.2-2 times more than this, at between $1.49-2.48 \times 10^4$ kCal.day⁻¹, for maintenance. Annually, at least $5.44-9.05 \times 10^6$ kCal would be utilised, and must be replaced by dietary energy.

Energy available for fat deposits

Assimilation efficiency of dietary energy is likely to be high (probably between 90–95%) for pilot whales, as it apparently is for other marine carnivores consuming fish and squid (Keiver *et al.*, 1984; Ronald *et al.*, 1984). At this efficiency level, dietary energy assimilated and available for satisfying energy demand would be approximately 2.84– $3.00x10^4$ kCal.day⁻¹ or 10.39–10.96x10⁶kCal.year⁻¹, using the energy consumption estimated above. Of this, 50–90% would be used for maintenance (see above) leaving a surplus of 1.34- $5.52x10^6$ kCal. The previously estimated energy credit (reserve) of 1.34– $2.16x10^6$ kCal or 12.9–19.7% of calculated annual assimilated energy should represent the balance between energy intake and metabolic expenditure. Without more data on actual metabolic expenditure and feeding rates, these estimates cannot be refined. It should be noted however that the estimates of the energy of fat storage and of that surplus to maintenance and metabolism are similar.

Energetics of reproduction

MALES

It appears that adult bulls are more mobile than females, are required to be more assertive and competetive in reproduction and not infrequently fight other males and become wounded (Bloch *et al.*, 1993a; Desportes *et al.*, 1993). The age distribution and sex ratio in schools (Kasuya and Marsh, 1984; Lockyer *et al.*, 1987; Martin *et al.*, 1987; Bloch, 1992; Bloch *et al.*, 1993b) indicate a high male mortality rate compared with females. This may in part be due to energy stresses related to male reproductive activity. This implies that the energy demands of reproduction for males are high. If breeding is energetically expensive for males, seasonal breeding (and here males are assumed to be active annually) would be energetically most efficient if commenced in late spring, when energy reserves are still high, at least in the blubber. Martin and Rothery (1993) showed that conception peaks in mid-July, although conceptions occur throughout neighbouring months, indicating that males must be active at this time. Desportes *et al.* (1993) found two peaks in male activity and the rapid body fat depletion in males during spring and summer, firstly in muscle fat and then in blubber, may be the result of such reproductive activities. By May (Fig. 7), muscle lipid is negligible. Percentage weight of blubber is down by July (Fig. 3) and blubber lipid reduced by August (Fig. 6). At this time, the breeding peak is past.

FEMALES

The female reproductive cycle appears broadly similar to that of the sperm whale (*Physeter macrocephalus*), (Best, 1968; 1973; 1974; Best *et al.*, 1984). Lockyer (1981) calculated the following energy budget for sperm whales, assuming a lactation period of 2 years after 14.5–15.5 months gestation. During the calf's first year, estimated net growth efficiency was *ca* 21% (*ca* 14% gross efficiency), and estimated ratio of growth energy: metabolic expenditure was *ca* 1:4. Estimated consumption by calves was *ca* 1% body weight per day of milk, at a milk energy density of $3.84 \times 10^3 \text{kCal.kg}^{-1}$. The cost of pregnancy to the mother amounted to a daily increase in food intake of 5–10% above consumption by non-pregnant females, depending on whether the female was physically mature or still growing. Milk production during lactation required an increase in daily food intake of 32–63% of non-lactating requirements, again dependent on the age of the female (energy drains were greater on still growing females due to energetics demands of growth). It was noted that differing feeding habits probably contributed to sexual segregation at certain times in the sperm whale, with females feeding more frequently and actively than males.

Energy cost of pregnancy

Pilot whale foetuses devote an estimated 1.43x10⁵kCal to growth in biomass from conception to birth (12 months). This estimate is derived from analysis of carcase composition (Table 4; Figs 10–12), assuming that birth weight is 75kg, and that energy densities of blubber, muscle and visceral organs approximate 6.95x10³kCal.kg⁻¹, 1.29x10³kCal.kg⁻¹ and 1.06x10³kCal.kg⁻¹ respectively. The energy densities have been calculated using the proximate lipid and protein residue analyses: blubber contains 70% lipid and 6% protein; muscle contains 5% lipid and 14.5% protein; visceral organs contain 2.5% lipid and 14.5% protein. The energy density of lipid and protein are 9.45Cal.g⁻¹ and 5.65Cal.g⁻¹ respectively (Brody, 1968). Proportional body weight of tissues comprise 22% blubber, 17.5% muscle, 14.5% viscera. Given the body composition described above, carcase energy density of pilot whale foetuses approximates 1.91x10³kCal.kg⁻¹. Total cost of pregnancy includes, in addition to growth biomass, the metabolic energy cost of growing both that biomass and the biomass of the placenta, estimated using the formula of Brody (1968):

$$Q_{\rm G} = 4400 M^{1.2},\tag{5}$$

where Q_G is 'heat of gestation' in kCal, and *M* is the foetal growth mass in kg. For the pilot whale this equals 7.83×10^5 kCal. The overall energy requirement of pregnancy is thus $(7.83+1.43) \times 10^5$ kCal = 9.26×10^5 kCal.

Energy cost of lactation

Lactational costs in the first two years can be estimated given certain assumptions. Faroese data indicate that the pilot whale calf grows from about 180cm and 75kg at birth to about

250cm and 195kg during the first year and 290cm and 285kg during the second year. Carcase energy density of calves is estimated to total 2.415x10³kCal.kg⁻¹ assuming body weight proportions are 23.5% for each of blubber and muscle, and about 9.5% for viscera. Lipid and protein contents of blubber, muscle and viscera are assumed to be 80% and 6%, 5% and 25%, and 2.5% and 17.5% of wet weight, respectively. Thus growth accumulates as 2.89x10⁵kCal during the first year, and as 2.17x10⁵kCal during the second year. The first year is probably the most energy-draining period for the mother, because the sole source of nourishment for the calf during most of this time is milk. If pilot whales are similar to sperm whales, after the first year milk becomes a nutritional supplement to ingested prey.

Metabolic requirements of calves can be calculated in the same way as for adult females, assuming an average body weight throughout the year of 135kg for the first year, and 240kg for the second year. In the first year these will be at least 1.2–2.0x10⁶kCal, and 1.85–3.1x10⁶kCal in the second year, allowing for maintenance. Total energy costs, including growth of 2.89x10⁵kCal and 2.17x10⁵kCal for first and second year calves respectively, metabolic expenditure as just calculated, plus an allowance for assimilation efficiencies of 95% (Lockyer, 1981), are thus 1.6–2.4x10⁶kCal and 2.2–3.5x10⁶kCal for first and second year calves, respectively.

Pilot whale milk is composed of 14.7–31% lipid, 60–75% water and 9–10.5% solids (mostly protein) giving an estimated energy density of 1.95–3.50x10³kCal.kg⁻¹, averaging 2.73x10³kCal.kg⁻¹. Assuming growth efficiencies are similar for pilot and sperm whale calves, average milk consumption, allowing for 95% assimilation efficiency, would gross 2.06x10⁶kCal in the first year or approximately 755kg milk (2.1kg.day⁻¹).

Assuming that the ratio of growth:metabolic expenditure for sperm whale calves (1:4), also applies to pilot whale calves, estimated values of annual metabolic energy expenditure for growth of pilot whale calves from birth through their first year ($1.2x10^{6}kCal$) is within the range of the first estimate above for yearlings, at the low end of the scale. Total estimated food energy requirement for these first year calves, using this

	Caloric int	ake in kCal.kg ⁻¹
Method	Year 1	Year 2
1. (Growth + Metabolism)	$1.6 - 2.4 \times 10^6$	2.2 - 3.5x10 ⁶
¹ Assimilation efficiency		
2. Growth	2.1x10 ⁶	No calculation
² Gross growth efficiency		
^{3.} Growth x 4	1.6x10 ⁶	No calculation
 Food ingestion at 0.01 x body weight in kg 	1.4x10 ⁶	2.4×10^{6}

Table 6

Annual caloric intake predicted for calves using different methods of estimation.

 1 0.95; 2 0.14; 3 Ratio of Growth:Metabolism = 1:4.

basis, including energy devoted to annual growth, metabolism and assimilation amounts to 1.6x10⁶kCal, also at the lower end of the range above.

If a 1% wet weight.day⁻¹ ingestion rate is used for the calf, as in the sperm whale, the milk energy consumed amounts to 1.4x10⁶kCal in the first year, and 2.4x10⁶kCal in the second (no adjustments have been made for solid food taken during the second year of suckling). Estimates of total energy costs from the above methods fall within a close range (Table 6), suggesting that they are probably reasonable until accurate field data can be acquired. Caloric intakes for first and second year calves are thus likely to be less than 2.4x10⁶kCal and 3.5x10⁶kCal respectively.

From this, and allowing for a mammary gland efficiency of milk production of 90% (Lockyer, 1987b), milk production will demand up to 2.67×10^6 kCal from the mother during the first year of the calf. It is difficult to assess the cost of suckling during the second year because the calf will probably be consuming squid in addition to milk. If only milk was taken, this would require 3.89×10^6 kCal. If half the calf's diet is squid or fish, then the demand on the mother will approximate 1.95×10^6 kCal, rather less than in the first year, which is probably more realistic. If energy costs of lactation are a problem for the female in the first year, any surplus energy in the second and in subsequent years may allow simultaneous lactation and pregnancy. This reproductive condition is in fact often observed in the Faroese catches (Martin and Rothery, 1993), with >38% of females still lactating when they become pregnant again and 7.7% of mature females simultaneously pregnant and lactating in the population.

A summary of the energy utilisation by an adult female pilot whale is presented in Fig. 13. The depletion of the energy store is depicted as part of reproductive costs. Lactational costs are shown in relation to energy consumption and utilisation by the calf in both the initial and subsequent year after birth. It seems clear that even with these approximations, the presence of an energy depot is of considerable importance to the reproductive cycle, and is probably underestimated because subcutaneous and bone lipid depots have not been included in calculations.

CONCLUSIONS

The energy reserve built up by spring in an adult female of body weight 1,000kg, has been estimated at 1.34-2.16x10⁶kCal. This is less than, but close to, the annual reproductive cost in terms of lactation as estimated above, and rather more than the estimated costs of pregnancy. Not all of the energy required for reproduction may come from these stored resources because the process is protracted and feeding occurs during the whole year, unlike the cyclical feeding and breeding pattern of baleen whales where stored energy is vital for reproductive success (Lockyer, 1981; 1984; 1987a; b). However, most pilot whale births off the Faroes appear to coincide with movement into the area for feeding, from August onwards, and with subsequent winter fattening. Lactational demands may thus be met initially by feeding in the fall and early winter, and later on in spring from reserves.

Very lean body condition in Faroese pilot whales appears at about the start of summer, after conception, and hence mating has taken place. The observed dramatic decrease in muscle lipid, and subsequently in blubber, may be related to reproductive demands, as has been speculated in the case of bulls which must be active in their quest for females. Both male and female pilot whales would thus be expected to be in their worst body condition by about July, the males having used their energy stores in mating activities, and the females in reproductive activities.



The need to store fat reserves seasonally for reproduction has been reported for many species of mammal, both terrestrial and marine. Examples include reindeer (caribou) Rangifer tarandus (Leader-Williams and Ricketts, 1981; Adamczewski et al., 1987), grey seals Halichoerus grypus (Anderson and Fedak, 1987) and fin whale Balaenoptera physalus (Lockyer, 1981; 1987a; b). Andersen and Harwood (1985) speculate that breeding behaviour can be affected by both energy reserves and terrain. Anderson and Fedak (1985) observed that body size was very important for successful breeding by males and that energy stresses incurred during the grey seal breeding season left males with a very depleted body condition. This situation may bear comparison with that in the pilot whale, where adult males may need to compete with other males for control of breeding favours in schools. Pond (1984) has suggested that energy storage is a mammalian strategy primarily evolved for reproduction, namely, for lactation. Such a strategy will help to free the female from excessive foraging activities at a time when the young require close supervision and regular food. Although it is not certain that the fat reserves in pilot whales are primarily for reproduction (energy reserves also increase in juveniles), the timing of reproductive events and distribution with food at certain times of year do indicate that this may be an important association.

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DDT and PCB Pollution in Blubber and Muscle of Long-Finned Pilot Whales from the Faroe Islands

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ABSTRACT

The blubber and muscle of 183 individuals pertaining to seven different schools of longfinned pilot whales from the Faroe Islands were analysed for organochlorine pollutants. Organochlorine levels in these schools were similar to those detected in conspecifics from other localities in the North Atlantic, and are at an intermediate level in the range for cetaceans inhabiting eastern North Atlantic waters. No significant differences in organochlorine blubber concentrations were found between sexually mature and immature males, but sexually mature females carried significantly lower concentrations than immature ones. Differences between sexes were only apparent in adults. Thus, concentrations in sexually immature males and females were not statistically different, but sexually mature males carried significantly higher organochlorine burdens than sexually mature females.

KEYWORDS: PILOT WHALES – LONG-FINNED; NORTH ATLANTIC; POLLUTION – ORGANOCHLORINE.

INTRODUCTION

Organochlorine compounds are a family of synthetic chemicals that have been widely used since the mid-1940s in agriculture as pesticides and in industry for a variety of applications. During the last 15 years there has been a dramatic decrease in the use of PCBs (polychlorinated biphenyls) and especially DDT (dichlorodiphenyl-trichloroethane) because these substances have been banned in developed countries. However, both compounds are still in use in many developing countries. The high stability and poor biodegradability of some of their forms have made them one of the most important groups of xenobiotic pollutants found in the tissues of wildlife. Organochlorines have been claimed to be responsible for several different alterations of mammal physiology, the most important of which are related to pathological changes in the reproductive system and cycle, almost invariably leading to depressed reproductive rates (e.g. Fuller and Hobson, 1986; Reijnders, 1986; Subramanian *et al.*, 1987).

Marine mammals accumulate organochlorines to a varying degree, depending on the particular ecological and physiological characteristics of each species. Small cetaceans, especially those of smaller body size feeding at the top levels of the trophic web, often carry extremely high levels of these xenobiotics. This is especially true for some highly persistent forms of DDT and for PCBs. Moreover, recent research has shown that the capacity of small cetaceans to metabolise even PCBs is extremely low as compared to that of birds and terrestrial mammals (Tanabe *et al.*, 1988).

The present paper reports the results from a survey of organochlorine compounds in blubber and muscle from long-finned pilot whales (*Globicephala melas*) caught off the Faroe Islands. Blubber and muscle were selected because they are expected to be the largest body compartments in terms of organochlorine storage, and also because they represent the bulk of products for human consumption extracted from pilot whales.

MATERIALS AND METHODS

The tissue samples for organochlorine analysis were collected from whales from seven schools caught during 1987. The overall sample totalled 183 pilot whales (26 males and 157 females). The higher representation of females is explained because females were surveyed in a parallel study on the pattern of variation of organochlorine levels between schools (Aguilar *et al.*, 1993) and considerably more effort was devoted to determine pollutants in this sex. Table 1 summarises the sex and length of the sampled animals by school.

Muscle and blubber samples were collected from animals captured at Miðvágur (2 August 1987) and Tórshavn (10 April 1987). For the remainder, only blubber was collected. The tissue samples, each weighing at least 10g, were taken from the dorsal region behind the dorsal fin, wrapped in aluminium foil and deep frozen until analysis.

In the laboratory, the tissue samples were ground with anhydrous sodium sulphate using a mortar and pestle. The mixture was extracted with n-hexane for four hours in a *Soxhlet* apparatus. The extract was then concentrated to 40ml, from which a 10ml subsample to determine tissue fat content was taken. An aliquot of the remaining extract containing 100mg of lipid was mixed with sulphuric acid for the clean-up, following the procedures described by Murphy (1972).

After centrifugation and phase separation, the lipid-free extract was concentrated to 1ml and injected into a *Perkin Elmer Sigma* 3B gas chromatograph (injector temperature: 250° C), equipped with an electron capture detector of 63 Ni (temperature: 350° C), and a *Perkin Elmer Sigma* 15 computing integer. For all the analysis, a fused-silica capillary column of 0.25mm internal diameter, 60m length, and a stationary phase SPB-1 with a film thickness of 0.25µm was used. Pure nitrogen at a flow rate of 1ml/min was used as the carrier gas.

The temperature was programmed according to the following sequence: injection at 40°C; oven steady for the first 2mins and then increased to 160°C at a rate of 25°C/min; oven steady for 1min and then increased to 250°C at a rate of 2°C/min; from this point until the end of the analytical run, the column remained isothermal at a temperature of 250°C.

Heptachlor was used as an internal standard to calibrate fluctuations in the operational conditions. The identity of the DDT group compounds was confirmed by an alkali conversion to their respective olefins and re-analysis by GLC. PCBs were identified and quantified by their peak characteristics and retention times in relation to a 1:1 standard mixture of Aroclors 1254 and 1260, and confirmed by their resistance to the chemical derivations detailed above.

Locality	Leynar	Tórshavn	Vagur	Leynar	Miðvágur	Vagur	Tórshavn
Date	23.0 3.87	10.04.87	16.05. 87	22.07.87	02.08.87	20.08.87	08.10.87
Mean bod	ly length						
Males	378	450	552	-	415	-	-
Females	364	416	-	435	415	383	381
Total	365	417	552	435	415	383	38 1
Sample si	ze						
Males	2	1	5	0	18	0	0
Females	32	45	0	8	25	23	24
Total	34	46	5	8	43	23	24

Table 1

Mean body length (in cm) of long-finned pilot whales and sample size for each school surveyed.

Eight replicates of samples fortified with standards gave the following percentages of recovery for the whole analytical process (mean \pm CV) : p, p' – DDE : 72.56% \pm 15.8; p, p' – TDE : 87.41% \pm 8.4; o, p' – DDT : 81.91% \pm 8.3; p, p' – DDT : 98.13% \pm 7.6; PCB : 90.97% \pm 8.0. Ten replicate chromatographic runs of a mixture of the DDT and PCB standards gave the following CVs in the quantification: p, p' – DDE : \pm 7.9%; p, p' – TDE : \pm 6.5%; o, p' – DDT : \pm 5.5%; p, p' – DDT : \pm 8.2%; PCBs (mean of the eight peaks commonly used in the quantification): \pm 8.7%.

Tissue organochlorine concentrations in this paper are expressed in parts per million (ppm) calculated on the basis of either the fresh weight of the tissue (fresh weight basis) or the weight of the extracted lipids (lipid basis). Total DDT (tDDT) levels are expressed as the sum of all DDT forms (p, p' – DDE, p, p' – DDT, o, p' – DDT and p, p' – TDE). The DDE percentage was calculated as p, p' – DDE * 100/tDDT.

The sexual maturity of the whales sampled was determined by gonadal examination. Females were considered sexually mature when at least one corpus was present in either of the two ovaries. Males were taken as sexually mature when spermatogenic activity was observed in the tubules.

RESULTS AND DISCUSSION

Differences between tissues

Table 2 details the mean DDT and PCB levels in the blubber and muscle of the pilot whales from which both tissues had been sampled. Because of the much higher lipid content of blubber, this tissue carries about 40–70 times more organochlorines than muscle when concentrations are expressed on a fresh weight basis. This is the result of the different biochemical composition of the two tissues and the high lipophilicity of organochlorine pollutants (Aguilar, 1985). Blubber is a much more lipid-rich tissue than muscle (Table 2) and thus, organochlorine compounds dissolve and accumulate at much higher levels in it. As expected, therefore, the pollutant levels of blubber and muscle are only of a similar order of magnitude when calculated on the basis of the lipid content of the tissue (lipid basis).

expressed	ու թթ	in on a m	lip	id conte	nt of the	tissue (l	ipid basis)).	ppm on		s of the
				Blu	ibber				Muscl	e	
			FV	WВ	LB			FV	VB	LB	
	N % lipid	tDDT	РСВ	tDDT	РСВ	% lipid	tDDT	PCB	tDDT	PCB	
Tórshavn	46	79.28	8.47	15.17	10.68	10.13	5.40	0.41	0.84	7.59	15.56
Migvágur	44	69.79	29.32	39 .90	42.01	57.17	0.54	0.15	0.43	27.78	79.63
Total	90	74.59	18.78	27.40	26.17	33.39	3.07	0.28	0.64	17.57	47.24

Table 2

Mean percentage lipid content and organochlorine concentrations in the muscle and blubber of pilot whales from the Tórshavn (10.04.1987) and Miðvágur (02.08.1987) schools. FWB: concentrations expressed in ppm on a fresh weight basis. LB: concentrations expressed in ppm on the basis of the lipid content of the tissue (lipid basis).

Comparison with other pilot whale populations

According to Bloch and Hoydal (1987), the blubber of four Faroese long-finned pilot whales analysed in 1974 contained a mean concentration of 42ppm of tDDT and 39ppm of

PCB. These values appear somewhat higher than the corresponding mean values for the overall population analysed in the present survey, although they fall within the ranges of variation observed. Given the small sample size of the Bloch and Hoydal survey, it is not possible to ascertain whether the difference between the means should be attributed to sampling heterogeneity or to variation with time in the pollutant load of the population. The body lengths of the whales they examined (mean length: 382cm) suggests that most were juveniles (see Table 3), which we have found carry high pollutant levels, typically in the 30–70ppm range.

Table	3
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Mean body length and organochlorine residue levels and associated standard deviations in the blubber of long-finned pilot whales from different reproductive categories. Levels are in parts per million (ppm) calculated on a lipid basis.

Reproductive category	N	Body length	tDDT	РСВ	Reproductive category	N	Body length	tDDT	РСВ
Immature females	44	304 ± 50	37.16 ±26.94	47.80 ±29.53	Immature males	15	362 ±68	49.14 ±32.49	61.39 ±27.30
Mature females	113	431 ±28	9.21 ±9.10	15.54 ±12.42	Mature males	11	546 ± 48	50.85 ±20.71	57.35 ±24.59



Fig. 1. Pollutant levels in the blubber of North Atlantic long-finned pilot whales. White bar: tDDT. Black bar: PCBs. Data from the present survey and from Holden (1975), Taruski et al. (1975), Alzieu and Duguy (1979) and Muir et al. (1988).

As can be seen in Fig. 1, tDDT and PCB levels in the blubber of long-finned pilot whales from the Faroes are relatively low when compared to those detected in the blubber of their conspecifics inhabiting most other regions in the North Atlantic. Especially noteworthy are the high concentrations found in long-finned pilot whales from Rhode Island and Maine on the coast of the United States (Taruski *et al.*, 1975) and in those from France (Alzieu and Duguy, 1979). The sole exceptions to this are the Canadian specimens, which carried consistently lower tDDT and PCB residue levels than those from the Faroes (Muir *et al.*, 1988).

The only information on organochlorine pollutant levels available from long-finned pilot whales other than from the North Atlantic, came from seven stranded individuals analysed in Tasmania in 1981–82 (Anonymous, 1983). No PCB levels were reported, but, blubber tDDT concentrations seemed to be extremely low (mean: 1ppm).

Organochlorine residue levels in the blubber of the congeneric short-finned pilot whale (*Globicephala macrorhynchus*), appeared to be high (tDDT: 83ppm, PCB: 11ppm) on the Pacific coast of the United States in 1974–76 (O'Shea *et al.*, 1980), but were significantly lower in the Antilles in 1972 (tDDT: 2ppm, PCB: 4–8ppm) (O'Shea *et al.*, 1980; Tanabe *et al.*, 1987).

Comparison with other cetaceans inhabiting the eastern North Atlantic

The organochlorine levels in the blubber of Faroese long-finned pilot whales are in the mid-range of those found in the same tissue of other cetacean species from neighbouring waters of the North Atlantic (Table 4, overleaf).

There are two reasons for this. First, organochlorine compounds tend to concentrate through the trophic web. Second, the accumulation of pollutants in tissues depends on the feeding rate of the species, which is roughly proportional to its metabolic rate and, therefore, inversely related to body size. Long-finned pilot whales feed mainly on cephalopods and benthic fish (Desportes, 1983; Desportes and Mouritsen, 1993), and are thus at an intermediate trophic level, while their body length (4.5m in adult females and 6m in adult males) is also intermediate for cetaceans.

It is because of these two factors that baleen whales such as fin (*Balaenoptera physalus*) and sei whales (*Balaenoptera borealis*), which are massive and feed mostly on planktonic crustaceans situated low in the food web, carry comparatively much lower concentrations of pollutants in their tissues (Borrell and Aguilar, 1987; Aguilar and Borrell, 1988). At the other end of the range, small odontocetes such as harbour porpoises (*Phocoena phocoena*), striped dolphins (*Stenella coeruleoalba*), bottlenose dolphins (*Tursiops truncatus*) and common dolphins (*Delphinus delphis*) typically feed at the highest trophic levels and carry much higher levels of tDDT and PCB than the long-finned pilot whales from the same region (Clausen and Andersen, 1988; Morris *et al.*, 1989; Granby and Kinze, 1991; Borrell and Aguilar, unpublished data).

Differences associated with sex and length of the whales

Pollutant concentrations are known to vary among schools and this is probably because they do not all feed on the same grounds (Aguilar *et al.*, 1993). This means that data from different schools cannot be pooled and because the sample size for each sex in any single school is too small, a proper search for age-related variation in pollutant concentrations could not be carried out. However, some indication of overall age trends can be obtained by comparing blubber concentrations of pollutants in juvenile (sexually immature) and adult (sexually mature) individuals for each sex.

Species	Area	Years	u	tDDT	PCB	References
Phocoena phocoena	Denmark	1986-88	27	14.94 (0.7-61.4)	32.75 (0.75-121)	Granby and Kinze, 1991
Phocoena phocoena	Denmark	1980-81	51	23.49 (1.4-180)	82.37 (3.75-340)	Clausen and Andersen, 1988
Phocoena phocoena	Wales	1988	4	13.40 (4-17.7)	55.60 (23.5-93)	Morris, et al., 1989
Tursiops truncatus	Wales	1988	1	150.00	290.00	Morris et al., 1989
Stenella coeruleoalba	Wales	1988	1	49.00	21.50	Morris et al., 1989
Stenella coeruleoalba	Southern Irish Sea	1984	7	17.09 (43.5-5.6)	21.43 (43.1-7.8)	Unpub. data Borrell & Aguilar
Stenella coeruleoalba	Gibraltar	1982	ę	63.01 (129.4-27.7)	43.49 (64.2-29.8)	Unpub. data Borrell & Aguilar
Delphinus delphis	Southern Irish Sea	1984	18	4.29 (10-0.4)	9.38 (31.8-1.2)	Unpub. data Borrell & Aguilar
Physeter macrocephalus	Iceland	1982	10	4.17 (5.6-3)	10.20 (6.2-3)	Unpub. data Borrell & Aguilar
Balaenoptera borealis	Iceland	1982-85	40	0.164 (0.67-0.02)	0.157 (0.44-0.032)	Borrell & Aguilar, 1987
Balaenoptera physalus	Spain	1982-84	172	0.70 (1.9-0.14)	0.87 (2.22-0.11)	Aguilar & Borrell, 1988
Lagenorhynchus acutus	Faroe Islands	1987	13	18.40 (32.3-0.8)	29.13 (47.4-2.5)	Unpub. data Borrell & Aguilar
Globicephala melas	Faroe Islands	1987-88	184	16.45 (123.7-0.5)	23.53 (123.4-1.7)	Present survey

Pollutant levels (fresh weight basis) in the blubber of eastern North Atlantic cetaceans (only during the 1980s).

Table 4

For most schools, the number of samples from males was so small that variation related to age could not be examined. The only school containing a relatively large number of males (n=18) was that at Miðvágur (2 August 1987); but observed differences between juveniles and adults were not statistically significant.

For females from all schools, however, a different trend emerged, with tDDT and PCB concentrations decreasing with age. Overall, blubber pollutant levels (lipid basis) were 2-3 times higher in sexually immature individuals than in sexually mature animals.

The differences in tDDT and PCB levels between immature males and immature females were not significant but, overall, adult males had higher pollutant levels than adult females.

This overall pattern of variation is consistent with that commonly found in the marine mammal species hitherto studied (Aguilar, 1987). Thus, in most cetacean species, organochlorine pollutant loads are very variable during the juvenile stages, but quite often decrease with age during the first years of life as a consequence of rapid tissue growth and subsequent dilution of pollutants. In males, this pattern reverses in the sub-adult stage and concentrations increase throughout life until reaching a plateau in old specimens. In females, however, pollutant concentrations usually decrease after reaching sexual maturity because of the appreciable quantities of lipophilic contaminants that are transferred to offspring during gestation and lactation. In the adult stage, these diverging trends produce substantially higher organochlorine tissue concentrations in males than in females.

The average DDE percentage for all the schools studied was 42.7%. This percentage is indicative of the degree of metabolisation of tDDT in a given environment and trophic level, and is somewhat lower than that expected for an odontocete according to the general time-dependent pattern of variation previously observed for North Atlantic marine mammals (Aguilar, 1984). The DDE percentage in blubber was significantly higher (p<0.001) in males (50.9%) than in females (41.4%). This is due to the fact that this index depends on the intensity of induction of the enzymatic systems responsible for the degradation of organochlorines (Borrell and Aguilar, 1987). Males carry overall higher tDDT levels than females, for which reason it is expected that their enzyme systems could be more intensively activated. Therefore, the rate of conversion of DDT to DDE in males would be higher overall, eventually resulting in higher DDE percentages.

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Heterogeneities in Organochlorine Profiles of Faroese Long-Finned Pilot Whales: Indication of Segregation Between Pods?

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ABSTRACT

Blubber samples from 114 female long-finned pilot whales belonging to five schools captured in the Faroe Islands during 1987 were analysed for organochlorines to determine differences in pollutant profiles. One pod could be statistically distinguished from the rest by its higher PCB and tDDT concentrations and another by its higher p, p'-DDE/tDDT ratio. These differences between pods are not related to geographical locality or date of sampling, nor dissimilarities in age composition, nutritive condition or reproductive status. Rather, they probably reflect the use of different food resources by pods. Although the heterogeneity observed in the pollutant profile of pods does not necessarily correspond to a heterogeneous genetic structure in the population, it suggests the existence of some segregation, either geographical, seasonal or behavioural, between two of the pilot whale schools studied and the remainder.

KEYWORDS: PILOT WHALES – LONG-FINNED; NORTH ATLANTIC; POLLUTION; BEHAVIOUR; SOCIAL; FEEDING; PREY.

INTRODUCTION

Recent research into the genetic composition of the long-finned pilot whales (*Globicephala melas*) exploited in the Faroe Islands indicated that the allele frequencies of some pods significantly differed from those of the others. The difference could not be attributed to variation in the capture location or to seasonal or yearly change in stock composition (Andersen, 1988; 1993). In a parallel survey of heavy metal contamination, some schools were also found to differ in levels of cadmium (Caurant *et al.*, 1993).

Amos *et al.* (1991) applied DNA fingerprinting techniques to Faroese long-finned pilot whales and found that, while males from different pods presented indistinguishable genetic patterns, indicative of a high level of male gene flow between pods, significant allelic biases occurred between adult females from different groups. This finding suggests that, while males freely move between pods, females do not, and probably form a tightly-knit matriline.

Organochlorines are synthetic chemicals that have become ubiquitous environmental pollutants in the last two decades. They are incorporated into the bodies of mammals mostly via food and reach fairly high concentrations in those species, such as pilot whales, which are medium-sized and feed at the top of the oceanic food webs. The composition, concentration and chemical profiles of organochlorines differ among water masses because of geographical variation in the timing and intensity of discharges into the environment, and these dissimilarities are reflected in the pollutant load of the animals which inhabit and feed in these water masses. This is a potential tool for discriminating among marine mammal populations that have an allopatric distribution during at least

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part of the year and for studying their home ranges and migration routes (Aguilar, 1987; 1988).

