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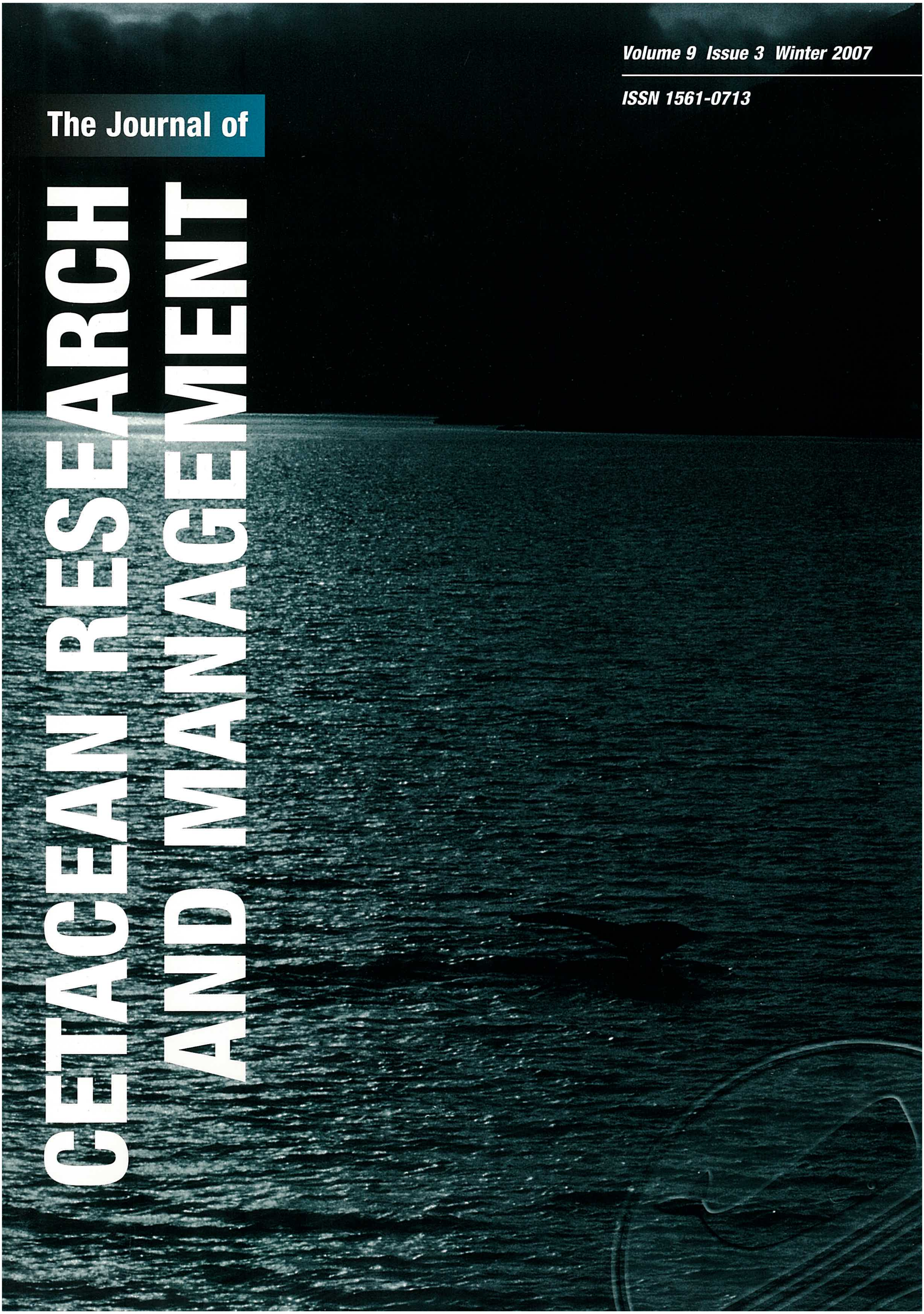

Contents

Editorial

Welcome to this the final issue of Volume 9 of the *Journal of Cetacean Research and Management*.

2007 has been another successful year for the Journal. A total of 31 papers have been published this year covering a wide range of subjects related to the conservation and management of cetaceans. There have been a total of 85 authors from Europe, Asia, Australia, Africa and North and South America. This year's supplement included the full report of the Scientific Committee held in St Kitts and Nevis in May-June 2006, as well as the results of five important intersessional workshops. The author and subject index can be found at the end of this issue.

Knowledge of the prey species of whales is important to management at many levels, from interpreting short- and long-term changes in distribution to consideration of interactions with fisheries. There are two papers relevant to prey (Windsland *et al*.; Leaper and Lavigne) and one to fishery interactions (Benjamins *et al*.) in this issue. Good conservation requires good knowledge of the abundance of populations and there are a number of papers relevant to that topic. Two of these relate to diving behaviour, an important correction factor in abundance estimates, one (Teilmann *et al*.) relating to harbour porpoises that uses data collected from telemetry and the other referring to large whales off West Greenland (Heide-Jørgensen and Simon). One of the most encouraging pieces of information on cetacean conservation in recent years is the evidence that Antarctic blue whales, although still at a very small percentage of their original population size, are recovering. The most recent estimates are given in the Branch paper in this issue. It is the policy of the journal to encourage good quality cetacean research in areas where cetacean studies are rare and/or in their infancy. I am pleased to include work from Angola (Weir) and off India (Jayasankar) here. Interactions with vessels is becoming an increasingly important topic for cetacean conservation in some areas and Morete *et al*. discuss the response of mother and calf humpback whales to vessels off Brazil. This issue also includes a fascinating paper on the use of genetic data to investigate the mating system of the common minke whale (Skaug *at al*.).

Finally, I would like to thank the 50 scientists that have acted as anonymous reviewers for the papers published in Volume 9 (Baker, C.S.; Bejder, L.; Berggren, P.; Best, P.B.; Borchers, D.L.; Bravington, M.V.; Brown, M.W.; Buckland, S.T.; Butterworth, D.S.; Cañadas, A.; Clapham, P.J.; Cockcroft, V.G.; Durban, J.W.; Findlay, K.P.; Forcada, J.; Gales, N.; George, J.C.; Gordon, J.C.D.; Hammond, P.S.; Hedley, S.L.; Hiby, A.R.; Hoelzel, R.; Kasuya, T.; Larsen, F.; Laake, J.L.; Lawson, J.; Lesage, V.; Lusseau, D.; Martien, K.K.; Martin, A.R.; Mate, B.; Mead, J.G.; Moore, M.; Øien, N.; Otani, S.; Palsbøll, P.J.; Perrin, W.F.; Pike, D.G.; Reeves, R.; Ridgway, S.H.; Rogan, E.; Rosenbaum, H.C.; Rowntree, V.; Teilmann, J.; Van Waerebeek, K.; Víkingsson, G.; Westgate, A.J.; Winship, A.; Williams, R.; Whitehead, H.). Without their diligence and hard work, the papers in the *Journal*, and more importantly the contribution they make to the wise management and conservation of cetaceans, would be considerably poorer. A full list of the reviewers and their affiliations can be found at: http://www.iwcoffice.org/publications/contents_reviewers.htm#review.

G. P. DONOVAN
Editor

Relative abundance and size composition of prey in the common minke whale diet in selected areas of the northeastern Atlantic during 2000-04

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ABSTRACT

A total of 210 common minke whales (*Balaenoptera acutorostrata*) were sampled in five different areas in the northeastern Atlantic during May-June 2000-04. Analysis of forestomach contents revealed a relatively mixed diet at the population level, whereas on an individual level, each whale had fed upon mainly one species. There were significant differences in diet composition between areas and some differences between years. The importance of krill in the Barents Sea increased with latitude and krill dominated the Spitsbergen diet. Capelin dominated the diet around Bear Island and contributed considerably to the diet along the coast of northern Norway. In the latter area, herring and haddock were also a great part of the diet. The diet in the Norwegian Sea consisted of mainly mature herring, while the diet in the North Sea was dominated by sand eels and mackerel. The minke whales were found to feed on a wide range of prey sizes, apparently determined by the availability of different size classes.

KEYWORDS: COMMON MINKE WHALE; ECOSYSTEM; FEEDING GROUNDS; FOOD/PREY; NORTH ATLANTIC; NORTHERN HEMISPHERE; BARENTS SEA; NORWEGIAN SEA; NORTH SEA

INTRODUCTION

Common minke whales (*Balaenoptera acutorostrata*) are mobile predators that undertake extensive seasonal migrations between low latitude breeding areas and temperate and polar regions where they exploit the biological production (e.g. Jonsgård, 1951). Their abundance (Skaug *et al*., 2004) and opportunistic feeding habits (Folkow *et al*., 2000; Haug *et al*., 2002) make them one of the most conspicuous high trophic-level predators in northeastern Atlantic ecosystems, including the Barents Sea, Norwegian Sea and North Sea. Quantifying the interactions between minke whales and their prey may be important for the management of the economically important species which are targeted by minke whales.

In the 19th century, the minke whale was described as a herring (*Clupea harengus*) predator (Sars, 1897) and as ichthyophagous in Norwegian waters (Grieg, 1894). Later observations made during commercial (Jonsgård, 1951;1982) and scientific catching operations (Haug *et al*., 1995a; Haug *et al*., 1996; Haug *et al*., 1997) revealed that the minke whale in the northeastern Atlantic is euryphagous, eating a wide variety of species. This is in strong contrast to its close relative in the Southern Hemisphere, the stenophagous Antarctic minke whale (*B. bonarensis*) which mainly feeds on krill (Bushuev, 1991; Ichii and Kato, 1991). The common minke whale has a flexible feeding pattern, i.e. it is able to adapt to local prey densities and it displays a type III functional response towards its major prey (Smout and Lindstrøm, 2007; Tjelmeland and Lindstrøm, 2005). Thus, it appears that changes in the abundance of preferred prey species have less effect on minke whale body condition than might be expected (Haug *et al*., 2002). According to earlier studies, the diet of the minke whales in Norwegian waters consists of several species of zooplankton and fish (Haug *et al*., 1995a; Haug *et al*., 1995b; Haug *et al*., 1996; Haug *et al*., 2002; Haug *et al*., 1997; Lindstrøm *et al*., 1997; Olsen and Holst, 2001). Energy rich species such as herring and capelin (*Mallotus villosus*) are preferred (Skaug *et al*., 1997), but gadoid species (Gadidae), sandeels (*Ammodytes* sp.), krill (*Thysanossa* sp.) and copepods (*Calanus* sp.) are also part of the diet. The diet may however vary in space and time due to spatio-temporal heterogeneity in prey abundance.

The Barents Sea, a large and highly productive shelf sea capable of supporting large populations of pelagic fish (Hamre, 1994; Wassmann *et al*., 2006), has experienced major changes in species abundance in the last 30 years; the most conspicuous are the populations fluctuations of capelin (Gjøsaeter, 1998) and juvenile herring (Dragesund *et al*., 1997). Key fish species in this ecosystem are cod (*Gadus morhua*), capelin and juvenile herring, of which only capelin resides in the Barents Sea year round. Herring, predominantly juveniles, stay in the Barents Sea for 3-4 years; thereafter they join the adult stock in foraging areas in the Norwegian Sea. Cod feeds in the Barents Sea and spawns along the Norwegian coast (Bergstad *et al*., 1987). Comparative surveys have shown variations in minke whale diet between different sub areas in the Barents Sea region; the diet was dominated by capelin and krill in the northernmost areas (Spitsbergen and Bear Island) whereas in the southern part of the Barents Sea, along the coast of Northern Norway, herring and various gadoids dominated the diet (Folkow *et al*., 2000; Haug *et al*., 1996; Haug *et al*., 2002).

The Norwegian Sea is an important feeding area for three of the most commercially important populations of pelagic fish; spring spawning herring, blue whiting (*Micromesistius poutassou*) and mackerel (*Scomber scombrus*) (Skjoldal, 2004). The population sizes vary, but in good years, as much as 20 million tons of pelagic fish may forage in the Norwegian Sea (Michalsen, 2004). The migration patterns of the different species are also known to vary among years, and this might affect the availability of prey for the minke whale (e.g. Hamre, 1994). A recent study has shown that adult herring is the most important prey item in this area

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(Olsen and Holst, 2001). Towards the coast of northern Norway, small herring and, in spring, gadoids, especially cod, replace adult herring in the diet of minke whales (Haug *et al*., 1995a; Haug *et al*., 1995b; Haug *et al*., 1996; Lydersen *et al*., 1991).

The North Sea is very different from the Barents Sea and the Norwegian Sea; it is a closed, shallow ecosystem, heavily affected by human activity and it can be divided into four areas, each with its own characteristic ecological profile. Cod, saithe (*Pollachius virens*), herring and, in autumn, mackerel are important species in the northern part (Michalsen, 2004). In the central part, cod is replaced by haddock (*Melanogrammus aeglofinus*) and whiting (*Merlangius merlangus*) and the adult herring are replaced by juvenile herring. The shallow eastern and southern areas are important sandeel areas in addition to being nursery areas for herring and cod. The last part, the Norwegian trench, starts outside the Stad on the southwest coast of Norway and follows the coast of southern Norway to the Oslofiord. The most dominant species in the Norwegian trench are adult herring and mackerel. Observations from 1975 and 1976 (Oritsland and Christensen, 1982) showed that sandeel and mackerel dominated the minke whale diet in this area. This was supported by Olsen and Holst (2001) who, in addition to sandeels and mackerel, found whiting and herring as important prey items.