This study was carried out as a part of a general survey on the organochlorine pollutant load of long-finned pilot whales inhabiting the waters of the Faroe Islands. In order to understand better the composition of the stocks and the social structure of the species, we determined the existence of heterogeneities in organochlorine pollutant profiles in different schools of long-finned pilot whales caught off the Faroes. The comparison was restricted to females because they form the most stable segment within pods (see Discussion).

MATERIAL AND METHODS

Pollutant analysis

Blubber samples for organochlorine analysis were collected from 114 females from five schools (Table 1) caught in different localities in the Faroe Islands during 1987 (Fig. 1). The tissue samples were collected, preserved and analysed following the procedures and techniques detailed by Borrell and Aguilar (1993).

Body fat and tissue lipid content is known to vary seasonally in Faroese long-finned pilot whales (Lockyer, 1993). Because organochlorines are highly lipophilic compounds and are soluble in neutral fats (Aguilar, 1985), changes in body fat content may influence concentrations of pollutants expressed as a fraction of the wet weight of tissue. In order to avoid this problem, organochlorine concentrations in the present paper are expressed as parts per million (ppm) of the weight of total lipids extracted (lipid basis). This way of calculating concentrations should remove the effect of possible dilution or concentration of blubber organochlorine concentrations produced by seasonal changes in nutritive condition.

Total DDT (tDDT) levels were expressed as the sum of all the DDT forms (p, p'-DDE; p, p'-DDT; o, p'-DDT; and p, p'-TDE). PCB concentrations were calculated as the sum of all congeners detected, and quantified in relation to a 1:1 standard mixture of 1254 and 1260 Arochlors. The p, p'-DDE/tDDT ratio was calculated as p, p'-DDE*100/tDDT, and the tDDT/PCB ratio as tDDT*100/PCB.

Statistical analysis

Screening statistical analyses were performed on several different combinations of organochlorine pollutants and ratios. However, five variables were finally selected for the comparison between schools: tDDT, p, p'-DDE and PCB concentrations, and the p, p'-DDE/tDDT and tDDT/PCB ratios. These are the most meaningful variables for

				Mean				Age cla	isses	
Code	Locality	Date	N	age	SD	0-6	6-12	12-18	18-24	24-30
M	Mídvágur	02 August	20	15.5	7.7	4	3	3	7	3
L	Leynar	23 March	23	12.3	7.8	4	9	2	5	3
T1	Tórshavn	08 October	19	12.1	8.1	6	4	3	4	2
T2	Tórshavn	10 April	36	15.3	7.1	2	10	11	7	6
+V	Vágur	20 August	16	13.8	8.6	5	1	3	5	2

	lable	1	
Characteristics	of the	schools	sampled.

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Fig. 1. Location of capture of the five pilot whale pods studied.

describing organochlorine load profiles and are also thought to be the most useful for discriminating among groups of marine mammals that segregate geographically (Aguilar, 1987).

Because female mammals in each reproductive cycle transfer part of their organochlorine load to their offspring through lactation and pregnancy, age is an important factor determining an animal's tissue pollutant concentrations (Aguilar, 1987). Therefore, the sample used for this study contained only specimens aged 0–30 years in order to keep the age-distributions of schools within comparable ranges. Age distribution, mean ages and their associated standard deviations (SDs) for the schools surveyed are detailed in Table 1.

Age was also used as a covariate in all statistical analyses. However, preliminary screening showed that the relationship between age and organochlorine concentrations was not linear, so the pollutant concentrations and ratios used in subsequent analyses were

log-transformed (base 10) to linearise the relationship. This transformation also had the advantage of reducing skewness and contributing to homogeneity in variance among pods.

To test the hypothesis of equality of means of organochlorine concentrations or ratios between schools, a standard one-way analysis of variance taking age as a covariate was used (ANCOVA). The assumption of homogeneity of the slopes (Tabachnik and Fidell, 1983) between age and the variables examined in the different pods was also tested. In the cases where the omnibus hypothesis had been rejected, pairwise comparisons between all possible pairs of pods were carried out using the Bonferroni inequality to keep an overall alpha level of 0.05. Thus, we used the alpha/10 level in each comparison, a value which is clearly conservative because the 10 contrasts performed were not independent (Morrison, 1976). Assumptions of normality were checked using a Shapiro-Wilks test (Sprent, 1989) and those of homogeneity of variances between sample groups were verified by a BOX M test (Sokal and Rohlf, 1981). All statistical calculations were carried out using the SPSS-X statistical package (SPSS Inc, 1983).

RESULTS

Given the importance of age as a factor determining organochlorine concentrations, the age composition of pods was carefully screened in order to ensure that the results from different sample groups were comparable. The age compositions among pods were not statistically different (Kruskal-Wallis test, X=3.92, p>0.4) and thus can be considered fairly similar among the pods surveyed (Table 1).

Table 2 depicts statistics describing raw organochlorine pollutant concentrations in the blubber of females belonging to each pod, and Table 3 details the log-transformed values for the same variables and the ratios used. Differences in log tDDT, log p, p'-DDE, log PCB, log (p, p'-DDE/tDDT) and log (tDDT/PCB) between pods were tested with an ANCOVA. Except for the log tDDT and log p, p'-DDE in pod T2, the distributions of variables of the other pods were not significantly different from normality. The hypothesis of homogeneity of variances was not rejected in any of the cases. The assumption of homogeneity of the slopes between age and the different variables was accepted in all cases except for the p, p'-DDE/tDDT ratio, which in pod M appeared to be significantly higher.

The omnibus comparison test for the variables log tDDT and log p, p'-DDE rejected the hypothesis of equality between the pods surveyed (F=7.28, p<0.001 for tDDT and F=5.20, p<0.001 for log p, p'-DDE). From the adjusted means, it appears that the highest tDDT and p, p'-DDE concentrations were found in pod M and that the levels in the other pods followed the decreasing order T1 > L > V > T2, the three last pods exhibiting very similar loads of this pollutant (Table 3). The pairwise comparison tests showed that pod M carried significantly higher tDDT and p, p'-DDE blubber concentrations than the remainder. The difference in the adjusted means between pod T1 and L, V and T2 is significant for p, p'-DDE but not for tDDT, although the statistics in this latter case were near their critical value for rejection, and it is likely that the test failed in rejecting the hypothesis of equality of means because of the highly conservative method used to ensure the overall alpha level of 0.05.

Regarding log PCB concentrations, the analysis yielded a very similar result to that for tDDT. The hypothesis of equality in the omnibus comparison test was also rejected (F=11.56, p<0.001); pod M had the highest residue levels, followed by pod T1, and then pods T2, V and L (Table 3). However, the results of the comparison tests indicate that differences among pods in PCB loads were smaller than for tDDT. Only pod M proved to carry significantly higher PCB concentrations than pods T1, T2, V and L.

The ratio log (tDDT/PCB) did not appear to differ among pods. The differences existing between the adjusted means are much smaller than in previous cases (Table 3), and as a consequence of this, the omnibus test performed through the ANCOVA did not show a significant pod effect (F=1.92, p>0.1).

The ratio log p, p'-DDE/tDDT yielded quite different results from the variables previously tested. Because of the different slope of pod M, this variable could only be compared among the other pods. Table 3 shows that the highest mean value for this ratio was for pod T1, followed by L, V and T2, an order which is also retained in the means adjusted by age. The ANCOVA reveals a clear pod effect for this variable (F=14.32, p<0.001) and the comparison between pairs of pods yielded results consistent with the differences observed in the analyses of the tDDT and p, p'-DDE loads. Thus, pod T1 showed significantly higher values than the other pods.

In conclusion, pods M and T1 could be clearly distinguished from each other and from the rest, whereas pods L, T2 and V were more similar in organochlorine loads.

DISCUSSION

The studies by Andersen (1988; 1993) and Amos *et al.* (1991) on the genetic and social structure of the long-finned pilot whales caught by the Faroese fishery have suggested that, while fathers do not stay in a pod for a long time but move frequently between different pods, adult females remain most of their lives in the same pod and, indeed, form its core and give it cohesiveness and stability. It is for this reason that we only analysed organochlorine loads in females and, of course, it should be remembered that the conclusions from this study should be applied only to this sex.

The relationship between age and the log (p, p'-DDE/tDDT) and log(tDDT/PCB) ratios is weaker than for the absolute concentrations, a fact that is borne out by the great similarity existing between the observed and the adjusted means of these ratios for each

	calculate	ed on a lipid basis.	
	DDE	tDDTs	PCBs
School	Mean SD	Mean SD	Mean SD
	(lowest - highest)	(lowest - highest)	(lowest - highest)
М	10.5 12.2	24.2 23.0	40.7 29.6
	(1.2 - 47.7)	(4.1 - 82.0)	(10.7 - 103.1)
L	7.6 8.9	14.9 15.2	21.6 15.8
	(2.5 - 66.9)	(2.5 - 66.9)	(5.0 - 72.3)
T 1	10.9 9.6	20.4 16.5	28.3 17.2
	(1.5 - 35.2)	(3.8 - 58.4)	(7.7 - 65.1)
T2	4.9 5.5	11.2 10.9	20.2 16.1
	(0.8 - 20.8)	(2.5 - 41.0)	(6.1 - 79.2)
V	6.8 8.7	15.1 18.1	23.0 21.0
	(0.8 - 32.7)	(2.1 - 67.3)	(6.8 - 77.0)
Overall	7.7 9.0	16.3 16.7	25.8 20.9
	(0.8 - 47.7)	(2.1 - 82.0)	(5.0 - 103.1)

Mean, associated standard deviation (SD) and ranges for the organochlorine pollutant loads detected in the blubber of females from the schools studied. All concentrations are expressed in ppm

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Mean for the log-transformation (base 10) of organochlorine pollutant loads in the blubber of females from the schools studied, associated standard error of the nean (in parentheses), and adjusted means obtained from the ANCOVA (Adj. Mean).	
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	Lo	g DDE	Log	t tDDTs	r	og PCBs	Log(tDI)Ts/PCBs)%	Log(DD	E/tDDTs)%
Pod	Mean	Adj. Mean	Mean	Adj. Mean	Mean	Adj. Mean	Mean	Adj. Mean	Mean	Adj. Mean
×	0.76 (0.11)	0.836	1.20 (0.09)	1.270	1.50 (0.07)	1.552	1.70 (0.03)	1.718	1.56 (0.02)	
L	0.64 (0.10)	0.572	0.99 (0.08)	0.932	1.24 (0.06)	1.196	1.75 (0.03)	1.736	1.65 (0.01)	1.644
Tı	0.85 (0.10)	0.777	1.16 (0.09)	1.089	1.37 (0.06)	1.325	1.78 (0.03)	1.764	1.70 (0.01)	1.692
2T	0.46 (0.07)	0.528	0.88 (0.06)	0.942	1.20 (0.05)	1.249	1.68 (0.02)	1.692	1.58 (0.01)	1.587
^	0.55 (0.13)	0.546	0.93 (0.12)	0.928	1.22 (0.09)	1.218	1.71 (0.03)	1.710	1.62 (0.01)	1.619
IIA	0.63 (0.04)		1.01 (0.04)		1.29 (0.03)		1.72 (0.01)		1.61 (0.01)	

pod. Ratios are less affected by age, and they are potentially more reliable than absolute concentrations when the age composition of samples to be compared is unknown or is known to be heterogeneous (Aguilar, 1987).

The results clearly indicate substantial differences in the profile of organochlorine contamination between some of the pods. The pollutant load (both for p, p'-DDE, tDDT and PCB) was significantly higher in pod M than in the remainder, although pod T1 appeared to average slightly higher concentrations than pods L, T2 and V. This effect seems not to be caused by any intrinsic factor of pod M, such as age composition, nutritive condition or reproductive status and suggests that pilot whales from this pod had been feeding on a prey that was substantially more contaminated by organochlorines than individuals belonging to other pods.

Moreover, specimens from pod T1 stood out by their characteristic p, p'-DDE/tDDT ratios which were significantly higher than those corresponding to individuals from the other pods. This difference may reflect dissimilarities in the pollutant content of the prey consumed by each pod. However, high tDDT tissue levels are known to induce enzyme liver activity, which in turn produces an increase in the p, p'-DDE/tDDT ratio (Borrell and Aguilar, 1987) and, for this reason, the difference in this ratio may be indeed the consequence of the high tDDT concentrations detected in pod T1.

Overall, the differences in pollutant loads observed among the various pods can be attributed to several factors: (i) differences in the 'age' of the organochlorines present in the ecosystem inhabited by the prey; (ii) differences in the distances from the prey line to the main source of pollution; and (iii) differences in the trophic levels of the prey eaten by the various pods (Aguilar, 1984; 1987).

Reasons (i) and (ii) both imply that in the past the geographical range of pod T1 was different to that of the other pods. Reason (iii) may be explained by differences in feeding behaviour but, since the composition of the various pods is similar in age, reproductive condition and other biological variables, the most likely reason is the different availability of food resources to pod T1, which in turn would again imply an allopatric distribution between this pod and the others studied.

Pollutant concentrations in the blubber of marine mammals do not fluctuate readily following changes in pollutant intake (Aguilar, 1984; 1987). The overall results obtained from the ANCOVA suggest that pods M and T1 had been feeding in the past in grounds that were located geographically distant from each other and from those where pods L, T2 and V fed. These three latter pods do not necessarily need to have consumed their prey in the same area but in areas where organochlorine pollution was qualitatively and quantitatively similar.

Examination of geographical locality and date at which the pods had been captured does not solve this question. Pods M and T1 were driven to Miðvágur and Tórshavn, two harbours in the central region of the Islands and very close to where pods L and T2 were caught. Indeed, these four pods were captured within a 10 n.mile range. Pod V, the only pod caught far from the others, in fact had a pollutant profile that was almost identical to that of pods L and T2. The pods sampled were more or less evenly distributed across the year and the two that had differences in their organochlorine loads, M and T1, were not caught at the same period. In fact, pods M and V, the two that showed the most dissimilar pollutant loads of the range, were caught within 18 days of each other (Table 1).

Differences in pollutant loads between two groups of wild mammals can only appear when their home ranges are allopatric over a significant portion of their life cycle, a circumstance that is also likely to result in a reduced gene flow between them. In an electrophoretic survey of Faroese pilot whales, Andersen (1988; 1993) found that the pod isozyme composition did not vary geographically or seasonally, but observed that pod T1 had a significantly different electrophoretic profile from pods M, T2, L and V. She considered this difference to be a result of pilot whale social behaviour, with schools organised along strong matrilineal lines. However, the coincidence of her study and ours in considering T1 as a 'distinct' pod strongly suggests the existence of some segregation, either geographical, seasonal or behavioural, between this and the other schools studied. By contrast, the genetic survey found no apparent differences between pod M and the others (Andersen, 1993).

Julsham *et al.* (1987) put forward the hypothesis that more than one population occupies Faroese waters, a possibility that was not supported by Andersen's (1993) study. Our results are inconclusive in this respect because heterogeneities in pollutants profile do not necessarily correspond to heterogeneities in genetic structure.

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Factors Influencing the Accumulation of Metals in Pilot Whales (*Globicephala melas*) off the Faroe Islands

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ABSTRACT

This study of the ecotoxicology of trace elements is part of a comprehensive investigation of the biology of the long-finned pilot whales (Globicephala melas) caught in the drive fishery of the Faroe Islands. Arsenic, copper, selenium, zinc, cadmium and mercury were analysed in some 131 individuals from five schools. Levels in the liver (in which bioaccumulation occurs to a large extent) were analysed for each school; levels in muscle and kidney tissues were analysed for two schools. The concentrations of trace elements were determined in each organ, and the influence of different factors on their bioaccumulation (such as body length, age, sex, reproductive status of the females and the school of origin) was studied. The trace elements tend to concentrate in the liver, the centre of numerous metabolic processes. Mercury and cadmium were always significantly correlated to the age of the individuals. Zinc showed very high levels in the liver of young individuals but was regulated in adult liver. The relationships of zinc in the kidney and copper in the liver, with age or body length vary according to the school. In one school, the zinc concentrations increased with age/length which suggests that homeostasis is altered. Intraorganic correlations such as Hg-Se and Cd-Zn or Cd-Cu would reflect certain detoxification mechanisms. Compared with other marine mammals from the North Atlantic, levels of cadmium in pilot whales were high, but varied from one school to another. This may reflect the existence of at least two subpopulations of Faroese pilot whales. Cadmium concentrations in the liver of the lactating females were significantly lower than in other adult females. Cadmium concentrations in the milk differed by school, thus the exposure of suckling calves to this toxic metal also varies. Levels of mercury and cadmium were detected in the liver of foetuses showing that a transplacental transfer of these elements occurs.

KEYWORDS: PILOT WHALES–LONG-FINNED; NORTH ATLANTIC; POLLUTION-HEAVY METALS; PHYSIOLOGY.

INTRODUCTION

Cadmium and mercury are generally considered to be the heavy metals most likely to give rise to pollution problems in marine ecosystems (Bryan, 1984). Since marine mammals are relatively long-lived species and occupy the higher trophic levels, they would be expected to accumulate relatively high levels of metals; 'natural' levels of these metals are unknown for marine mammals. The range of concentrations may vary greatly among species without it always being possible to attribute high levels to environmental pollution problems. Most previous studies of the bioaccumulation of heavy metals in marine mammals have involved small sample sizes. The programme of research on the pilot whale fishery in the Faroe Islands (Bloch *et al.*, 1993a) allowed us to obtain sufficient samples to statistically evaluate trends in the distribution and concentration of the toxic elements (mercury and cadmium) and the essential elements (arsenic, copper, selenium and zinc) and to examine the main factors influencing their accumulation in the pilot whale.

MATERIAL AND METHODS

Sampling and chemical analysis

Tissue samples for trace element analysis were collected from different tissues for whales from five schools caught in the drive fishery of the Faroe Islands (Table 1). Sampling procedures in the field are described by Bloch *et al.* (1993a).

Arsenic (As), cadmium (Cd), copper (Cu), mercury (Hg), selenium (Se) and zinc (Zn) concentrations were determined from fresh tissue (2g for liver, mammary gland and kidney; 4g for muscle) digested in suprapure nitric acid. Urine and milk samples were directly analysed, although insufficient milk was available to determine Hg and Se concentrations. Cu and Zn in all samples and Cd in kidney and liver were determined by Flame Atomic Absorption Spectrophotometry (AAS) using the Zeeman effect correction. Cd in muscle, mammary gland tissue, milk and urine, and As and Se in all the tissue samples, were determined by graphite furnace AAS using the Zeeman effect correction as described by Amiard *et al.* (1987). Total mercury was analysed by Cold Vapour AAS as described by Boiteau and Pineau (1988).

Standards from NRC Canada (Lobster hepatopancreas TORT1, dogfish liver DOLT1 and dogfish muscle DORT1) were carried through the procedure in the same way as the samples. Measurement methods for As, Cu, Se and Zn were validated by International Intercalibration Exercises (IAEA, 1987; 1988). Our laboratory is also involved in international interlaboratory comparisons organised by the Centre de Toxicologie du Quebec.

Statistical analysis

Each individual or school can be represented by the six determined parameters (As, Cu, Zn, Se, Cd and Hg concentrations). However, as it is difficult to visually represent more than three parameters graphically, we have chosen to employ factorial principal component analysis (Morrison, 1976).

The metabolism of certain trace elements is known to vary with age in marine mammals and thus the comparison of mean levels in schools or groups of individuals can only be carried out if the age structures of the sub-samples are comparable statistically. Similarly, as a complete range of tissues could not always be obtained for each individual, the study of accumulation for the different organs required different groups to be established. Again, comparison requires there to be no significant difference in the age structure of

Information	n on the	sampled s	schools:	milk w	as obtained	from th	e mammary	/ gland	ls and sa	mples	were
discarded i	f visibl	y contami	inated w	ith bloc	od. Key:	IMM,	immature;	MM,	mature	male;	MF,
		matu	re femal	e; and T	OT, total.	* Uncer	rtain maturi	ty.			

			Number of whale analysed					
No.	Location	Date	IMM	MM	MF	TOT	Tissue analysed	
5	Øravik	15.09.86	31	3	18	52	Liver, muscle, kidney, milk	
16	Torshavn	23.12.86	0	0	6	6	Liver	
22	Torshavn	10.04.87	0	1 *	10	11	Liver	
25	Leynar	22.07.87	5	0	17	22	Liver, milk	
33	Torshavn	08.10.87	16	3	21	40	Liver, muscle, kidney, mammary gland, milk	

these groups. The non-parametric Mann-Whitney test (Zar, 1984) was used. Age data were obtained as described in Lockyer (1993) and Bloch *et al.* (1993b).

RESULTS

Levels of bioaccumulation and organotropism

Table 2 provides the mean levels of trace elements in liver, kidney and muscle of each school.

In all organs, As concentrations were similar and very low compared to other trace elements.

Concentrations of Hg and Cd varied among organs. Cd was stored primarily in the kidney (highest mean $93\mu g/g$ wet weight, school 5) followed by the liver (highest mean $41\mu g/g$ in the same school). In the muscle, Cd concentrations were up to one hundred times lower. Total Hg concentrated mostly in the liver (highest mean $84\mu g/g$ in school 33); kidney and muscle concentrations were markedly lower (mean of 4.9 and 1.4 $\mu g/g$ respectively in the same school). The pattern for Se levels in the three organs was similar to that for Hg. Zn concentrations were the highest in the liver (highest mean $87\mu g/g$, school 5) followed by the kidney ($37\mu g/g$) and muscle ($27\mu g/g$). Cu levels were similar in the liver and kidney (5.97 and $4.75\mu g/g$ respectively, school 5) and lower in the muscle ($0.86\mu g/g$, school 5). Within schools, the range of Hg concentrations in the liver and the range of Cd concentrations in the liver and kidney were very high (from $0.73 - 557\mu g$ Hg/g in school 33; from $1.4 - 158\mu g$ Cd/g and from $0.07 - 94\mu g$ Cd/g respectively in the kidney and the liver of the individuals of school 5).

In the liver, mean levels of Cd, Hg and Zn varied among schools. A difference was also clear in the kidney for Cd between school 33 and school 5 (55.3 and 93.1 μ g/g respectively).

School		As	Cd	Cu	Hg	Se	Zn
Liver							
33(n=40)	Mean	0.43	33.3	5.95	84.1	22.5	54.3
. ,	SD	0.13	18.5	1.69	92 .0	23.7	08.6
5(n=52)	Mean	0.55	41.1	5.97	56.0	19.7	87.3
	SD	0.23	31.7	1.87	82.7	25.1	34.1
25(n=19)	Mean	0.46	56.8	4.85	61.9	16.5	78.4
(/	SD	0.19	28.6	1.23	5 6. 8	14.6	14.7
22(n = 11)	Mean	0.20	79.6	5.60	52.1	13.6	75.8
22(II 11)	SD	0.12	28.6	0.93	37.7	08.9	15.7
Kidney							
33(n=31)	Mean	0.18	55.3	3.81	4.91	3.07	34.7
	SD	0.06	19.9	1.02	3.81	1.06	4.40
5(n=23)	Mean	0.37	93.1	4.75	5.70	4.53	36.6
5(m 25)	SD	0.19	44.5	0.90	3.78	1.61	5.30
Muscle							
33(n=31)	Mean	0.28	0.14	0.67	1.35	0.57	25.3
00(II)	SD	0.11	0.14	0.16	1.78	0.40	4.12
5(n = 50)	Mean	0.26	0.10	0.86	0.41	0.63	27.4
J(11- 50)	SD	0.18	0.07	0.24	0.35	0.23	12.8

Mean and standard deviation (SD) of arsenic, cadmium, copper, mercury, selenium and zinc concentrations ($\mu g/g$ wet weight) in pilot whales off the Faroe Islands (n = number of individuals).

In order to best understand the individual variations of metal concentrations (As, Cd, Cu, Se, Hg, Zn) in the liver, a principal components analysis (PCA) was performed among schools for the 66 mature females for which the age was known (Table 3).

Fig. 1 represents the position of the mature females in the first principal plane 1–2, and the projection of the associated axis. This first plane explained 72% of the total variation with respectively 40% for the first axis and 32% for the second. Hg, Se and Cu were correlated with the first axis (r=0.82, p<0.1%, r=0.92, p<0.1%; r=0.93, p<0.1%). [Arsenic, correlated with the third axis, is not represented in this plane.] Age, a supplementary variable, was correlated with the first axis (r=0.58, p<0.1%), and so with Hg, Se and Cu but not with Cd and Zn. The mature females of school 33 are quite well differentiated from others with lower levels of Cd and Zn. The difference in Cd concentrations between schools 33 and 5 was highly significant (Mann-Whitney: z=4.38, p<0.01%). For the same individuals, using the same test, the difference between the ages was not significant and was not responsible for the intergroup differences.

The mature females of schools 5 and 33 showed the highest Hg concentrations in the liver. Significant differences between Hg concentrations in this organ were only found between schools 5 and 22 (z=2.7, p<1%) and between schools 33 and 22 (z=2.58, p<1%). School 22, with the lowest concentrations, also had a lower mean age for females (15) than the other schools (19). This suggests that age is the main factor influencing Hg bioaccumulation.

Correlations

In all the PCAs performed with trace element concentrations, the third principal axis represented less than 15% of the total variation. The element As was always correlated with this axis, and thus never with the other elements, suggesting that its metabolism is independent of the others or at least follows different metabolic pathways.

Tables 4–6 show the correlation matrix of concentrations in liver, kidney and muscle for the two largest schools (5 and 33).

Bioaccumulation with age and length

ARSENIC

No relation between As content and age could be deduced from the data.

Mean and (standard deviation) of age (in years), cadmium, copper, mercury, selenium and zinc concentrations in liver tissue of mature females of the pilot whales off the Faroe Islands from five different schools (n=number of individuals). ($\mu g/g$ wet weight).

School	Age	Cd	Cu	Hg	Se	Zn
5(n=14)	19.3	75.5	7.52	143.2	49.2	78.7
- ((10.1)	(10.8)	(1.72)	(109.4)	(28.0)	(10.1)
22(n=10)	15.5	73.1	5.59	53.4	13.6	75.2
	(6.1)	(19.6)	(0.97)	(39.5)	(9.3)	(16.4)
25(n=14)	19.3	70.4	5.25	` 79.7 [´]	20.3	82.9
· · ·	(9.8)	(23.4)	(1.16)	(53.9)	(16.4)	(15.3)
33(n=22)	19.7	45.5	6.92	Ì 51 .7	34.9	55.6
	(10.3)	(15.2)	(1.56)	(140.0)	(24.9)	(7.6)
16(n=6)	22.9	100.3	6.92	113.2	29.7	94.0
	(13.2)	(39.4)	(1.82)	(81.7)	(20.0)	(27.6)



Fig. 1. Representation of the principal components analysis: distribution in the principal plane 1–2 of the mature females of the five different schools of pilot whales off the Faroe Islands, with the projection of the five associated variables axis– Cu, Se, Hg, Cd and Zn concentrations in the liver tissue. The age is plotted as a supplementary variable. The first principal axis determined by Cu, Se and Hg represents 40% of the total variation. The second principal axis determined by Cd and Zn represents 32% of the total variation. ■: school XXXI, □: school V, +: school XXII, ○: school XXV, ●: school XVI.

Correlation matrix of metals versus metals, length versus metals in school 5, age versus metals in school 33, in the liver tissue of the pilot whales off the Faroe Islands. Level of significance = 1% at least (n = number of individuals).

		Cd	Cu	Hg	Se	Zn	Length	
	Cd	-	0.44	0.59	0.68	-0.42	0.84	
School	Cu	0.91		0.42	0.55	0.38	-	School
33	Hg	0.59	0.61	-	0.88	-	0.58	5
	Se	0.74	0.70	0.92			0.70	n = 52
n = 40	Zn	0.42	0.50	-	-		-0.52	
	Age	0.59	0.63	0.76	0.81	-		

CADMIUM, MERCURY AND SELENIUM

Because it was not possible to determine the age of many individuals in school 5, only correlations between trace elements and length could be studied. In the liver, Cd, Hg and Se were correlated with age and length (Table 4). Fig. 2 represents the first principal plane 1–2 and the associated axes (Cd, Cu, Hg, Se, Zn in the liver and length) of the PCA performed with the 52 individuals of school 5. Length was treated as a supplementary

Correlation matrix of metals versus metals, length versus metals in school 5, age versus metals in school 33, in the kidney tissue of the pilot whales off the Faroe Islands. Level of significance = 1% at least (except * = 5%) (n = number of individuals).

		Cd	Cu	Hg	Se	Zn	Length	
	Cd	-	0.58	0.86	0.68	0.82	0.81	
School	Cu	-	-	0.74	0.71	0.75	-	School
33	Hg	0.64	-	-	0.85	0.81	0.67	5
	Se	0.48	-	0.66	-	0.78	0.54	
n = 31	Zn	0.79	-	-	-	-	0.53	n=23
	Age	0.40*	-	0.64	0.67	-	-	

Table 6

Correlation matrix of metals versus metals, length versus metals in school 5, age versus metals in school 33, in the muscle tissue of the pilot whales off the Faroe Islands. Level of significance = 1% at least (n = number of individuals).

		Cđ	Cu	Hg	Se	Zn	Length	
	Cd	_	-	0.66	-0.31	_	0.75	
School	Cu	-	-	-	-	-0.50	-0.59	School
33	Hg	0.73	-		-	-	-0.59	5
	Se	0.76	-	0.89	-	-	-0.39	
n=31	Zn	-	0.50	-	-	-	0.41	n=50
	Age	0.70	-	0.71	0.66	-	-	

variable in order to consider its influence without making it redundant. The sex and the maturity of each individual is shown, as is age, when known. The first plane explained 74% of the total variation with 48% for the first axis and 26% for the second one, respectively. Hg, Se, Cd and length were correlated with the first axis (r=0.89, p<0.1%; r=0.95, p<0.1%; r=0.83, p<0.1%; r=0.77, p<0.1%). The immature individuals are all situated on the side of the plane which represents low Hg, Se and Cd concentrations whereas the adult whales are distributed along the first axis according to their age. A similar pattern was found for the kidney and the muscle, except that Se and Hg in the muscle was negatively correlated with length for school 5 (Fig. 2, Table 6).

COPPER AND ZINC

The apparent relationship of Cu and Zn with growth parameters varied by organ and school. In school 33, Zn concentrations in the liver did not increase with age or length, whereas in school 5 a negative correlation was found for the liver (Table 4). This was the result of very high Zn levels (up to about $250\mu g/g$) in some small individuals (length < 250cm). Zn concentrations decreased rapidly after 250cm and were not correlated with length (Jean-Caurant, 1987). In school 33, with no individuals <250cm, Zn levels in the liver were lower and not correlated with length. In the kidney and the muscle, Zn concentrations increased with length in school 5, but not in school 33 (Tables 5 and 6). The presence of individuals <250cm hides the correlation between Cu concentrations in the liver and length; in 150–250cm individuals, Cu concentrations decreased from 9.5 to $4\mu g/g$; beyond 250cm, Cu increased with length as in school 33.



Fig. 2. Representation of the principal components analysis: distribution in the principal plane 1-2 of the 52 individuals, belonging to school 5, with the projection of the five associated variables axis- Cu, Zn, Se, Hg and Cd concentrations in the liver tissue. Length is plotted as a supplementary variable. The first principal axis determined by Se, Hg and Cd represents 48% of the total variation. The second principal axis determined by Cu and Zn represents 26% of the total variation. Where known, the age of the individuals is plotted. O: immatures, ●: immatures with milk, +: mature males, □: resting females, ⊠: pregnant females, ■: pregnant and lactating females, [3]: lactating females.