Based on data from 1992-99, Haug *et al*. (2002) investigated how ecosystem changes affected the feeding ecology of minke whales in the Barents Sea. The present study is a continuation of the 1992-99 minke whale studies and includes material collected in 2000-04. In addition to the Barents Sea, the present material also includes data from the Norwegian Sea and the North Sea. Comparisons can therefore be made between different ecosystems in the northeastern Atlantic with respect to minke diet composition. Possible year-to-year variations within the areas are investigated and the analyses also include information about the size and age composition of the most important prey species.

MATERIALS AND METHODS

Whale sampling

The whale stomachs were collected in three main areas (Fig. 1): The Barents Sea (with three sub-areas: Spitsbergen (SB; north of 75°N), Bear Island (BI; north of 73°N) and the Southern Barents Sea (SBS; east of 17°E, north of 69°N); the Norwegian Sea (NOS, here defined to include the area between 70-74°N and 7-9°E); and the North Sea (NS, including the areas south of 65°N). Stomach content samples from 210 whales were collected by scientific personnel on commercial whaling boats during May and June 2000-04 (see Table 1). In contrast to the scientific permit whaling in 1992-1994, where whales were caught randomly along predetermined transects (Haug *et al*., 1996), the animals were collected opportunistically in areas of high abundance. After being killed, the whales were immediately taken on board for dissection and biological sampling.

Table 1

The number of minke whales (males/females, N=210) sampled in Spitsbergen (SB), Bear Island (BI), Southern Barents Sea (SBS), Norwegian Sea (NOS) and the North Sea (NS) in May/June 2000-04.

Year	Sample period	SB	BI	SBS	NOS	NS
2000	23/05-21/06	11 (0/11)	2 (0/2)	22 (15/7)	-	-
2001	10/05-06/06	16 (0/16)	-	21 (11/10)	-	14 (2/12)
2002	15/05-12/06	3 (0/3)	6 (0/6)	26 (10/16)	10 (4/6)	13 (12/1)
2003	12/05-01/06	-	12 (0/12)	18 (2/16)	-	10 (5/5)
2004	13/05-21/06	8 (0/8)	4 (0/4)	14 (0/14)	-	-
Total		38 (0/38)	24 (0/24)	101 (38/63)	10 (4/6)	37 (19/18)

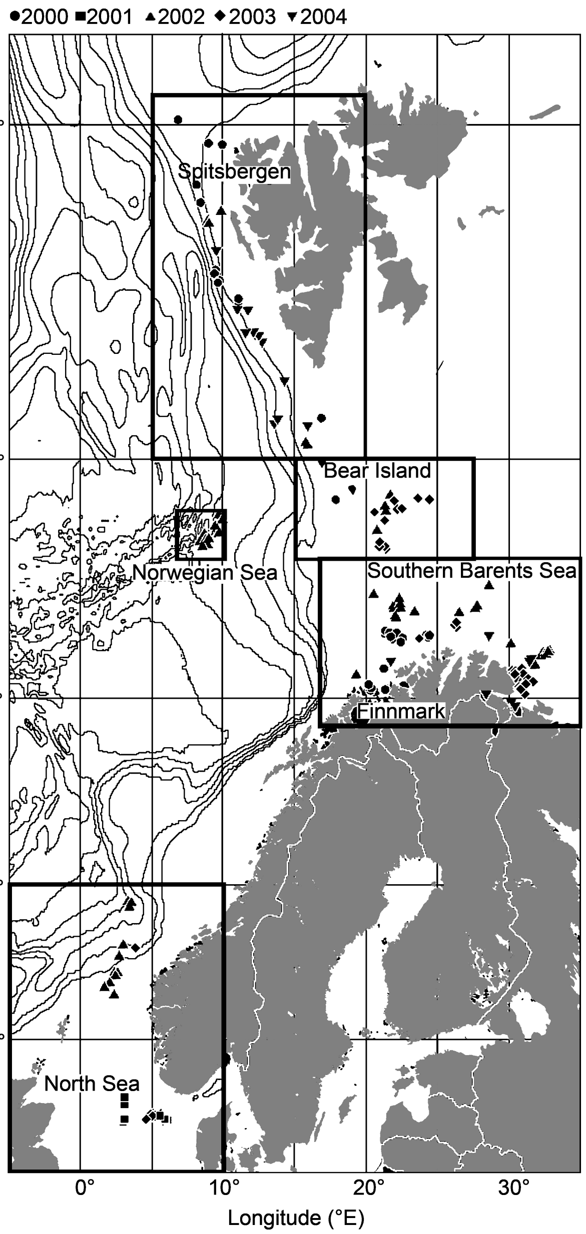


Fig. 1. Catch positions of the minke whales sampled in Spitsbergen (SB), Bear Island (BI), Southern Barents Sea (SBS), Norwegian Sea (NOS) and North Sea (NS) during May-June, 2000-04.

Treatment of stomach contents

The minke whale has relatively short intestines and its stomach consists of four compartments in order to utilise the energy in prey to the fullest (Olsen *et al*., 1994). The four compartments; the forestomach, the fundic chamber, the connecting channel and pyloric chamber retain food for long enough for it to be digested by both microbial and enzymatic degradation. Lindstrøm *et al*. (1997) showed that sampling and analysis from the forestomach was adequate to evaluate the diet of minke whales. Sampling in the present study was therefore restricted to the forestomach, where sub-samples of between 5 and 10 litres were taken from each whale. The degree of digestion and the observed species composition were also recorded.

In the laboratory, the forestomach contents were treated according to standard procedures (Haug *et al*., 1995a); the forestomach contents were filtered through a sieve system consisting of three sieves (20mm, 5mm and 1mm). Fresh and intact (length can still be measured, but not weight due to digestion) fish specimens were separated from the rest of the material and identified using gross morphological characteristics (Pethon, 1985), whereas sagittal otholiths were used to identify more digested fish which, together with krill, were identified to the lowest possible taxon (Härkönen, 1986). The total number of each species was calculated by adding the number of fresh and intact specimens, intact skulls and half the total number of free otoliths. Random samples of 100 undigested otoliths (or as many as possible) from each fish species were used to calculate the prey biomass at time of ingestion. The length, weight and otoliths of 30 undigested fish were collected and used to establish fish length-fish weight, otolith length-fish length and otolith length-fish weight regression equations (Table 2). When the number of fresh species was insufficient to make regression equations, equations from Härkönen (1986) were used instead. The age of fish collected from the stomachs in 2004 was estimated by counting annual zones in the otoliths.

The estimation of krill biomass at time of ingestion is a problem when reconstructing the forestomach content of common minke whales. Krill lacks hard parts resistant to the forestomachs microbes (e.g. Nordoy *et al*., 1993) and the passage and degradation rates are likely to differ from those of fish due to their size. Thus, the initial weight of the ingested krill was not determined. Instead, the weight of krill in the stomachs was used in this study.

By using traditional numerical and mass fractions of individual prey categories to describe the whale diet, forestomachs containing large amounts of food are given exaggerated importance compared to those containing little food (Lindstrøm *et al*., 1997). Previous studies indicate that minke whales feeding on small prey like crustaceans tend to have small continuous meals (Haug *et al*., 1997) and will at any time have small amounts of food in their stomachs, while whales that prey on larger prey will have large, well defined meals. The importance of large prey may therefore

Table 2

Regression equations for calculation of fish weight and fish length of prey eaten by minke whales in the northeast Atlantic in 2000-04 (*Härkönen, 1986).

	Fishweight-otolithlength	R^2	Fishweight-fishlength	R^2	Fishlength-otolithlength	R^2
2000						
Herring	FW=1.449*OL^3.238	0.96	FW=6*10^-7*FL^3.4751	0.91	FL=48.797*OL^1.2559	0.97
Capelin	FW=1.538*OL^2.778	0.78	FW=3.174*10^-7*FL^3.561	0.85	FL=44.333*OL+41.951	0.65
Sand-eel	FW=0.87*OL^2.52	0.88	-	-	FL=80.962*OL^0.7847	0.88
Haddock	FW=0.002096*OL^4.58 *	0.97	-	-	FL=8.785*OL^1.38 *	0.96
Polar cod	FW=0.178*OL^2.595	0.86	-	-	FL=20.86*OL+16.849	0.94
Cod	FW=0.006855*OL^4.435 *	0.95	-	-	FL=48.37*OL-202.13 *	0.92
2001						
Herring	FW=1.449*OL^3.238	0.96	FW=2*10e-5*FL^2.777	0.86	FL=48.797*OL^1.2559	0.97
Capelin	FW=1.2493*OL^2.8851	0.69	FW=2E-07*FL^3.5872	0.85	FL=75.396*OL^0.7811	0.78
Sand-eel	FW=2.1096*OL^2.2159	0.87	FW=0.2493*FL-24.751	0.94	FL=80.962*OL^0.7847	0.88
Smaller sand-eel	FW=3.3241*OL-1.5289	0.64	FW=0.0653*FL-3.5687	0.88	FL=50.82*OL+31.321	0.68
Haddock	FW=0.002096*OL^4.58 *	0.97	-	-	FL=8.785*OL^1.38 *	0.96
Cod	FW=0.006855*OL^4.435 *	0.95	-	-	FL=48.37*OL-202.13 *	0.92
Saithe	FW=0.007288*OL^4.501 *	0.99	-	-	FL=8.97297*OL^1.53 *	0.97
2002						
Large herring	FW=1.449*OL^3.238	0.96	-	-	FL=21.31OL+238.91	0.44
Herring	FW=1.449*OL^3.238	0.96	-	-	FL=49.961*OL+23.951	0.95
Capelin	FW = 3.8698*OL^1.6507	0.30	FW=0.3575*FL-37.364	0.67	FL=75.887*Ln(OL)+85.106	0.37
Sand-eel	FW = 2,1096*OL^2,2159	0.87	-	-	FL=80.962*OL^0.7847	0.88
Small sand-eel	FW=1.279*OL^2.3361	0.75	-	-	-	-
Haddock	FW=0.002096*OL^4.58 *	0.97	-	-	FL=8.785*OL^1.38 *	0.96
Polar cod	FW=0.178*OL^2.595 *	0.86	-	-	FL=20.86*OL+16.849	0.94
Cod	FW=57.619OL-459.61	0.81	-	-	FL=48.37*OL-202.13	0.92
Saithe	FW=0.007288*OL^4.501 *	0.99	-	-	FL=8.97297*OL^1.53 *	0.97
Mackerel	FW=1.094*OL^4.039 *	0.90	-	-	FL=87.59*OL-20.41 *	0.91
Pearlside	FW=0.1735*OL^3.8244	0.66	-	-	FL=44.012*OL-17.95	0.75
Blue whiting	FW=0.02628*OL^3.484 *	0.99	-	-	FL=0.63+23.884*OL *	0.98
2003						
Herring	FW=0.9956*OL^3.3508	0.94	-	-	FL=49.961*OL+23.951	0.95
Capelin	FW=4.0405*OL^1.6198	0.41	-	-	FL=91.148*OL^0.5506	0.49
Sand-eel	FW=2.1096*OL^2.2159	0.87	-	-	FL=80.962*OL^0.7847	0.88
Small sand-eel	FW=1.6187*OL^2.3446	0.79	-	-	FL=59.228*OL+24.703	0.76
Haddock	FW=0.002096*OL^4.58 *	0.97	-	-	FL=8.785*OL^1.38 *	0.96
Cod	FW=0.006855*OL^4.435 *	0.95	-	-	FL=48.37*OL-202.13 *	0.92
Pearlside	FW=0.5056*OL^1.7967	0.37	-	-	-	-
Whiting	FW=0.012692*OL^3.535 *	0.98	-	-	-	-
2004						
Herring	FW=0.9956*OL^3.3508	0.94	-	-	FL=49.961*OL+23.951	0.95
Capelin	FW=3.7355*OL^1.7898	0.50	FW=0.00001*FL^2.8334	0.84	FL=28.512*OL+78.528	0.29
Sand-eel	FW=2.1096*OL^2.2159	0.87	-	-	FL=80.962*OL^0.7847	0.88
Haddock	FW=0.0459*OL^3.2302	0.95	FW=0.00003*FL^2.7698	0.95	FL=24.541*OL-30.661	0.96
Large haddock	FW=0.0459*OL^3.2302	0.95	FW=0.00003*FL^2.7698	0.95	FL=8.785*OL^1.38 *	0.96

be overestimated and the importance of small prey underestimated. This problem can be reduced by using the Weight index (WI), which summarises the percentage of each prey species in each individual whale and dividing this by the total summarised percentage mass of all prey specimens from all whales. The WI is defined as:

$$WI_j = \frac{1}{n}\sum_{i=1}^{n}\frac{w_{ij}}{w_i}$$

Where w_{ij} is the relative contribution by weight (%) of species j in whales from area i, w_i is the total biomass of all prey species in whales from area i and n = number of stomachs examined (Lindstrøm *et al*., 1997).

To illustrate the prey diversity in the different regions, the frequency of occurrence (FO) of prey species was calculated. The FO is defined as:

$$FO_i = \left(\frac{s_i}{s_t}\right)\cdot 100$$

where s_i is the number of whales in which prey species i occurs and s_t is the total number of whales containing food.

The comparison of the diet data with available fish abundance data was qualitative not quantitative.

Minke whales exploit a variety of prey species. In order to determine whether they feed on several prey species at a time, the number of species observed in each stomach was recorded. To reduce the uncertainty of secondary ingestion of prey, i.e. prey categories that have been ingested by larger prey and then subsequently ingested by the whales, prey species contributing with less than 1% of the total prey biomass in a stomach was removed from the analysis concerning number of prey items in each stomach.

Statistical framework

A linear discriminant analysis (LDA) was performed on this data set to see whether the differences in diet between the different sampling areas were large enough to determine the origin of individual whales based on their stomach contents. The prey group ‘other’ was omitted from the analysis.

To illustrate and better understand the mechanisms behind temporal and spatial variation in diet composition, a principal component analysis (PCA) was used to ordinate the whale diet data along the first three axes of variation (see Legendre and Legendre, 1998). The site scores, i.e. the mean sample scores, were calculated from each sub-area and year and then plotted along with the environmental variables. A PCA is not a statistical test, but a way of representing multivariate data on a reduced number of axes that best describes the main trends of variation in the data (Legendre and Legendre, 1998). A redundancy analysis (RDA) can be seen as an extension of PCA and was used to check the amount of variance explained by the different explanatory variables. Three explanatory variables were examined: area, year and sex. The effect of area was tested on the entire dataset to look for significant differences among the five areas. Since an RDA can only be used on a fully factorial data set, the effect of year was tested on each of the five areas individually. Previous studies have showed a differentiation in diet between females and males (Haug *et al*., 2002). To rule out any covariance between year and sex, these two variables were tested together as well as separately. Only females were caught at Spitsbergen and Bear Island, hence, no analysis of sex was done for these two areas.

A 95% confidence interval for the relative importance of prey was constructed by bootstrapping the diet data 1,000 times. The intervals are corrected for possible acceleration and bias (see Efron and Tibshirani, 1993). Non-overlapping 95% confidence intervals were considered to indicate a statistically significant difference ($p \leq 0.05$). The method used analyses one prey item at a time.

RESULTS

Diet composition

A total of 14 different prey items were found in the 210 minke whale stomachs (Table 3), including 12 different species of fish in addition to krill and copepods. Krill, capelin, herring and haddock had a high frequency of occurrence in several areas. In addition, mackerel had high FO in the North Sea.

From the weight index, it was evident that the most conspicuous prey items were krill, capelin and herring which were all found in considerable amounts (>10% of WB; Table 3) in two or more areas. The same three prey items made up 72% of the total weighted biomass for all areas (when weighted for number of whales in each area). Other observed prey items were sandeels, haddock, mackerel, cod, pearl side, blue whiting, copepods, saithe, polar cod, and whiting (in order of importance). Fish dominated the diet in all but one area (Spitsbergen) and made up 74% of the total WB (when weighted for number of whales sampled in each area). Krill were mainly found in the two northernmost areas, Bear Island and Spitsbergen, where they made a large contribution to the weighted biomass. The diversity of diet was lowest off Spitsbergen where nearly 90% of weighted biomass consisted of krill.

In spite of the large number of observed prey species, the number of different prey species eaten by individual whales was low. The majority of all whales (69%) had fed on one prey item only, while 23% had fed on two different prey species (Fig. 2). The remaining minke whales had three or four different prey items in their stomachs. This dominance of single-prey stomachs was seen in all the sampling areas. The highest percentages of single prey stomachs were found off Spitsbergen (87%) and in the North Sea (84%). The lowest percentage was found in the southern Barents Sea (58%). Examination of all single prey stomachs showed that 32% contained capelin, 26% contained krill and 13% contained herring (Fig. 3). The remaining single-prey stomachs contained sandeels, haddock, mackerel, pearlside and copepods. The majority of single-prey stomachs from the southern Barents Sea and Bear Island contained capelin, while at Spitsbergen, nearly all single-prey stomachs contained krill. In the North Sea, sandeels and mackerel dominated the single prey stomachs, while herring was most important in the Norwegian Sea.

To simplify further statistical analysis, the stomach contents were divided into nine different prey groups: herring; capelin; sandeels; cod; haddock; other gadoid species (saithe, polar cod, whiting and blue whiting); mackerel; krill and other species (copepods and pearl side).

The PCA showed that krill was strongly separated from all fish species of prey and highly associated with the Spitsbergen area (Fig. 4). Capelin was somewhat segregated from the rest of the fish species. Furthermore, herring was often found together with codfish. With the exception of Bear Island, where there is large uncertainty concerning the estimates due to small sample size, the scores from the different years of various areas were very similar.

Table 3

Frequency of occurrence (FO) and weighted biomass (WB; both in %) of identified prey species found in minke whale stomachs caught in Spitsbergen (SP), Bear Island (BI), Southern Barents Sea (SBS), Norwegian Sea (NOS) and North Sea (NS) in 2000-04. *N* = number of stomachs.

		SB		BI		SBS		NOS		NS		Total	
		N=38		*N*=24		*N*=101		*N*=10		*N*=37		*N*=210	
		FO	WB	FO	WB	FO	WB	FO	WB	FO	WB	FO	WB
Crustacea													
Euphausiacea	*Thysanoessa* sp.	97.37	89.59	45.83	38.45	1.98	0.99	-	-	-	-	23.81	21.08
Copepoda	*Calanus* sp.	2.63	2.64	2.65	2.66	2.67	2.68	2.69	2.70	2.71	2.72	2.73	2.74
Pisces													
Clupeidae	*Clupea harengus*	-	-	4.17	0.58	41.58	14.32	100.00	95.88	16.21	6.16	28.10	12.60
Osmeridae	*Mallotus villosus*	18.42	1.57	75.00	51.15	73.27	58.90	20.00	0.15	2.70	0.00	48.57	34.46
Gadidae	*Boreagadus saida*	7.89	0.02	4.17	0.85	-	-	-	-	-	-	1.90	0.10
	Gadus morhua	5.26	4.79	4.17	1.42	5.94	2.68	-	-	-	-	4.29	2.32
	Melanogrammus aeglofinus	2.63	1.40	12.50	6.96	28.71	20.26	-	-	2.70	2.42	16.19	11.22
	Merlangius merlangus	-	-	-	-	-	-	-	-	2.70	0.28	0.48	0.05
	Micromesistius poutassou	-	-	8.33	0.60	0.99	0.01	20.00	3.97	-	-	2.38	0.26
	Pollachius virens	-	-	-	-	1.98	1.77	-	-	-	-	0.95	0.85
	Gadidae ssp.	2.63	0.01	4.17	0.01	2.97	0.63	-	-	-	-	2.38	0.30
Ammodytidae	*Ammodytes* ssp.	-	-	-	-	10.89	0.46	-	-	62.16	56.01	16.19	10.09
Scombridae	*Scomber scombrus*	-	-	-	-	-	-	-	-	29.73	29.72	5.24	5.24
Sternoptychidae	*Maurolicus muelleri*	-	-	-	-	-	-	-	-	10.81	5.42	1.90	0.95

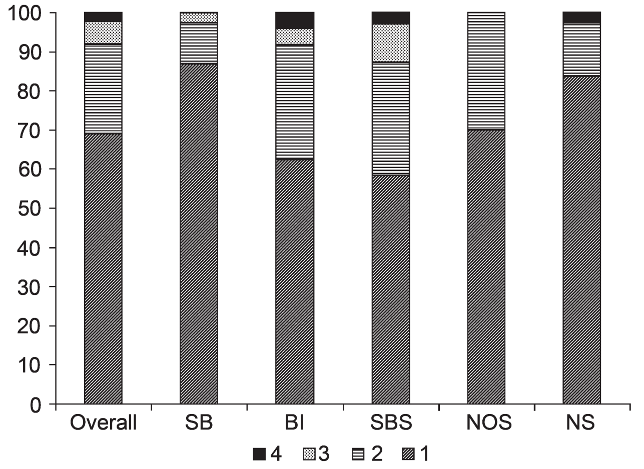


Fig. 2. The number of prey species in individual minke whale stomachs (% of all stomachs in each area) for the five sampling areas, with sampling years 2000-04 pooled.

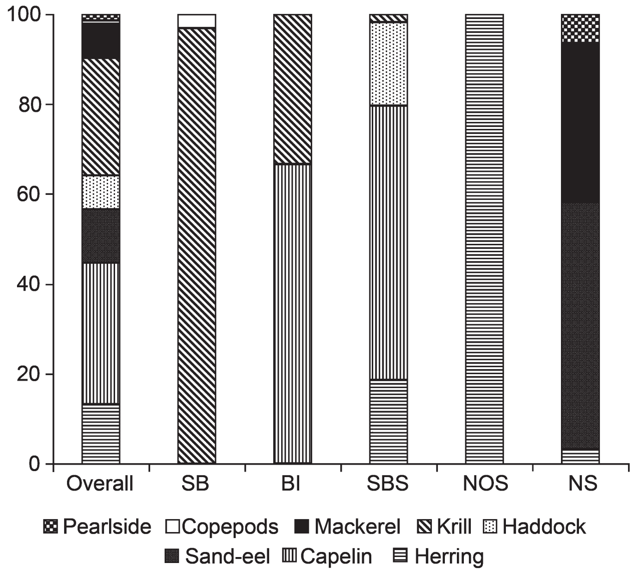


Fig. 3. Prey items in single prey stomachs (% of all stomachs in each area) of minke whales for the five sampling areas (Spitsbergen (SB), Bear Island (BI), Southern Barents Sea (SBS), Norwegian Sea (NOS) and North Sea (NS)) with sampling years 2000-04 pooled.

Area-to-area variation

According to the RDA analysis, area explained 42.7% of the constrained variance ($p<0.005$). In fact, the LDA showed that the differences in diet between areas were large enough to predict the area of origin of 82% of the whales, based on contribution of the different prey groups to the stomach contents. Krill and sandeels were the best prey items at discriminating among areas. These species together were sufficient in predicting the origin of 73% of the whales. The relative importance of prey was found to vary greatly both between and within the sub-areas (Fig. 5). The role of krill in the diet was most pronounced around Spitsbergen where it was significantly more important than the other prey items such as cod, haddock and capelin. These species showed no significant difference in importance between them.

Krill was also important in the diet around Bear Island, but was significantly less important than off Spitsbergen (Fig. 5). The greater part of the diet around Bear Island was a mixture of fish species (Table 3), with capelin as the significantly most important prey item. The rest of the diet consisted of haddock, cod and other gadoids which were equally as important as krill. There were no significant differences in importance between haddock, cod, gadoids and krill.

As for the Bear Island area, capelin was equally important in the southern Barents Sea (Fig. 5), where the diet consisted of capelin, haddock, herring and other gadoids (Table 3). Capelin and haddock were significantly more important than herring and other gadoids (Fig. 5).

Herring had a significantly greater importance in the Norwegian Sea than in all the other areas (Fig. 5). There, herring completely dominated the diet.