Intraorganic correlations

LIVER (TABLE 4)

In schools 5 and 33 the following correlations were found: Cd-Cu, Cd-Hg, Cd-Se, Cd-Zn, Cu-Hg, Cu-Se, Cu-Zn and Hg-Se. Hg-Se in both schools (33: r=0.92, p<0.1%; 5: r=0.88, p<0.1%) and Cd-Cu in school 33 (r=0.91, p<0.1%) showed the highest correlations. The young individuals in school 5 led to the negative correlation between Cd and Zn (r=-0.42, p<1%) and decreased the correlation coefficient between Cd and Cu (r=0.91, p<0.1% in school 33; r=0.44, p<1% in school 5). Excluding these individuals gave a positive correlation between Cd and Zn in school 5 (Jean-Caurant, 1987).

KIDNEY (TABLE 5)

In school 5, all the elements were highly correlated with each other, especially Cd and Hg, Cd and Zn, Hg and Se, Hg and Zn. In school 33 however although correlations existed between Cd and Hg, Cd and Se, Cd and Zn and Hg and Se, Cu was not correlated with any other element.

MUSCLE (TABLE 6)

In both schools, Cd and Hg, Cd and Se, and Cu and Zn were correlated. The correlations for Cd-Se and Cu-Zn in school 5 were again due to the very young individuals. Hg and Se were correlated in school 33 but not in school 5.

Inter-organ correlations

Fig. 3 shows the correlations between the organs for each element in schools 5 and 33. The patterns for each element differed between schools except for Zn concentrations where no correlation was found between the three organs in either school.

Cu concentrations were correlated between kidney and liver in school 5 but not in school 33.

For Hg and Se, the correlations varied between and within the two schools. Hg concentrations in the kidney were correlated with those in the muscle and the liver for school 5, whereas in school 33, the Hg concentrations in the liver were correlated to the kidney and the muscle. In school 33, all the organs were correlated for Se concentrations, whereas in school 5, only the liver and kidney were correlated.



Fig. 3. Correlations of metal concentrations (Cd, Hg, Sc, Cu and Zn) between liver (L), muscle (M) and kidney (K) tissues of the pilot whales off the Faroc Islands, belonging to schools 5 and 33. Levels of significance: ---: 1%, ==: 0.1%.

Schools 5 and 33 differed both in levels of Cd, and in the correlations between the organs, for the same element. In school 5 which showed the highest levels, correlations were significant between not only the liver and kidney, which are known to be involved in Cd metabolism, but also between these two organs and the muscle. In school 33 no correlation was found among the three organs.

Influence of sex

Since males were not numerous in either school, the levels of metals in the liver (for both schools pooled) were compared with those of females in the same age group (Table 7). The concentrations of each element were systematically higher in females.

Influence of reproductive status

A discriminant analysis (Cailliez and Pages, 1976) was performed with the 44 known age mature females in order to study the relationships between the metal concentrations in the liver and reproductive status. School 33, characterised by its low levels of Cd, was not used in the analysis. Fig. 4 represents the results of the analysis for various categories of mature female (pregnant, pregnant and lactating, lactating). The discriminant analysis correctly classified 66% of the females to reproductive category. This reflects the influence of reproductive status on the bioaccumulation of the trace elements.

Cd alone determined the first axis of the plane which represents 53% of the total variation. The second axis, determined by all the other elements, represents 47% of the total variation. The 'centre of gravity' of the lactating females is close to the Cd axis, and these females constitute a group which differs from the others by lower Cd concentrations (Table 8). Whereas the differences in Cd levels among classes were significant, the

Mean and (standard deviation) of cadmium, copper, mercury, selenium and zinc concentrations in liver tissue of males and females of the pilot whales off the Faroe Islands belonging to the same age range: 12 to 25 years old (n = number of individuals). ($\mu g/g$ wet weight).

Table 7

Sex	Cd	Cu	Hg	Se	Zn
Males	33.1	5.32	76.4	22.6	72.2
(n=10)	(17.9)	(0.79)	(28.4)	(11.1)	(26.1)
Females	62.3	7.61	119.6	40.2	67.9
(n=18)	(19.1)	(1.40)	(59.0)	(18.6)	(14.7)

Table 8

Mean and (standard deviation) of age (in years), cadmium, copper, mercury, selenium and zinc concentrations (μ g/g wet weight) in liver tissue of mature females of the pilot whales off the Faroe Islands (n = number of individuals). The females of school 33 were excluded because of their significantly lower levels of cadmium. PNL: Pregnant and non lactating; L: Lactating; PL: Pregnant and lactating.

Status	Age	Cd	Cu	Hg	Se	Zn
PNL Females	18.4	79.1	6.2	89.7	24.7	80.2
(n=28)	(9.6)	(24.5)	(1.3)	(66.0)	(18.5)	(19.1)
L Females	22.4	60.9	5.2	105.9	31.3	77.4
(n=8)	(11.2)	(12.3)	(1.2)	(136.7)	(35.3)	(7.6)
PL Females	17.9	84.1	7.8	121.9	43.1	89.3
(n=8)	(5.0)	(20.5)	(2.2)	(46.4)	(22.3)	(9.8)

Results of the comparison by a Mann Whitney test of cadmium in liver between the lactating, the pregnant and lactating, the pregnant and non lactating females of pilot whales off the Faroe Islands. The females of school 33 were excluded because of their significantly lower levels of cadmium. (NS=non significant).

Status	Lactating	Pregnant and non lactating
Pregnant and non lactating	z=2.05 (99%)	
Pregnant and lactating	z=2.41 (99%)	z=0.87 (NS)

differences between ages were not (Mann-Whitney test, Table 9). Hg concentrations remained correlated with the age (r=0.74, p<0.1%) as reported earlier for each school. The reproductive status of the females seems to influence mostly Cd bioaccumulation.



Fig. 4. Representation of the discriminant analysis: distribution in the principal plane 1-2 of the known age mature females. The females of school 33 which had significantly lower levels of Cd are excluded. The six associated variable axis- As, Hg, Se, Zn, Cu and Cd concentrations in the liver tissue – are represented. The first principal axis of the plane, determined by Cd represents 47% of the total variation. The second principal axis of the plane, determined by As, Hg, Se, Zn and Cu represents 47% of the total variation. ∆: pregnant and non lactating females, G1: centre of gravity. ○: lactating females, G2: centre of gravity. □: pregnant and lactating females, G3: centre of gravity.

	Cd	Cu	Zn
	(ng/g)	(µg/g)	(µg/g)
33(n=7)	11.5 (2.4)	1.26 (0.44)	15.3 (5.1)
5(n=6)	23.6 (14.8)	0.69 (0.37)	10.4 (5.0)
25(n=8)	43.7 (35.6)	0.58 (0.49)	9.6 (4.9)
Mean	26.4 (26.1)	0.85 (0.51)	11.8 (5.3)
Range	8.6-121.8	0.2 - 2.03	1.0-19.1
Harp seal ¹	57 (23)	0.54 (0.08)	6.0 (1.5)
Human milk ²	-	0.24 (0.08)	1.34(0.96)
Human milk ³		0.15 to 1.34	0.4 to 8.0

Mean and (standard deviation) of cadmium (ng/g), copper $(\mu g/g)$ and zinc $(\mu g/g)$ concentrations in milk of lactating females of pilot whales off the Faroe Islands from three different schools. Comparison with harp seal milk and human milk. (n=number of individuals).

Transfer during lactation and pregnancy

Transfer via milk

Cu and Zn concentrations in milk (Table 10) were higher than those reported in a study carried out by Wagemann *et al.* (1988) on harp seals in the Gulf of St. Lawrence and Underwood (1977) and Chan *et al.* (1984) for humans. Concentrations of these essential elements and also of Cd, vary greatly by species, and in the case of the pilot whale, by school.

Table 11

Mean (SD) of cadmium, copper and zinc concentrations in milk (mg/1), mammary gland, liver, kidney and muscle tissue of the six lactating females of school 33. (n=number of individuals). $(\mu g/g \text{ wet weight}).$

Tissue	Cd	Cu	Zn
Mammary gland	0.78 (0.19)	1.05 (0.28)	23.6 (7.0)
Milk	0.01 (0.003)	1.03 (0.44)	14.1 (5.3)
Liver	41.2 (10.5)	6.46 (0.56)	50.9 (7.3)
Kidney	64.3 (14.1)	3.89 (0.88)	34.7 (5.1)
Muscle	0.22 (0.18)	0.60 (0.08)	23.3 (2.2)

Only mammary tissue from school 33 has been analysed. The results are presented in Table 11 with the levels in the liver, kidney and muscle of the same females. Concentrations of each element were lower in the mammary glands than in liver or kidney but higher than those of muscle.

Transfer to the foetus during the pregnancy

Table 12 gives the results of metal concentrations in the livers of 13 foetuses from three different schools. Cu concentrations were higher in foetuses than in adults, as has also

Mean (SD) of cadmium, copper, mercury, selenium and zinc concentrations ($\mu g/g$ wet weight) in liver tissue of the foetuses from three different schools: 16, 25 and 22. (n=number of individuals).

School		Cd	Cu	Hg	Se	Zn
16(n=3)	Mean	0.004	39.1	0.36	0.90	33.0
. ,	SD	0.001	5.3	0.15	0.56	15.4
25(n=5)	Mean	0.020	41.9	1.07	1.22	47.5
	SD	0.010	10.0	0.53	0.48	24.6
22(n=5)	Mean	0.037	57.3	0.83	2.43	54.7
	SD	0.015	14.8	0.40	1.43	36.0

been found in humans (Riordan and Richards, 1980). Levels of non essential elements were detectable but much lower than in adults, showing that some transfer was possible. Cd and Hg concentrations in the foetus were not correlated with those in the mother but were with the length of the foetus, with the highest correlation coefficient for Hg (r=0.81, p<0.1%). These two metals are thus already beginning to accumulate in the foetus.

DISCUSSION

Arsenic bioaccumulation

Marine mammals do not accumulate more As than their prey and have low levels compared to those found by Bryan (1984) in primary producers, invertebrates and fish.

Levels of Cd, Cu, Hg and Zn in the liver

A comparison of the mean levels of metals in the liver of Faroese long-finned pilot whales with those found in the same tissue of other marine mammal species from different areas of the North Atlantic, shows that most variation occurs in Cd and Hg, both by species and by area (Table 13). The dependency of Hg content on age may explain the differences between the results of this study and those of Julshamn *et al.* (1987), who analysed only 22 animals.

If only studies with a large sample size are considered, only the Cd concentrations in the narwhal or the Hg concentrations in the common dolphin and ringed seal from the Gulf of Bothnia are similar to those found in pilot whales. Cd and Hg are thought to be the best metal indicators of pollution of marine ecosystems (Bryan, 1984). However, the levels in Faroese pilot whales are greater for Cd and comparable for Hg to species from the heavily industrialised Gulf of Bothnia. A similar situation was found for seabirds in the South Atlantic area (Muirhead and Furness, 1988) where birds from a 'non-polluted' area showed higher Cd and Hg concentrations than those from a contaminated North American system or for feral pigeons from highly polluted areas of London.

Around the Faroes, pilot whales feed mainly on squid (Desportes and Mouritsen, 1993) as did the South Atlantic seabirds in Muirhead and Furness' study (1988). Cd levels in marine fish are generally lower than in other organisms and thus the intake of Cd will be higher for squid eaters. This is supported by the Cd concentrations found in the urine of seven individuals from school 5 (9.1–30.7 μ g/g of creatinin). In humans, Cd is assimilated in larger quantities than it is excreted (almost entirely in urine). Normal levels in humans are about 2μ g/g of creatinin, but they can be much higher in exposed persons. The high levels of Cd in the urine of pilot whales indicates a diet rich in this element. Nevertheless all the cited species in Table 13 are at a similar level in the food chain. Striped dolphins

Mean of cadmium, copper, mercury and zinc concentrations (μg/g wet weight) in liver of different species from the North Atlantic Area. Sources: ^a Present study; ^b Julshamm *et al.* (1987);
^c Wagemann *et al.* (1983); ^d Andersen and Rebsdorff (1976); ^e Falconer *et al.* (1983); ^f Gaskin *et al.* (1979); ^g André (1983); ^h Johansen *et al.* (1980); ⁱ Helle (1981); and ^j Ronald *et al.* (1983).

Species	Geographical area	Cd (i	Cu in µg/g	Hg wet wei	Zn ght)	Source
Globicephala melas $(n=131)$	Faroe Islands	47.0	5.7	70.1	75.5	3
G. melas (n=8)	Faroe Islands (1977)	12.0	10.0	280 .0	110.0	b
G. melas $(n=14)$	Faroe Islands (1978)	45.7	5.3	61.1	65.3	b
Monodon monoceros $(n=37)$	Baffin Island (Canada)	32.0	5.3	6.1	38.8	c
Phocoena phocoena $(n=4)$	Coast of Denmark	-	4.5	22.0	59.0	đ
\dot{P} . phocoena (n=23)	E. coast of Scotland	0.2	7.2	4.7	43.5	e
P. phocoena $(n=146)$	Bay of Fundy (Canada)	-	-	16.0	-	f
Delphinus delphis (n=49)	Atlantic coast of France	-	-	51.0	-	g
\dot{P} hoca hispida (n=29)	West Greenland	7.3	11.6	2.4	46.0	Ъ
P. hispida $(n=22)$	Gulf of Bothnia	0.8	-	50.8	30.8	i
P. hispida $(n=152)$	Gulf of St. Lawrence	12.0	24.3	12.7	-	j

from the coast of Japan (Honda and Tatsukawa, 1981) had much lower Cd levels in the liver ($6\mu g/g$ wet weight) than those found in Faroese pilot whales, although they also feed mainly on squid. The same study found Cd concentrations ranging from 0.21 to 0.90 $\mu g/g$ wet weight in muscle tissue of the prey species, *Todarodes pacificus* (n=3, mean=0.65). This is comparable with our results for the levels in the muscle of *Loligo forbesi* caught by Faroese fishermen in the North Atlantic (0.10 to 0.94 $\mu g/g$ wet weight -n=9, mean=0.31, unpublished data). Thus environmental and feeding habits are not the only factors influencing the bioaccumulation of Cd. Uptake, storage and elimination processes may be characteristic of a given species, thus inducing a lower or higher bioaccumulation.

Comparative bioaccumulation of Cd and Hg

Cd and Hg concentrations are very low at birth and accumulate with age. In pilot whales, the rate of accumulation of these two metals differed. In the liver, Hg showed the best correlation with age, showing a consistent increase throughout life. Hg has been shown to be cumulative in numerous marine mammal species from different geographical areas (Gaskin *et al.*, 1979; Falconer *et al.*, 1983; Honda *et al.*, 1983; André *et al.*, 1990), with a similar pattern of accumulation in each study.

As in man (Gottofrey, 1984), Cd mainly accumulates in the kidney and liver. In pilot whales, the increase was particularly rapid during the first years of life, stabilising at about 15 years old. Honda and Tatsukawa (1983) found a similar pattern with age in striped dolphins and postulated that this might imply a higher absorption efficiency and accumulation of Cd *via* the digestive tract in calves. In this study, Cd concentrations were better correlated with length (or weight), which is in agreement with Boyden (1974) who reported that because of concomitant variation in weight, the increase in metal content continued even if the increase in concentrations stopped.

Cu and Zn: essential elements

Cu and Zn are essential elements and with most species, including man, their concentrations in the liver are higher in newborn than in adult animals. Based on studies of terrestrial mammals, Kirchegessner and Weigand (1983) concluded that Zn absorption and retention decreased with age, the change occurring at around weaning, although it was not possible to directly relate this to the transition to solid food. A similar pattern was found in school 5 where 61.5% of the individuals <250cm had milk or mixed milk and cephalopod beaks in their stomachs i.e. were at the weaning stage. Excluding these animals resulted in Zn concentrations no longer being correlated to length as had been found in school 33. Thus Zn is a non-cumulative metal, and as Kirchegessner and Weigand (1983) showed previously in man, concentrations remain the same until a great age: in pilot whales, liver Zn is at least partially regulated. Falconer *et al.* (1983) and Honda and Tatsukawa (1983) have shown the same in porpoises and striped dolphins, respectively.

In this study, Cu concentrations in liver increased with age; as far as we know, this has not been reported in other studies on marine mammals. Schroeder *et al.* (1967, cited by Yunice and Hsu, 1984), have shown that Cu concentrations in human liver gradually decreased from birth to maturity, and decreased again after the age of 60, whereas they remained unchanged in the kidney. However, the status of Cu in relation to age varies greatly from one species to another. Nevertheless in pilot whales, the increase of Cu with age in both schools, and the increase of Zn with length in kidney and muscle in school 5, could be attributed to the failure of homeostasis of these essential elements. In humans, Yunicce and Hsu (1984), suggested that this failure could be induced by increased dietary intakes or shifts in interorgan distribution because of changes in metabolic needs.

Intraorganic correlations: possible mechanisms of detoxification

Mercury-Selenium

Correlations between elements may reveal similarities in the mechanisms leading to their uptake in the organism or affinities for certain metabolic pathways. The high correlation between Hg and Se found in pilot whales, especially in the liver, has been found in early (e.g. Koeman *et al.*, 1973) and more recent studies of dolphins (Itano *et al.*, 1984; Julshamn *et al.*, 1987) and seals (Reijnders, 1980; Ronald *et al.*, 1984; Wagemann and Muir, 1984; Perttilä *et al.*, 1986; Nielsen and Dietz, 1990).

The protective effect of Se against Hg toxicity has been observed in a number of different organisms and several mechanisms have been postulated: the redistribution of Hg in the presence of Se; competition for binding sites between Hg and Se; formation of an Hg-Se complex; conversion of toxic forms of Hg to other forms; and prevention of oxidative damage (Cuvin-Aralar and Furness, 1991). Martoja and Berry (1980) carried out histological surveys which showed black particles located in the connective tissue of the liver portal vessels of *Ziphius cavirostris* and *Tursiops truncatus*. They identified these granules as mercuric selenide (tiemannite) which is presumed to play a role in preventing acute organic mercury toxicity by binding with the mercury and thus preventing it from reaching target tissues (Burk *et al.*, 1974, cited by Cuvin-Aralar and Furness, 1991). This Hg-Se complex could be the last stage of the detoxification process leading to the fossilisation of Hg and Se under the form of non biodegradable compounds.

In this study, the mean molar ratio of total Hg to Se was 1.5 in liver and 2.0 in the muscle and kidney. These differences can be explained by the different ratios of methylmercury to total mercury in the organs. In the liver most of the mercury is recovered in the inorganic form (analysis of 14 pilot whales gave an average percentage of organic mercury with respect to total mercury of 33% ranging from 3–62% – Schintu *et al.*, 1992). These results were similar to those reported by Julshamn *et al.* (1987) for the same species in the same

area. In the muscle, the mean methylated fraction of Hg found in 15 mature females was 81% (range 68-99%, unpublished results), showing that most of the mercury is recovered as organic mercury.

However, the proportion of organic mercury in the liver decreased with age even though older individuals had higher total mercury levels (Schintu et al., 1992). This is in agreement with findings for other marine mammal species (Gaskin et al., 1979; Reijnders, 1980; Falconer et al., 1983; Wagemann et al., 1988). But concomitantly with the age, the school and also the reproductive status of the individual seemed to influence the molar ratio of total Hg to Se, since it reached almost two in the liver of the lactating females in the present study. This may suggest the occasional occurrence of a limit to the processes of detoxification. Poor availability of Se in the food may also be a cause, but a detailed examination of this question is outside the scope of this study. Fish, and especially squid, form a significant part of the pilot whale diet and presumably play an important role in the transfer of Hg and Se. The observation of a 1:1 molar relationship between Hg and Se in marine mammals does not hold true for a large number of marine fish, and Hg and Se relationships are seldom included in reports on squid. Numerous studies have been carried out to determine the effectiveness of different chemical forms of Se against Hg poisoning. There are some indications of different modes of action of the different forms of Se. The varying results suggest that the interactions between different Se and Hg compounds are extremely complex; they are not well understood at present (Cuvin-Aralar and Furness, 1991).

Cadmium-copper-zinc

Cd and Cu concentrations and Cd and Zn concentrations were respectively correlated in liver and kidney indicating some similarities in their metabolism. In numerous marine mammals (Helle, 1981; Honda and Tatsukawa, 1983; Julshamn *et al.*, 1987), as in terrestrial mammals or in humans (Schroeder *et al.*, 1967), Zn concentrations increase with Cd concentrations in liver or kidney.

In this study, the increase of Zn with Cd was more pronounced in the kidney than in the liver, but in both organs the molar ratio Zn/Cd was less than 0.5. This is quite different from Honda and Tatsukawa's (1983) results. They found a Zn/Cd molar ratio of 3 in liver and 1 in the kidney of Stenella coeruleoalba. They also found that in the kidney, if Cd concentrations were higher than in liver, the Zn/Cd relationship was broken when the levels of Cd reached $50\mu g/g$ wet weight. In pilot whales, the mean levels were $42\mu g/g$ wet weight in liver (range 0.01 - 94) and $93\mu g/g$ wet weight in the kidney (range from 1.4 -158), whereas they were considerably lower, 6 and 30µg/g respectively, in striped dolphins. Moreover despite the Zn/Cd correlation, they found that Zn was regulated in both the liver and kidney. Regulation occurred in the liver but not in the kidney (where it accumulated with age) in pilot whales. Most Cd present in the body is found in the liver and the kidney, where more than 80% is bound to the metalloprotein metallothionein (Webb and Cain, 1982). Kagi and Vallee (1960, cited by Webb and Cain, 1982) established that this protein was able to bind Cd, Zn and Cu. Later studies carried out by Piscator (1964, cited by Webb and Cain, 1982) confirmed that the protein was synthesised in response to the presence of Cd, as a protective detoxifying mechanism.

In their studies on striped dolphins, Honda and Tatsukawa (1983) assumed the increase of Zn to be a compensation for the increase in Cd concentration and related this to the formation of metallothionein. Metallothionein has been found in the liver and kidney of several marine mammal species: California sea lions (Lee *et al.*, 1977; Ridlington *et al.*, 1981); fur and grey seals (Olafson and Thompson, 1974); sperm whales (Ridlington *et al.*, 1981); striped dolphins (Kwohn *et al.*, 1986); and narwhals (Wagemann *et al.*, 1984). In

this last study, Cd was associated almost exclusively with metallothionein which is in agreement with studies with humans and terrestrial mammals. In the Faroese pilot whales, metallothionein was found in the liver and the kidney of the mature individuals as well as in the foetuses (unpublished results).

However, the increase in Zn concentrations should not be considered as a 'compensation' for the increase in Cd but more as a consequence of the bioaccumulation of Cd. It is well established that the primary function of metallothionein is to ensure the homeostasis of the essential elements Cu and Zn (Webb and Cain, 1982), which also induce its synthesis. The detoxification mechanism in the light of chronic exposure to Cd may be nothing more than the fortuitous interaction of this foreign cation with the normal homeostasic mechanism for Cu and Zn (Rose, 1983).

Correlations between Hg and Cu and Hg and Zn also exist and metallothionein synthesis in response to mercury is also possible (Webb and Cain, 1982). In pilot whales, if Cd is present in high quantities, it is believed to bind to metallothionein as soon as it is newly synthesised. *In vivo* zinc-thionein has a short half-life and the rates of zinc turnover and protein breakdown are the same. However, when Cd is incorporated in the metallothionein molecule, the half-life is longer than zinc-thionein (Feldman *et al.*, 1978) and increases with the Cd/Zn ratio (Cain and Holt, 1979, cited by Webb and Cain, 1982). This may affect Zn and Cu homeostasis and may explain the lack of regulation of Zn and Cu in the kidney of pilot whales from school 5 and of Cu in the liver from both schools.

Influence of sex

Pilot whale males grow more rapidly than females and attain a greater length at the same age (Bloch *et al.*, 1993b). Desportes and Mouritsen (1993) found that the size of the prey increases with the size of the animal. From this, one might expect that at the same age the quantities of trace elements assimilated by males would be higher than those assimilated by females. However, faster growing animals have more storage tissue than the slower growing animals and larger animals will have a lower metabolic rate (Borrell and Aguilar, 1993). This would then result in the lower concentrations actually found in males.

Differences between schools

School 33 appears to be different from the others. The most obvious differences are in the significantly lower levels of Cd, the slower rate of accumulation and an apparently better maintained Cu and Zn homeostasis.

When compared with school 5, the differences were even more pronounced when considering the element concentrations between organs (cf Fig. 3). In school 5 (the most contaminated individuals), correlations in Cd concentrations were found between the liver, kidney and even muscle (which is not involved in Cd metabolism). Cd is probably transported throughout the body via the blood as associated proteins. No such correlation was found in school 33, where Cd levels were significantly lower.

Similarly, Cu concentrations in the kidney, which were higher in school 5, were correlated to those in the liver. No such correlation was found for school 33. This may also reflect problems in the regulation of Cu in school 5.

The different nature of school 33 was also found in the isozyme analysis carried out by Andersen (1993), who found this school in particular to differ from the others, suggesting the possibility of at least two sub populations of Faroese pilot whales.

Food is the principal source of trace elements in marine mammals and Cd levels may be used as an indicator of pollution levels in the waters where the animals feed. It is assumed that the pilot whales in Faroese waters are part of a larger population (or populations) in the North Atlantic Ocean, although little is known about the population structure
(Hoydal, 1986; Amos *et al.*, 1993). Borrell and Aguilar (1993) suggested that the schools feeding around the Faroes in the summer may have an 'allopatric distribution' during the rest of the year. This might explain the pattern shown in Fig. 5. In humans, the biological half-life of Cd in the kidneys is about 10-30yrs (Friberg *et al.*, 1974) and the bioaccumulation of Cd in the kidneys reflects the long-term contamination of the individual. Pesch *et al.* (1989) consider the liver as 'the yardstick organ' for the current metabolic Cd burden.



Fig. 5. Comparison of Cd concentrations in the kidney and liver for schools 5 and 33.

In Fig. 5, the range of Cd concentrations in the liver was the same for the two schools studied $(10 - 90\mu g/g \text{ wet weight})$ reflecting the fact that their recent diet was the same (i.e. they were both feeding in Faroese waters). However, the range of Cd concentrations in the kidney was different in both schools $(0 - 60\mu g/g \text{ wet weight in school 5 and } 20 - 100\mu g/g \text{ wet weight in school 33})$ suggesting that the long-term contamination was different for each school.

Transfer during lactation and pregnancy

The observed influence of reproductive status on the bioaccumulation of trace elements in the liver may reflect a change in the organotropism of the elements during pregnancy or the transfer of these elements from the females to the calves via the milk, or to the foetuses via the placenta.

Transfer via milk

The amounts of essential elements in milk vary both by species and the time within lactation; in all species colostrum is substantially richer in Cu and Zn than milk (Underwood, 1977). This makes the interpretation of different values quite difficult. In this study, Cu and Zn concentrations varied by school and were lower in those schools where the females showed higher Cd concentrations in the liver; these lower levels may be the result of Cd contamination. Nevertheless, several studies carried out on humans gave conflicting results. According to Underwood (1977) and Chan *et al.* (1984), the maternal dietary intake does not affect Cu and Zn concentrations in milk. However, other studies reported by Chan *et al.* (1984) show that geographical location influenced the Cu content of milk, and that socio-economic status was correlated with both Cu and Zn concentrations in milk.

The most obvious feature of the discriminant analysis of the mature females (Fig. 4) was the low level of Cd in the liver of lactating females. One explanation is that it is eliminated via the milk. (For a simultaneously pregnant and lactating female the quantities of milk would have become too low for this to represent an efficient way of elimination). This hypothesis of elimination via the milk is supported by the fact that the same differences in the Cd concentrations in milk existed between the schools, school 5 showing the highest levels. A consequence of this is that suckling calves will be differently exposed to Cd according to their school. Lockyer (1993) estimated milk consumption to be 2.4 and 3.9kg/ day for first and second year calves respectively. Therefore calves in school 33 would ingest 28µg Cd/day during the first year whereas those in school 5 would ingest 57µg Cd/ day. Although Cd concentrations were found to be much lower in the liver $(6.6\mu g/g)$ and the kidney $(27.7\mu g/g)$ of harp seals (Wagemann *et al.*, 1988), the mean levels of Cd in milk are comparable (and even lower in the pilot whales, Table 10) in the two species. The role of the mammary gland in control in rats has been examined by Lucis et al. (1972) who injected them with Cd and Zn after parturation. They found that after lactation, Cd remained in the mammary tissue whereas Zn was depleted. However the possibility that the mammary gland has a role in control can not be excluded because of the difference of Cd concentrations between this organ and the milk.

Transfer to the foetus during the pregnancy

Until the 1960s it was thought that the placenta was a barrier against the flux of Cd to the foetus. However numerous studies on humans and animals have since shown that the transfer does occur but that it varies with species and within the time of pregnancy.

Organic forms of Hg can cross the placenta and reach the developing foetus. Total Hg concentrations were very high in the liver of pilot whales but, because of the role of Se in the detoxification of Hg, the foetus' exposure to methylmercury is not yet known. In the liver of the foetus there was no correlation between total Hg and Se concentrations. This was also found by Wagemann *et al.* (1988) for harp seals. Total Hg concentration was positively correlated with Se in the liver of the mothers but not the pups. This might be the result of selective transport of Hg and Se, as experiments with rats have shown that small amounts of Se compounds administered during pregnancy or lactation decrease the passage of Hg from the mother to the offspring (Parizek *et al.*, 1969, cited by Reijnders, 1980). However, it may also indicate that the foetus has not developed the same ability as the adult to demethylate methylmercury by the formation of tiemannite with Se. Further analyses that include metallothionein and methylmercury will examine mother-foetus transport in more detail.

CONCLUSION

Cd and Hg concentrations increase with length or age in the pilot whales of the Faroe Islands. This is a general phenomenon in marine mammals which occupy the highest levels of the marine food chain and are long-lived species.

The high correlation between Hg and Se in pilot whales suggests (as do numerous previous studies) that Se may have a protective effect against the toxic action of mercuric compounds.

The influence of age is clearly predominant for Hg whereas for Cd the contamination levels also appear to be dependent on the reproductive status of the females and more strongly on the school to which the individuals belong. Because of the lower levels of Cd in lactating females, milk appears to be another way of eliminating Cd but consequently exposes their newborns to this toxic metal as soon as they are suckled. Hg and Cd concentrations are detectable in foetuses, but the levels are too low to constitute an efficient method of elimination for pregnant females.

Compared with other marine mammals from the same area, Cd levels are very high in pilot whales from the Faroes and are even higher than in species from highly industrialised areas. This suggests that these high levels, which would have severe toxic effects at the same concentrations in man (H.L. Boiteau, pers. comm.), are due more to adaptative processes of accumulation than to anthropogenic effects, and raises the question of the response of pilot whales to metals. Differences appear in Cd levels between individuals of different schools. This suggests that there may be more than one population of pilot whales found around the Faroes and that either Cd constitutes a 'tracer' for the different distribution of whales when they are not in Faroese waters or that the metabolism and bioaccumulation mechanisms differ by school. Nevertheless most of the Cd is bound to metallothionein in marine vertebrates and the main function of this metalloprotein is to ensure the homeostasis of the essential elements Cu and Zn. In the school showing the highest Cd levels, the regulation of Cu and Zn appeared to be less efficient. This may be among the first effects of 'abnormal' levels of Cd and qualifies the idea of the adaptive responses to metals.