Whale sampling in the North Sea occurred in two distinctly separated parts. In 2001 and 2003, all but one whale were collected in the eastern North Sea. In 2002, all

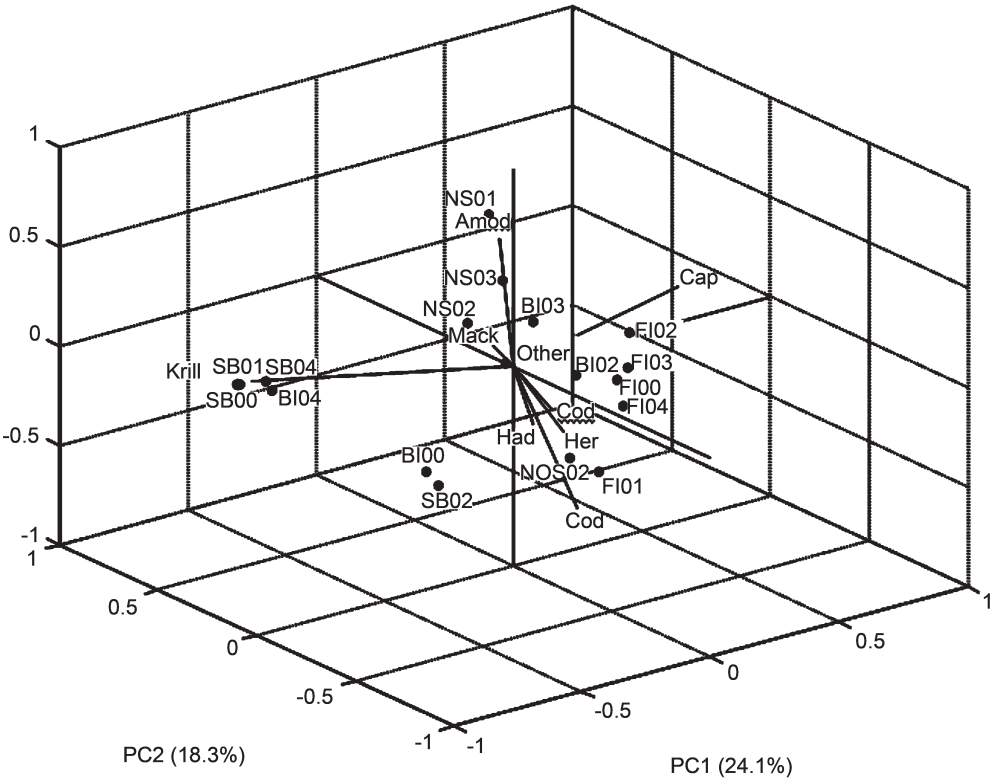


Fig. 4. PCA ordination plot of axes 1, 2 and 3 with prey species (arrows) and sampling sites for minke whales from the areas North Sea (NS), Norwegian Sea (NOS), Bear Island (BI), Spitsbergen (SB) and Southern Barents Sea (SBS) in the different sampling years. The first three axes 1-3 accounts for 24.1, 18.3 and 11.8 % of the variation in the prey species data, respectively. The sampling years are given along with the sampling sites, e.g. SB00, corresponds to Spitsbergen 2000.

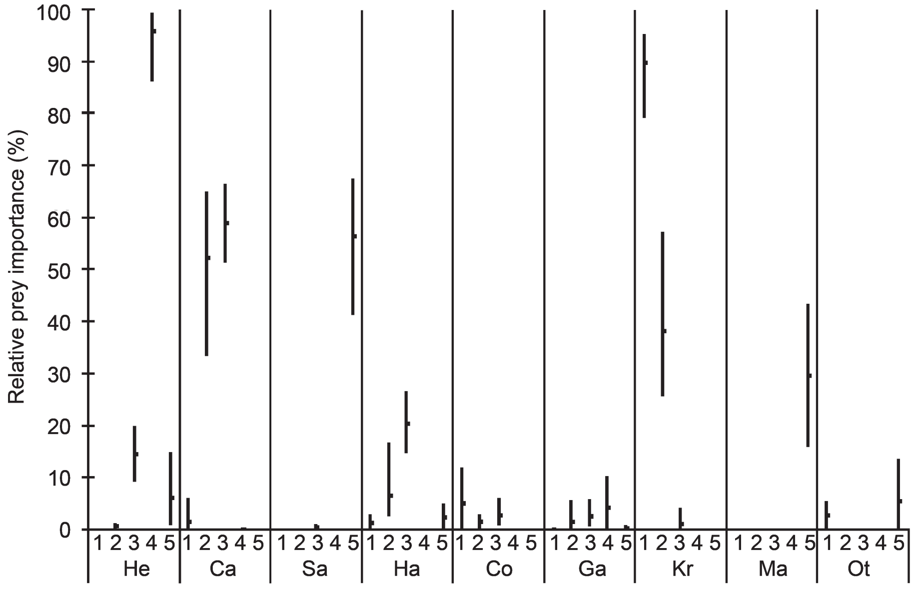


Fig. 5. Importance of different minke whale prey (WI) in the five different areas; Spitsbergen (1), Bear Island (2), Southern Barents Sea (3), Norwegian Sea (4) and North Sea (5). The means are given with a 95% confidence interval obtained by bootstrapping. All sampling years (2000-04) are pooled. The different prey items are herring (He), capelin (Ca), sandeels (Sa), haddock (Ha), cod (Co), gadoids (Ga), krill (Kr), mackerel (Ma) and Other (Ot).

but one whale were collected in the northern North Sea. The diet of whales collected in the eastern North Sea consisted mainly of sandeels (Table 3), with minor elements of herring and haddock. In the northern North Sea, all minke whales had fed exclusively on mackerel, with the exception of one whale who had fed exclusively upon pearlside.

Year-to-year variation

A considerable amount of the diet in the Spitsbergen area was explained by year (Table 4). The importance of krill was fairly stable, appearing in considerable amounts every year. The other prey items occurred only in one of the years. In 2000, capelin and haddock made large contributions to the

Table 4

Results of the RDA analysis of the percentage variance in diet of common minke whales explained by year and sex. Significance codes: 0***0.001** 0.01*0.05, NS: not significant.

	Year		Sex		Year + sex	
	% var. explained	F	% var. explained	F	% var. explained	F
SB	37.0	0.7831**	-	-	-	-
BI	39.9	0.8841***	-	-	-	-
SBS	16.2	0.3394***	4.8	0.35***	19.1	0.3299***
NOS	-	-	25.5	0.15 NS	-	-
NS	0.1	0.1027 NS	4.2	0.087 NS	-	-

diet, but were significantly less important than krill (Fig. 6a). In 2002, the diet contained large amounts of cod, which were of equal importance to krill.

There were significant differences in diet at Bear Island among the sampling years (Table 4). In 2000, most of the diet consisted of gadoids and krill. In 2002, capelin and herring were the dominant species. In 2003, capelin made up most of the diet, while in 2004 only krill was found. The small sample size in some of the years makes it hard to determine whether the changes are significant or not, but it appears that the importance of krill was greater in 2000 and 2004 than in the other years.

The southern Barents Sea was the only area in which sampling occurred in all five years of the study. This allows for a thorough analysis of year-to-year variation in diet. The dominance of capelin, haddock and herring was maintained from year to year but the relative amount of the individual species fluctuated between years. Compared to the other areas, year did not explain much of the constrained variance (Table 4). The importance of herring decreased in the beginning of the sampling period and herring was significantly more important in 2000 than in 2002 (Fig. 6b). In 2003, the importance of herring rose and was now significantly higher than in 2002. In 2004, herring was nearly absent in the diet.

Sampling in the eastern North Sea occurred in two years when the diet in both years contained large amounts of sandeel, which were significantly more important than smaller amounts of herring (Fig. 6c). There were no significant differences in diet between the two sampling years (Table 4). However, in 2003, the dietary contribution of sandeel was smaller than in 2001. At the same time, haddock made a contribution to the diet, being as important as herring. Diet of minke whales collected in 2002 in the northern North Sea was completely different, consisting primarily of mackerel.

Sex-effect

There was a significant difference in diet according to sex-composition of the minke whales. In the southern Barents Sea, sex explained 4.8% of the variance (Table 4). In years with a high amount of herring in the diet, the number of males in the samples was high compared with years with smaller amounts of herring.

The differences in diet among sexes in the North Sea was not significant (Table 4).

Size composition of prey

The capelin consumed in the southern Barents Sea were larger than those consumed in the northern Barents Sea (Table 5). The size of consumed capelin in the southern Barents Sea showed a normal distribution. The size distribution in the northern Barents Sea, on the other hand, was slightly bimodal (Fig. 7).

Herring was consumed in all three sampling areas but only mature herring were consumed in the Norwegian Sea (Table 5). The size range of consumed herring in the southern Barents Sea was much wider than in the Norwegian Sea and North Sea and the size distribution was bimodal (Fig. 8).

The size range of consumed sandeel in the North Sea was wider than in the southern Barents Sea due to a large proportion of smaller sand eel not present in samples from the southern Barents Sea samples (Table 5). The size distribution of consumed sandeel in the North Sea was thereby bimodal (Fig. 9).

The size range of consumed haddock was much wider in the southern Barents Sea than in the northern Barents Sea and the North Sea (Fig. 10, Table 5). The largest haddock was consumed in the northern Barents Sea.

In less frequently consumed prey there were great variations in size, from small species as pearlside and polarcod, to larger prey such as saithe and cod which were eaten at both small and large sizes (Table 6).

Age composition of prey

The majority of capelin consumed in the southern Barents Sea was 3 and 4 years old (Fig. 11). Sandeel were consumed at an age of primarily 1 and 2 years. The otoliths of haddock were difficult to interpret, and so the results should be viewed with that in mind. However, it is clear that a considerable amount of the consumed haddock were very small. Adult herring was the main minke whale prey in the Norwegian Sea.

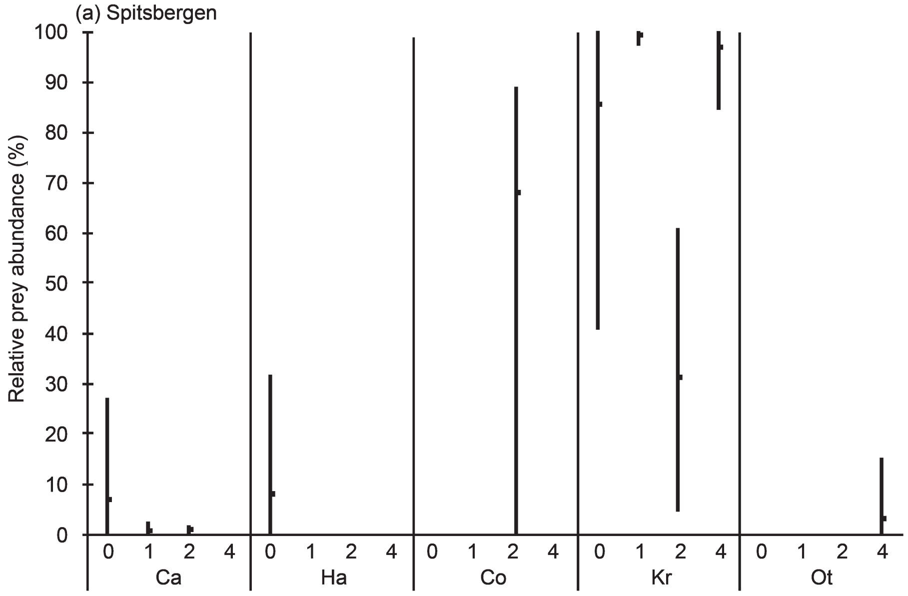
DISCUSSION

This study confirms the euryphagous nature of North Atlantic common minke whales described in earlier studies (Haug *et al*., 2002; Larsen and Kapel, 1981; Nordoy and Blix, 1992; Sergeant, 1963; Sigurjónsson *et al*., 2000), a feeding behaviour also observed in common minke whales in Japanese waters (Kasamatsu and Hata, 1985; Tamura and Fujise, 2002). Consistent with earlier studies which indicated a preference for fish (Skaug *et al*., 1997), the results show a clear dominance of fish in the diet. Six of 12 observed species of fish dominated the common minke whale diet in at least one of the areas examined. However, the number of different prey species in individual stomachs was low; the majority of the stomachs were single prey stomachs. Similar to previous minke whale feeding studies (Haug *et al*., 1997; Tamura and Fujise, 2002) the majority of the whales had fed upon only one prey species This shows that in spite of the minke whale's ability to forage on a variety of species, the number of prey species eaten at any one time is usually very low. In Haug *et al.* (1997) krill, herring and capelin made up 92% of the single prey stomachs. The majority of the single prey stomachs in this study also contained capelin, krill and herring, confirming their importance in the minke whale diet.

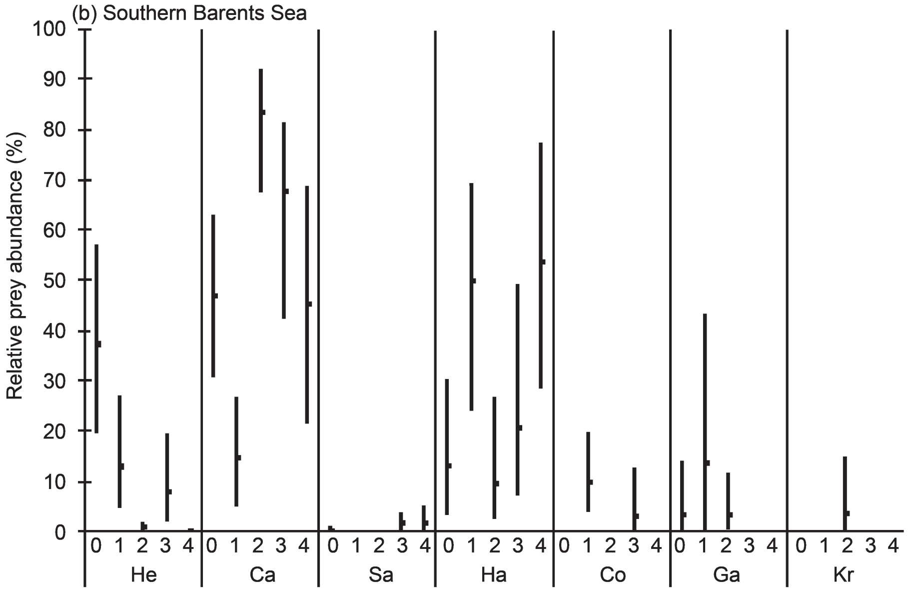
Barents Sea

Previous studies have shown that the proportions of capelin and krill in the diet in the northernmost areas are closely related to the state of the capelin population, following its collapses and recoveries. In 1989 and 1993, when the capelin stock had collapsed (Gjøsaeter, 1995), the diet of minke whale in the northernmost areas consisted mostly of

(a) Spitsbergen



(b) Southern Barents Sea



(c) North Sea

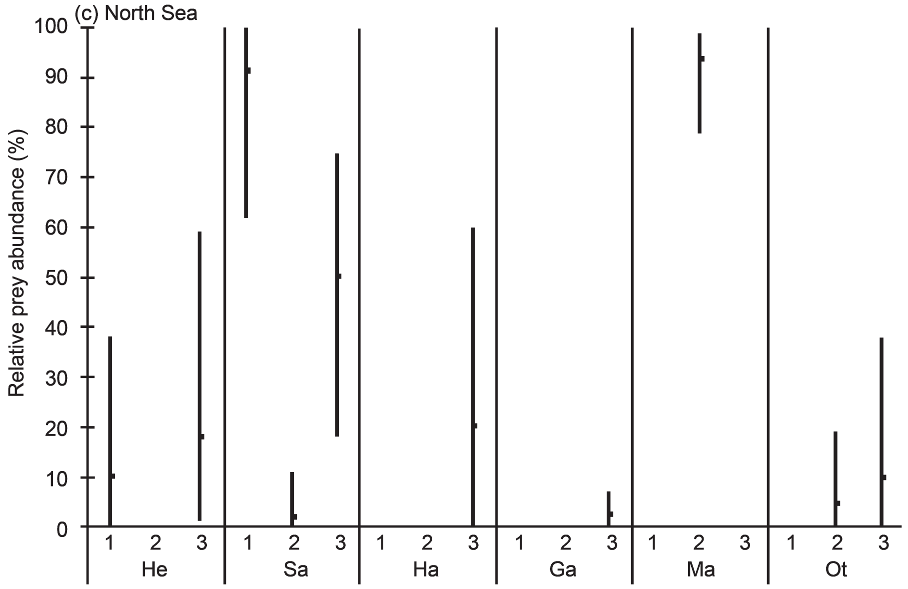


Fig. 6. Importance of different prey of minke whales in Spitsbergen (a), Southern Barents Sea (b) and North Sea (c) in 2000 (0), 2001 (1), 2002 (2), 2003 (3) and 2004 (4) (weighted biomass). The means are given with a 95% confidence interval obtained by bootstrapping. The different prey items are herring (He), capelin (Ca), sandeels (Sa), haddock (Ha), cod (Co), gadoids (Ga), krill (Kr), mackerel (Ma), other (Ot).

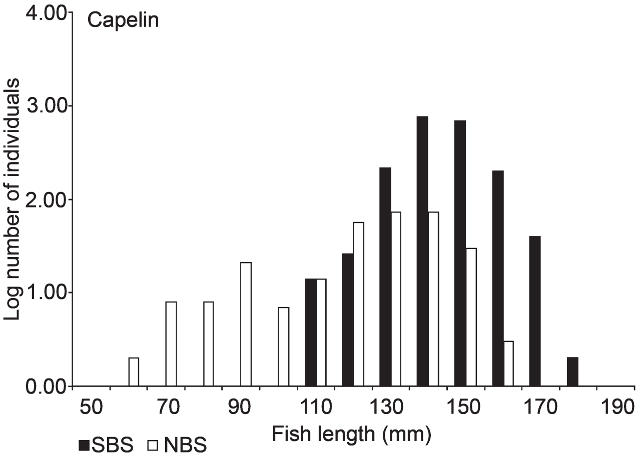


Fig. 7. Size distribution of capelin eaten by minke whales in the Southern Barents Sea (SBS) and Northern Barents Sea (NBS = Spitsbergen and Bear Island pooled) in 2000-04. Log transformed number of individuals of each size class (N).

Table 5

Minimum, maximum, average and median fish length (mm) of frequent prey of minke whales in the northern Barents Sea (NBS), Southern Barents Sea (SBS), Norwegian Sea (NOS) and North Sea (NS) in 2000-04. *N* = number of prey specimens. N_w = number of whales from which prey was collected.

Species	Area	Min.	Max.	Av.	Med.	*N*	N_w
Capelin	SBS	107	190	149	149	1,947	71
	NBS	58	170	134	139	436	22
Herring	SBS	85	355	187	180	510	39
	NS	162	301	204	185	55	6
	NOS	320	440	345	242	171	10
Sand-eels	SBS	100	192	135	133	170	10
	NS	53	228	105	85	671	23
Haddock	SBS	37	636	288	222	237	29
	NBS	460	626	550	553	18	4
	NS	278	411	340	335	16	1

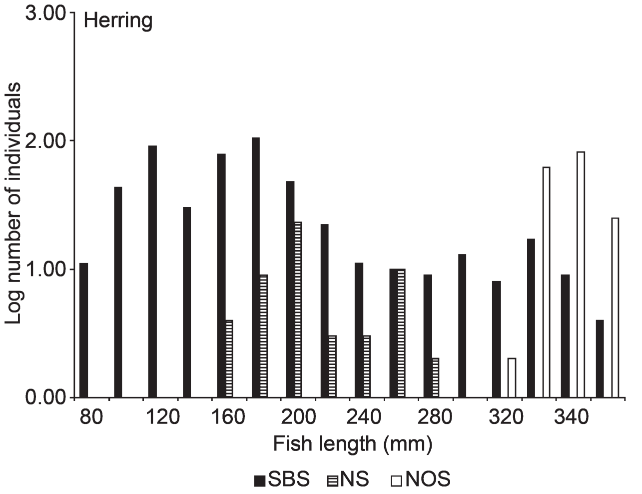


Fig. 8. Size distribution of herring eaten by minke whales in Southern Barents Sea (SBS), North Sea (NS) and Norwegian Sea (NOS) in 2000-2004. Log transformed number of individuals of each size class (N).

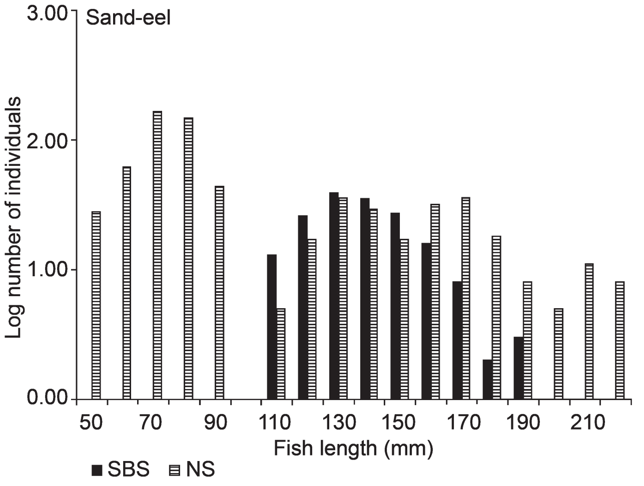


Fig. 9. Size distribution of sand eel eaten by minke whales in Southern Barents Sea (SBS) and North Sea (NS) in 2000-2004. Log transformed number of individuals of each size class (N).

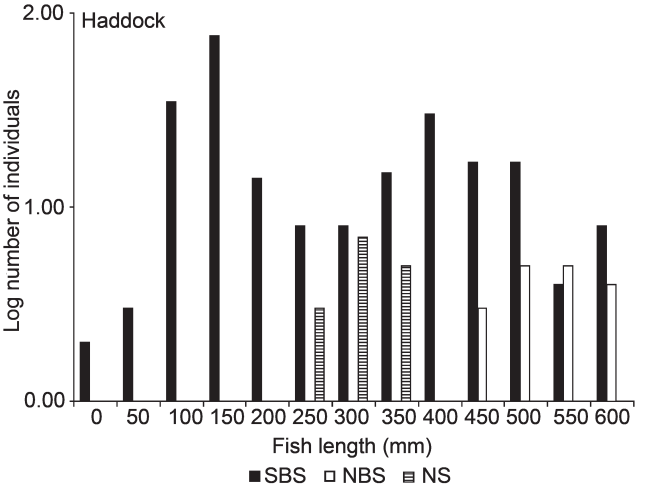


Fig. 10. Size distribution of haddock eaten by minke whales in the Southern Barents Sea (SBS), Northern Barents Sea (NBS = Spitsbergen and Bear Island pooled) and North Sea (NS) in 2000-04. Log transformed number of individuals of each size class (N).

Table 6

Minimum, maximum, average and median fish length (mm) of less frequent prey of minke whale in the northeast Atlantic in 2000-04. *N* = number of prey specimens, N_w = number of whales from which the prey was collected.

Species	Min.	Max.	Av.	Med.	*N*	N_w
Cod	205	795	382	320	36	9
Saithe	359	850	544	524	14	2
Polar cod	65	189	134	131	36	1
Blue whiting	185	311	224	216	59	5
Mackerel	290	425	246	339	61	11
Pearlside	43	65	53	54	78	2

krill (Haug *et al*., 1995b; Haug *et al*., 1996; Nordoy and Blix, 1992). In 1992, after the recovery, capelin dominated the diet completely (Haug *et al*., 1995a; Haug *et al*., 1995b). In this study, capelin and krill were found in all three subareas of the Barents Sea, but in different amounts depending on latitude. The importance of krill in the minke whale diet in the Barents Sea was highest in Spitsbergen waters and decreased with decreasing latitude, a pattern also observed in the 1990s (Haug *et al*., 2002). The importance of fish increased with decreasing latitude and was lowest in Spitsbergen waters, where only small amounts of capelin were found. In the southern Barents Sea krill had been

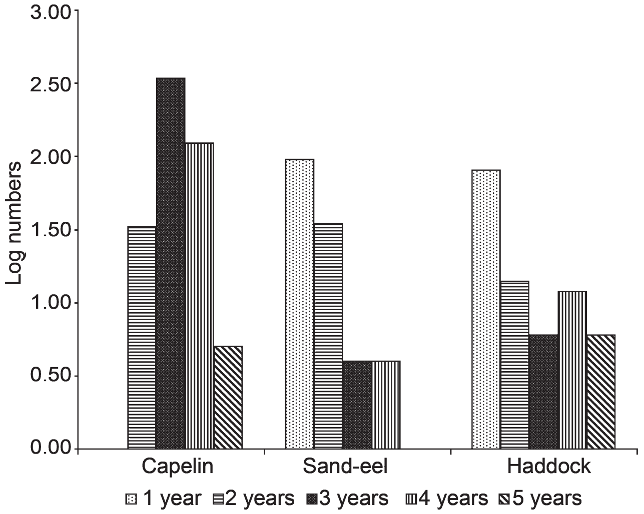


Fig. 11. Estimated age of prey by counting of otolith year rings of capelin (n=506), sand eel (n=139) and haddock (n=119) consumed by minke whales in the Southern Barents Sea in 2004.

replaced by a mixture of fish species including capelin. The diet in the Bear Island area was a combination of the diet in the southern Barents Sea and that around Spitsbergen. The only abundance estimates available for capelin apply to the entire Barents Sea. It is therefore difficult to discuss any correlations between the amounts of capelin in the diet in any of the three sub-areas and abundance estimates for capelin. The recent collapse of the capelin population in 2003 (see Wassmann *et al*., 2006) may however explain the complete absence of capelin in the diet in the Bear Island area in 2004.

The capelin consumed in the southern Barents Sea was mainly three and four years old, which is the age of mature capelin (Gjøsaeter, 1998). The abundance of mature capelin in the minke whale diet in the southern Barents Sea was related to the fact that during winter and early spring, the adult Barents Sea capelin migrate to the coast of northern Norway to spawn (Gjøsaeter, 1998). The capelin eaten by minke whales north of the spawning grounds, around Spitsbergen and Bear Island, were considerably smaller with only 56 and 48% of the capelin being above the size of mature females and males, respectively.

Herring has in numerous studies proven to be one of the most important species in the diet of the northeastern Atlantic minke whale, at least in the southern Barents Sea during summer (Haug *et al*., 1995a; Haug *et al*., 1995b; Haug *et al*., 1996). In this study, herring was found in smaller quantities than capelin in the southern Barents Sea. The abundance of juvenile herring in the Southern Barents Sea diminished from 2000 to 2002 due to the small year classes of 1998-2001 (ICES, 2005). With the exception of 2004, the importance of herring in the whale diet is well correlated with the abundance of herring in the sea. This is an indication that herring is a preferred prey item. In 1992, capelin was almost completely absent from the diet of common minke whales sampled off the coast of north of Norway (Haug *et al*., 1995a; Haug *et al*., 1995b) in spite of high abundance in the sea. The diet consisted mostly of herring, which was also found in great abundance. This suggests that minke whales may prefer to feed on herring when available (see Sivertsen *et al*., 2006). An additional explanation for the decrease and increase in the dietary importance of herring from 2000 to 2004 may be a difference in the male to female ratio between the years, where the females were found to feed more intensively on capelin while males seemed to prefer herring. The sudden lack of herring in the diet in 2004 in spite of higher abundance in the sea might be explained by the fact that stomach samples were collected from females only. This differentiation in diet between males and females has also been found by Haug *et al.* (2002).