Further studies on the locations and forms of stored metals, comparison between schools and transfers between mother and calf or mother and foetus are underway.

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Parasites of the Long-Finned Pilot Whale, Globicephala melas (Traill, 1809), in European Waters

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ABSTRACT

Long-finned pilot whales from three European regions (Faroe Islands, French Atlantic waters and Spanish western Mediterranean) were surveyed for ecto- and endoparasites in order to provide information on the taxonomy, biogeography, host relationships and pathogenicity of the parasites and epizoics of the pilot whale in European waters. Twentyone species were detected; two of them new to science. The helminth fauna from animals taken in the Faroes comprised both cosmopolitan species and those apparently restricted to cold waters. Differences found in the parasite fauna between this study and those previously described for pilot whales from Newfoundland waters are possibly due to methodology and sampling effort, environmental conditions (especially water temperature) and differences in the pool of intermediate hosts available in each area. A greater prevalence and abundance of the whale-lice Isocyamus delphini on mature males appears to be related to a higher incidence of wounds from sexual fights. The prevalence of the stomach parasites, Anisakis simplex and Pholeter gastrophilus, is significantly higher in animals over three years old. Infestation appears to begin early in life with the onset of feeding on solid food. The high prevalence of A. simplex in pilot whales from the Faroes is possibly a consequence of its low specificity and to the high abundance of larval stages in fishes and cephalopods in the North Atlantic. The abundance of the most common intestinal helminth species was significantly higher in whales over ten years in age, which is likely to be due to a greater chance of infestation among older animals. Males were more severely infested than females, perhaps due to physiological and behavioural differences. Significant differences in the abundance of intestinal helminths across schools supported the hypothesis of segregated groups of pilot whales around the Faroes. However, seasonal fluctuations in prey availability may also contribute to the differences observed. Some parasite species were associated with pathological lesions. The most prevalent pathology consisted of ulcers caused by A. simplex (81.4%) on the stomach walls, especially in the main stomach. Crassicauda sp. appeared in the mammary glands. It has been proposed that these infestations can lower milk production, jeopardising the reproductive success of schools.

KEYWORDS: PILOT WHALES-LONG-FINNED; NORTH ATLANTIC; MEDITERRANEAN; PARASITES; PATHOLOGY; FEEDING; SQUID; AGGRESSION; REPRODUCTION; BEHAVIOUR.

INTRODUCTION

Cetaceans possess a peculiar parasite fauna due to their colonisation of the marine ecosystem. Only some of the ancestral parasitic helminths appear to have been able to respond to the adaptative pressures imposed by the new environment. This resulted in a little-diversified helminth fauna, indicating the long isolation of the hosts from terrestrial mammals. This is illustrated, in some cases, by the preservation of fairly primitive taxa which have almost disappeared or are scarcely represented among land mammals, e.g. the pseudaliid nematodes (commonly known as lungworms). However, helminth species were also acquired from other vertebrates after adaptation to the marine environment, particularly seabirds (Hoberg, 1989; Bush *et al.*, 1990; Balbuena, 1991). In addition, cetaceans also established associations with crustaceans which, apart from some sporadic

reports of cirripeds on pinnipeds, are unique among mammals. These associations may range from phoresis and commensalism to parasitism *sensu stricto* (Raga, In press).

In general, the life cycles of cetacean parasites are either completely or almost completely unknown. Only in a very few instances have they been elucidated with any certainty, e.g. those of the anisakid nematodes (Smith, 1983; Oshima, 1987). However, heteroxenous (indirect) life cycles can be assumed for some helminths, particularly the cestodes, digeneans and acanthocephalans, in the light of their phylogenetic relationships.



Fig. 1. European regions studied in the present survey: Faroe Islands, French Atlantic and western Mediterranean.

As is true for most cetaceans, parasitological studies of the long-finned pilot whale, *Globicephala melas* (Traill, 1809), have been restricted almost exclusively to taxonomic work. Until the present study, 18 parasitic or epizoic species had been recorded from this host. This relatively high number may be due to availability of specimens of the long-finned pilot whale in the Northern Hemisphere, where most studies have been carried out. Information from European waters comes mostly from occasional necropsy reports (e.g. Dollfus, 1968; Raga and Balbuena, 1988) or listings of specimens deposited in zoological collections (Gibson and Harris, 1979; Raga *et al.*, 1987). Data on the parasites and parasitic lesions of a relatively large number of animals had only been provided by examination of pilot whales taken in the fishery off Newfoundland in the 1960s (Cowan, 1966; 1967). These investigations gave rise to the description of a new cestode genus (Rausch and Margolis, 1969).

The present study is based mainly on long-finned pilot whales caught in the Faroese drive fishery in the course of a comprehensive research programme on the biology of this species in the Northeast Atlantic (e.g. Bloch *et al.*, 1990). Pilot whales stranded along the Spanish Mediterranean coast were also systematically surveyed. In addition, during a French-Spanish joint research project, parasite specimens collected by members of the Centre National d'Étude des Mammiféres Marins, La Rochelle, from pilot whales stranded on the Atlantic French coast were examined. This study uses these data to examine the taxonomy, biogeography, host relationships and pathogenicity of the parasites and epizoics of the pilot whale in European waters.

MATERIALS AND METHODS

Pilot whales from three European regions (Fig. 1) were studied: Spanish western Mediterranean; French Atlantic (Bay of Biscay and the English Channel) and the Faroe Islands (North Atlantic). Five animals stranded on the Spanish Mediterranean coast between June 1982 and July 1988, six on the Atlantic French coast between November 1972 and June 1988 and 170 taken in the Faroese drive fishery were surveyed for parasites. In the latter case, 13 schools caught in seven localities from July 1987 to June 1988 were examined (Table 1). Additional information on stomach helminths of 590 whales caught off the Faroes between July 1986 and June 1988 and epizoic and helminth specimens collected during opportunistic sampling of these animals were kindly supplied by G. Desportes (Faroese Museum of Natural History).

Data concerning body length, sex, age, feeding habits and sexual status were made available to us by D. Bloch and G. Desportes (Faroese Museum of Natural History).

The specimens stranded on the Spanish coast and those caught in the Faroes were systematically necropsied and examined. The external surface and natural openings of the whales were scrutinised for ectoparasites and epizoics. Lungs, air sinuses, heart, kidneys and mammary glands were examined in the field. Complete digestive tracts were collected and kept frozen at -20° C prior to examination in the laboratory. There, the various stomach compartments and bile and hepatic ducts were opened and examined for helminths. The intestine was divided into approximately 2m long sections for site-selection studies (see Balbuena, 1991). Each intestinal section was examined separately.

The sampling implemented in the Faroe Islands was restricted by working conditions (see Bloch *et al.*, 1993). This precluded a thorough examination of every whale: the blubber and mesenteries of 114 animals, lungs of 53, air sinuses of 31, kidneys of 28, mammary glands of 92, stomachs of 761 and livers and intestines of 170 animals were surveyed for helminth parasites. In addition, the skin and natural openings of 152 individuals were examined for ectoparasites and epizoics. All parasites were washed in

		Age (yrs)	No of whales examined			
Locality	Date	Mean (SD)	Males	Females	?1	Total
Leynar	22 Jul 1987	10.7 (8.8)	3	12	0	15
Miðvágur	24 Jul 1987	17.8 (11.4)	4	6	0	10
Miðvágur	2 Aug 1987	14.5 (9.7)	6	8	0	14
Vágur	19 Aug 1987	8.5 (6.6)	4	4	0	8
Klaksvík	29 Aug 1987	15.2 (12.9)	3	3	0	6
Vágur	18 Sep 1987	10.8 (9.1)	8	4	2	14
Tórshavn	8 Oct 1987	10.0 (10.7)	9	10	0	19
Vágur	20 Oct 1987	11.5 (12.4)	6	12	2	20
Hvalvik	24 Oct 1987	1.4 (1.1)	5	9	0	14
Tórshavn	17 Feb 1988	2.7 (1.9)	2	4	0	6
Miðvágur	13 Mar 1988	2.5 (1.5)	5	5	0	10
Bour	20 Apr 1988	2	6	9	0	15
Leynar	10 Jun 1988	10.5 (8.6)	9	10	0	19
Totals for who	ole sample	9.8 (9.8)	70	96	4	170

Data concerning 170 long-finned pilot whales surveyed for parasites off the Faroe Islands. Whales were sampled from 13 schools taken in the Faroese drive fishery.

Table 1

¹ Sex not recorded; ² Data not available.

saline solution or sea water and then fixed and preserved in 70% ethanol. Samples of lesions due to parasites were fixed and stored in 10% formalin and processed using standard histological techniques.

The presence or absence of parasites in each organ or tissue was noted. The parasites and epizoics recovered from the skin, intestine, blubber and mesenteries from each host were counted with the exception of three cases of mass infestations with the whale-louse *Isocyamus delphini* Guérin-Méneville, 1837.

In the case of the stomach helminths, Anisakis simplex Rudolphi, 1809 and Pholeter gastrophilus Kossack, 1910, their numbers were estimated. Four intensities of infestation levels for A. simplex were established: light (1–100 worms), moderate (101–300), heavy (301–500) and mass infestations (500+). P. gastrophilus was found within cysts in the stomach submucosa. The number of cysts was counted and is assumed to be an index of the number of worms. Three intensities of infestation levels were considered: light (1–5 cysts), moderate (6–15 cysts) and heavy infestations (15+ cysts).

Independence of host age, host sex and the prevalence of A. simplex (and ulcers caused by this nematode) and P. gastrophilus was tested using log-linear models and a likelihoodratio chi-square statistic (L^2) (Norusis, 1986). For this purpose, whales were distributed into three age classes: 0–3yrs, 4–10yrs and 10+yrs. These age classes were established to allow a comparison of the prevalence of A. simplex and P. gastrophilus between juvenile and adult pilot whales. Interactive terms were added singly to the model and those that were found to be significant (P<0.05, determined by partitioning L^2) were retained (Norusis, 1986).

Classical techniques in parasitology were used for species determination. Specimens were deposited at the collections of the Faroese Museum of Natural History, Museé Océanographique of La Rochelle, Museum National d'Histoire Naturelle of Paris, The British Museum (Natural History) and the Department of Animal Biology of the University of Valencia.

Definitions of abundance (mean number of parasites per host), intensity of infestation (number of parasites on each infested host), prevalence (percentage of hosts infested with a given parasite species) and other ecological terms referring to the parasites are in accordance with Margolis *et al.* (1982).

Parasite and epizoic species of <i>Globicephala melas</i> detected in three European localities (Far	oes =
North Atlantic; France = French Atlantic; Spain = Spanish western Mediterranean.) +/- ind	licates
presence/absence of a given species.	

Table 2

	Faroes	France	Spain
Digenea			
Hadwenius delamurei	+	-	+
Hadwenius subtilus	+	-	-
Orthosplanchus arcticus	+	-	-
Pholeter gastrophilus	+	+	+
Cestoda			
Plicobothrium globicephalae	+	-	-
Diphyllobothrium stemmacephalum	+	-	-
Diphyllobothrium cf. polyrugosum	+	-	-
Diphyllobothrium sp. A.	+	-	-
Diphyllobothrium sp. B.	+	-	-
Trigonocotyle globicephalae	+	-	+
Phyllobothrium delphini	+	+	+
Monorygma grimaldii	+	+	+
Nematoda			
Anisakis simplex	÷	+	-
Stenurus globicephalae	+	+	+
Crassicauda carbonelli	-	-	+
Crassicauda sp.	+	-	-
Acanthocephala			
Bolbosoma capitatum	+	+	+
Copepoda			
Pennella sp.	-	-	+
Cirripedia			
Conchoderma auritum	+	-	-
Xenobalanus globicipitis	+	+	+
Malacostraca			
Isocyamus delphini	+	+	+

RESULTS AND DISCUSSION

Taxonomic remarks

In all, 21 metazoan parasite or epizoic species were detected (see Table 2). The occurrence of two species new to science is worthy of note: *Hadwenius delamurei* Raga and Balbuena, 1988, a digenetic trematode from the intestine (Raga and Balbuena, 1988) and *Crassicauda carbonelli* Raga and Balbuena, 1990, a spirurid nematode found in the penis. Both were first found in animals from the Spanish Mediterranean. The *Crassicauda* sp. specimens reported by Dollfus (1968) from a pilot whale off the Gibraltar Strait area seem to represent the same species as *C. carbonelli* (Raga and Balbuena, 1990). Moreover, the

digenean *Hadwenius subtilis* Skrjabin, 1959, has been redescribed by Balbuena *et al.* (1989). Both *H. delamurei* and *H. subtilis* are designated according to a recent taxonomic revision of the family Campulidae (Adams and Rausch, 1989).

Due to the scarcity or poor condition of the specimens recovered and the uncertain taxonomy of some parasitic groups, four species were identified to genus and one to family only. Three of them occurred in pilot whales off the Faroe Islands: *Crassicauda* sp. was found in the mammary glands; *Diphyllobothrium* sp. A, *Diphyllobothrium* sp. B and *Diphyllobothriidae* sp. were recovered from the intestine. The remaining species, *Pennella* sp., a copepod, was detected on Mediterranean pilot whales.

H. subtilis, Orthosplanchus albamarinus (Treshchev, 1968); *Diphyllobothrium stemmacephalum* Cobbold, 1858; D. cf. *polyrugosum* (Delyamure and Skrjabin, 1966) and *Pennella* sp. are reported for the first time in the pilot whale (Balbuena and Raga, 1993a). Likewise, the occurrence of *H. subtilis*, *H. delamurei* and *O. albamarinus* in the North Atlantic (Faroe Islands) constitute new locality records.

Parasite fauna off the Faroes - comparison with other localities

Nineteen epizoic or parasite species were detected in the animals caught in the Faroes. Sixteen are parasitic helminths (4 digenean, 8 cestode, 3 nematode and 1 acanthocephalan species) and three are epizoic or ectoparasite crustaceans. Prevalence, intensity of infestation and abundance are given in Table 2. Three species, *O. albamarinus*, *Diphyllobothrium* sp. B and *Conchoderma auritum* (L., 1767), were not found during the systematic sampling of 170 animals, but were occasionally observed in, and collected from, other whales in the larger sample.

Due to sampling heterogeneities and the low number of whales examined in the French Atlantic, a comparison with the other two localities was only possible in terms of presence or absence of species. Given the low sample size in the western Mediterranean, prevalence should be regarded as providing a relative rather than an absolute indication. Moreover, because of the scarcity of previous studies, few data are available on the distribution and host range of the parasite species. Bearing all this in mind, caution must be exercised in the comparison of the parasite faunas.

Among the ectoparasites and epizoics, only *I. delphini* and *Xenobalanus globicipitis* Steenstrup 1851, occurred in all three regions. Both possess a wide geographical distribution (Raga, 1985; Balbuena and Raga, 1991). Generally, crustaceans were more prevalent on the pilot whales from the Mediterranean (Table 3); relatively warm waters may be more appropriate to their life cycles (Clarke, 1966; Arvy, 1982). However, *Conchoderma auritum* appeared only in the Faroes despite being a cosmopolitan species (Raga, 1985). This may be due to its rare occurrence on odontocetes (Clarke, 1966) and/or the low number of whales examined in the French Atlantic and western Mediterranean (Table 3).

Most species (12) from the Faroese pilot whales were found in the digestive system (all digenean, 6 cestode, 1 nematode and 1 acanthocephalan species). The remainder were located as follows: two cestode species, *Phyllobothrium delphini* Bosc, 1802 and *Monorygma grimaldii* Moniez, 1889, occurred as larval (plerocercoid) stages encysted in the blubber and mesenteries respectively; the nematode, *Stenurus globicephalae* Baylis and Daubney, 1925, was found in the air sinuses and respiratory system and, another nematode, *Crassicauda* sp., within the mammary glands and ventral muscles (Table 2).

Five helminth species, S. globicephalae, P. gastrophilus, Bolbosoma capitatum von Linstow, 1821, M. grimaldii and P. delphini, were found in all three regions (Table 3). According to the references available, these species show a wide geographical range

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Table 3

		Preval	ence	Intensity	of infestation	Abunda	ance
Species	Site	n/Exam.	(%)	Range	x ± SE	x ± SE	z
Hadwenius delamurei	Intestine	21/170	12.35	1-3179	159.4 ± 151.1	23.5 ± 18.8	3,989
Hadwenius subtilus	Intestine	37/170	21.76	1-4310	119.6 ± 116.4	31.6 ± 25.4	5,377
Orthosplanchus arcticus *	Liver	·	•	ı	ſ	ı	ı
Pholeter gastrophilus	Stomach	263/659	39.91	ı	•	ı	ł
Plicobothrium globicephalae	Intestine	1/170	0.59	ı	·	1	1
Diphyllobothrium stemmacephalum	Intestine	1/170	0.59	ı	·	ı	-
Diphyllobothrium cf. polyrugosum	Intestine	1/170	0.59	ı	ı	•	
Diphyllobothrium sp. A.	Intestine	ı	ı	·	ı	,	2
Diphyllobothrium sp. B.*	Intestine	8/170	4.71	1-33	7.9 ± 3.8	0.4 ± 0.2	59
Trigonocotyle globicephalae	Intestine	18/170	10.59	1-9	2.1 ± 0.2	0.3 ± 0.1	45
Phyllobothrium delphini	Blubber	7/114	6.14	1-2	1.1 ± 0.1	0.07 ± 0.03	×
Monorygma grimaldii	Mesenteries	4/114	3.51	1-3	1.5 ± 0.4	0.05 ± 0.03	9
Anisakis simplex	Stomach	612/761	80.42	'	ı	ı	,
Stenurus globicephalae	Air sinuses	23/31	74.19	•	ı	J	ı
•	Lungs	11/53	20.75	ı	ı	ı	ı
Crassicauda sp.	Mammary glands	17/92	18.48	١.	ı		·
Bolbosoma capitatum	Intestine	79/190	46.47	1-53	6.3 ± 1.0	3.0 ± 0.5	504
Conchoderma auritum*	Teeth	ı	ı	ı	•	ı	
Xenobalanus globicipitis	Skin	2/152	1.32	2-3	ı	,	S
Isocyamus delphini	Skin	46/152	30.26	ı	ı	ı	ł

(Delyamure, 1955; Raga, 1985). Two of them, S. globicephalae and B. capitatum, seem to be common in the long-finned pilot whale although both have been recorded in other odontocetes (Delyamure, 1955; Arnold and Gaskin, 1975; Balbuena, 1991). In contrast, the remaining species are fairly unspecific among toothed whales (Raga, 1985; In press). M. grimaldii and P. delphini occur more frequently and abundantly in warm and tropical waters (Delyamure, 1955; Walker, 1990), accounting, perhaps, for their more common occurrence in the Mediterranean pilot whales (Table 3).

According to previous studies, other helminth species seem restricted to relatively cold localities. This might be the case with *H. subtilis*, *O. albamarinus* and the diphyllobothriid cestodes (Treshchev, 1968; Wardle *et al.*, 1974; Balbuena *et al.*, 1989; Balbuena and Raga, 1993a), which were only found in pilot whales off the Faroes.

Some differences between the helminth fauna of the animals from the Faroes and those caught in Newfoundland were found (see Cowan, 1967; Rausch and Margolis, 1969). The number of species detected at the Faroes is larger. Of particular interest is the absence of some digeneans (*P. gastrophilus* and *Hadwenius* spp.) in the Canadian whales. Five of the seven species detected in Newfoundland were also found in the Faroese pilot whales. In addition, *Diphyllobothriidae* sp. found in the present study may correspond to *Plicobothrium globicephalae* first reported in Newfoundland by Rausch and Margolis (1969) but the poor condition of our specimens precluded further identification (Balbuena, 1991).

Quantitative differences between these two localities were also observed. *B. capitatum* showed a higher prevalence in the Faroe Islands (46.7% vs 5.5%). However, the most striking discrepancies concerned larvae of the tapeworms *M. grimaldii* and *P. delphini* (Cowan, 1967 applied to both of them the designation *Phillobothrium* sp.). All whales in the Canadian locality were infested with at least one of these species, while they were uncommon in the Faroese individuals (3.5% for *M. grimaldii* and 6.1% for *P. delphini*). In contrast, the occurrence of other species such as *A. simplex* and *Trigonocotyle globicephalae* Baer, 1954 (*T. lintoni* according to Cowan, 1967) were similar in both regions. It should be remembered that the observed differences across these areas may, to a greater or lesser degree, be explained by differences in sampling conditions and the number of animals surveyed. However, other factors such as prevailing environmental conditions and intermediate (or paratenic) hosts available in each region may also be contributory.

Environmental conditions, particularly water chemistry and temperature and the productivity of the local ecosystem, are regarded as important factors influencing the distribution of marine parasites (Rohde, 1982; Holmes, 1990). In fact, water temperature is generally accepted as the most important single factor affecting the distribution of marine organisms at large (Rohde, 1982). The pool of intermediate hosts available to parasites is obviously dependent on such factors. The question of intermediate host availability is of great importance in the case of digeneans because of the high specificity between the first intermediate host (a mollusc) and the miracidium. In the case of marine teleosts, it has been demostrated that the local molluscan fauna is crucial in the shaping of the digenean community of the definitive host (Koie, 1983). An additional factor might be temporal (both short- and long-term) and geographical variations in prey availability, which would be reflected in helminth abundances. Diet variations of this sort have been reported in pilot whales from European waters (see Desportes, 1985; Desportes and Mouritsen, 1993). In addition, pilot whales are known to locally specialise on certain prey items in the North Atlantic: Illex illecebrosus Le Sueur, 1821 and cod (Gadus morhua L., 1758) off Newfoundland and Todarodes sagittatus Lamarck, 1798 and Gonatus sp. at the Faroes (Sergeant, 1962; Mercer, 1975; Desportes and Mouritsen, 1993).

Factors affecting parasitism

The large number of animals sampled at the Faroe Islands allowed us to examine the relationship between parasitism by some species and various intrinsic (sex, age and reproductive status) and extrinsic (school) host factors.

The whale-louse *I. delphini* was the only ectoparasite or epizoic species which occurred regularly enough to allow statistical analyses. Its prevalence and abundance on mature males was significantly higher than for other individuals and severe infestations were only observed on these males (Balbuena and Raga, 1991).

The nature of the life-cycle of whale-lice and behavioural differences between the male and female pilot whales and between the adults and the juveniles might account for these results. These crustaceans possess a direct life cycle without active-swimming stages. Consequently, transfer from one host to another is only possible by bodily contact between individuals (Leung, 1976).

Fighting scars occur more frequently on male rather than female pilot whales and on adults rather than juveniles (Martin *et al.*, 1987; Bloch, 1992). This may be due to sexual fights for dominance or access to mature females in the pod. These lesions may provide additional shelter for *I. delphini*, accounting for the higher prevalence on these animals. Severe wounds caused by fighting would provide appropriate sites for feeding and reproduction of whale-lice resulting in the occasional heavy infestations observed on mature males (Balbuena and Raga, 1991). These males may also be crucial in transferring the infestations to other schools since recent studies suggest that adult male pilot whales mate with females in schools other than their own (Andersen, 1993).

The occurrence of the stomach helminth species, A. simplex and P. gastrophilus, was positively associated with host age. In both cases, the inclusion of an age-by-prevalence interaction significantly improved the fit of these data over the model of independence $(L^2 = 6.39, 5 \text{ df}, P > 0.20, \text{ for } A. simplex \text{ and } L^2 = 6.38, 5 \text{ df}, P > 0.20 \text{ for } P. gastophilus).$ This was independent of host sex although, in the case of A. simplex, the partial contribution of the sex-by-prevalence interaction was almost significant ($L^2 = 3.31, 1 \text{ df}, 0.10 > P > 0.05$). However, when the 0-3yr age class was omitted from the analysis, the occurrence of both species became independent of host age and sex ($L^2 = 4.09, 4 \text{ df}, P > 0.30 \text{ and } L^2 = 2.03, 4 \text{ df}, P > 0.70$ respectively).

Thus parasitism by A. simplex appears to begin in young pilot whales. The first infestations were observed within the first year of life with the onset of weaning. A sharp increase in occurrence was observed, with all age classes showing values greater than 90% (Fig. 2a). This suggests a high abundance of larval stages of A. simplex in prey species of the pilot whale and frequent reinfestations among weaned whales. In fact, simulations using host-parasite encounter models have shown that, in cases in which infestive stages were continuously available, the prevalence of a parasite rises rapidly to nearly 100% (Janovy and Kutish, 1988).

The pattern of infestation of *P. gastrophilus* with host age follows a similar pattern (Fig. 2b).

The high prevalence of A. simplex is probably due to its low host specificity (both final and intermediate hosts). Previous studies on some commercially exploited fish species such as cod and whiting in the North Atlantic revealed high levels of occurrence of larval stages of this nematode (Wootten and Waddell, 1977). Infestation by these larvae in cod caught off the Faroes is close to 100% (Sørensen, 1988). The first larval stages of A. simplex also occur in euphausiids in this region but at lower levels, as might be expected in first intermediate hosts (Smith, 1971; 1983). The presence of A. simplex larvae in squid in the North Atlantic is less well documented, but the abundance of larval stages appears greater in fish than in squid (Smith, 1984). However, among the cephalopod species of the



Fig. 2. Prevalence of (a) Anisakis simplex and (b) Pholeter gastrophilus related to host age classes and sex.

North Sea and Scottish waters, T. sagittatus, the favourite prey of the pilot whales off the Faroes (Desportes and Mouritsen, 1993), appeared to show the highest prevalence of larval anisakids (Smith, 1984).

Marine mammals are essential for the completion of the life cycle of *A. simplex*. This nematode mates in the stomach and the eggs are shed into the environment through the faeces. Its high prevalence in the pilot whales off the Faroes may contribute to the apparently high abundance of larval *A. simplex* in these waters. In fact, in areas with large concentrations of marine mammals, high percentages of fish infested with *Anisakis* spp. have been found (Dailey, 1985).



Fig. 3. Relative intensity of infestation of (a) Anisakis simplex and (b) Pholeter gastrophilus related to host age classes. Levels of infestation as defined in Materials and Methods Section.

For most pilot whale age classes, the intensities of infestation of A. simplex were light or moderate. Heavy or mass infestations, although more frequent in the oldest animals, can still be considered exceptional (Fig. 3a). The intensities of infestation of P. gastrophilus appeared greater in whales of medium age (Fig. 3b). In the oldest pilot whales, a decrease in severe infestations of both species was observed (Fig. 3). Since these helminths produce some kind of lesions on their hosts, this decrease may indicate a higher mortality rate of the most severely infested individuals.

In spite of the small number of hosts examined for S. globicephalae (no statistical analyses were possible), its occurrence seemed to increase with the age of the whales. It appeared in 46.7% of whales 0–3yrs old, but in all hosts >3yrs old. Only the younger animals appeared to be free of this helminth (none $\leq 2yrs$ was found infected). These results are similar to those reported by Geraci *et al.* (1978b) for a school of mass-stranded

Atlantic white-sided dolphins (*Lagenorhynchus acutus*). They did not find *S. globicephalae* in nursing animals, but did detect it in late-weaned calves and older individuals; again it was most abundant in the oldest animals. This pattern may indicate a heteroxenous life cycle, the infestive stages of the nematode being ingested with prey. Although some recent evidence points to the possibility of a transplacentary transmission of pseudaliid species (Dailey et al., 1991), this does not exclude an alternative indirect mode of transmission (Dailey, 1985).

In most (74.2%) cases, S. globicephalae was found in the air sinuses and tympanic bullae, but it was also found in the respiratory ducts of some animals (20.8%). The latter, however, may not be a usual site because very few worms were found there and they were exclusively in the trachea and main bronchi and not in the more peripheral bronchioles.

With regard to the intestinal parasites, first results indicate that the abundance of the most common species (prevalence >10%) was significantly higher in whales >10yrs old than those \leq 10yrs old (Balbuena and Raga, 1993b). Since a heteroxenous life-cycle is assumed for these helminths, such differences in abundance may be explained by: (i) a higher exposure time to infestive stages of the parasites in whales >10yrs old (i.e. the longer the whale has been feeding, the higher the risk of becoming infested) and (ii) a greater food intake in older animals, both in total volume (daily food intake in pilot whales is correlated with body size – Lockyer, 1993) and mean prey size. The latter may be of relevance also. Evidence indicates that young pilot whales off the Faroes feed on smaller prey species (Desportes and Mouritsen, 1993). Several authors have pointed out that the abundance of anisakid larvae tends to increase with the size of their second intermediate or paratenic host (Scott and Martin, 1959; Wootten and Waddell, 1977; McClelland *et al.*, 1983; Smith, 1984; Sørensen, 1988).

Differences in the abundance of the most common species (especially *H. subtilis*) between male and female whales were observed, suggesting a higher resistance to infestation among females. This may lie in differences between the sexes related to physiological (the immuno-suppressive effect of male sexual hormones) and behavioural factors (stress derived from sexual competition between males) (Zuk, 1990). Sexual dimorphism in size among adults may also account for this, given the relationship between daily food intake and body weight (Lockyer, 1993); as males are larger, an increased chance of infestation should be expected.

Significant variations among schools in intestinal helminth abundances were also noted, particularly for the acanthocephalan *B. capitatum* (Balbuena and Raga, 1993b). These results were consistent with previous evidence in favour of the existence of several populations (or segregated groups) of pilot whales off the Faroes (Andersen, 1988; 1993; Aguilar *et al.*, 1993). However, seasonal fluctuations in the abundance of *B. capitatum* might also contribute to these differences (Balbuena and Raga, 1993b).

Parasitic pathologies

The epizoic species detected, *C. auritum* and *X. globicipitis*, seemed to have little, if any, pathogenic effect. Generally, most parasites did not appear to pose a serious health hazard to the whales. In the case of the external parasites, *I. delphini* only produced occasional inflammatory processes on the superficial layers of the skin, especially on unhealed wounds, while the attachment of *Pennella* sp. to its host only caused local inflammatory responses (which may reach the muscle layer). Among the endoparasitic helminths, only *A. simplex*, *P. gastrophilus*, *B. capitatum* and *Crassicauda* spp. were associated with pathological changes. The effect of the remaining species appeared to be restricted to nutrient extraction.

A. simplex was usually related to the presence of ulcers on the stomach walls, which were the most common parasitic lesions (prevalence: 81.4%). These injuries seem to be provoked by the action of the larvae on the gastric mucosa (Young and Lowe, 1969; Smith and Wootten, 1978; Smith, 1989). The prevalence of stomach ulcers was significantly dependent on whale age but not sex. The inclusion of the prevalence-by-age interaction caused the data to fit the model (L²= 6.38, 5 df, P > 0.20), but when the 0-3yr whale class was deleted, its prevalence was independent of both host age and sex (L²= 2.98, 4df, P > 0.50), a pattern very similar to that observed for A. simplex (see above). The ulcers tended to occur in the main stomach (97.8% of the cases in which ulcers were detected), followed by the pyloric chamber and forestomach (49.5% and 25.2% respectively). However, in harbour porpoises (Phocoena phocoena) from Scotland and Denmark, these ulcers are found mainly in the forestomach (Smith, 1989; personal observation). Characteristics of the host species, and particularly the relative size of the different stomach compartments, may influence host-parasite relations (Smith, 1989). This may account, at least partly, for these differences in location.

P. gastrophilus occurred within cysts in the stomach and duodenal ampulla (prevalence: 39.9%). Lesions caused by this trematode have been extensively described by Woodard et al. (1969). The influence of host sex and age on the prevalence of these cysts was discussed above and is very similar to that observed for A. simplex ulcers. Most of the cysts appeared in the pyloric stomach (84.2% of all cases), followed by the main stomach and forestomach (52.3% and 2.3%, respectively). The walls of the forestomach might not provide a suitable habitat for *P. gastrophilus*, explaining its low prevalence there.