The southern Barents Sea serves as a nursery area for juvenile herring and the majority of the observed and estimated lengths of herring eaten in the southern Barents Sea were below 200mm which corresponds to two year old herring (Pethon, 1985). The few otoliths available confirmed this age, although the sample size was too small to present in any figure. In addition, a bulk of adult herring was also found. These were possibly consumed farther west where adult herring may be encountered (Dragesund *et al*., 1997).

The amount of haddock in the whale diet varied from year to year but did not appear to show any correlation with current abundance estimates from the southern Barents Sea. The reason why gadoid species are not targeted more often may be that minke whale require a minimum foraging threshold level of prey (Piatt and Methven, 1992). With the exception of small saithe (Bergstad *et al*., 1987), gadoid species do not generally aggregate in dense schools and may therefore not always be an optimal prey for the whales. Nevertheless, 7% of the single prey stomachs in the present study contained haddock. This high occurrence of haddock in single prey stomachs from the southern Barents Sea can be explained by the fact that dense schools of gadoids may occur in spring in their spawning areas along the Norwegian coast (Bergstad *et al*., 1987). Haddock made a considerable contribution to the diet of minke whales in the southern Barents Sea, where they had a wide size distribution including both juvenile and large adult individuals, although both length and age analysis showed that the majority were smaller haddock. In the other areas the distributions were narrow but the number of individuals was also considerable lower. The haddock consumed in the northern Barents Sea were considerably larger than those consumed in the North Sea.

Norwegian Sea

The Norwegian Sea is an important feeding area for adult herring during late spring, summer and autumn. They migrate between the feeding areas in the Norwegian Sea, wintering areas in Norwegian fjords and spawning areas along the Norwegian coast (Dragesund *et al*., 1997). The whales were caught in the summer feeding area of the Norwegian spring spawning herring. The diet of the whales caught there consisted almost entirely of large herring and the size analysis revealed that the herring consumed by minke whales in that area were adult individuals, supporting earlier studies (Folkow *et al*., 2000; Haug *et al*., 1996).

North Sea

The eastern part of the North Sea is an important area for sand eel and this was also reflected in the whale diets; 87.5% of the whales had fed more or less exclusively on this prey item. Of all whales collected in this area, regardless of year (n=24), only three whales had not fed more or less exclusively on this prey item. In 2003, the dietary contribution of sandeels was smaller than in 2001; haddock, which was not present in 2001, contributed greatly to the diet. This could be a result of the poorer recruitment of sandeels in recent years (Michalsen, 2004), perhaps caused by overfishing. The landings of industrial fishing, targeting one and two year old fish can be used as an indication of the amounts of adult fish 3-4 years later when it is a target for the minke whale. The landings of 1997 and 1998 were extremely high, approximately 350,000 tonnes each year (Michalsen, 2004). The landings of 1999 and 2000 however, were considerably smaller, measuring 188,000 and 119,000 tonnes, respectively. The higher average size of sand eel consumed in 2001 was a result of a higher proportion of large sandeel present in the area. When splitting the two years, it was evident that the bulk of large sand eel present in 2001 were absent in 2003, confirming the poor year classes of previous years. The poor year classes may therefore be the reason behind the decrease in sand eel importance in minke whale diet in 2003.

The smaller size of the herring consumed by minke whales in the North Sea compared to the Norwegian Sea is consistent with size differences between these two herring populations (Tjelmeland and Lindstrøm, 2005).

The minke whales were found to prey almost exclusively on mackerel in the northern North Sea, which is known as an important mackerel area.

The considerable size range of consumed prey (0.2-78cm) confirms the flexible foraging behaviour of minke whales (Tamura and Fujise, 2002) and also that minke whales are not particular size selective on a population level. The size of prey seems to be determined by the availability of different size classes, rather than selectivity by the minke whale. A lack of size selectivity was previously found by Lindstrøm and Haug (2001).

In summary, this study confirms the euryophagous nature of the northeastern Atlantic minke whales; they appear to feed on the most available prey in each area. The diet composition of minke whales varies much in both time and space; fish dominates the diet in all but one area (Spitsbergen). The minke whales were found to feed on a wide variety of size classes, probably proportional to what can be expected by random feeding behaviour in areas where there is a variety of prey size classes.

ACKNOWLEDGEMENTS

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How much do large whales eat?

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ABSTRACT

Estimates of the amount of prey consumed by cetaceans have been used in ecological models and also directly compared to human fisheries yields. Most of these estimates have been based on assumptions about energy requirements. However, the lack of direct measurements for large whales has necessitated extrapolation beyond the data points available from smaller species. A number of different parameterisations of general regressions in which energy requirements or consumption are estimated as proportional to body mass raised to some power B, were compared with estimates of Basal Metabolic Rate (BMR) from the widely used Kleiber equation. The choice of values has a large impact on estimates, which can differ by an order of magnitude, but modellers are frequently forced to make rather arbitrary decisions due to lack of data. Nevertheless, neither data nor theory appear to support values of $B > 0.75$. Although some parameter values have obtained status through common usage, these have not always been based on actual data and estimates of consumption by whales need to reflect this uncertainty. Comparison of generalised relationships with data from other sources, including rates of filter feeding, oxygen consumption and seasonal changes in energy stores, suggest upper bounds on average daily metabolic rate of large whales. Estimates based on stomach contents also indicated average daily metabolic rates of less than four times the BMR from the Kleiber formula, but these are critically dependent on estimates of digestion time for which there appear to be little data. Estimates of stored energy suggest that large whales that migrate to seasonally productive feeding areas either have relatively low energy requirements for their size or need to meet a considerable proportion of their annual energy requirements outside of the feeding grounds.

KEYWORDS: ENERGETICS; FOOD/PREY; FEEDING; MODELLING; MANAGEMENT; NORTHERN BOTTLENOSE WHALE; NORTH ATLANTIC RIGHT WHALE; BLUE WHALE; BOTTLENOSE DOLPHIN; NARWHAL; ANTARCTIC MINKE WHALE; COMMON MINKE WHALE; SPERM WHALE; SEI WHALE; KILLER WHALE; FIN WHALE

INTRODUCTION

Several studies over the last three decades have generated estimates of how much prey is consumed by large whales. These studies have arisen both from concerns that whales may have a negative impact on fisheries and also that fisheries be managed in order to leave sufficient prey available for whales. Most estimates have been intended to inform ecological models; others have been used to examine hypotheses that prey resources may be limiting predator population recovery (Baumgartner and Mate, 2003; Kenney *et al*., 1986), whilst some have been used for direct comparison with human fisheries (Tamura and Ohsumi, 2000). Such comparisons have generated much public debate, often poorly informed. Within the International Whaling Commission (IWC) some Commissioners have stated that 'whales consume huge quantities of fish making the issue a matter of food security for coastal nations' (IWC, 2007) despite the conclusion of the IWC Scientific Committee that 'for no system at present are we in the position, in terms of data availability and model development, to provide quantitative management advice on the impact of cetaceans on fisheries, or of fisheries on cetaceans' (IWC, 2004). Given such a level of interest over quantities that have not been directly measured, there is a clear need for understanding the uncertainties surrounding the available estimates of food consumption. This paper reviews a number of estimates of prey consumption in an attempt to allow comparisons between different approaches.

Most of the methods for estimating prey or energy consumption of whales are based on generalised formulae related to body size. These formulae usually relate to body mass, although Hunter *et al*. (2000) suggested that maximum body length is a more accurate independent variable than body mass. Most calculations have relied on estimating the energy requirements of whales and using this to estimate the amount of prey that would need to be consumed to meet these requirements. These calculations face a number of challenges: (1) estimates of metabolic rates in large whales need to be extrapolated well beyond the range of available data; (2) estimates of Basal Metabolic Rate (BMR) need to be adjusted to Field Metabolic Rate (FMR) or Average Daily Metabolic Rate (ADMR) and to allow for the energy requirements of growth and reproduction; (3) large whales may make long migrations and feed for only a proportion of the annual cycle; and (4) energy content of prey needs to be estimated and adjusted for assimilation efficiency (i.e. the amount of energy that becomes available to the whale).

RELATIONSHIPS WITH BODY MASS

Some of the studies reviewed here used direct empirical relationships between mass of food ingested and body mass while others were based on estimates of energy requirements. Where the energy content of the prey can be expressed as an average value per kg, then consumption rates follow directly from the energy estimates. Thus in the cases considered, daily consumption rates, R, can be expressed in the general form

$$R = AM^B \qquad (1)$$

Where R is mean consumption rate in kg d^{-1} over the whole year, A and B are constants and M is the body mass in kg. This equation can also be expressed in terms of energy

$$E = KM^B \qquad (2)$$

Where E is the mean daily energy requirement over the whole year (kJ d^{-1}) and K is a constant. The energy balance for an individual is frequently written as

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$$T = E/c \tag{3}$$

Where T is the total energy intake (kJ d^{-1}), E is the metabolisable energy and c is the product of digestive efficiency and assimilation efficiency.

The value of B will clearly become increasingly influential with increasing body mass, and so is particularly significant for large whales.

Energy requirements

Kleiber (1975) suggested the generalised formula of Eqn 2 for BMR (expressed in kJ d^{-1}) in homeotherms, including mammals, with an exponent of B=0.75.

$$BMR = 293.1M^{0.75} \tag{4}$$

Although some studies have suggested that marine mammals have elevated metabolic rates compared to the Kleiber formula, none of these have proved to be consistent with all the available data. The hypothesis that marine mammal metabolic rates are higher than those of carnivorous terrestrial mammals (or mammals generally) has been tested on more than one occasion by comparing all available standardised metabolic rate determinations for marine mammals (specifically pinnipeds and cetaceans) with relationships generated for terrestrial mammals. Lavigne *et al*. (1986) concluded that the previous perception that marine mammals have higher metabolic rates in relation to body size than terrestrial mammals was not supported by data when comparisons were made under standardised conditions. Innes *et al*. (1987) also reached similar conclusions for comparisons of feeding rates and on further analysis of BMR estimates based on O_2 consumption (Innes and Lavigne, 1991). These results were confirmed by Hunter *et al*. (2000) who included additional data, but still were unable to reject the null hypothesis that BMR in marine mammals is the same as in terrestrial mammals of similar body size.

More recently, Williams *et al*. (2001) calculated BMRs of Weddell seals (*Leptonychotes weddelli*) and bottlenose dolphins (*Tursiops truncatus*) resting on the water surface of 1.6 and 2.3 times the predicted levels for similarly sized domestic terrestrial mammals. Their estimates involved measuring oxygen consumption. It is interesting to compare their estimates of BMR in bottlenose dolphins to measurements of actual food consumption of this species in captivity. Kastelein *et al.* (2002) found that estimated average annual food consumption of adult males and non-pregnant, non-lactating females was approximately 176×10^5kJ for a mean adult body mass of 260kg. This would correspond to a total energy requirement around 2.5 times the predicted BMR from the Kleiber formula and similar to the BMR estimated by Williams *et al*. (2001). There is clearly a discrepancy in this case given the expectation that the total energy content of the prey consumed would be some larger multiple of BMR. However, even if the BMR estimates of Williams *et al.* (2001) were correct, this would not justify their conclusion 'that the metabolic rates of many species of carnivorous marine mammal are elevated when compared to levels for carnivorous terrestrial mammals', since their finding only applies to two species. By taking selected data points for a few other species (as Williams *et al.* did) it is not correct then to reject a hypothesis supported by a much larger and more standardised data base. There have also been suggestions that marine mammals may require elevated metabolic rates to maintain body temperatures (Kshatriya and Blake, 1988). However, in response to Kshatriya and Blake (1988), Lavigne *et al*. (1990) recalculated the lower critical temperatures of blue whales (*Balenoptera musculus*) and found that they, like many smaller marine mammals, should not be obligated to increase their heat production in order to maintain homeothermy, even in sea water at its minimum temperature of about −2°C.

Based on the evidence that metabolic rates in marine mammals were not exceptional, Lavigne (1996) suggested the following formula for *ADMR*, based on Eqn 4.

$$ADMR = \beta(293.1M^{0.75}) \tag{5}$$

Where ADMR is the average daily metabolic rate in kJ, β is a multiplicative factor greater than one and M is the mass in kg (a daily energy requirement of 293.1kJ corresponds to 70kcal or a power output of 3.39W). Based on the assumption that FMR is a simple multiple of BMR, ADMR should approximate average FMR throughout the year. For cetaceans, β is often assumed to be in the range of 2-5. Some authors have used β=2.5 which was a choice made by Kenney *et al*. (1997) for all cetaceans and subsequently followed by Hooker *et al*. (2002) and Laidre *et al*. (2004) for northern bottlenose whales (*Hyperoodon ampullatus*) and narwhal (*Monodon monocerus*) respectively. Baumgartner and Mate (2003) used a value of two for the ratio of diving metabolic rate to BMR in North Atlantic right whales (*Eubalaena glacialis*) with a note that 'It is very important to bear in mind, however, that the selection of Diving Metabolic Rate=2BMR, though based on sound reasoning, is truthfully only a guess.' This caution is applicable to most studies that assume a value for this ratio. Although some particular values have gained status through repeated use, these are not necessarily supported by actual data.

Alongside the debate about whether marine mammals have elevated metabolic rates is the debate about the value of B. Despite considerable attention being given to estimation of B within the literature (Hunter *et al*., 2000; Kleiber, 1975; Koteja, 1991; Lavigne *et al*., 1986) the problem remains of very few data points at higher body mass on which to base regression lines. Regressions that are not significantly different can nevertheless result in different values of B that result in considerable differences in predictions of consumption rates at large body mass. For example, the regression analysis of Lavigne *et al.* (1986) for the relationship between body mass and metabolic rate in phocid seals gave a value of B of 0.87. However, this was not significantly different from Kleiber's equation. The relationship between metabolic rate and body mass in marine mammals has also been reviewed by Boyd (2002). He suggested an allometric relationship in which FMR (expressed in kJ d^{-1}) varied with body mass to the power 0.524.

$$FMR = 2529.2M^{0.524} \tag{6}$$

Other recent reviews have also challenged the 0.75 figure as a general value for B in mammals. For example, White and Seymour (2005) argue that the best estimate of B for BMR is 0.69 across all mammalian taxa. In an extensive regression of 619 species from 19 mammalian orders, the same authors had previously made the case that BMR in mammals is proportional to body mass raised to the power 0.67 (White and Seymour, 2003). However, it should be noted that large whales are outliers to all these studies in terms of body mass.

COMPARISONS OF DIFFERENT STUDIES OF CONSUMPTION

Comparison of different estimates of the amount of prey consumed by large whales is complicated by whether these estimates are expressed in terms of energy or mass and whether they are mean daily values throughout the year or just for seasonal consumption within a region. For the studies reviewed here, we have presented comparisons in terms of mean daily energy throughout the year, relative to the predicted BMR from the Kleiber formula (Eqn 4).

Estimates of prey consumption by large whales based on allometric extrapolations

Kenney *et al*. (1997) used the approach of Eqn 5 in a study of the trophic impacts of cetaceans in the USA northeast continental shelf ecosystem. They assumed assimilation efficiency to be 80% and an average FMR/BMR ratio of 2.5. This gave an estimate of total energy intake of 3.125 times BMR. They also applied an additional factor for baleen whales to take into account seasonal differences in feeding rates. The study area was a known summer feeding ground for baleen whales and the calculated ADMR was multiplied by 1.2 to account for higher feeding rates when whales were in the study area. Such corrections highlight important issues when comparing estimates. For some modelling studies, it is the consumption within the area of the model that is of interest; for others it is the average consumption throughout the year. Daily consumption rates may vary by orders of magnitude between areas of high feeding activity and low feeding activity, especially for species that make long migrations and are able to store large amounts of energy.

To move from ADMR to estimates of prey consumption, data are required on the relative composition of the diet and energy content of the different prey species and assimilation efficiency. In many cases, such data are not available. In a study of the North Pacific, Trites *et al*. (1997) used a direct approximation for an individual's daily consumption or ration,

$$R_{i,s} = 0.1M_{i,s}^{\ 0.8} \qquad (7)$$

Where $R_{i,s}$ is the daily prey consumption in kg and $M_{i,s}$ is body mass in kg, for each species i and sex s. The value of 0.8 was taken from Innes *et al*. (1987). Okamura *et al*. (2001) used the same formula for an *Ecopath*/*Ecosim* model of the western North Pacific. Eqn 7 is shown on Fig. 1 assuming a mean prey calorific value of 5,450kJ kg^{-1} (this is a commonly used value for fish prey and is used in this paper to standardise comparisons between estimates based on intake and estimates based on energy requirements) and an assimilation efficiency of 80% (this value is also used in this paper to standardise comparisons).

Sigurjonsson and Vikingsson (1997) used two different parameterisations to estimate consumption by whales around Iceland, which were used as input in an ecosystem model by Stefansson *et al*. (1997). They used the suggestion of Armstrong and Siegfried (1991), based on the results of Innes *et al*. (1986), that feeding rates could be described as

$$R = 0.42M^{0.67} \qquad (8)$$

Where R is the daily consumption and M is body mass in kg. This is shown in Fig. 1 for a prey calorific value of 5,450kJ kg^{-1} and an assimilation efficiency of 80%.

Sigurjonsson and Vikingsson (1997) also calculated ingestion rates based on estimates of energy requirements using

$$G = 863.6M^{0.783} \qquad (9)$$

Where G is the daily requirement in kJ.

This was based on the near-basal metabolic rate of Lockyer (1981) with an assumed assimilation rate of 80% and an activity coefficient of 1.5. Mean daily feeding rates for baleen whales were also adjusted seasonally based on the assumption of 83% of the annual intake being during a 120 day summer feeding period and that feeding rates for the intensive feeding period were ten times that during the rest of the year, also based on Lockyer (1981). Thus the summer ingestion rate was assumed to be $2.53G$ and the winter ingestion rate $0.235G$. In the absence of data on the seasonal variation in energy content of prey species they assumed an average of 3,900kJ kg^{-1} for crustaceans and 5,450kJ kg^{-1} for fish and cephalopods. These values were then used to calculate consumption rates from Eqn 9.

Tamura and Ohsumi (2000) used three different parameterisations to calculate regional estimates of prey consumption by cetaceans, referred to as Methods 1, 2 and 3 in their paper. Method 1, uses Eqn 8 directly, Method 2 uses Eqn 9 and Method 3 uses the formula suggested by Klumov (1963),

$$R = 0.035M \qquad (10)$$

Where R is daily consumption in kg and M is average body mass, kg. This is shown on Fig. 1 for a prey calorific value of 5,450kJ kg^{-1} and an assimilation efficiency of 80%. The relevance of the data from Klumov (1963) have subsequently been questioned by Reilly *et al*. (2004) who commented that the data used 'do not provide a sound basis for extrapolation'. For Method 2, Tamura and Ohsumi (2000) assumed the mean energy content of prey to be 4650kJ kg^{-1} for baleen whales in the Southern Hemisphere and 5,450kJ kg^{-1} for baleen whales in the Northern Hemisphere and odontocetes around the world. Tamura *et al*. (2004) used the mean of Methods 1, 2 and 3 and this is also shown in Fig. 1.

In a study of biomass and energy transfer to baleen whales in the South Atlantic sector of the Southern Ocean, Reilly *et al*. (2004) reviewed various options for estimating mean daily consumption for a number of species. They used data on estimates of feeding rates of minke whales (*B. bonaerensis*) in the Antarctic (Tamura *et al*., 1997) that appeared to be in good agreement with the Blix and Folkow (1995) FMR estimates. At the other end of the body mass range for great whales they extrapolated using Eqn 8 to blue whales. Fitting the generalised relationship between consumption and body mass given in Eqn 1 to these points gave their preferred relationship

$$R = 1.66M^{0.559} \qquad (11)$$

for mean daily consumption in kg during the high feeding period in the Antarctic. This is shown in Fig. 1 adjusted for seasonal feeding based on the same assumption as in Eqn 9, of 83% of annual intake during the high feeding period, assuming mean energy content of prey to be 4,650kJ kg^{-1} and an assimilation efficiency of 80%. However, they did consider a range of possibilities within the model, based on a maximum daily consumption for blue whales as a percentage of body mass.

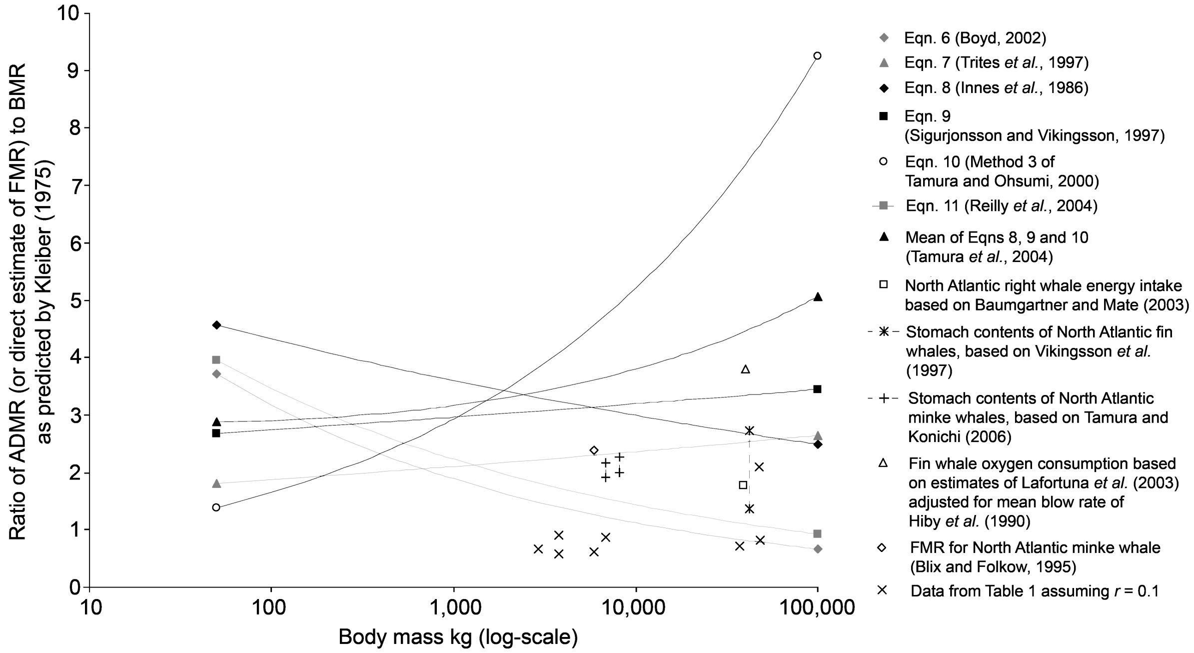

Fig. 1. Comparison of different studies expressed as a ratio to BMR as predicted by the Kleiber formula. For comparative purposes estimates based on seasonal energy intake were adjusted to approximate ADMR throughout the year (direct estimates of FMR were not adjusted for possible seasonal differences). Where estimates were originally expressed in terms of prey mass these were converted to energy based on estimated prey energy content and an assimilation efficiency of 80%.

OTHER METHODS OF ESTIMATING CONSUMPTION RATES

Possible alternative approaches to extrapolation based on allometry include direct measurement of intake from behavioural studies, estimates of intake based on analysis of stomach contents, estimates of respiration based on oxygen exchange, and estimates of energy requirements based on utilisation of energy stored in body tissues.

Direct observations of consumption rates

Estimates of quantity of prey consumed from behavioural studies of free living cetaceans have rarely been possible in the short term and become even more problematic over an annual cycle. For baleen whale species that feed by 'gulping' on prey that may take evasive action, measuring the amount of prey consumed is unlikely to be practicable. However it may be possible to make some inference for filter feeding species such as the *Balaenidae* if it can be assumed that the prey take no avoiding action. This has been done for North Atlantic right whales based on assumptions of swimming speed, projected area of the mouth, proportion of time spent feeding and measurements of copepod densities in the vicinity of feeding whales (Baumgartner and Mate, 2003; Beardsley *et al*., 1996; Kenney *et al*., 1986). Such an approach also provides an additional theoretical consideration for the choice of *B*. If body proportions remain constant with growth then the projected area for filtering will increase with body length raised to the power two whereas mass increases with length to the power three. Thus unless larger whales swim faster or spend a greater proportion of their time feeding, then *B* would be have to be 0.67 or less.