The action of *B. capitatum* on the pilot whales did not seem to be severe. It caused inflammatory processes on the intestine walls, resulting from the penetration of the proboscis in the mucosa. The highest density of this species was five worms per metre. Intestinal obstruction due to inflammation induced by *B. capitatum* was only observed in one young animal, but the intestinal wall was not perforated (Howard *et al.*, 1983).

Crassicauda carbonelli specimens were detected in the penis of a Mediterranean pilot whale. These worms occurred with the cephalic ends deeply embedded in the cavernous bodies, with the caudal extremities hanging freely in the urethra. They caused capillaries to break and the destruction of cavernous tissue leading to necrosis, leucocyte infiltration and hyperplastic proliferation of conjunctive tissue (Raga and Balbuena, 1990).

Eggs and adult worms of *Crassicauda* sp. were found within the mammary glands of whales from the Faroes (prevalence: 18.5%). Histological sections showed three kinds of lesions according to their severity: congestive processes accompanied by light haemorrhages; acute lesions as indicated by abundant lymphocyte infiltration; and chronic lesions defined by intense fibrosis and replacement of glandular parenchyma by non-secretory tissue. The latter appeared with a prevalence of 39.1%. The higher prevalence of these lesions with respect to that of *Crassicauda* sp. seems to indicate that either there is another agent provoking such lesions or that we were unable to detect the nematodes in every case. The latter possibility seems more likely since they usually appeared in low intensities. Eggs occurred in milk samples accompained by neutrophil leucocytes and lymphocytes, indicating a chronic inflammatory process.

Infestations by *Crassicauda* spp. in the mammary glands and adjacent tissue are known in several cetacean species and have been discussed by Dailey and Perrin (1973) and Dailey and Stround (1978). Their pathogenicity was discussed by Geraci *et al.* (1978a). According to them, the occurrence of these worms in the mammary glands may lower the milk production, jeopardising the reproductive success of the herd. However, even though some female pilot whales in this survey showed severe pathologies, we are unable, at present, to assess the impact of this parasitosis in the host population.

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Two Mass Strandings of Pilot Whales (*Globicephala melas*) on the Coast of Iceland

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ABSTRACT

Mass strandings of long-finned pilot whales (*Globicephala melas*) occurred at Rif (West Iceland) in August 1982 and at Thorlákshöfn (Southwest Iceland) in October 1986, involving the death of 38 (out of a herd of approximately 280 animals) and 148 animals (probably the entire school), respectively. Only a few of the animals examined had traces of food in the stomach, the rest were empty. All identifiable food remains belonged to the cephalopod *Todarodes sagittatus*. The age of the animals ranged from 0–34yrs, based on growth layer counts in teeth. Body lengths ranged from 212–595cm in males and 174–475cm in females. Females appear to attain higher ages on average than males. Sexual maturity in this small sample was reached between 6 and 12 yrs of age in females and 11 yrs or more in males. Of the 21 sexually mature females in 1982, 13 (61.9%) were lactating, 4 (19.0%) were resting, 2 (9.5%) were pregnant and 2 (9.5%) animals were pregnant and lactating.

KEYWORDS: PILOT WHALES-LONG-FINNED; NORTH ATLANTIC; STRANDINGS; POPULATION PARAMETERS; REPRODUCTION; MORTALITY; FEEDING; SQUID.

INTRODUCTION

Mass strandings of long-finned pilot whales (*Globicephala melas*) around the coast of Iceland have been known to occur at least several times a century (Sæmundsson, 1937; 1939). Unlike the Faroes (Joensen, 1962; 1976; Hoydal, 1986), no organised Icelandic pilot whale drive fishery developed, probably due to the less regular occurrence of this species in coastal Icelandic waters. However, in the past, both schools of stranded pilot whales and driven schools of pilot whales were a most welcome addition to an often rather poor selection of food (Kristjánsson, 1986). Most of the catches and strandings have occurred in autumn and early winter in southwestern, western and northwestern Iceland, although there have been a few on the northern coast and at least one on the east coast. Sæmundsson (1937; 1939) suggested that the strandings are linked to rather irregular migrations of squid into the shallow waters of Iceland. In recent years, pilot whales have been observed frequently around the coast of Iceland (Gunnlaugsson *et al.*, 1988; Sigurjónsson *et al.*, 1989; Buckland *et al.*, 1993 *et al.*, 1993b) especially to the west and southwest of Iceland in late summer (Sigurjónsson and Gunnlaugsson, 1990).

In the summer of 1982 and early winter of 1986, two mass strandings of pilot whales occurred in Iceland. Biological observations and collections were made at both sites, the first ever made on the species in the area. This paper reports on results of the study.

The stranding at Rif, August 1982

The stranding at Rif or Rifshöfn town (64°53'N, 23°49'W) occurred on 20 August 1982. A large school (around 280 animals, see below) of pilot whales approached the harbour at



Fig. 1. Rif harbour in West Iceland, the site of the stranding in August 1982.

around 0700 hrs at high tide. The weather was good, the wind calm and the sky clear. Rifshöfn is located on the northern side of the Snaefellsnes peninsula (Fig. 1). The harbour inlet is sheltered from the north by a sand reef and faces the large Breidafjördur bay. The mean range of spring tides at Rif is 3.7m and a spring tide of 4.19m occurred at 1957 hrs on the stranding day. The sea bottom off Rif is mostly composed of sand and gravel (median diameter >0.063mm, Gudrún Helgadóttir, MRI, pers. comm.).

At 0730 hrs, a local resident noted that the herd was within 1–2 n.miles northeast of the lighthouse (Fig. 1) and a small fishing vessel was in the vicinity, north of the school. An hour earlier a fisherman leaving the port at Rif had not noted anything unusual. By 0815 hrs, three vessels were north of the animals, apparently preparing for an organised drive of the whales into the harbour area. The whales seemed to be scared by the vessels and passed the lighthouse towards the harbour opening, where the whole school stopped shortly afterwards, the animals milling at the surface close together.

It soon became clear to the local people that they were not well enough equipped to make use of this large herd of pilot whales. They also found it difficult to herd the school into the harbour and, despite repeated efforts, attempts were abandoned at approximately 0945 hrs. Later in the morning, they initiated an organised rescue operation (Fig. 2a), with fishing vessels and rubber skiffs being placed at the harbour





Fig. 3a. A part of the school moving in concentrated subgroups, after being driven out of the harbour at Rif (photo J. Sigurjónsson).



Fig. 3b. Attempts to rescue the stranded whales (photo: K. Einarsson).



Fig. 4. Pilot whales stranded at Rif, W-Iceland near the southern harbour wall (photo J. Sigurjónsson).

opening to scare the animals away. Attempts were made to tow animals away by attaching a rope around the tail stock and some people went into the sea to help the animals to move away from the harbour. However, instead of turning towards open water (by the passage southeast of the lighthouse), the animals headed towards the sand reef north of the harbour mouth. A group of animals then turned in the opposite direction along the south harbour wall, where they finally reached the shore and were stuck on the rocky wall and along the sandy beach to the south (Fig. 2b). At around noon, the low tide made swimming very difficult and despite the desperate efforts of the locals to help the animals out, including actively towing out some animals and cooling them with water, the operation proved unsuccessful; animals gradually beached where the first animals were stranded and some died.

At the rise of the tide later in the afternoon, part of the herd started moving northeast with the active help of the locals (Fig. 3) and at 1700 hrs, when one of the authors arrived at the stranding site, the part of the school that had survived during the day had passed the lighthouse and was moving in smaller groups outside the harbour area. The animals appeared disorientated, but 1–2 hours later they reacted normally towards vessels when approached and at 1830 hrs, 8–10 groups of some 25 whales each moved to the north and northwest, 5–10 n.miles from the coast.

From aerial photographs, it was estimated that there were approximately 280 whales in the entire herd, of which 38 died at or near the southern harbour wall (Fig. 4) in the afternoon. They were examined immediately and at low tide the following day. Some of the whales were flensed by the locals and the meat used for human consumption.

The stranding at Thorlákshöfn, October 1986

On 25 October 1986, a mass stranding occurred near Thorlákshöfn (63°51'N, 21°23'W), Southwest Iceland (Fig. 5). During the preceding night, a school of 148 pilot whales beached and in the morning when the local residents of Thorlákshöfn noted the stranding, most animals were dead. Since the few live animals were in a severe condition and on dry land, the local authorities decided to kill them shortly after they were found. The animals were scattered in groups of 2 to 15 animals along approximately 1km of the gradually



Fig. 5. Thorlákshöfn harbour in SW Iceland, the site of the stranding in October 1986.

sloping sandy beach (Fig. 6), which is unsheltered from the North Atlantic to the south (Fig. 5). The sea bottom off the stranding site is composed of sand and mud, i.e. is of somewhat finer texture than that at Rif. During the stranding the weather was good, with a light wind from the north and the east. The mean range of spring tides at Thorlákshöfn is 2.8m, but the stranding occurred near neap tides, when the mean range in sea water level is around 1.3m. Two of the authors visited the stranding site and made observations the following day, before the local authorities removed the carcasses during the afternoon and evening of the same day. As far as possible, the whales were fully utilised for human consumption or animal fodder.

MATERIALS AND METHODS

The animals were examined and measured on site. Total body length was measured in a straight line parallel to the long axis from the tip of the snout to the apex of the fluke notch. For the 1982 sample, detailed morphometric data were also collected for most animals. The anterior part of the lower jaw (incl. 5–10 teeth) was usually removed with a chain-saw for later study. Few animals were sampled for stomach analysis or reproductive studies in



Fig. 6. The pilot whales stranded at Thorlákshöfn, lying in groups of 2–10 along approximately 1km of the sandy beach (photo J. Sigurjónsson).

1986, while most reproductive organs (including ovaries, cornua width, mammaries, foetuses and testes) and some stomach contents were examined in 1982. An effort was made to collect both ovaries, but in most cases a single testis was chosen randomly for weighing and sampling. Samples were fixed and stored in a 10% formalin solution. Scarring and body condition (blubber thickness measured at two sites) was recorded in 1982 and for several animals in 1986, and blood samples were collected for electrophoretic studies (see preliminary results in 'Arnason and Spilliaert, 1987; Spilliaert and 'Arnason, 1987). A sample of photographs of body colouration was obtained from the 1986 stranding and will be reported elsewhere.

In the laboratory, ovaries were sliced in approximately 2mm sections and examined for numbers of corpora. The diameter of *corpora lutea* and *c. albicantia* were measured to the nearest 1mm on three and two axes, respectively. Ovaries and testes (without the epididymis) were weighed in the laboratory to the nearest gram. Teeth were removed from the jaw, cleaned and decalcified. Each tooth was sectioned centrally through the crown and pulp cavity on a freezing microtome at about 35μ in thickness and stained with Hematoxylin according to Lockyer (1993). Finally they were read three times by the same reader (CL).

RESULTS

Length and sex composition

Fig. 7 show the length distribution of the animals examined in both strandings. Of a total of 38 whales examined in 1982 (Table 1), 12 (31.6%) were males (mean length 433.0cm, SD 118.43) and 26 (68.4%) females (mean length 408.8cm, SD 64.05). Of the 148 whales



Fig. 7. Length frequency distribution of animals that stranded at Rif and Thorlákshöfn. The lower limits of the 50cm length groups are indicated in the figure, i.e. 151: animals 151–200cm of length.

stranded near Thorlákshöfn in 1986, 43 (31.6% of known sex, mean length 425.5cm, SD 122.58) were males and 93 (68.4%, mean length 372.5cm, SD 76.76) were females. The sex of 12 animals (8.1% of the sample) was not determined as they were not accessible at the time of sampling. Although the mean lengths were somewhat higher for the Rif stranding, this was only statistically significant for females (df=109, t=2.184, p<0.05).

No significant difference was found in the sex ratio between the two Icelandic strandings. However, the Icelandic groups had a significantly higher female/male ratio (chi-square = 4.15, p<0.05) than the mean ratio for the Faroese drive fishery, with the value being similar to the pods with the highest female/male ratio (Bloch *et al.*, 1993).

Age and growth

Figs 8 and 9 show the age distribution of males and females in both strandings. Of the 38 successfully aged males, the mean age was 12.4 yrs (SD 7.92) and the range was 1–34 years. The mean age of males in the 1982 sample was 14.8 yrs (n=10 and SD 6.97) and for the 1986 sample 11.6 yrs (n=28 and SD 8.19). This difference was not statistically significant (t-test, p=0.275). In 1986, 25 (89.3%) males were 20 yrs or less, 13 (46.4%) 10 or less and 6 (22.2%) 5 yrs or less.

Table 1

Data on age (years), length (cm) and sexual status of the animals from the strandings at Rif and Thorlákshöfn. The maturity percentage of the Rif-sample is based on examination of gonads, but in the Thorlákshöfn sample maturity was calculated by extrapolation from age (length) data.

	Rif		Thorlákshofn		
	Males	Females	Males	Females	
N	12	26	43	93	
Sex ratio	0.316	0.684	0.316	0.684	
Mean length (cm)	433	409	426	373	
(range)	(212-576)	(219-475)	(170-595)	(174-465)	
Mean age	14.8	17.9	11.6	12.3	
% Mature	50.0	85.7	58(65)	46(42)	



Fig. 8. Age distribution (in years) of stranded animals at Rifshöfn, August 1982.

The female sample from Rif was significantly older (t-test, p<0.01) than the Thorlákshöfn sample with an average of 17.9 yrs (n=26, SD 9.05) compared to 12.3 yrs (n=66, SD 8.44). The total average was 13.9 yrs (n=92, SD 8.94), ranging from less than 1 yr to 34 years. In 1986, 65 (98.5%) females were 30 yrs or less, 55 (83.3%) 20 or less, 31 (47.0%) 10 or less and 18 animals (27.3%) were 5 yrs or less.



Fig. 9. Age distribution (in years) of beached animals at Thorlákshöfn, October 1986.

Fig. 10 shows the age-length relationship in both sexes. Males exhibit relatively rapid growth until reaching 10–12 yrs of age and 4.5–5m of length. The pattern is similar for females, except that growth slows down when they have reached a length of 4–4.5m (10–12 yrs). The animals aged at less than 1 yr or calves of the year (4 females) ranged from 205 to 235cm, while yearlings (2 females and 3 males) ranged from 234 to 283cm. One foetus was near full term (176cm), while the remaining five foetuses were all relatively small, 16.1cm (71g), 20.3cm (170g), 20.7cm (220g), 22.4cm (204g) and 28.5cm (409g).

Apparent annual mortality rates in the Thorlákshöfn sample, calculated by the method of Robson and Chapman (1961) were 0.0766 (SE 0.011) for females and 0.0836 (SE 0.0152) for males. Similar values were obtained from the slope of a log-linear regression analysis, i.e. 0.082 (SE 0.0105) for females and 0.0955 (SE 0.018) for males.



Fig. 10. Age-length relationship in male (a) and female (b) pilot whales beached in Iceland in 1982 and 1986 combined.

Sexual condition and maturity

Males

The growth of the testis in respect to age and length of the animals is shown in Fig. 11. The single testis weight ranged from 0.07 to 4.7kg. Despite the small sample size it seems that a rapid increase in testis weight occurs at a length of less than 5m and at an age of 11 years or more. Six animals of around 5m or less all had a single testis weighing less than 1.5kg, while the remaining nine in the sample were larger than 510cm and had a testes weighing



Fig. 11. Growth of testis (single testis weight; mean or randomly chosen) in relation to age (a) and length (b).

over 2.5kg. These criteria (1.5kg testis weight and approximately 5m body length) correspond to the late maturing stage in animals studied in the Faroe Islands (Desportes *et al.*, 1993).

The testes of eight males were examined for presence of sperm in the epididymis. None of the three testes weighing 1.2kg or less from animals <510cm had sperm present. Of the remaining five animals larger than 510cm and with testes weighing greater than 3kg, two had sperm fluid present.

Females

Measurements of cornua width are available for 20 animals. Average values found were: immature whales 3.75cm (n=2, SD 1.061); resting females 4.78cm (n=4, SD 0.352); and lactating females 5.15cm (n=13, SD 1.038). A single pregnant animal with a 22.4cm foetus had cornua width of 22.0cm. The depth of the mammary gland was measured in 18 females. It ranged from 1.8–9.5cm, averaging 2.95cm (n=4, SD 0.802) for mature resting females, 7.11cm (n=13, SD 2.063) for lactating females and 2.40cm (n=2, SD 2.404) for pregnant females. Table 2 gives data on the four pregnant animals and their foetuses from the 1982 stranding. The two simultaneously pregnant and lactating animals had relatively little milk in the mammaries, and had a slightly smaller *corpus luteum* than the nonlactating pregnant animals.

Serial no.	Age (yrs)	Mammary depth (cm)	Milk	No. of corpora	Diameter of corpus luteum	Sex of foetus	Foetus length (cm)
r. 3	19	5.8	no	7	47.0	M	203
r.6	20	-	yes	5	39.6	Μ	161
r.16	24	2.4	no	8	43.1	F	224
r.3 1	16	5.5	yes	?	39.8	М	207

Table 2

Biological data on foetuses and their mothers from the 1982 stranding. No. of corpora includes both corpora lutea and corpora albicantia.

Two primiparous females (9.5% of mature animals) were found in 1982, both aged at 11 yrs; one measuring 407 and the other 410cm. Both were lactating and had one young *corpus albicans*, i.e. had conceived at age 9–10 yrs. All aged mature females (n=31 in both strandings) were 11 yrs or older except one 397cm lactating animal, aged 8 yrs. The oldest sexually immature female (n=6) was 6 yrs. One female for which only one ovary was examined (no corpora were found) was aged 10 yrs. The largest immature female measured 347cm. Of the 21 sexually mature females in 1982, 13 (61.9%) were lactating, 4 (19.0%) resting, 2 (9.5%) pregnant and 2 (9.5%) animals were simultaneously pregnant and lactating.

The maximum number of ovarian corpora (*corpus luteum* + *corpora albicantia*) was 11. The relationship between the total number of corpora accumulated in pairs of ovaries, with age, is shown in Fig. 12. Regression analysis of corpora numbers on age in animals with one or more corpus gave the following relationship:

age = 1.543C + 11.799 (p=0.0006),

where C is the total number of corpora. This implies a mean age of around 13 years at sexual maturity. This estimate is considerably higher than that indicated from the newly



Fig. 12. Relationship between total corpora number and age in years.

matured females discussed above, as well as that from other areas (Martin and Rothery, 1993; Kasuya *et al.*, 1988b). The regression value is probably biased upward due to the small number of examined animals at ages 6–10.

Other observations

Tooth counts from 11 males that seemed to have a 'normal' set of teeth ranged from 18 to 24 in both the upper and lower jaw. One 20 yr old bull (548cm) had only 12 teeth in the upper jaw and 22 in the lower jaw. A 212cm calf had no teeth while a 260cm calf had 20 and 12 teeth in the upper and lower jaws, respectively. Of twenty-one females examined, the normal number of teeth appeared to be 20 in the upper jaw and 22 in the lower. Of six animals that had lost one or more teeth or had serious tooth wear, all except one were older than 25 yrs and 450cm or larger. The exception was a 12 yr old female (433cm) that had only four teeth in the upper jaw and nine in the lower jaw, most of which were badly worn down. The tooth formulae for the three youngest females were 0:0 (total number in upper and lower jaws) for a 219cm calf of the year with three teeth about to erupt on each side of the lower jaw, 20:20 for a 239cm 2 yr old animal and 18:16 for a 3yr old animal.

In the 1982 stranding, 24 animals were examined for stomach contents. Sixteen (67%) had no trace of food of which three were half full or full of sand. Eight (33%) had traces of food, 4 with distinguishable remains of squid flesh/beaks and the remaining 4 only digestive fluid. All identifiable food remains were of the cephalopod species *Todarodes sagittatus*. Measurements of the cephalopod beaks are given in Table 3 together with calculated mean mantle lengths and wet weights according to the formulae given by Clarke
			wet weight.		
Whale no.	Sex	No. of beaks	LRL (mm)	Mantle length* (mm)	Wet weight* (g)
R.5	М	24	4.20	162.4	127.0
R .7	F	5	3.99	153.7	109.9
R.22	F	5	3.76	144.2	92.9
R.23	F	1	4.39	170.3	144.0

Table 3

Measurements of lower rostral length (LRL) of squid beaks (Todarodes sagittatus) found in the stomachs of pilot whales stranded at Rif. Also given are calculated mean values of mantle length and wet weight.

* Calculated according to formulae given by Clarke, 1986.

(1986). The mean size of the prey is somewhat smaller than the mean figure reported from the Icelandic catch of the species (Jónsson, 1980) sampled somewhat later in the season.

Only 10 animals from the 1986 stranding were examined for food in the stomach; all were empty. In both years, stomach parasites were collected, but these have not, as yet, been analysed.

DISCUSSION

The two strandings under consideration are somewhat different in nature. It seems that fishermen were a causative factor in the 1982 stranding, although it is not impossible that the whales may have already been moving towards the beach. However, the 1986 stranding has no human link. In terms of school structure, the first sample may not be representative of pilot whale pods off Iceland, since the larger part of the herd of around 280 animals was rescued. The difference in length and age distributions in the two samples may simply be due to the higher probability of rescue of smaller animals.

Although the number of animals examined is small, the estimated length and age distributions are similar to those found in other studies on North Atlantic pilot whales, such as those using samples from drive fisheries off Newfoundland (Kasuya et al., 1988a) and the Faroes (Bloch, 1992; Block et al., 1993), and in recent mass strandings that have occurred at the British Isles (Martin et al., 1987). Females have a sharp peak frequency at 4-4.5m, while males are more evenly distributed. No marked departure from growth curves published in the above North Atlantic areas was found. Disregarding the (probably overestimated) regression analysis, the present study indicates an age at sexual maturation of 6-10 yrs in females and at or above 11 yrs in males. These values are not significantly different from those found in more extensive Faroese studies that indicated the onset of sexual maturity at age 9-10 yrs and around 370cm in females and at 12-14 yrs and 480cm in males (Martin et al., 1987). Using these values, 42-46% of the males, and 58-65% of the females in the 1986 stranding had reached sexual maturity (Table 1). The 176cm foetus was probably near-term (Martin et al., 1987; Martin and Rothery, 1993; Bloch et al., 1993), while the small calves of 170cm and 174cm must have been newborns although no umbilical cord was observed. The length distribution of the foetuses coincides with the peaks of conception and births, observed in April-July and July-October, respectively (Sergeant, 1962; Martin and Rothery, 1993; Martin et al., 1987).

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North Pacific

Non-Reproductive Mating In Short-Finned Pilot Whales

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ABSTRACT

The uterine fluid from a total of 87 short-finned pilot whales, *Globicephala macrorhynchus*, caught off Japan by drive or harpoon fisheries was sampled and examined for spermatozoa as an indication of recent copulations that had concluded with ejaculation. Data on the occurrence of spermatozoa on various days after driving indicated that the whales rarely copulated between driving and death, and that sperm can survive in the uterus for three to four days after copulation. The presence of uterine sperm was not correlated with mating season, age or reproductive status of mature females. High sperm concentrations were found in females in oestrus or early pregnancy but also in some anoestrus females; lower concentrations were detected often in mature non-oestrus females including post-reproductive females. The highest sperm density was found in one of five post reproductive females. Although we do not have knowledge on the partners of these females or on the proportion of copulations that ended with ejaculation, we consider that the occurrence of non-reproductive mating probably enhances school stability and increases reproductive success of female kin.

KEYWORDS: PILOT WHALES-SHORT-FINNED; REPRODUCTION; SOCIAL; BEHAVIOUR; NORTH PACIFIC.

INTRODUCTION

Most female mammals only mate during a relatively brief period in the oestrus cycle which may itself be strictly seasonal. Indeed, in many mammalian species such as some rodents (Asdel, 1965), mating outside oestrus is physically impossible since the vagina is fused shut or covered with an epithelial membrane. Departures from this generalised mammalian pattern of a strictly circumscribed oestrus period have been recorded in many catarrhine primates. As summarised by Hrdy (1981), such species exhibit a greater flexibility in the timing of proceptive and receptive behaviours, and a longer duration of oestrus. Some species are sexually receptive throughout all or much of the cycle under natural conditions, even though all primates retain a tendency (which ranges from slight to pronounced in different species) to concentrate matings at mid-cycle. This tendency differs even among species of great apes in the wild (Graham, 1981). The capacity for flexible receptivity of these primates is 'not typically found in other mammals' (Hrdy, 1981). In this paper we report on matings outside the peri-oestrus period in wild shortfinned pilot whales, *Globicephala macrorhynchus* Gray 1846.

MATERIALS AND METHODS

Specimens were collected from the catch of Japanese pilot whale fisheries operating on two geographical forms of the short-finned pilot whale off the Pacific coast of Japan, i.e. 'northern form' and 'southern form' (Kasuya *et al.*, 1988a; Kasuya and Tai, 1993). Our sample was selected arbitrarily by reproductive status and age, and is not a representive sample of the total population.

Thirty-four southern form specimens were collected from three schools which were driven to Taiji (33°35'N, 135°55'E) off central Japan in March (when the incidence of conception is high in this population; Kasuya and Marsh, 1984) and October (when it is low) in 1982 and 1984 (Table 1). Sampling was carried out within four days of driving, and between 0.5 to 5 hours of death. After driving, the whales were held in a net enclosure set in a small bay before being killed.

The 53 northern form specimens were obtained in October and November in 1984 and 1985 at the conception peak of the stock (Kasuya and Tai, 1993) from the 'small-type' whaling catch landed at Ayukawa (38°20'N, 141°30'E), northern Japan. These animals were killed at sea from numerous schools on different occasions (Kasuya and Tai, 1993), and sampled within 5 to 10 hours of death.

The uteri and ovaries (from the cervix to the bursae) were collected from each female. The uterus was injected with 2–3ml of 10% formalin via a new disposable pipette introduced through a small slit made near the proximal end of the uterine horn. The same pipette was then used to transfer 3–4ml of mucus and formalin from the distal portion of the uterus near the Fallopian tube. This mixture was then fixed in 20–30ml of 10% formalin. This was done by a single scientist and care was taken to avoid contaminating the sample. This procedure was repeated if the first sample was contaminated by blood. The sample was collected non-selectively from either the right or left uterus of resting (neither pregnant nor lactating adult), lactating and ovulating females, but usually from the non-pregnant side of pregnant females. This was because the pregnant uterus was usually filled by embryonic membranes which created difficulties in collecting the fluid.

After the samples had settled for at least a week, the bottom layer was removed with a clean micro-pipette, smeared on 3–5 glass slides and stained with 0.2% water solution of toluidine blue for several minutes. The slides were then rinsed, dried and examined under a microscope (magnification 100-200x) without cover slips being used. The mean count of spermatozoa per slide per individual whale was then used as a rough index of the density of sperms in the uterus. Presumed degenerate spermatozoa were recorded separately (Kasuya and Amino, 1985).

Pregnancy in the southern form animals was identified only by macroscopic examination of the uterus. In the northern form animals this was supplemented by histological examination of the endometrium. This latter technique allowed identification of early pregnancy for some females which may have aborted small foetuses after harpooning (Kasuya and Tai, 1993).

The ovaries of southern form animals were examined macroscopically and histologically as outlined by Marsh and Kasuya (1984). Adult females having only old corpora albicantia and no Graafian follicles of measurable size (≥ 1 mm) which were not atretic were classified as post-reproductive (Marsh and Kasuya, 1984). The three diameters of the largest Graafian follicles which were not atretic were usually measured, but one or two diameters were measured for some of the small follicles. The ovaries of the northern form animals were examined only macroscopically for the presence of corpora and the two diameters of the largest Graafian follicles were measured; it was not recorded if the follicles were atretic or not. The geometric mean of these diameters was used as an index of follicle diameter. Although the resultant follicle diameters may not be directly comparable between the two forms, we believe that both are useful as rough indicators of follicular development and for the identification of non-estrous females.

The growth of males was classified using testicular histology and the criteria of Kasuya and Marsh (1984) into four stages, i.e. immature, early maturing, late maturing and mature. Spermatogenesis does not occur at the 'immature' stage (≤ 20 years old). It starts in limited testis tissue at the 'early maturing' (7–16 years old) or 'late maturing' stage (14–29 years old), and occurs in the entire tissue at the 'mature' stage (15–45 years old). The testes weight of these mature males further increases until an age of about 25 years. School structure analysis suggests that males may be socially mature at the mature stage (Kasuya and Marsh, 1984; Kasuya and Tai, 1993).

The absolute ages of the whales were estimated from counts of complete annual growth layers in dentine and cementum following the technique of Kasuya and Matsui (1984). Fractions of a year were rounded down to the nearest integer.

RESULTS

The sample

Each of the three southern form schools contained between two and six sexually mature males (Table 1). The sample of 34 southern form females consisted of one immature, 14 lactating and 19 resting adults. Three of the resting females had a 'corpus luteum of ovulation' *sensu* Marsh and Kasuya (1984). One of these animals also had a large Graafian follicle, but the other two had no measurable follicles. Eight of the 33 adult females were identified as post-reproductive. There were no spermatozoa in the uterus of the immature female that had no measurable Graafian follicles, and it was excluded from subsequent analyses.

The sample of 53 northern form females comprised 2 immature, 5 pregnant, 7 simultaneously pregnant and lactating, 20 lactating (including three having a corpus

School no. Date of driving	29 23/10/82	30 25/10/82	31 01/03/84
Males Immature ¹	5	22	8
Early maturing ¹	4	6 0	2 0
Sexually mature	2	6	3
Females Immature Pregnant Resting Lactating Unidentified	$ \begin{array}{c} 7 \\ 4^2 \\ 8 \\ 10 \\ 1 \end{array} $	$ \begin{array}{c} 6 \\ 12^{2} \\ 6 \\ 11 \\ 9 \\ 2 \end{array} $	6 (1) 6 14 (14) (9) 0
Unknown sex	4	0	26
Total	45 (9)	71 (1)	74 (24)

Table 1

School composition and uterine fluid samples (in parentheses) of southern form short-finned pilot whales. Maturity was determined by gonad examination unless indicated otherwise.

¹ Maturity for some individuals was based on the body length criteria of Kasuya and Marsh (1984).

² Includes one pregnant and simultaneously lactating female.

luteum of ovulation) and 19 resting individuals (including seven with a corpus luteum of ovulation). The reproductive status of two females in early pregnancy was determined using endometrial histology and the foetal length was assumed to be less than 5cm. Out of the 53 female samples, seven resting females (41–61 years old) were older than the ages of the oldest pregnant (36 years) or ovulating (40 years) females known to this population (Kasuya and Tai, 1993), and were considered to be post-reproductive. Two immature females (one 5 years old with a Graafian follicle of 2.0mm; one 6 years old with no measurable Graafian follicle) had no spermatozoa in the uterus and were excluded from the subsequent analyses.

Homogeneity of samples and significance of the sperm density

The estimated index of abundance for the number of sperm in the uterus was based usually on the examination of three slides (occasionally four or five). When the sperm densities are relatively high (1.6-2,990 sperm/slide), sperm are seen on each slide, and the possibility of misallocating these to the 'sperm absent' category is negligible. However, in the case of lower sperm densities (0.2–1 sperm/slide), only one or two spermatozoa were seen on one (12 individuals), two (four) or three slides (one) examined for each individual and misallocation is to be expected; it is likely that examination of more slides would have revealed sperm in some of the samples from the 45 females currently identified as having no sperm in the uterus. A sampling simulation suggested that of the 45 females, 2–3 would perhaps have been misclassified (T. Miyashita, pers. comm.).

For only one northern form animal were both uterine horns sampled. This was a female in early pregnancy that had a 3.5cm foetus in the left uterus and a corpus luteum in the left ovary; it was also lactating. The sperm densities were 11.0 sperm/slide (SD=8.2) in the right uterus and 68.0 (SD=27.8) in the left. The difference was statistically significant (ttest, p<0.05). It is known that the position of ejaculation varies between mammal species from the vagina to the uterine horn (Toyota, 1983), but nothing is known of the position of ejaculation and subsequent sperm transportation in the reproductive tract of female toothed whales. This makes it difficult to evaluate the difference in sperm density between the two uterine horns.

Further potential sources of error in the estimated sperm densities arise from: (1) the great variability in the quantity of uterine fluid among females which presumably reflects changes in the reproductive cycle; (2) the amount of uterine fluid sampled and (3) the procedures used in slide preparation. These have not been evaluated in the present study.

However, we have found in subsequent analyses that high sperm densities are only found in females of a particular reproductive status even when (almost) random samples collected from one of the two uterine horns are utilised. This suggests that the index of uterine sperm density we have adopted is useful in confirming the presence of sperm in particular individuals and in examining the tendency of high sperm density to occur among certain groups of females. However, the index is not suitable for determining the absence of uterine sperm in particular females or in evaluating the importance of differences of sperm densities among individuals.

Persistence of spermatozoa in the uterus

The proportion of southern form females with sperm in the uterus changed with time after driving (Table 2). Combining the data from the three schools gives 11/18 females with uterine sperm on days 0-2 (day 0 is the day on which the driving occurred) and 2/15 on day 4. No sample was available on day 3. The difference was statistically significant (G with William's Correction = 8.02, 1 df, p<0.005). The trend was similar among smaller

Days after driving	0	1	2	3	4	Total
School 29 School 30		1.0	1:3		1:4	2:7
School 31	1:1	1.0	8:3		1:9	10:13
Total	1:1	1:0	9:6			
		11:7			2:13	13:20

Change in uterine sperm occurrence with time after driving, for sexually mature southern form short-finned pilot whales (present:absent).

Table 2

samples taken in March when the incidence of conception was high. Such changes may occur if (1) transport of sperm to the uterus occurs quickly after mating, (2) mating is not common in the enclosure and (3) spermatozoa persist in the uterus for less than three or four days.

In humans, sperm transport to the Fallopian region takes about 15 minutes, while in mammals in general it can take from a few minutes to several hours (Settlage *et al.*, 1973). Human sperm survives in the Fallopian tube for up to 85 hours (Ahlgren, 1975). Among the 51 sexually mature northern form females which were sampled in the wild, 17 had both normal and decayed sperm in the uterine cavity, while nine females had only normal sperm and five females had only decayed sperm. The remaining 20 females had neither. This would occur if sperm only survive in the uterus for a short period and the dead sperm are promptly discharged, as is the case for many mammals (Iriya, 1972).

Therefore, it seems that the presence of sperm in the reproductive tract of female shortfinned pilot whales indicates recent copulation. Although the availability of mates is a key factor in an analysis of this type, it is not considered here as all short-finned pilot whale schools contain some mature males (Kasuya and Marsh, 1984) and our study is directed mainly at the occurrence of mating for females of a certain reproductive status and does not use information on the absence of sperm.

Seasonal change in the presence of spermatozoa in the uterus

Among the southern form females killed on days 0–2, 61% had sperm in the uterus. The proportion was higher (9 of 13 specimens in one school) in March (a month of high conception) than in October when conception is low (2 of 5 specimens in two schools), but the difference was not significant (G with William's correction = 0.43, 1 df, p>0.5). Of the 51 adult northern form females collected during the mating season, sperm was found in 26 individuals (51%), which was similar to the value for the southern form.

The proportion of females having spermatozoa in the uterus varied with reproductive status (Tables 3 and 4), but the sample size was insufficient for further splitting. In the following analyses we have ignored the effect of the sampling season.

Matings in pregnant females

The uterine fluid of pregnant females was examined only in the northern form. Technical problems meant that only early pregnant (foetal body length ≤ 13.3 cm) females were considered (Table 3). Of the 12 pregnant females, only one (with a 5.0cm foetus) did not have sperm present. The sperm density for the 11 females was relatively high, ranging from 1.3–57.7 sperm/slide, with a mean of 17.8 (SD=18.3).

Age ¹ (year)	Follicle diameter ¹ (mm)	Foetal length (cm)	Sperm density (no./slide)	% with sperm	Sample size (no. whales)
Pregnant	· · · · · · · · · · · · · · · · · · ·		<u>, , , , , , , , , , , , , , , , , , , </u>		
21-32	0-6	0-5	1.7-39.5	100	5
6-32	<1	5-10	0-57.7	75.0	4
16-36	<1	10-14	1.3- 9.0	100	3
Total	0-6	0-14	0-57.7	91.7	12
With corpu	s luteum of ovula	tion ²			
27-40	<1	-	0-252.7	50.0	4
21-36	1-10	-	0-341.3	83.3	6
Total	0-10	-	0-341.3	70.0	10
Resting ^{3,4}					
≤ 4 0	<1	-	0.3- 0.7	100	2
≤40	5-14	-	0- 62.7	50.0	2
≥41	<1	-	0-2990	20.0	5
≥41	1-14	-	0- 172.0	50.0	2
Total	0-14	-	0-2990	41.7	12
Lactating ³					
11-30	<1	-	0- 0.7	16.7	6
7-34	1-9.3	-	0- 0.3	18.2	11
Total	0-9.3	-	0- 0.7	17.6	17
Immature 5-6	0-2	-	0	0	2

Table	3

Occurrence of uterine sperm by reproductive status for northern form short-finned pilot whales.

¹ Follicles may include atretic ones. Ovulation is known in this species only up to age of 40 years.

² Three lactating females and seven non-lactating females (none of which were pregnant).

³ Having neither corpus luteum of ovulation nor foetus.

⁴ The total number includes a female with unknown follicle size.

We do not have direct estimates of the dates of conception. However, with an average neonatal body length of 185cm and a mean gestation time of about 15 months for this population (Kasuya and Tai, 1993), the average foetal growth rate is 0.41 cm/day. This includes an increased growth rate in the later part of pregnancy and certainly overestimates the rate in early pregnancy (Laws, 1959). Thus the estimated age of the largest foetus in the present sample, 32 days, is an underestimate. From this we conclude that females in early pregnancy are highly receptive and mate frequently for over one month after conception.

Matings in ovulating females

Three southern form (non-lactating) and 10 northern form (three lactating and seven non-lactating) females were not pregnant but had a corpus luteum of ovulation (Tables 3 and 4).

Sperm were detected in 10 (77%) of these 13 ovulating females. In the northern form females, the sperm density was either low at below 2 sperm/slide (three individuals) or high at 20-400 (four individuals), but it was intermediate (3-20 sperm/slide) in the three southern form females (Fig. 1). The apparent difference in sperm densities between the

Table 4

Occurrence of uterine sperm by reproductive status for southern form short-finned pilot whales.

Senile ¹ or not	Follicle diameter (mm)	Sperm density (no./slide)	% with sperm	Sample size (no. whales)
luteum of ovu	lation ²		·····	
no	0-27	4- 10.3	100	3
				-
no	2-22	0-1562	66 7	3
no	0-12	0	0	5
yes	<1	0 - 1.0	33 3	6
yes	<1	0- 15	50.0	2
n+y	0-22	0-1562	31.3	16
-				
no	0-8	0- 0.8	44 4	Q
no	0-5	0 -0.2	25.0	4
yes	<1	0	0	1
n+y	0-8	0- 0.8	35.7	14
-	-	0	0	1
	Senile ¹ or not luteum of ovul no no no yes yes n+y no no yes n+y	Senile1 or notFollicle diameter (mm)luteum of ovulation2 no $0-27$ no $0-27$ no $0-12$ yesyes<1 n+y $0-22$ no $0-12$ yesyes<1 n+y $0-22$ no $0-8$ no 0-5 yesno $0-8$ no 0-5 yesno $0-8$ no 0-5 yesno $0-8$ no 0-5 yesno $0-8$ no 0-7	Senile1 or notFollicle diameter (mm)Sperm density (no./slide)Inteum of ovulation2 no $0-27$ 4-10.3no0-274-10.3no0-120yes<1	Senile1 or notFollicle diameter (mm)Sperm density (no./slide)% with spermInteum of ovulation2 no $0-27$ 4-10.3100no $0-27$ 4-10.3100no $0-27$ 4-10.3100no $0-27$ 4-10.3100no $0-12$ 00yes<1

 $\frac{1}{2}$ Sensu Marsh and Kasuya (1984).

² Neither pregnant nor lactating.

³ Having neither corpus luteum of ovulation nor foetus.



Fig. 1. Variation in uterine sperm densities in the northern form (shaded box) and southern form (black box) short-finned pilot whales. The 'ovulating females' are defined here as sexually mature females having a corpus luteum but no foetus, which can be either lactating or non-lactating, and 'resting females' are sexually mature females that are not 'pregnant', 'lactating' or 'ovulating'.

two forms is not statistically significant. Sperm density apparently has no correlation with follicle size in the northern forms (Spearman rank correlation coefficient r=0.16; n=8; p>0.25 one side). The southern form sample was too small for testing.

From this we conclude that females with a corpus luteum of ovulation are as receptive as females in early pregnancy.

Matings in lactating females

Of the 17 northern form and 14 southern form lactating females that were neither pregnant nor ovulating, sperm were found only in three (17.6%) northern form and five (35.7%) southern form animals. These proportions were the lowest among the four reproductive stages classified in the present study (Tables 3 and 4). The sperm densities in these eight lactating females were low at less than 1 sperm/slide. Presence or absence of sperm showed no correlation with follicle size or age (Table 5).

 Table 5

 Comparison of follicle size (mm) of short-finned pilot whales between females having uterine sperm and those without.

Status	Range	Mean	SE	Sample size
Resting northern forms		· · · · · · · · · · · · · · · · · · ·		
With uterine sperm	0-14.4	4.4	2.7	5
Without uterine sperm	0-14.5	3.0	2.3	6
Resting southern forms				
With uterine sperm	0-22.2	5.2	4.2	5
Without uterine sperm	0-12.5	1.8	1.1	11
Lactating northern forms				
With uterine sperm	0- 3.0	1.5	0.8	3
Without uterine sperm	0- 9.3	2.3	0.7	14
Lactating southern forms				
With uterine sperm	0- 8.0	4.8	1.4	5
Without uterine sperm	0- 8.5	2.3	1.0	9

From this we consider that lactating females can be receptive to males irrespective of the level of follicular development.

One southern form female in lactation (52 years old with no measurable Graafian follicle) was identified as post-reproductive and no sperm were detected. All the lactating females of the northern form were younger than the age of the oldest known ovulating female and could not be classified as post-reproductive on the basis of age (Table 3).

Mating in resting females

We examined 12 resting northern form and 16 southern form females that had no corpus luteum of ovulation (Table 3 and 4). Sperm were found in five (41.7%) northern form and five (31.3%) southern form animals (Tables 3 and 4). The densities were apparently bimodal at below 2 sperm/slide and over 60 sperm/slide (Fig. 1). The former corresponds to that found in lactating females and some ovulating females, while the latter corresponds with densities found for many ovulating females and females in early pregnancy.

Sperm density apparently has no correlation with follicle size or age (Fig. 2). The mean follicle sizes did not differ between females with or without sperm (Table 5). Sperm were even found in resting females with no measurable follicles (<1mm, four individuals with 0.3–1.0 sperm/slide) and high densities were found for animals with barely measurable follicles (1mm, one northern form female with 2,990 sperm/slide).



Fig. 2. The relationship between uterine sperm density, the female's age and the diameter of Graafian follicles in the northern form (open circle) and southern form (closed circle) short-finned pilot whales. The sperm density is expressed by the average number of spermatozoa per slide. Graafian follicles of less than 1mm are plotted as 1mm, but larger follicles on the correct scale. U indicates individuals of unknown age. For female reproductive status see Fig. 1.

Eight resting females of the southern form were determined as post-reproductive from ovarian examination (Marsh and Kasuya, 1984), although three had some sperm in the uterus (0.25–1.5 sperm/slide). Of the seven northern form females which were estimated as post-reproductive from their ages (41–61 years old), one (41 years old) was found with uterine sperm density of 172.0 sperm/slide and a 14.4mm Graafian follicle, and another (44 years old) with 2,990 sperm/slide and a 1.0mm follicle (Fig. 2). It is not possible to consider the case of the former individual in any more detail because its age was too close to the age of the oldest ovulation known to this population (40 years) and it was not known if the large follicle was attretic or normal. However, the latter individual shows that post-reproductive females (thus in anoestrus) can be receptive and copulate successfully with mature males.

DISCUSSION

Short-finned pilot whales are oceanic, and to date most information on their social behaviour has been deduced from carcase analysis (Kasuya and Marsh, 1984; Kasuya and Matsui, 1984; Marsh and Kasuya, 1984; 1986; Kasuya and Tai, 1993). They live in cohesive schools of 15–50 whales that are breeding units composed of adult males, adult females spanning the entire range of age and reproductive status, and immature animals of both sexes. They have a multi-male polygynous breeding system; mature males are about twice as heavy as females and on average there are eight mature females in a school per mature male. All schools contain several mature males which produce spermatozoa continuously. Schools also contain an average of approximately one early or late maturing male per 10 mature females. Such males produce spermatozoa at least seasonally. From the age composition of the schools it appears that males leave their mother's school at puberty, while females perhaps remain there for life.

Our data on the female short-finned pilot whale suggest a similar trend away from strict hormonal control of sexual receptivity to that found in some higher primates. Hrdy (1981) identified a continuum of sexual activity in primates, from those species in which receptivity appears to be under strict hormonal control and is advertised by conspicuous sexual swellings, to those species which are fairly continuously receptive throughout their cycle and do not advertise receptivity with any conspicuous displays. An exception to this generalisation would be the pygmy chimpanzee (*Pan paniscus*), which has a conspicuous cycle of sexual swelling but is receptive in the wild (Kuroda, 1982) and in captivity (Savage-Rumbough and Wilkerson, 1978) during any period of the cycle. Michael and Zumpe (1970) have shown that the only measure of reproductive activity in rhesus monkeys (*Macaca mulatta*) reliably correlated with a particular stage of a female's reproductive cycle under laboratory conditions is the frequency of male ejaculation which is highest at his partner's mid-cycle.

The female short-finned pilot whale probably exhibits no morphological display, although the possibility of some other displays (e.g. chemosensory) cannot be excluded at present (Herman and Tavolga, 1980; Kuznetzov, 1990). In the absence of behavioural data, it is difficult to place the short-finned pilot whale in such a continuum as it is not known whether it is the frequency of copulations, ejaculations, or both that is greatest at oestrus and is responsible for the frequency and density variations in sperm found in the uterus.

Learning from experienced partners is essential for the accomplishment of normal copulation among chimpanzees (*Pan troglodytes*), particularly males (reviewed by Nadler, 1981). The precocious sexual behaviour (including intromission) commonly observed between immature male and adult female chimpanzees (Tutin and McGinnis, 1981) has an educational function. Such a possibility cannot be excluded for short-finned pilot whales, and the common occurrence of low density sperm common in non-oestrus females might, in part, be attributable to copulation with males before full maturation.

In the higher primates, the tendency away from strictly cyclical female receptivity is characteristic of species both with and without pair bonding and of species both with and without extensive male parental investment (Hrdy, 1981). These observations have challenged the theory espoused by Morris (1981) that 'continuous' female sexual receptivity is an uniquely human characteristic which evolved to strengthen the pair bond and thereby increase paternal investment. This theory is also challenged by our knowledge of the social behaviour of the short-finned pilot whale. Short-finned pilot whales live in schools which are apparently highly cohesive; they are frequently involved in massstranding incidents (e.g. Casinos and Bou, 1980). Although we have no information about paternal investment in the short-finned pilot whales, maternal investment is substantial. A single calf is born after a gestation period of about 15 months and is nursed for a minimum of about two years. The calves of older females may be nursed for considerably longer than this, and the care of successive offspring frequently overlaps. Females may live for over 60 years but stop bearing calves before age 40. Only about 10% of adult females become pregnant each year, usually after about two diffusely seasonal ovulations. This averages out to only about 1.6 oestrus females per mature male per year. However, even though the mortality rate of mature males is significantly greater than that of mature females, there is no morphological evidence of the rigorous inter-male fighting in the short-finned pilot whale such as that known for the sperm whale, *Physeter macrocephalus* (Kasuya and Marsh, 1984; Kato, 1984).

We suggest that there has been selection in favour of receptivity by female pilot whales at times when pregnancy is unlikely as a mean of enhancing school stability: firstly, by reducing inter-male fighting; and secondly by reducing the need for mature males to move among schools in search of mates. The presence of adult males will also be beneficial for fertilization of female kin as well as in defending the school from predators. A similar explanation was proposed to explain such behaviour in the pygmy chimpanzee (Savage-Rumbough and Wilkerson, 1978; Kuroda, 1982). This can be regarded as a generalisation of Morris's (1981) explanation for the 'continuous' sexual receptivity of the human female, a generalisation applicable to species both with and without pair bonding and with and without extensive male parental investment.

A stable social environment would be important to the success of species such as these with low reproductive rates and long offspring dependency. However, there appears to be a wide variety of social and reproductive strategies among odontocetes with such a life history pattern. Amos et al. (1991) identified paternity for foetuses in schools of longfinned pilot whales (G. melas) and found that only for foetuses smaller than 20cm could the fathers be identified as coming from the same school. This suggested relatively rapid alternation of adult males in the school. However, females of this species do not show a distinct age-dependent decline in pregnancy rate or an extended post-reproductive life as found in the short-finned pilot whale (Kasuya et al., 1988b; Martin and Rothery, 1993). Further work is needed to determine whether both species of pilot whales have a similarly stable social structure. Killer whales (Orcinus orca) in the Vancouver Island area are another toothed whale species whose social structure has been studied extensively (Bigg et al., 1990). Although they live in stable matrilineal schools and have a low reproductive rate, both sexes appear to remain in their school of birth even after reaching sexual maturity. This suggests that they have achieved a stable social structure in a different manner to that of short-finned pilot whales, and have possibly evolved a different mating system. Sperm whales are also known to form stable matrilineal nursing schools and have a low reproductive rate (Best, 1979; Best et al., 1984; Whitehead and Waters, 1990). Adult males move in the mating season to lower latitudinal waters, and join the nursing schools for mating only for 3-6 hours each (Whitehead and Waters, 1990). Intra-male fighting is common on the breeding grounds as deduced from the tooth marks on the body (Best, 1979; Kato, 1984). Examination of foetal length distributions suggest that synchronous ovulation occurs with the arrival of adult males in the school, with the function of minimising the disruption caused by mating on the stability of the schools (Best and Butterworth, 1980). These examples illustrate the possibility of various types of mating system evolving within the toothed whales that all result in a stable social structure, extended maternal investment or low reproductive rates.

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Life History of Short-Finned Pilot Whale Stocks off Japan and a Description of the Fishery

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ABSTRACT

The life history of the short-finned pilot whale off the Pacific coast of northern Japan (the northern form) is analysed using samples taken at the beginning of the most recent period of exploitation by the small-type whaling in the southwestern part of the stock's range. The results are compared with those previously reported for the same species off southern Japan (the southern form), which differs in the shape and brightness of the saddle mark and in the shape of the melon of adult males. The two stocks are similar in age at maturation, breeding life span, age dependent decline in reproductive activity and longevity. However, the northern form is larger by about 45cm in neonatal length and 1-2m in asymptotic length, and breeds more seasonally with a breeding peak about 5-6 months later. This breeding pattern was probably derived from that of the southern stock, and was modified to enable yearlings to switch their major source of nutrition from milk to solid food during the summer season when squid are abundant. The larger body size may increase the survival of newborn calves produced in colder months. The differing morphology, geographical segregation and similarity in the life history strategy of these two stocks suggest that they are members of two geographical races or subspecies, which might be found to include several stocks in the greater geographical area of the North Pacific.

KEYWORDS: PILOT WHALES-SHORT-FINNED; NORTH PACIFIC; WHALING-MODERN; STOCK IDENTITY; TAXONOMY; MORPHOLOGY/ANATOMY; POPULATION PARAMETERS; REPRODUCTION; MORTALITY; GROWTH/ LENGTH DISTRIBUTIONS.

INTRODUCTION

Previous studies on the life history of the short-finned pilot whale, *Globicephala* macrorhynchus Gray, 1846, off southern Japan (Kasuya and Marsh, 1984; Marsh and Kasuya, 1984; 1986; Kasuya et al., 1993) have revealed their specialised social structure and reproductive strategy. The estimated annual pregnancy rate of 13% was one of the lowest in the toothed whales, and the rate was found to decline rapidly with increasing age until age 36 years when it reached zero although females of this age still have a mean life expectancy of 14 years. Pilot whales appear to live in cohesive matrilineal schools and the mother-calf association is thought to last until around the age of sexual maturation in males (at 15–22 years) and perhaps after maturation in females (at 7–12 years). The old, low- and post-reproductive females comprise a significant part of the school and probably contribute towards its maintenance and the survival of its younger individuals.

After about a 25 year pause in exploitation and following the rise in the price of whale meat, in 1982 some Japanese small-type whaling vessels¹ resumed the hunting of short-finned pilot whales off the Pacific coast of northern Japan. Miyazaki (1983; 1993), using

¹ Vessels less than 50 gross tons and using a 50mm or smaller calibre harpoon gun, licensed to take minke whales and toothed whales other than sperm whales.



Fig. 1. Saddle marks of adult male short-finned pilot whales off the Pacific coast of Japan. Top: northern form. Bottom: southern form.

materials obtained in the 1982 season, showed that the animals were morphologically distinct from conspecifics off southern Japan and this stimulated further studies on the stock. Kasuya *et al.* (1988) listed the visual characteristics separating the two forms as the shape and brightness of the saddle mark (Fig. 1) and the contour of the adult male melon when seen from above (Fig. 2). They described the segregation between the two forms in the western North Pacific and suggested that the short-finned pilot whales in the eastern North Pacific might similarly be segregated. Miyashita (1992) estimated the population size from sightings data to be about 5,300 individuals. Wada (1988), based on isoenzyme analyses, reported that the genetic differentiation between the two forms was of a magnitude normally expected between stocks.



Fig. 2. Shape of the melon of short-finned pilot whales off the Pacific coast of Japan. Left: northern form adult male (720cm in body length). Middle: southern form immature male (409cm). Right: southern form mature male (518cm). The scale is different between the three photographs.

The present study analyses the life history of the northern form of the short-finned pilot whale using material collected from the small-type whaling catch. It compares the life history strategies of the two stocks off Japan at an early period of significant exploitation for both. The description of the whaling operation and its regulation are given in some detail, in order to facilitate understanding of the nature of the samples and to provide a historical record of the fishery.

MATERIALS AND METHODS

Information on whaling operations

The records of the whaling operations that have been routinely submitted by the industry to the Fisheries Agency of Japan are used in this study. These include numbers of short-finned pilot whale sightings (number of whales and schools), numbers caught, level of fishing effort, position of catch and surface water temperature at the capture position (Tables 1 and 2). Fishing effort was expressed as the number of catcher's working days (CDW) and daily operation hours. The latter is the total time spent by each vessel in searching, chasing and handling (i.e. excluding the time spent securing and towing the catch). Although operational data are available from 1982–1988, the 1982 data are not used in this paper due to the uncertainty in both the number of whales captured and the accompanying operational data (see below).

Biological materials

Biological material was obtained from northern form whales taken by Japanese small-type whaling off the southern part (37°30'N to 39°30'N) of the Sanriku region on the Pacific coast of Japan and landed at Ayukawa (38°15'N, 141°30'E) in October and November from 1982–1988 (Table 3). Of the 378 animals sampled, 368 (223 females and 145 males) were taken between 1983 and 1988 when 51–100% of the reported catch was sampled (87/125 in 1983, 141/160 in 1984, 62/62 in 1985, 28/28 in 1986, 50/98 in 1988). The 1982 sampling (by N. Miyazaki) was exploratory and the objective was to collect taxonomic materials from a small number of adult individuals. Samples from the 1986 and 1988 seasons (56 females and 32 males) have not been aged.

The majority of the data and samples were collected by the primary author or by trained biologists. Some length data and reproductive samples were collected by industry personnel when biologists were absent from the whaling station, although the teeth of these animals were later collected by biologists (usually only maturity could be identified for these females since the mammary glands were often missing). The identification to stock was made without difficulty using the shape and brightness of the saddle mark behind the dorsal fin as described by Kasuya *et al.* (1988).

Although some biological data (e.g. length, sex and reproductive status) were also recorded in the industry reports, they are not used here because it was not possible to verify their accuracy by examining the relevant biological samples.

Collection of materials and subsequent laboratory analyses used the methods described by Kasuya and Marsh (1984), except for the two minor improvements described below.

(1) The mammary glands of most of the females were examined histologically for the presence of lactation using hematoxylin and eosin stained sections. This avoided misclassification of lactation due to the insufficient experience of some biologists and/or the long postmortem time of the specimen.

Four females reported by two biologists as non-lactating were later identified as lactating as a result of histological analysis. Colostrum was histologically identified for two

pregnant females, one with a 180cm foetus and one with a near term foetus of unknown body length (the foetus was aborted at death but the size of the umbilical cord left in the uterus gave a rough indication of the foetal stage). These two females were classified as pregnant but not lactating.

(2) The endometria of all the females, except for some that were certainly immature or pregnant, were examined to determine pregnancy using criteria described by Benirschke *et al.* (1980) and hematoxylin and eosin stained sections prepared from each uterus or the larger side of each individual. This was necessary because of the possibility that some foetuses could have been lost through the slitting of the carcass in the sea or could have been aborted at death. The latter supposition was confirmed on several occasions by the umbilical cord remaining in the intact uterus or by the observations of gunners.

Histological observation of the endometrium can confirm pregnancies for foetuses over 2.3cm (the smallest foetus of this study) and was used to correct or establish the reproductive status of 20 females (10 pregnant, 1 pregnant and simultaneously lactating and 9 non-pregnant) and to confirm other records of biologists. The ten pregnant females included two that were reported in the field as having aborted at death, one with a fragment of embryonic membrane collected from the uterus and four that were recorded by the biologist as non-pregnant. The nine non-pregnant females included two with embryonic membranes (3 and 15cm long) but without an embryo visible under the dissection microscope (see below).

Age was estimated by counting growth layers in the cementum and dentine of hematoxylin-stained, decalcified, thin longitudinal sections of teeth. An annual deposition of tooth layers was assumed, by analogy with the southern form (Kasuya and Matsui, 1984). Any individual aged between n and n+1 years (n being an integer) was expressed as n+0.5 years.

As the body length was measured either to the nearest 1cm (by biologists) or to the nearest 10cm (by industry personnel), we have grouped all the measurements to the nearest 10cm for most of the following analyses.

In the final section, information on the life history of the northern form is compared with that previously reported for the southern form by Kasuya and Marsh (1984), Kasuya and Matsui (1984) and Marsh and Kasuya (1984; 1986).

WHALING OPERATIONS

Exploitation of the northern form stock prior to 1982

Kasuya and Marsh (1984) reviewed the catch of Globicephalids in Japan. Although they did not distinguish between the southern and northern forms of short-finned pilot whales, recent studies have shown that the two forms segregate at around Choshi Point (35°45'N) on the Pacific coast of Japan (Kasuya *et al.*, 1988). Here we have reconstructed the catch history of the northern form by assuming that takes of short-finned pilot whales north of this point (mainly off Sanriku and Hokkaido) represent the northern form (Fig. 3). All catches of short-finned pilot whales have been identified to stock since the 1983 season.

All catches of the northern form have been made by small-type whalers. Catches reached a peak in the 1949 season and then declined to the 1957 season, possibly due to both socio-economic factors and the depletion of stocks (Kasuya and Marsh, 1984). No statistics are available for the period 1958–67 except for 1965, but from tables 2 and 3 of Kasuya and Marsh (1984) we have estimated the mean annual small-type whaling catch of Globicephalid species throughout Japan as 178. This figure includes northern and southern form short-finned pilot whales, killer whales (*Orcinus orca*), false killer whales



Fig. 3. Numbers of northern form short-finned pilot whales (closed circle and solid line) and all globicephalid species (open circle and dotted line) taken by the Japanese small-type whaling. For years 1958–1964 and 1966–1967, the northern form is not separated from other globicephalid species taken by the fishery throughout Japan (see text). Based on data in Kasuya and Marsh (1984) and Japan Small-type Whaling Association.

(*Pseudorca crassidens*) and Risso's dolphins (*Grampus griseus*), and certainly overestimates the northern form catch. An examination of the total Globicephalid takes in the 1957, 1965 and 1968 suggests that about 30% of the annual take would have been of the northern form (about 50 animals). Thereafter smaller catches were taken until 1982, when Japanese small-type whaling increased.

Operations since 1982

Since 1982, national regulations have been changed annually in an attempt to decrease the annual catch to a level close to 1% of the estimated population size. The 1% rule was arbitrarily decided for tentative use based on the analogy to the killer whale off the Vancouver Island area, which had a similar life history and showed a population increase of about 2.5% (Bigg, 1982) or 1.3–2.6% (Olesiuk *et al.*, 1990).

There were no regulations in force for the 1982 season which lasted from October to November. Initially a catch of 85 pilot whales was reported. In response to doubts expressed by the primary author, this figure was later altered to 172 whales. However, this revision was not accompanied by changes in the reported operation statistics such as effort records and sightings. Although it may be closer to the true catch, we have no basis to test its veracity and we have thus excluded it from most of our analyses. Of the 17 short-finned pilot whales taken by two catcher boats and examined by N. Miyazaki (National Science Museum, Tokyo) from 28 October-8 November, all seven individuals taken on 5 November were of the southern form. The gunners were unfamiliar with the 'chunky' body of this form. Similar individuals were taken by other vessels on the same day, but were not taken during the rest of the 1982 season (Y. Toba, pers. comm.) or during the following seasons (this study). We consider the occurrence of the southern form off Ayukawa to be uncommon (Kasuya *et al.*, 1988).

For the 1983 season, on the advice of the government and biologists, the industry autonomously set the season from 1 October to 30 November with a quota of 175 whales. This quota was divided between seven vessels and resulted in a take of 125 whales for a total effort of 100 vessel-days.

In 1984, the quota and fishing season remained the same but the number of operating vessels was decreased to six. The catch was reported as 'good'. However, the primary author discovered 'hidden' whales being processed by one whaling company, when its reported catch was approaching its limit. Thus, although the total reported catch was 160 whales, this may be an underestimate.

In the 1985 season, the quota system was abandoned because it was thought to encourage under-reporting if the limit was approached before the end of the season; only the length of the fishing season and the number of operating vessels were therefore set. Each of the seven vessels was allowed to operate from 1 October and then for various periods of 10 to 61 days. The period allocated to each vessel was decided by the industry, taking into account the minke and Baird's beaked whale quotas of each vessel. The total number of days was 255, about 77% of the equivalent figure for the previous seasons. In fact, the actual number of operating days was considerably less due to bad weather. This season was felt poor, and ended with a reported take of 62 short-finned pilot whales for a total effort of 77 vessel-days. However, we were informed that one vessel had seen another taking northern form short-finned pilot whales during the minke whale season (i.e. before the pilot whale season began).

In 1986, despite biologists' doubts on its effectiveness, the quota system was reintroduced and a quota of 50 whales set for a season lasting from 5 October to 18 November. A total of 100 days was allowed for the three operating vessels and the quota allocated amongst them. In general those vessels with a longer season received a higher quota. The season was also felt to be poor by the whalers and ended with a reported catch of 28 whales for a total effort of 14 vessel-days.

Operations were suspended in 1987 so that the quota (50 whales) could be carried over to the 1988 season when it was expected that there would be no minke whale quota.

During the 1988 season, five catcher boats operated. The quota was 100 whales (50 + 50 see above) and the season was from 5 September to 30 November. The total number of fishing days allocated was 285. The total reported catch was 98 for a total effort of 90 vessel-days.

The total reported catch for the six seasons (in the seven year period) was 645 whales (Table 1). This is a minimum estimate as it does not include possible under-reporting or mortality of struck-and-lost whales (for which we have no statistics). In recent seasons, heads from hand-harpoons have been recovered from some northern form whales taken by small-type whalers (Y. Yoba, pers. comm.). This suggests that some of the fishermen who take Dall's porpoises using hand harpoons may have tried to take pilot whales. Although no actual takes have been reported during the study period (Anonymous, 1984; 1985; 1986; 1987; 1988; 1989; 1990), it is technically possible to kill pilot whales using electric harpoons and this needs to be examined and monitored in future.

Whaling grounds

Northern form whales are hunted within about 30 n.miles of the coast and between 37°30'N and 39°50'N. The northern range is limited by the time required to tow the catch to the whaling stations at Ayukawa while the offshore range is determined by safety considerations due to the west wind prevailing at this time of the year. In general, northern form whales are found in cold coastal waters extending from the north and are absent in the warm waters near the periphery of the Kuroshio Current (Figs 4–6). This

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Table 1

Year		1982			1983			1984			1985		1986		198	~	
Month	Oct.	Nov.	Total	Oct.	Nov.	Total	Oct.	Nov.	Total	Oct.	Nov.	Total	Oct.	Sep.	Oct.	Nov.	Iotal
Vessels (V)	5	5	5	7	s	7	9	s	9	9	s	9	ю	3	4	2	4
Operation times Days (<i>OD</i>)	68	51	119	40	60	100	46	48	94	56	21	11	14	22	36	32	6
OD/V	13.6	10.2	23.8	5.7	12.0	17.7	7.7	9.6	17.3	9.3	4.2	13.5	4.7	7.3	9.0	16.0	22.5
Hours (OH)	608.7	441.4	1050.1	340.9	514.3	855.2	293.1	364.1	657.3	412.0	139.7	551.7	36.7	187.5	299.5	195.1	582.1
OH/V	9.0	8.7	8.8	8.5	8.5	8.6	6.4	7.6	7.0	7.4	6.7	7.2	5.5	8.5	8.3	6.1	7.6
Sightings Schools (N)	89	85	153	58	115	173	74	139	213	69	35	104	15	80	93	5 8	201
Whales (W)	1670	1400	3070	970 2	2280	3250	667 1	577	2244]	1017	476 1	493	525	975 1	283	535 2	793
S/OD/V	1.0	1.7	1.3	1.5	1.9	1.7	1.6	2.9	2.3	1.2	1.7	1.4	1.1	3.6	2.6	0.8	2.2
WIODIV	24.6	27.5	25.8	24.3	38.0	32.5	14.5	32.9	23.9	18.2	22.7	19.4	37.5	44.3	35.6	16.7	31.0
Whaling	32 ¹	53 ¹	172 ²	34	91	125	50	110	160	36	26	62	28	33	45	20	98
C/OD	1	1	1.42	0.85	1.52	1.25	1.09	2.29	1.70	0.64	1.24	0.81	2.00	1.50	1.25	0.63	1.08
CIOH	١	1	0.16	0.10	0.18	0.15	0.17	0.30	0.24	0.09	0.19	0.11	0.37	0.18	0.15	0.10	0.14
¹ Figure in the in	itial repo	nt. ² La	iter amenk	Jment.													



Fig. 5. Catch positions (closed circles) of northern form short-finned pilot whales and the ground for the squid fishery (shaded area), 1984 season. The species of squid are the flying squid *O. bartrami* (right bottom ground in 1–10 October), and the common squid *T. pacificus* (other grounds) (Gyogyo Joho Service Center, 1984). For other marks see Fig. 4.

Fig. 4. Catch position (closed circle) of northern form short-finned pilot whales. 1983 season. No squid ground was formed within this range. The surface isotherms are from Gyogyo Joho Service Center (1983). The arrow indicates the position of Ayukawa and the numerals at the top left indicate the number of pilot whale catches listed.



Fig. 6. Catch position (closed circles) of the northern form short-finned pilot whale and ground of the common squid *T. pacificus* (shaded area), 1985 season. (Gyogyo Joho Service Center, 1985). For other marks see Fig. 4.

oceanographic information and the fact that the summer range of the stock is centred further north (see Discussion), suggests that the fishery operates near the southern limit of the autumn range of the stock. Whaling operations in such a peripheral location may be greatly affected by fluctuations in oceanographic conditions.

The surface water temperature at the position of catch ranged from 12° to 22°C (Table 2). The upper temperature range in November was about 4°C lower than in October, due to seasonal oceanographic changes not a shift in the grounds. The reported temperature range and its seasonal change roughly concur with Kasuya *et al.* (1988), who found from an analysis of sighting data that the temperature boundary between the two forms of short-finned pilot whales changed seasonally from 18°C (winter) to 24°C (summer).

When the fishing grounds for flying squid (*Ommastrephes bartrami*) or common squid (*Todarodes pacificus*) were within the range of the whaling operation, northern form whales tended to be caught there. This may have been due to the fact that: (1) northern form whales aggregate there for food; and/or (2) whalers tended to visit the squid grounds with the expectation of finding pilot whales there.

Indices of abundance

Small-type whaling vessels exchange information on pilot whale sightings during operations and hunt the same school simultaneously. Therefore the records reported by the gunners may include frequent duplicate sightings. The annual mean number of sightings per operation day per catcher boat ranged between 1.1–2.3 schools (19–33 individuals). This concurs with the general view that each catcher boat may sight one or

Surface	e water	temperatures	at the	catch	position boat	for capt	northern ain.	fo rm	animals	recorded	by	the c	atcher
						-	oce water	temp		C ¹			

Table 2

					Surfa	ce water	tempera	ature °C	1		
Year	Month	12	13	14	15	16	1 7	18	19	20	21
1983	Oct.	_	-	-	2	-	8	17	4	2	1
	Nov.	9	42	26	10	-	4	-	-	-	-
	Total	9	42	26	12	-	12	17	4	2	1
1984	Oct.	-	-	-	3	9	22	16	-	-	-
1704	Nov.	-	-	13	19	62	16	-	-	-	-
	Total	-	-	13	22	71	38	16	-	-	-
1985	Oct.	-	-	-	1	4	10	18	2	-	-
	Nov.	-	-	1	-	12	12	-	-	-	-
	Total	-	-	1	1	16	22	18	2	-	-
83-85	Oct.	-	-	-	6	13	40	51	6	2	1
	Nov.	9	42	40	29	74	32	-	-	-	-
	Total	9	42	40	35	87	72	51	6	2	1

¹ Temperature between n and n+1 is indicated by n (n being an integer).

two schools per day, take several whales from them often within the sight of other catcher boats and tow them to their whaling station at Ayukawa. If no catches were made they would usually return to a nearby port in the evening. With this type of operation the number of pilot whales or schools sighted per unit of effort (SPUE) is probably an imprecise index of whale density.

Catcher boats often chase one school for several hours before they take the first whale and thus the number of whales taken per catcher's operating hours or catcher's working day (CPUE) will also be a crude and insensitive index of whale density.

In fact, both SPUE and CPUE increased from October to November in the five seasons 1982–86 (Table 1). This probably reflects the southerly movement of northern form whales towards the fishing ground in the latter part of the season, presumably following the cooling of the sea and/or migration of food species. In the 1988 season, either the SPUE or CPUE declined from September to November. This may reflect the decline in the number of operating vessels in the latter part of the season rather than any real change in whale density.

Catch composition

The sex composition and reproductive status of our sample is given in Table 3. The percentage of sexually mature individuals in the total female catch was 96.0%; this varied little with month (October – 94.8%; November – 97.3%). The corresponding values are lower for males (56.7% – October to 56.3% – November) and reflect their greater body size. The percentage of sexually mature males in the catch decreased from 65.2% (62 mature and 33 immature or maturing individuals) in the 1983 and 1984 seasons to 38.1% (16 mature and 26 immature or maturing males) for the following three seasons. The difference is statistically significant (Chi-square test, p < 0.01).

Kasuya and Marsh (1984) examined the sex ratio of short-finned pilot whales taken by Japanese small-type whaling after the Second World War, and found a decline in the male proportion for both northern and southern form stocks over time. They interpreted this as reflecting depletion of males which were selectively hunted by the industry. However, it is

Table 3

			Fe	emale	;				Male	;		
Year	Month	I	М	U	Total	I	E	L	М	U	Total	Total
1982 ¹	Oct.	0	0	0	0	0	0	0	0	2	2	2
	Nov.	0	5	0	5	2	0	0	1	0	3	8
	Total	0	5	0	5	2	0	0	1	2	5	10
19 83 ²	Oct.	1	24	0	25	2	3	0	3	0	8	33
	Nov.	1	31	0	32	2	3	Ŏ	17	Ő	22	54
	Total	2	55	0	57	4	6	Õ	20	Ő	30	87
1984	Oct.	0	25	1	26	3	4	1	15	1	24	50
	Nov.	1	42	0	43	2	8	5	27	6	48	91
	Total	1	67	1	69	5	12	6	42	7	72	141
1 985	Oct.	3	29	0	32	0	3	0	1	0	4	36
	Nov.	1	18	0	19	4	3	0	0	0	7	26
	Total	4	47	0	51	4	6	0	1	0	11	62
1986	Oct.	2	14	0	16	3	3	1	5	0	12	28
1988	Oct.	0	17	0	17	0	3	0	10	0	13	30
	Nov.	0	13	0	13	3	3	0	0	1	7	20
	Total	0	30	0	30	3	6	0	10	0	20	50
83-88	Oct.	6	109	1	116	8	16	2	34	3	63	179
	Nov.	3	109	0	112	13	17	5	45	7	87	199
	Total	9	218	1	228	21	33	7	79	10	150	378

Northern form short-finned pilot whale samples used in the present study (1986 and 1988 samples are not aged, no operation in the 1987 season). Maturity: I = immature; E = early maturing; L = late maturing; M = mature; U = unknown.

¹ Non-random sample in October and November.

² Excluding 20 females and eight males examined by industry personnel while biologist was absent from Ayukawa.

unclear whether higher fishing mortality, learning to avoid ships, or a combination of both has led to the decline in the proportion of males in the catch. Adult males may have experienced much more severe chasing than females because of their greater body size and because there are usually fewer adult females than males in the same school (Kasuya and Marsh, 1984). This may result in males learning more quickly than adult females to avoid catcher boats.

LIFE HISTORY

Males

Sexual maturity and breeding longevity

Males were classified into the four maturity classes of Kasuya and Marsh (1984) using the proportion of mature tubules (i.e. those having spermatozoa, spermatids or spermatocytes) found histologically from samples taken from the centre of testis, i.e. *immature* (100% immature tubules), *early maturing* (<50% mature tubules), *late maturing* (>50% and <100% mature tubules) and *mature* (100% mature tubules).

The weight of a single testis of a northern form male is correlated with its maturity status (Fig. 7 and Table 4). After a rapid increase in weight at between ages 13 and 18 (Fig. 7), the testes apparently cease to grow at around 25 years and at variable testis weights over 2.5kg (the largest testis weighed 7.2kg). Larger individuals tended to have heavier testes, as was observed in the southern form (Kasuya and Marsh, 1984). The restricted sampling season prevented the examination of any seasonal changes in the testis. The present sample probably represents the status in the mating season (see below). The mean weight of a single testis at the attainment of the 'mature' stage is approximately 0.9kg, over twice the corresponding value for the southern form (0.400kg) calculated by Kasuya and Marsh (1984).

Body length is also correlated with maturity in northern form males (Table 4 and Fig. 8). Sexual maturity is attained at between 5.0 and 5.9m (the average is around 5.5 to 5.6m). It is likely that the fishery may be selective by body length but not by maturity, although the hiatus in body lengths at around 5.5m suggests that pubertal males will be underrepresented in the sample. This would result in our estimate of average body length at sexual maturation being an underestimate.

An examination of the mean growth curve gives a length of 5.6m for age 17 years, the average age at sexual maturity. This is the present estimate of the average body length at sexual maturity of male northern form short-finned pilot whales. This is in good agreement with the above range, 5.5–5.6m, in view of the possible bias mentioned above and other uncertainties that surround the mean growth curve and the average age at sexual maturity. The average body length at sexual maturity was 4.22m in the southern form males (Kasuya and Marsh, 1984).

Maturity is also correlated with age in northern form males (Fig. 8 and Table 4). Spermatogenesis begins at various ages between 4 and 18 years (and even earlier in a few individuals as indicated by testicular smear examination), although the major increase in the proportion of fully mature individuals occurs between ages 14 and 19 years (Fig. 9). The age at which 50% of the individuals are mature is between 16 and 18 years, which is close to 16.5 years or the midpoint of the above age range of full maturation. Kasuya and Marsh (1984) reported the corresponding age of the southern form as 17.0 years.

Kasuya and Marsh (1984) found that male maturity was correlated with both body length and age in the southern form and thus that larger individuals tended to mature at a younger age. It seems probable that this will also be the case for the northern form. If the fishery selects larger individuals then the sample will contain more adult individuals since they are larger than immature individuals of the same age. This will lead to an overestimate of the proportion of mature individuals in each age class, and thus an underestimate of the age at 50% maturation. Although selection for large individuals will not

Maturity	stages for northern form males determined from testicular histology (sample	sizes	in			
parentheses). Body length and testis weight data: 1982-1986 and 1988 seasons.						
Age data: 1982-1985 seasons.						

Table 4

Maturity stages	Body length (m)	Age (Year)	Weight of single testis (g)
Immature	3.1-5.4 (21)	2.5-17.5 (14)	30- 250 (21)
Early maturing	3.5-5.9 (33)	4.5-17.5 (24)	58- 450 (32)
Late maturing	4.5-5.9 (7)	13.5-18.5 (6)	450- 960 (8)
Mature	5.0-7.2 (79)	14.5-44.5 (59)	675-7200 (76)







Fig. 8. Male maturity by body length (top, 1982–1985 and 1988 seasons) and age (bottom, 1982–1985 seasons) in northern form short-finned pilot whales. The white column in the bottom graph represents the total of the above three categories. Maturity was determined based on histology of testis tissue.

bias the age range between the oldest immature and youngest mature individuals, the range will vary considerably with sample size. Given these problems we consider that there is no significant difference between the mean age at sexual maturation for the two short-finned pilot whale stocks off Japan.



Fig. 9. Age related changes in the relative density of spermatozoa in the epididymal and testicular smears of northern form short-finned pilot whales (1983–1985 seasons). a: absent, b: doubtfully present, c: scanty, d: intermediate, e: copious.

The above analyses use a somewhat arbitrary criterion of male maturity that is independent of the actual ability to reproduce. Fig. 9 shows the relationship between age and relative abundance of spermatozoa in testicular and epididymal smears. Sperm density has been classified following Kasuya and Marsh (1984) into the following categories: (1) *absent*; (2) *doubtfully present* (one or two spermatozoa in several fields); (3) *scanty* (less than ten per field); (4) *intermediate* (a level common on smears of active testes); and (5) *copious* (a level found usually only on epididymal smears of active males). Kasuya and Marsh (1984) found that for the southern form, sperm production was seasonal in the early stages of maturation (usually with a low level of sperm production) but became aseasonal as maturation progressed. As the material from the northern form was probably collected during the mating season (see below), sperm production may be maximal for all growth stages. Although sperm formation and transport to the epididymis began in some northern form individuals even before three years of age, high sperm densities (categories 4 and 5) were not attained until after 14 years in both tissues.

After about 18 years of age, the sperm density in the epididymal smear ceases to increase with age. This is a few years after the density in the testicular smear reaches a plateau. Although it is unclear whether younger males can successfully participate in reproduction, it is safe to conclude that northern form males are physiologically able to reproduce at age 18 years. This is similar to the average age found for the histologically defined mature status. From a comparison of histological maturity of males and school structure, Kasuya and Marsh (1984, p.307) concluded that southern form males are 'socially mature' when they attain histologically mature status, i.e. at 17 years of age.

The histological examination of testis tissue in this study was probably too coarse to indicate an age-dependent decline in the reproductive activity in males, if one exists. However, the analysis did show that: spermatogenesis occurred even in the oldest male (age 44.5 years); testis weight did not decline in old age; and sperm density in the testicular and epididymal smears did not decline with increasing age (Fig. 9). These data suggest that, as for the southern form (Kasuya and Marsh, 1984), males of the northern form are physiologically capable of reproduction for the remainder of their lives after attaining maturity.

At the beginning of the most recent period of exploitation (1983 and 1984) about 2.8 times as many adult females as adult males (218:79) were taken (Table 3). Males, of course, have a larger body size and are thus preferable to the industry. It has also been confirmed that several adult males were often taken from a single school (Kasuya, unpublished data). This suggests that the northern form has a multi-male polygynous reproductive system, similar to that indicated for the southern form (Kasuya and Marsh, 1984). In such a community, males will not recognise their own offspring and paternal



Fig. 10. Male body length plotted on age, northern form short-finned pilot whales (1982–1985 seasons). Star indicates southern form of the same sex taken by the fishery in 1982 and examined by N. Miyazaki.
investment in rearing the calves will be minimal. The death of the father will thus have a negligible effect on the survival of the newborn calves, and selection can work towards males that breed for their entire post-pubertal life.

Growth curve

Due to the selection for large individuals, the current sample cannot, in a strict sense, be used to obtain the true length/age relationship (Fig. 10). The resultant bias is probably greater for individuals <12 years or 4.5m, which corresponds to the left side slope of the female body length frequency (Fig. 11). We have not therefore constructed a growth curve for immature males.

After reaching puberty at around 15 years, the male growth rate declines with age (Fig. 10) until growth ceases between 25 and 30 years. This is similar to the value of 27 years found for the southern form (Kasuya and Marsh, 1984). The mean length of the 11 males over 30 years of age was 6.5m (SD=0.33) (Table 5). This represents the present best estimate of the mean asymptotic length. Fishing selectivity will have little effect on this

		Female			Male		
Age	n	Body length	SD	n	Body length	SD	
0.5	_	-	-	-	-	-	
1.5	1	286.0	-	-	-	-	
2.5	-	-	-	2	315.0	5.0	
3.5	-	-	-	-	-	-	
4.5	1	355.0	-	1	354 .0	-	
5.5	1	380.0	-	5	389.4	24.1	
6.5	4	385.5	16.2	3	418.7	20.4	
7.5	2	399.5	1.5	3	429.0	11.5	
8.5	1	434.0	-	1	440.0	-	
9.5	-	-	-	2	469.0	1.0	
10.5	4	415.0	6.1	4	467.3	10.4	
11.5	3	426.0	3.6	6	486.2	24.5	
12.5	1	452 .0	-	1	520.0	-	
13.5	1	410.0	-	5	512.0	26.1	
14.5	1	438.0	-	4	555.8	70.5	
15.5	4	436.3	2.6	5	506.6	39.7	
16.5	4	438.5	5.1	3	575.3	10.5	
17.5	3	456.0	13.6	4	551.8	44.0	
18.5	5	454.8	11.4	7	571.1	82.1	
19.5	4	440.0	0.0	5	612.2	21.7	
20.5	6	456.8	5.6	6	604.3	23.6	
21.5	6	461.0	10.2	3	587.3	14.5	
22.5	5	449.8	15.8	4	598 .0	30 .0	
23.5	14	459.4	20.1	5	587.8	40.4	
24.5	9	465.6	15.9	3	639.3	7.4	
25.5	9	467.3	25.3	5	654.2	23.4	
26.5	5	462.0	9.8	1	629.0	-	
27.5	10	466.6	17.5	2	633.5	15.5	
28.5	5	465.8	16.4	2	650.5	7.5	
29.5	6	458.2	18.7	8	651.6	26.7	
≥30.5	58	467.4	14.6	11	650.4	33.5	

Table 5					
Age-length key for northern form animals; mean body length in cm (1982-1985 seasons).					

estimate as the fishery also took a large number of adult females, most of which were smaller than any of the adult males in the catch. The estimated asymptotic length is about 1.8m larger than the 4.73m estimated for the southern form by Kasuya and Matsui (1984).

Females

Sexual maturity

Females having at least one corpus luteum or corpus albicans were classified as sexually mature.

The body lengths of the smallest mature and the largest immature northern form females were 4.0m and 4.2m, respectively (Fig. 11). Half the females are sexually mature



Fig. 11. Female maturity by body length, northern form short-finned pilot whales (1982--1985 and 1988 seasons). Black column represents mature individuals, white immature, and shaded squares an individual of unknown maturity. Maturity was determined based on the presence of at least one corpus luteum or albicans in the ovaries.



Fig. 12. Female maturity and reproductive status by age, northern form short-finned pilot whales (1982-1985 seasons).

at between 3.9 and 4.0m, considerably larger than the mean body length at attainment of sexual maturity for the southern form (3.16m; Kasuya and Marsh, 1984).

The youngest mature and the oldest immature females were aged at 5.5 and 11.5 years, respectively (Figs 12 and 13), although it must be remembered that the sample size is small. The middle value of 8.5 years may be considered close to the average age at attainment of sexual maturity, although the selection for large individuals by the industry may possibly render this an underestimate. The limited evidence available does not



Fig. 13. Female body length plotted on age, northern form short-finned pilot whales (1982–1985 seasons). Individual in parentheses was excluded from the analyses.

suggest that the values for the northern form are significantly different from those (7–12 years, mean 9.0 years) for the southern form as estimated by Kasuya and Marsh (1984). However, further work is necessary to confirm or refute this.

Growth curve

The selection for larger individuals in the catch will produce an upward bias in the female growth curve. Although the magnitude of the bias is unknown, it will be larger than for males as adult females are both smaller and more abundant, providing more chance for the fishery to choose larger individuals. The growth curve will be totally unreliable for ages below 15 years, when most females are less than 4.6m (the peak of female length frequency, Fig. 11).

After age 15, the mean body length continues to increase but at a slower rate until between ages 25 and 30 (Fig. 13). The lower end of this range is not to dissimilar to the 22 years estimated for the southern form (Kasuya and Matsui, 1984). The mean body length of the 58 northern form females over 30 years was 4.67m (SD=0.15) (Table 5). Again, this value will not be too affected by fishing bias, and can be considered the best estimate of the mean asymptotic length of the females. It is about 1m larger than the corresponding figure (3.64m) for the southern form estimated by Kasuya and Matsui (1984).

Foetal lengths, breeding season and gestation time

Any analyses of the available data to examine breeding season and foetal growth will suffer from selection for larger individuals and the short sampling season.

Two non-pregnant females (27.5 and 17.5 years old) each with a corpus luteum were found with embryonic membranes in the uteri (3cm and 15cm in length) with some abnormal features including unusual thickness, low transparency or an irregular surface. No embryos could be identified under a dissecting microscope (10–20x) and the endometria did not show features characteristic of pregnant females. However, the former contained a structure sometimes termed a 'cystic placental mole' that Benirschke and Marsh (1984) considered might be derived from a degenerated embryo. This suggests the occurrence of intra-uterine mortality of embryos soon after conception, as has also been found for the southern form (Benirschke and Marsh, 1984).

Foetal lengths in the sample ranged from 2.3 to 180cm, and had two modes, <15cm and >150cm (Fig. 14). Although the latter peak represented fewer foetuses, this may not reflect a true difference because uteri containing large foetuses are more likely to be lost by slitting the carcass on the boat and by being discarded. Large foetuses were only brought to the whaling station after requests were made to the gunners. The two modes appear more distinct than those reported by Kasuya and Marsh (1984) for the southern form. This supports a not unreasonable hypothesis that the boreal stock has a more distinct seasonality in breeding.

Kasuya (1977) obtained the following interspecific relationship between mean neonatal length (X, cm) and daily foetal growth rate for the linear part of the growth curve (Y, cm/day) for seven small cetacean species:

$$Y = 0.001462X + 0.1622.$$

Substituting a mean neonatal length of 185cm (see below) gives an estimated foetal growth rate of 0.433 cm/day. Since the length difference between the two foetal groups is about 135cm, then the difference between the two conception peaks is about 135/0.443=312 days or 10.3 months. Although this calculation is crude, it seems reasonable to conclude that the northern form whales have only one breeding season and that the two foetal length modes represent mating peaks in two successive years.



Fig. 14. Foetal length frequencies, northern form short-finned pilot whales.

The above analyses suggest that mating had begun prior to the fishing season (October and November) and probably continued during it. This view is supported by the fact that some 12% of adult females possessed corpora lutea of ovulation (smaller than those of pregnancy) but for which the persistence was yet unknown (Table 6). If it is assumed that northern form foetuses take 2–3 months to reach 15cm by analogy with the southern form (Kasuya and Marsh, 1984), the breeding season will begin in about August. If the peak of the season is in October/November, then the full season will last for 5–6 months, i.e. from August to January.

The larger foetuses (150 to 175cm) will be near term. However, the decline in foetal length frequency over 170cm may not be due solely to parturition but may also reflect seasonality of conception. Ohsumi (1966) obtained the following interspecific relationship between mean neonatal length (Y, m) and the mean body length of females at sexual maturation (X, m): $Y = 0.532X^{0.916}$

Substituting the range 3.9 to 4.0m found in this study gives an estimated mean neonatal length of 1.85 to 1.89m.

For the southern form females, Kasuya and Marsh (1984) estimated mean body lengths at birth and sexual maturation of 1.40m and 3.16m, respectively. If the latter value is used in Ohsumi's equation this gives a mean neonatal length of about 1.5m, slightly larger than the value calculated directly from the length frequencies of neonates and foetuses. This suggests that the equation might slightly overestimate the true value and so in the absence of good biological data, we have tentatively assumed that the average neonatal length of the northern form is about 185cm (the lower end of the above range). This is about 45cm larger than the value for the southern form.

Table 6

	Month		Number of females					Percentage		
Year		P	PL	L	LOV	R	ROV	Total	(P+PL)	(OVs)
1983	Oct.	11	0	5	0	7	0	23	47.8	0.0
	Nov.	3	1	12	0	8	1	25	16.0	4.0
	Total	14	1	17	0	15	1	48	31.3	2.1
1984	Oct.	5	2	6	0	5	4	22	31.8	18.2
	Nov.	4	7	9	3	11	7	41	26.8	24.4
	Total	9	9	15	3	16	11	63	28.6	22.2
1985	Oct.	7	1	11	0	5	2	26	30.8	7.7
	Nov.	4	2	8	0	1	1	16	37.5	6.3
	Total	11	3	19	0	6	3	42	33.3	7.1
1986	Oct.	2	0	9	1	0	0	12	16.6	8.3
1988	Oct.	1	1	6	0	5	0	13	15.4	0.0
	Nov.	3	0	6	0	4	0	13	23.1	0.0
	Total	4	1	12	0	9	0	26	19.2	0.0
1983-88	Oct.	26	4	37	1	22	6	96	31.3	7.1
	Nov.	14	10	35	3	24	9	95	25.3	12.6
	Total	40	14	62	4	46	15	191	28.3	10.1

Reproductive status of northern form adult females in the catch (no operations in the 1987 season).
P: pregnant (not lactating), PL: pregnant and simultaneously lactating, L: lactating, LOV: lactating with corpus luteum of ovulation, R: resting, ROV: resting with corpus luteum of ovulation, OVs: LOV+ROV.

Foetuses in the larger group (Fig. 14) will reach neonatal length at about (185-160)/ 0.433=58 days, giving a parturition peak in December/January. This suggests that gestation is about 14–15 months.

Perrin *et al.* (1977) obtained the following interspecific relationship between gestation time (Y, months) and mean neonatal length (X, cm) from data for four species (five stocks):

Log Y = 0.4586 log X + 0.1659

Using the estimated neonatal length of 185cm gives an estimated gestation time of 16.1 months. Given the inherent approximation in interspecific relationships and the fact that there is no reason to assume that such a relationship will necessarily apply for sub-stocks within the same species, this value is not dissimilar from the value obtained above. With our present level of information, we presume that gestation time for the northern form is within the range 14–16 months.

General features of the female reproductive cycle

The presence of a considerable number of pregnant and simultaneously lactating females indicates that northern form females often conceive during lactation. The numbers of early pregnant (foetus <60cm) and simultaneously pregnant and lactating females were about the same (12:10, see Table 7). This suggests that similar proportions of females conceive either during lactation or after it. Although the proportions of lactating and resting females were similar in the population (Table 6), the number of lactating females below the maximum reproductive age (36.5 years) was about 1.7 times the number of

Table 7

Foetal length (cm)	Pregnant (non-lactating)	Pregnant and lactating	Unknown
0-9	6	6	
10- 19	5	2	-
20- 29	-	1	-
30- 39	-	-	-
4 0- 49	1	-	-
50- 59	-	1	-
60- 69	1	-	-
- 90- 9 9	1	_	_
100-109	-	-	-
110-119	-	-	1
- 140-149	1		
150-159	2	-	-
160-169	2	-	-
170-179	- 1	-	-
180-189	1	-	-
Total	20	10	1

Comparison of foetal length frequencies between pregnant females and those pregnant and simultaneously lactating, northern form animals (1983-1986 and 1988 seasons).

resting females in the same age range (50:30, see Table 8). This suggests that the probability of a reproductive female conceiving in a season is greater after the completion of lactation than before it.

Although about half of the early pregnant females were in lactation, lactating females had a corpus luteum of ovulation less often than resting females (4:15, Table 6). This indicates that incidence of oestrus in the population in a season is higher among resting than lactating females, but that the probability of an ovulation being followed by conception is lower among resting females. This may be due to the fact that only young females or those of high reproductive capacity will ovulate during lactation. The fact that ovulations in older females less often result in pregnancy was also observed for the southern form (Kasuya and Marsh, 1984).

Table	8
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Age-dependent changes in the reproductive status in northern form mature females, 1983-1985 (percentage in parentheses)¹. Key: P, pregnant (not lactating); PL, pregnant and simultaneously lactating; L, lactating; R, resting.

Age (yrs.)	Р	PL	L	R	Total
5.5-14.5	5 (42)	2 (17)	3 (25)	2 (17)	12 (100)
15.5-24.5	14 (26)	4 (7)	26 (48)	10 (19)	54 (100)
25.5-34.5	12 (22)	6 (11)	21 (39)	15 (28)	54 (100)
35.5-44.5	2(13)	0 (0)	1 (6)	13 (81)	16 (100)
45.5-54.5	0 (0)	0 (0)	0 (0)	8 (100)	8 (100)
55.5-64.5	0 (0)	0 (0)	0 (0)	2 (100)	2 (100)
No age	1 (14)	1 (14)	3 (43)	2 (29)	7 (100)
Total	34 (22)	13 (9)	54 (35)	52 (`34)	153 (100)

¹ See Table 6 for the 1986 and 1988 data, which are not aged.

Only non-lactating pregnant females were found to have near term foetuses (Table 7). Two non-lactating females (not listed in Table 7) were reported by gunners to have foetuses of about 1ft (30cm). This suggests that females that conceive during lactation are those near the end of lactation and/or that once lactating females become pregnant they cease lactation soon afterwards perhaps before the end of the summer, a suitable weaning season (see Discussion).

Age-related change of reproductive activity in females

Age-related changes in the reproductive status of northern form females are shown in Fig. 12 and Table 8. Those for the southern form are shown in Table 9 which is based on data from the 14 drives detailed in Kasuya and Marsh (1984) and Marsh and Kasuya (1984) and an additional 7 drives examined between 1981 and 1984.

In the northern form, the two oldest pregnant females were 36.5 years, the oldest lactating female was 43.5 years and the two oldest resting females were 61.5 years. All resting females with a corpus luteum of ovulation were less than 40.5 years. The proportion of pregnant females decreased with increasing age from 58% (ages from 5.5–14.5 years, including pregnant and simultaneously lactating individuals) to 0% (ages 37.5 years or older), while that of resting females increased from 17% (ages 5.5–14.5 years) to 100% (ages 45.5 years or older). None of the 21 females (14% of adult females) \geq 37.5 years was pregnant. Despite the limited sample size, it seems reasonable to conclude that the reproductive activity of northern form females declines with increasing age and ceases at around 37 years. This is also the case for the southern form, which is believed to have significant numbers of post-reproductive females in the population (Kasuya and Marsh, 1984; Marsh and Kasuya, 1984; 1986).

1974-1964 (percentage in parentileses). Key as Table 6.						
Age (yrs.)	Р	PL	L	R	Total	
5.5-14.5	38 (60)	2 (3)	11 (17)	12 (19)	63 (100)	
15.5-24.5	41 (43)	1 (1)	33 (35)	20 (21)	95 (100)	
25.5-34.5	23 (26)	2(2)	34 (38)	31 (34)	90 (100)	

14 (22)

6 (19)

0(0)

13 (37)

111 (29)

49 (77)

25 (81)

13 (37)

157 (41)

7 (100)

64 (100)

31 (100)

35 (100)

385 (100)

7 (100)

0 0

0 (0)

0 (0)

0 (0)

5 (1)

1 (2)

0(0)

0(0)

9 (26)

112 (29)

Table 9

Age-dependent change in the reproductive status in southern form mature females, 21 drives in 1974-1984 (percentage in parentheses). Key as Table 8.

Annual pregnancy rate

35.5-44.5

45.5-54.5

55.5-64.5

No age

Total

About 28% of adult females were pregnant (including those simultaneously lactating) and this did not vary much annually or by month (Table 6). Although this is similar to the apparent pregnancy rate estimated for the southern form (30%), this similarity is probably superficial since the sampling periods were very different. The present sample was collected in a two-month period near the peak of the breeding season and the start of the calving season, whereas the southern form data were taken over an eight-month period that included both mating and calving peaks.

The proportion of ovulating non-pregnant females showed considerable annual variation, being high (22%) in 1984 and low (0–8%) in the other seasons (Table 6). This cannot be explained by the annual variation in either the apparent pregnancy rate or the proportion of females older than the oldest pregnant female (\geq 37.5; 19% in 1984, 7–17% in 1983 and 1985), and requires further examination.

The estimation of the annual pregnancy rate for the northern form is complicated by two factors: (1) separating females into early and late pregnancy; and (2) confirming whether the foetal length frequency in the sample correctly reflects the seasonality of conceptions. Although the first can be approximated using foetal length criteria, the uncertainty surrounding the second is more serious. The breeding season was still underway and the calving season may have started at the time of sampling. Therefore, it is possible that neither of the foetal groups may fully represent the conceptions in one mating season. In addition, the possibility remains that the females representing the two foetal groups are segregated from each other. Finally, only 31 foetuses of 54 known pregnancies were measured and the larger foetuses were certainly under-represented in the sample.

For the southern form, Kasuya and Marsh (1984) estimated that the apparent pregnancy rate may overestimate the true annual pregnancy rate by a factor of 1.062–1.443 depending on the sampling season. The higher value corresponds to samples taken after the peak of the breeding season and before the calving peak, as in the present sample. Since the northern form has a more distinct breeding season but a similar gestation time, the corresponding value for the present sample would be over 1.443, but certainly be below 2.0 (expected only if the samples are obtained after completion of the breeding season and before the calving season). Using this range and data in Table 6, and assuming that there is no segregation between females of various reproductive and gestation stages, the possible range of the true annual pregnancy rate for the northern form of all ages is estimated at between 0.196 (54/191/1.443) and 0.141 (54/ 191/2), and the mean calving interval between 5.1 and 7.1 years.

If only data for the 1983–85 seasons (i.e. the smaller number of aged data which allow direct comparison with values obtained in the next section) are used, the range in the true annual pregnancy rate becomes 0.213–0.154 and that of the mean calving interval 4.7–6.5 years. These ranges overlap and are not significantly different from those above.

Reproductive cycle of females before senescence

Reproductive senescence occurs among southern form females at ages over 28 years, although identification of the status of individual females is not simple (Marsh and Kasuya, 1984). This is also true for the northern form. Analyses of the reproductive cycles of females using only those below 36.5 (the age of the oldest pregnancy) will exclude most post-reproductive females and give a better view of the reproductive cycle prior to the onset of senescence. The 125 mature females of the northern form in this age range comprised 33 (26.5%) pregnant, 12 (9.6%) pregnant and simultaneously lactating, 50 (40.0%) lactating and 30 (24.0%) resting individuals (Table 8). These values and the above procedure give an annual pregnancy rate of 0.249-0.180 and a mean calving interval of 4.0-5.6 years, about one year less than if senescent females are included.

Although estimation of each component of the mean reproductive cycle is difficult using this seasonally biased sample, an approximate estimate can be made using the above data. The average length of a particular stage in the reproductive cycle (Y, year) can be calculated from the number of females in that category (X) and the total number of pregnant females (33 + 12 = 45 individuals) by:

Y = X [Gestation in years]/[Total no. pregnant females].

Using a gestation period of 15 months (1.25 years), the average reproductive cycle (in years) is approximately:

Pregnancy (without lactation)	0.92
Overlap of pregnancy and lactation	0.33
Lactation	2.00-2.78
Resting	1.20-1.67
Mean reproductive cycle	4.45-5.70

where both the numbers of pregnant but not lactating and pregnant and simultaneously lactating females were corrected by factors of 1.443 or 2.0 respectively. The magnitude of error in this calculation using seasonally biased data is unknown, but the sum of each component (4.5–5.7 years) is close to the average calving interval (4.0–5.6 years) calculated for southern form females in the same age range and the mean lengths of pregnancy and simultaneous lactation are also within the probable range estimated.

Age composition and mortality rate

The age distribution for the northern form given in Fig. 15 includes 28 individuals (20 females and eight males) collected by industry personnel while the primary author was absent from Ayukawa in 1983. These data have not been used in the biological analyses because of the uncertainty of the reproductive status of the mature females.

For the three years of data collection, the modal age class for females was 23.5 years. Using the segment analysis of Robson and Chapman (1961) for female age data between 23.5 and 61.5 years gives an estimated apparent annual total mortality rate of 0.100 (SD=0.009). Kasuya and Marsh (1984) found that for the southern form, female natural mortality increased from 2.5% for 18–46 year old females to 13.5% for females over 45 years. Although a similar age-dependent mortality change may occur in the northern form, it has not been detected in the present sample. This may be because it does not occur or may be due to the small sample size and the fact that the stock was not stable for the 25–45 year period before the present sampling. Heavy exploitation occurred from the late 1940s to early 1950s followed by relatively low and declining exploitation for 28 years, when the population might have been recovering. The apparent mortality rate estimated above will be greater than the natural mortality rate.

The male sample was too small to enable any analyses of the age structure to be carried out.

DISCUSSION

Growth

Life history parameters and mean growth curves for the northern and southern forms are given in Table 10 and Fig. 16, respectively. All parameters associated with absolute body size (neonatal length, length at sexual maturation, asymptotic length and weight of testis at maturation) were greater in the northern form. Such differences would accompany those in age at maturation and reproductive rates if the length differed solely due to density or postnatal food availability. However, as those parameter values are similar it seems reasonable to assume that the size differences are at least in part due to genetic differentation. From published length distributions, Kasuya and Matsui (1984) suggested the presence of geographical variation in the size of short-finned pilot whales, i.e. Indian Ocean animals were slightly larger than those off southern Japan and off the eastern United States (records in Ross (1984) also confirmed this). Animals from the last two areas were of similar body size.



Fig. 15. Age composition of northern form short-finned pilot whales.

Table 10

Comparison of life history parameters between the northern and southern forms of short-finned pilot whales off the Pacific coast of Japan.

			Northern form	Southern form ¹
A.	Body size	· · · · ·		
	(1) Average neonatal length (m)		1.85	1.40
	(2) Average body length at sexual maturity (m)	male	5.6	4.22
		female	3.9-4.0	3.16
	(3) Asymptotic length (m)	male	6.50	4.74
		female	4.67	3.64
	(4) Largest body length (m)	male	7.2	5.25
		female	5.1	4.05
	(5) Mean weight of testis at maturity (g)		900	400
B.	Maturity and growth stages			
	(6) Age at maturity (year), male	mean	17.0	17.0
		range	14-19	15-30
	(7) Age at maturity (year), female	mean	8-9	9.0
		range	5-12	7-12
	(8) Age at asymptotic length (year)	male	25-30	27
		female	25-30	22
	(9) Age of the oldest whale (year)	male	44.5	45.5
		female	61.5	62.5
C.	Breeding seasonality in females			
	(10) Mating season, peak month		Oct./Nov.	May
	(11) Mating season, major range		AugNov.	JanAug.
	(12) Parturition peak		Dec./Jan.	July/Aug.
D.	Age dependence in female reproduction			
	(13) Age of the oldest pregnancy (year)		36.5	35.5
	(14) Age of the oldest pregnancy accompanied			
	by lactation (year)		32.5	34.5
	(15) Age at the oldest ovulation (year)		40.5	39.5
	(16) Age at the oldest lactation (year)		43.5	50.5
	(17) Percentage of females over 35 years in		17.8	29.1 ²
	total adult lemales			
E.	Reproductive cycle in females			
	(18) Apparent pregnancy rate (%)		28.3	32.2
				30.4^{2}
	(19) Annual pregnancy rate, all ages (%)		14-20	12.8
	(20) Mean calving interval, all ages (yr)		5.1-7.1	7.78
				7.83^{2}
	(21) Age of reproductive females (yr)		≤ 36.5	≤ 35.5
	(22) Reproductive cycle (yrs) for reproductive females	$(see 21^{3})$		
	pregnancy (no lactation)	```	0.92	1.10^{2}
	pregnancy with lactation		0.33	0.13^{2}
	lactation		2.00-2.78	2.23^{2}
	resting		1.20-1.67	1.75^{2}
	total length of cycle		4.45-5.70	5.21 ²
	(23) Gestation length (months)		ca 15	14.9

¹ Kasuya and Marsh (1984) and Kasuya and Matsui (1984), or recalculated using their data and method;
² Error data in Table 0.

From data in Table 9;

³ Gestation time for the northern form assumed as 15 months.



Fig. 16. Mean growth curves for the two forms of short-finned pilot whales off Japan. Solid lines represent the northern form and dotted lines the southern form. For each form upper lines indicate males and lower lines females. The mean age and the mean body length at the attainment of sexual maturity are indicated for both forms. The accuracy of the growth curves for the northern form are inferior to the southern form due to the small sample size and fishery selection for large individuals. Growth curves are drawn by eye.

Our study reveals the Japanese northern form animals to be larger than the Indian Ocean animals or the long-finned pilot whales (G. melas) off Newfoundland studied by Sergeant (1962) and Kasuya et al. (1988). In fact they are the largest known animals of the genus Globicephala. Pigmentation variation is also known among populations of long-finned pilot whales (Davies, 1960; Bloch et al., 1993). Thus neither length nor colouration alone are sufficient to identify pilot whale species, although they may indicate genetic isolation among stocks.

Reproduction

The estimated reproductive parameters of the two forms differed in two respects: (1) a considerably greater proportion of pregnant and simultaneously lactating females was found in the northern form (14 in 191 adult females, Table 6) – the proportion was negligible in the southern form (1 in 283 from Kasuya and Marsh, 1984 or 5 in 385, Table 9); and (2) a considerably smaller proportion of northern form females continued lactation after the age of the oldest pregnant female (one 43.5 years old female, Fig. 12) – 12 were found in the southern form sample (16% of the total lactating females, aged up to 50.5 years; Kasuya and Marsh, 1984).

The first difference can be partly explained by previously mentioned differences in sampling season and by differences in the age composition of the catch. A smaller percentage (17.8% mature females) were aged over 35.0 years in the northern form (Table 8), than in the southern form (29.1%; Table 9). This suggests that the proportion of post-reproductive females is lower in the northern form population, and explains point 2 above.

This difference in the age composition of the catch may not only reflect differences in natural or fishing mortality rates but may also arise out of a difference in recent trends in recruitment (see above); it does not necessarily reflect genetic differentiation. We consider it more important to note that pregnancy rate declines with age for both forms, from which we conclude that northern form females may also have a significant postreproductive life time extending in some individuals for over 25 years (the time between the oldest observed pregnancy and maximum longevity).

The average calving interval for all adult northern form females (5–7 years) is slightly less than that for the southern form (7.8 years; Kasuya and Marsh, 1984). This remains the case if recent southern form data (Table 9) are incorporated and a method similar to that of Kasuya and Marsh (1984) is used (modified only to use a new value of $F_2=0.405$ as the correction factor for the over-estimation of pregnant females). This produces estimates of 1.12 years for pregnancy, 0.12 years for pregnancy and simultaneous lactation, 2.73 years for lactation, a 3.86 year resting period and a mean calving interval of 7.83 years.

However, the mean calving interval (4.0 to 5.6 years) estimated for northern form females below the age of the oldest known pregnancy (36.5 years) is similar to the estimated value for the southern form (5.21 years for females \leq 35.5 years using data in Table 8 and the above method). This again suggests that the apparently higher annual pregnancy rate for the northern form reflects the higher proportion of females of a reproductive age in the sample, and not any true difference in the reproductive capacity of those females.

Ecological implications

The warm Kuroshio Current turns east at about 35°N and the cold Oyashio Current reaches about 42°-43°N, forming an area of coastal mixing bounded by northern Honshu and Hokkaido in the west/northwest, the front of the Oyashio Current in the north/ northeast and the front of the Kuroshio Current in the south/southeast. The Tsugaru Current, a branch of the warm Tsushima Current running east through the Tsugaru Strait, flows into the northwestern part of this area and contributes to the high productivity of this area (Ishino, 1975).

The usual geographical range of the northern form concurs with the above area (Fig. 17). They are found at surface water temperatures of below 24°C (summer) or 8°-21°C (winter). The southern form however is found in the wider waters of the Kuroshio Current and the Kuroshio Counter Current area with surface water temperatures of over 24°C (summer) or over 20°C (winter). The range of southern form short-finned pilot whales off Japan extends offshore to 158°E and south to 22°N; they have not been seen to the east or south of this range despite considerable sighting effort by Japanese research vessels (Kasuya *et al.*, 1988).

The gestation time and mating season of mammals are usually such that birth occurs in the season most suitable for the survival of the offspring (Kiltie, 1984). Calving in the southern form peaks in the summer (July/August), but the season is not strongly defined and births may occur in any month. The standard deviation of the mean parturition date is about 70 days (Kasuya and Marsh, 1984). This suggests that the date of birth has only a limited effect on the survival of southern form calves.

The circum-equatorial distribution of the short-finned pilot whale (Gaskin, 1976) and its widening in the northern form (this study) suggest that the northern form has derived from an ancestral type inhabiting equatorial waters. The calving season of this ancestral form was probably closer to that of the current southern form, from which the calving season of northern form animals presumably evolved to be one with calving in winter. Although no direct benefit seems apparent, one possible indirect benefit is that weaning will then take place during the most productive (summer) season. Southern form calves are known to start taking solid food at about 6 months and the importance of milk as the major source of nutrition is limited to this period, although the mother and calf bond and suckling may last



Fig. 17. Segregation of two forms of short-finned pilot whales off Japan and the oceanography of the habitat. Isotherms are for 1985 and show the temperature in centigrade at 100m depth (Japan Meteorological Agency, 1985). The front of the Kuroshio Current agrees with the 15°C isotherm at 100m depth, and that of the Oyashio Current with 5°C (spring) or 8°C (autumn) isotherms (Kawai, 1972). O indicates the Oyashio Current, K the Kuroshio Current, and T the Tsugaru Current. Closed circles indicates sightings of northern form short-finned pilot whales and open circles southern forms (Kasuya *et al.*, 1988; Kasuya unpublished data obtained by the end of 1987). January-March sightings are plotted in February, April-June sightings in May, July-September sightings in August, and October-December sightings in November.

longer (Kasuya and Marsh, 1984). The similarities in the calving cycle and reproductive strategy suggest that the northern form will have a similar age at weaning.

The stomach contents of the limited number of northern form animals taken in October/ November revealed that they feed mostly on cephalopods with some additional fish species. The following prey species were found (Dr T. Kubodera, pers. comm. in 1987): in 1982, Japanese common squid (*Todarodes pacificus*), two species of flying squid (*Eucleoteuthis luminosa* and *Ommastrephes bartrami*) and a further squid species (*Histioteuthis dofleini*); in 1983, North Pacific giant octopus (*Octopus dofleini*), Japanese common squid and the two species of flying squid found in 1982. From this, the major stable prey, at least at this time of year, appears to be three squid species (*T. pacificus, E. luminosa* and *O. bartrami*).

Shingu *et al.* (1983) reported that *T. pacificus* is a coastal species that spawns off southern Japan and summers off northern Japan. The catch off the Pacific coast of Hokkaido and northern Honshu (the habitat of northern form short-finned pilot whales) showed a single distinct peak between September and October (varying annually from 1965 to 1969, when the stock was abundant). *O. bartrami* lives further offshore and also makes north/south migrations each year. Catches of this species off the Pacific coast of northern Japan have increased since 1974 following the depletion of *T. pacificus* and had a single peak in September from 1978 to 1981 (Murata *et al.*, 1983). The monthly landings of these species from November to July ranged from 0–30% of that in the peak months. This suggests that peak food availability for the northern form is probably from late summer to early Autumn, coinciding with the period when most calves are expected to switch their major source of nutrition from milk to solid food.

Thermal tolerance in mammals is related to body size, and the lower critical temperature (T_{lc}) , below which metabolic heat production rises to offset heat loss and stabilise body temperature, is predicted by Peters (1983):

$$T_{lc} = T_b - 14.6W^{0.182}$$

where T_b represents body temperature (°C) and W represents body weight (kg). The estimated mean neonatal body weights of short-finned pilot whales can be obtained from the estimated neonatal lengths (140cm – southern form; 185cm – northern form) using the length/weight relationship obtained for the southern form by Kasuya and Matsui (1984):

$$\log W = 2.8873 \log L + \log 2.377 \times 10^{-5}$$

as 37.4kg and 83.6kg, respectively. T_b for cetaceans is 36°-37°C (Gaskin, 1982). Using these values gives a predicted lower critical water temperature of 7.8°-8.8°C and 3.3°-4.3°C for the southern and northern forms, respectively. The latter value is some 5°C below the minimum surface water temperature in which northern form animals have been found. It has been suggested (Gaskin, 1982) that cetacean metabolic rates are similar to those of land mammals. However, even if this is not the case the relative difference in thermal tolerance between newborn calves of the two forms remains and it appears that selection would favour larger neonates in the northern form population, where births occur in autumn/winter and in higher latitudes than those in the southern form stock (which has births in spring/summer and in lower latitudes). Although the predicted lower critical temperatures for adults will not be encountered in their usual habitat, larger individuals are more resistant to food shortages (Peters, 1983). Seasonal or annual variations in food availability will be greater in coastal waters between two major opposing ocean currents. This again suggests that natural selection may have favoured larger animals more in the northern form even among adults.

A limited amount of interbreeding does not exclude the possibility of maintaining the separate genetic identity of stocks, if they are under different selection pressures (Crow, 1987). The geographical differences in water temperature and seasonality in food availability will result in different selection pressures on the two stocks of short-finned pilot whales. While the Kuroshio Current can be identified as a physical barrier inhibiting free interbreeding or gene exchange, there are additional factors that may decrease the rate of gene exchange.

Firstly, the 5–6 months difference in mating peaks will decrease the chance of interbreeding. Secondly, even if some 'straying' southern form males breed with northern form females, the probability of the introduced genes surviving in the population will be smaller because they will tend to be linked with genes of smaller body size or of seasonally diffuse mating. The reverse case (northern form males and southern form schools) will not lead to significant changes in the gene composition since the southern form population is large (about 53,000; Smith and Read, 1992). Movements of females between stocks will be infrequent given the matrilineal cohesiveness of schools suggested for both the southern form (Kasuya and Marsh, 1984) and the northern form (this study). Even if it does occur the effects will be as cited above, at least for characters of Mendelian heritage.

Differences in social behaviour represent a third plausible mechanism that would inhibit free gene exchange. A similar cohesive matrilineal social structure is likely to occur in both forms. This was also found in morphologically and behaviourally different sympatric killer whale stocks off Vancouver Island (Bigg, 1982; Ford and Fisher, 1982; Bigg *et al.*, 1990), yet they are known not to interbreed, presumably for social reasons (Bigg *et al.*, 1990; Morton, 1990). A similar mechanism could have evolved between the two allopatric stocks of short-finned pilot whales off Japan.

The long-finned pilot whales studied by Sergeant (1962) and Kasuya *et al.* (1984) differ from both forms of short-finned pilot whales in many of the features relating to an agedependent decline in reproductive rates. Additionally, both short-finned pilot whale stocks feed almost exclusively on squid (although some northern forms of animals had fish, e.g. *Trachypterus* sp., in the stomach; Kasuya, unpublished data). This suggests that both have similar life history strategies and occupy similar niches in different geographical areas. It is more appropriate therefore to consider them as separate geographical races or subspecies rather than as species. This concurs with the suggestion of taxonomic closeness revealed through isoenzyme analysis (Wada, 1988) and osteological studies (Miyazaki, 1983; Miyazaki and Amano, 1993).

Kasuya *et al.* (1988) suggested that two forms of short-finned pilot whales comparable to the western North Pacific might be present in the eastern North Pacific south of Vancouver Island. If this is the case, the northern form animals studied here may be considered as one of the populations within a group (cf. subspecies) inhabiting greater geographical range, that may have originated from the major stock of the species (similar to the southern form) and become adapted to the cold temperate North Pacific. Further study on morphology, life history and genetics should throw some light on this question.

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Sightings, Strandings and Incidental Catches of Short-finned Pilot Whales, *Globicephala macrorhynchus*, off the British Columbia Coast

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ABSTRACT

Records of the short-finned pilot whale, Globicephala macrorhynchus, from within the Canadian 320km (200mi) extended economic zone off the coast of British Columbia, are presented, with a total of 19 occurrences to 1989. Six animals were incidentally caught in Canadian waters in an experimental driftnet fishery for flying squid (Ommastrephes bartrami) in 1986-7, and an additional five animals were taken by this fishery outside of Canadian waters in 1983–7. This fishery has now been discontinued. Sighting records are infrequent. Water depth at sighting and incidental catch localities ranged from 10 to 1,200 fathoms. Mean group size was about 15, with a range from 1 to 150 individuals (n=15). Single individuals were sighted most frequently. Records have been obtained from April through October but since search effort in winter months is greatly reduced, it is difficult to determine if this distribution reflects seasonal changes in their presence in BC waters. Although there are large gaps in the sighting record (1962–76, 1978–84), it can probably be assumed that the increased number of records in recent years is due to an increase in search and recording effort. Based on this information the short-finned pilot whale should be considered rare in the waters off British Columbia. They may be present in these waters in most years, but usually only with a few records each year. Sighting programs are limited, and no information is available on sightings per unit effort.

KEYWORDS: NORTH PACIFIC; PILOT WHALE-SHORT-FINNED; SIGHTING-OPPORTUNISTIC; STRANDINGS; DISTRIBUTION; INCIDENTAL CAPTURE.

INTRODUCTION

In the eastern North Pacific the range of the short-finned pilot whale (Globicephala macrorhynchus) extends northward as far as Alaska (Leatherwood et al., 1988). From the waters off the British Columbia (BC) coast, however, only Pike and MacAskie (1969) appear to have presented accepted published records of this species. Osgood (1901) and Wailes and Newcombe (1929) reported that this species is common in some areas of BC, but Pike and MacAskie (1969) subsequently discounted these reports. Home (1980) also noted recent records from the coast of southeastern Alaska, and suggested that the earlier records discounted by Pike and MacAskie may be valid. He overlooked a sighting of six animals mentioned by Spong et al. (1972). We believe that Pike and MacAskie's (1969) suggestion that these early records are most likely mis-identifications or misnamed killer whales (Orcinus orca) is probably correct, and that short-finned pilot whales are not 'common' as Osgood (1901) and Wailes and Newcombe (1929) noted. However, assessment of status based on published records leads one to conclude that short-finned pilot whales might be accidental or vagrant in these waters. Based on recent records presented here, and those of Home (1980), and considering the lack of search effort in the waters off the BC coast, such a conservative assessment might be unwarranted.

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Fig. 1. Map showing localities of records from within the BC 320km (200mi) extended economic zone.

RESULTS AND DISCUSSION

Thirteen previously unpublished records, and the seven records noted by Pike and MacAskie (1969) from within the Canadian 320km (200mi) extended economic zone are presented in Table 1, with locations shown in Fig. 1. Previously unpublished records were obtained from the Canadian Wildlife Service, Royal British Columbia Museum, the National Marine Fisheries Service's National Marine Mammal Laboratory, the Canadian Department of Fisheries and Oceans' Pacific Biological Station, and the BC Cetacean Sighting Program. There are several repositories for cetacean records in BC, but none are currently accepted by all researchers, thus other records may exist, but are unavailable. No regular sighting surveys are currently undertaken in BC waters, and public knowledge of unusual species is generally poor, so it is likely that this species occurs more often than records indicate. Inexperienced observers may not discriminate between pilot whales and similar species found in BC, such as the false killer whale, Pseudorca crassidens (Baird et al., 1989). In fact, the common name 'blackfish' is still sometimes used for pilot whales, false killer whales and killer whales, further confusing species identification. Additional unsubstantiated records of animals that may be pilot whales do exist, but the lack of details or documentation preclude positive identification.

During an experimental Canadian driftnet fishery for flying squid (Ommastrephes bartrami) in 1986-7, six animals were incidentally caught in Canadian waters (Jamieson

and Heritage, 1987; 1988; Table 1). This fishery has now been discontinued. An additional five animals were caught in this fishery outside Canadian waters in 1983–7. Recording of incidental catches during this fishery by qualified observers allowed for a detailed record of species taken. Incidental catches probably occur in other fisheries in Canadian waters, but are not recorded due to a lack of observers.

A total of 16 sighting records have been obtained, 15 of which include group size. Group size ranged from 1–150 animals (mean = about 15). Leatherwood *et al.* (1988) note that pilot whales are gregarious and rarely found alone. For the BC records however, the

Date	Location ^A	Number	Туре ^в	Source ^C
August 1954	Barkley Sound	?	1	1
30 May 1958	Swiftsure Bank	6	1	1
6 June 1958	Swiftsure Bank	1	1	1
2 July 1958	Clarke Pt.	1	1	1
29 July 1958	Laredo Channel	3	1	1
22 April 1959	48°28'N, 125°30'W	1	1	2
10 June 1959	5mi W of Pachena Pt.	1	1	1
14 August 1961	48°43'N, 125°13'W	4	1	1
August 1971	Johnstone Strait	about 6	1_	3
23 November 1977	Metchosin, V.I.	1	2 ^D	4,5
23 August 1985	50°6'N, 129°58'W	2	1	2
18 July 1986	47°27'N, 129°18'W	12-15	1_	6
14 August 1986	50°25'N, 132°20'W	2	3 ^E	6
14 August 1986	50°25'N, 132°20'W	2	4 ^E	6
23 August 1986	51°40'N, 136°0'W	1	3 ^E	6
23 August 1986	51°40'N, 136°0'W	150	1 ^E	6
15 September 1986	48°10'N, 129°15'W	4	1	4
13 July 1987	47°27'N, 130°5'W	1	3	6
10 May 1988	53°30'N, 131°10'W	1	1	7
30 August 1988	48°5'N, 128°10'W	9	1	8
14 April 1989	48°21'N, 123°50'W	3 0	1	7
10 July 1989	48°18'N, 123°39'W	1	1	7

Records of Globicephala macrorhynchus off the British Columbia coast.

Table 1

Notes:

^A Location of previously published records given as presented in the original source.

^B Type: 1. Sighting; 2. Stranding; 3. Incidental catch, dead; 4. Incidental catch, released alive.

^C Source: 1. Pike and MacAskie, 1969; 2. D. Cheng, Platforms of Opportunity Program, National Marine Mammal Laboratory; 3. P. Spong (pers. comm.), Spong *et al.* (1971); 4. M.A. Bigg, Pacific Biological Station; 5. Royal British Columbia Museum, Victoria, BC. 6. D. Heritage, Pacific Biological Station; 7. BC Cetacean Sighting Program, c/o authors; 8. K. Morgan, Canadian Wildlife Service.

^D This appears to be the only specimen record from British Columbia, a 4.52m female (BCPM 9775). Although reported in November, the animal had been dead for greater than a month (M. Bigg, pers. comm.). Thus in interpreting seasonal presence this record was listed from October.

^E When a single group of animals was both seen and one or more animals were incidentally caught, they are dealt with as if they are independent records of different types in this Table, but for the purposes of the total number of occurrences in BC waters they are considered only once.

modal group size was one (n=6). It is possible that this high proportion of single animals may be an artifact of the small number of records, or that single animals may be more prevalent in the fringes of the range of this species. Alternatively it is possible that records of single animals are a result of incomplete observations or documentation of a larger group, especially considering that the sightings were not made as part of a marine mammal sighting survey.

Water depth of sighting and incidental catch localities ranged from 10 to 1,300 fathoms. Sea surface temperatures were only recorded for six sightings, three reported in Pike and MacAskie (1969) as 12°C, 12°C and 14°C, and three unpublished records, from 23 August 1985, 30 August 1988 and 14 April 1989 as 14°C, 16°C and 8°C respectively. Records have been from April to October, but since search effort in winter months is greatly reduced, it is difficult to determine if this seasonal distribution reflects seasonal changes in their presence in BC waters. Although pilot whales frequently strand in other parts of their range, only one stranding, that of a single animal, has been recorded from BC (Table 1, Fig. 2). Pilot whales are frequently found associated with other species of cetaceans. In the records presented here, one interspecific association was noted, on 30 August 1988, with a group of 5 northern right whale dolphins, *Lissodelphis borealis*, and 25 Pacific white-sided dolphins, *Lagenorhynchus obliquidens* (Baird and Stacey, 1991; Stacey and Baird, 1991).

There are large gaps in the record from 1962–76 and from 1978–84. However, search effort has not been consistent. There has been an increase in search, reporting and recording effort in recent years, and based on these sightings the short-finned pilot whale should be considered rare in BC waters, occurring in most years, but with only a few records per year. Further research on short-finned pilot whales would be necessary to clarify their status in Canadian waters. By itself such research may not be warranted, but could be undertaken in combination with offshore sighting surveys for other cetaceans.



Fig. 2. A 4.52m stranded female short-finned pilot whale from Metchosin, 1977; the only specimen record from British Columbia (BCPM 9775). Photo by M.A. Bigg.

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