Kenney *et al*. (1986) estimated a maximum possible daily filtering rate of 9.9×10^4 m^{3}d^{-1} for right whales in the Cape Cod area assuming that they were feeding around the clock during submerged periods. This was based on a swim speed of 1.5ms^{-1}. These estimates led them to conclude at the time that the required prey densities were from one to three orders of magnitude greater than the densest concentrations sampled in the vicinity of North Atlantic right whale aggregations in the Great South Channel. Subsequent studies have tried to measure plankton concentrations in the vicinity of feeding right whales, and the results highlight the large variability in copepod densities. More recent studies of skim feeding right whales suggest that a 1.5ms^{-1} swim speed may be too high. Leaper *et al.* (1999) observed maximum swim speeds of 1.2ms^{-1} and a mean of 0.6ms^{-1} with the mouth open, similar to a mean of 0.64ms^{-1} for feeding whales observed by Mayo and Marx (1990) in Cape Cod Bay and 0.7ms^{-1} from Goodyear (1995). The mean density of plankton observed near feeding right whales in the Great South Channel was 5.9gm^{-3} (Wishner *et al*., 1995) and 3.9gm^{-3} in Cape Cod Bay (Mayo and Marx, 1990). Subsequently, Beardsley *et al.* (1996) reported some very high copepod densities in the Great South Channel. They calculated that the highest observed densities from a single bucket sample in front of a feeding whale (3.3×10^5 copepods m^{-3}) would enable a right whale to satisfy its daily energy requirement in around nine minutes of feeding. However, such high densities are not commonly observed and are much greater than mean values close to feeding whales. For example, the mean copepod density reported by Baumgartner and Mate (2003) beside feeding right whales in the Bay of Fundy was 6,618 copepods m^{-3} i.e. only 1/50 of the peak observed by Beardsley *et al.* (1996). Using the mean ingestion rate of Baumgartner and Mate (2003) for feeding right whales provides an energy intake of 2.96BMR. However, right whales are known to make long migrations and clearly do not feed every day of the year. Given the time spent by female right whales on the calving grounds and travel times between feeding areas it seems unlikely that all right whales could feed at this rate for more than nine months of the year. This would suggest a mean annual energy intake of 2.2BMR as predicted by Kleiber. Assuming an assimilation efficiency of 80% would suggest

FMR=1.76BMR and this is shown in Fig. 1 for comparison. No correction was made to this estimate to allow for less than 100% filtration efficiency (Mayo *et al*., 2001). Baumgartner and Mate (2003) concluded that many of the tagged right whales in their study ingested prey at sufficient rates to meet daily metabolic requirements assuming DMR = 2BMR. However, if DMR values for right whales exceeded four times BMR, then only 4 of the 22 individuals with tag attachments lasting over 1hr would have been ingesting prey at a sufficient rate to meet daily energy requirements.

Stomach contents

Some estimates of feeding rates have been based on analysis of stomach contents including Vikingsson (1997) for fin whales (*B. physalus*) feeding off Iceland, Tamura *et al*. (1997) and Tamura and Konishi (2006) for Antarctic minke whales. Vikingsson (1997) predicted daily feeding rates for fin whales of between 677 and 1,356kg based on quantity of fore stomach contents and assumptions about the evacuation rate of the fore stomach. This range of values is plotted on Fig. 1 assuming a prey energy density of 5,450kJ and an assimilation efficiency of 80%, for a mean body mass of 42 tonnes adjusted to an average daily rate through the year using the assumption of Sigurjonsson and Vikingsson (1997) that $I=2.53R$ where I is the summer feeding rate and R is the mean throughout the year.

The ability of whales to exploit a super-abundance of prey will be limited by the size of the mouth and stomach, the duration of the conditions that maintain prey at high densities, the extent of the dense patches and the rate at which the stomach is evacuated. There is thus a maximum rate of food intake regardless of prey density. In studies of Antarctic minke whales during commercial whaling Bushuev (1986) found that only 3% of Antarctic minke whales caught between 04:00-05:00 hrs had empty stomachs but that this rose to 96% between 17:00-18:00 hrs. He concluded that in good feeding areas Antarctic minke whales only exhibited one period of peak feeding per day. Tamura and Konishi (2006) also reported a similar but less pronounced diurnal pattern in Antarctic minke whale stomach contents and used this to estimate daily consumption based on assumed digestion rates. Their consumption estimates of 4.36%-4.95% of body mass per day, adjusted for a mean daily rate based on 120 days feeding at high rate and 83% of annual energy intake during this period are shown in Fig. 1 for minke whales of body mass 6,800 and 8,100kg assuming a mean prey energy content of 4,473kJ kg^{-1}. Approximate times for digestion cite Bushuev (1986) although in fact this paper does not provide any actual data on digestion times. If the proportion of prey digested in each time interval, d, is constant (i.e. exponential decay) then there will be a linear relationship between estimates of daily consumption and estimates of d. Thus without data on d, it is not possible to relate stomach contents to consumption rates.

Respiration rates

Lockyer (1981) estimated that 30 and 70 tonne fin whales had BMRs of 1.4 and 1.8 times respectively of the values predicted by the Kleiber formula on the basis of lung capacity. Subsequent studies have also attempted to estimate metabolic rates from estimates of oxygen consumption. These are based on measured respiration rates, estimates of lung capacity (tidal volume) and assumptions regarding the exchange efficiency of oxygen. Lafortuna *et al*. (2003) derived a relationship for tidal volume, $V_T=0.074M^{0.9}$, from measurements for three cetacean species in captivity. Extrapolation to large whales was based on a similar regression of measurements of total lung volume that did include sei (*B. borealis*) and fin whales and also appeared to scale with body mass to an exponent around 0.9. They also made the assumption that whales control their ventilatory output, mainly, if not exclusively, by frequency modulation. This assumption was based on physiology and may be challenged on the basis of numerous reports from field observations of variation in the apparent strength of blows for several species. One implication of the assumptions is that if tidal volume scales as body mass 0.9 and metabolic rates scale as body mass to some smaller exponent, then ventilation rates would decrease with size. There is some evidence of this from intra-specific comparisons. For example, Gordon and Steiner (1992) calculated mean blow intervals of 70.6s for small sperm whales (*Physeter macrocephalus*) and 107.1s for large males. Lafortuna *et al*. (2003) estimated an average oxygen consumption of 150L min^{-1} for a 40,000kg whale with a conversion factor of 20.1kJ per litre of O_2. The observed blow rate in that study (mean 1.16 breaths min^{-1}) was rather higher than the mean respiration rate from a review of fin whale blow rates (mean 0.87 breaths min^{-1}) by Hiby (1992). Fig. 1 shows the FMR for fin whales based on Lafortuna *et al*. (2003) but adjusted for 0.87 breaths min^{-1} (giving an O_2 consumption of 113L min^{-1}). This should be a more representative estimate of average FMR values, but nevertheless is only valid for whales on their feeding grounds.

Blix and Folkow (1995) used respiratory rates and lung volumes combined with respiratory data from other cetacean species to estimate an FMR of 80kJ kg^{-1} per day for North Atlantic minke whales (*B. acutorostrata*). This is shown in Fig. 1 for a body mass of 5,900kg. This estimate has been widely used in a number of studies including the *MULTSPEC* multi-species model for fish and marine mammals in the Barents Sea (Bogstad *et al*., 1997). In this model, average gross energy intake within the study area, allowing for muscle growth, blubber and visceral fat deposition was assumed to be 125kJ kg^{-1} per day. Folkow *et al*. (2000) present similar calculations for northeastern Atlantic minke whales but stratifying energy requirements by season and by sex and reproductive status. Their values for gross energy intake range between 88kJ kg^{-1} for physically mature males in spring to 143kJ kg^{-1} for immatures in autumn. They estimate an average consumption of all prey by minke whales of 117kg per whale per day over a 183 day feeding season. In a model of interactions between minke whales, cod and herring fisheries in the Greater Barents Sea, Schweder *et al*. (2000) used an average daily consumption of 90kg per whale per day. By contrast, Laws (1977) had previously assumed that minke whales in the Antarctic fed at 3.9% of their body mass a day for 365 days a year. If krill is assumed to have an energy content of 4,500kJ kg^{-1} then the mean daily gross energy intake would be 175.5kJ kg^{-1}. This is more than double the FMR estimates by Blix and Folkow (1995) and 5.6 times BMR as predicted by Kleiber for an 8,000kg whale and seems highly unlikely.

Energy stores

Brodie (1975) used estimates of the amount of lipid stored by fin whales on feeding grounds in the Southern Ocean and North Pacific to estimate consumption rates on the feeding grounds and energy requirements over the period for which whales are assumed not to be feeding. These estimates were taken from whaling data from 245 whales in the North

Pacific and 1,948 whales in the Antarctic by subtracting mean yields per whale at the start of the feeding season from those at the end. For a 48 tonne Antarctic fin whale he estimated a net gain in oil of 3,585kg over a 120 day feeding period. For a 37 tonne North Pacific fin whale he estimated a net gain in oil of 2,189kg over a 182.5 day feeding period. These would result in average available daily energy from stored reserves over the assumed non-feeding period of 550 and 451MJ per day for Antarctic and North Pacific fin whales respectively, based on an estimate of 38MJ kg^{-1} from whale oil. These values represent 56% of BMR calculated by the Kleiber formula (Table 1). However, it is possible that whales may also feed during the low-feeding rate part of the year, when they are using up energy stores. To investigate how this would affect the conclusions reached by Brodie, suppose S is the energy stored during the high-feeding rate period, D is the number of days of high feeding rate (where energy available from intake exceeds demands) and L is the number of days of low feeding rate (where energy demands exceed that available from intake; also $D+L = 365$).

Then, while lipid is being deposited

$$S = D \times f(I - FMR) \qquad (12)$$

where f is the efficiency by which energy from food intake is converted into lipid and I is the daily energy intake during the high feeding period. If all the stored energy is used during the low feeding period (with an assumed 100% efficiency) and assuming the daily intake during this period can be expressed as a proportion of high feeding intake, rI, then

$$S = (L \times FMR) - (rI \times L) \qquad (13)$$

Giving

$$FMR = \frac{S}{(1-r)}\left(\frac{1}{L} + \frac{r}{D \times f}\right) \qquad (14)$$

For an assumed set of values of D, L, f the ratio of low feeding rate to high feeding rate, r, will determine FMR. This is illustrated in Fig. 2 based on Brodie's data for the amount of energy stored by an Antarctic fin whale. The solid lines in Fig. 2 assume D=120 and L=245. The dotted lines assume D=182.5, L=182.5. In both cases the spread of lines cover the range of values of f from 0.5-0.8. This figure shows that the relationship between FMR and the ratio of low feeding rate to high feeding rate is relatively insensitive to the assumptions made regarding D, L and f within the parameter space explored in this study, particularly for low values of r. Although $0<f<1$ there are no data on which to base f for whales.

Some estimates of the rate of low season feeding have been made, but based on rather sparse data. For example, Lockyer (1981) predicted that 17% of annual food intake for Southern Ocean baleen whales was outside the high feeding period. This is equivalent to r=0.1 for D=120 and L=245. This estimate has also been used by other authors including Sigurjonsson and Vikingsson (1997) in the North Atlantic. Based on the energy stored from Brodie (1975) and assuming f=0.7 this estimate of low season food intake would result in estimates of FMR of 71% and 81% of the Kleiber prediction of BMR for North Pacific and Southern Hemisphere fin whales respectively (Table 1).

Brodie (1981) also estimated a mean daily energy requirement of 7.98×10^5 kJ for a 46 tonne bowhead whale (*Balaena mysticetus*) based on what he described as metabolically effective surface area (the surface area of the muscular body core), rather than body mass – this would equate to 0.86 of BMR as calculated by Eqn 5. He estimated a lipid store of 4,000kg built up over the feeding season. This figure would suggest slightly more available stored energy in relation to body size than for Antarctic fin whales (Brodie, 1975). Based on this estimate of energy requirements, Brodie estimated that the lipid store could last the whales up to six months of not feeding. Lockyer (1981) estimated rather more stored energy for Antarctic fin whales (Table 1) than Brodie (1975) based on classifying them as either lean or fat and using total weight difference rather than oil yield. Tamura and Konishi (2006) and Folkow *et al*. (2000) also present analyses of energy stores in Antarctic and North Atlantic minke whales respectively. These are compared in Table 1. For r=0.1 all these studies that measure stored energy would indicate FMRs of less than the Kleiber BMR except for Lockyer (1981) where the ratio of FMR to BMR would be 2.1. The minke whale data are consistent with Folkow *et al*. (2000) who concluded that North Atlantic minke whales would be unable to survive the winter on energy stores built up in summer alone. For the studies of minke whales, Table 1 shows the values of r required to support the ADMR of 80kJ kg^{-1} estimated by Blix and Folkow (1995). These vary from 0.34-0.42 for Antarctic minke whales and around 0.6 for North Atlantic minke whales. These values do not seem consistent with current theories of Antarctic minke whales making long migrations to breeding areas with poor food resources. Although it is perhaps not surprising that minke whales in the North Atlantic appear to store less energy than Antarctic minke whales, some North Atlantic minke whales are still believed to undertake long migrations. Either theories about low season consumption rates need to be revised or these data on stored energy would indicate metabolic rates of minke whales rather lower than other estimates.

DISCUSSION

The current situation is that developers of ecological models involving large whales tend to make rather arbitrary, but potentially highly influential decisions on selecting an approach from published sources on which to base estimates of prey consumption. We have not attempted a comprehensive review of all previous studies, but studies were selected to illustrate the range of estimates. Nevertheless, it is apparent from our review that several of the extrapolated curves, principally Eqn 10 and the mean of 8, 9 and 10 lie outside of the range of available data points for large whales (Fig. 1). These equations involve values of B>0.75 and our conclusion is that they are not supported either by theory or data.

It is also difficult to reconcile data on energy stores and widely held beliefs that large whales spend long periods without feeding without assuming lower values for FMRs than the BMRs predicted by the Kleiber equation. In this regard, observational studies of feeding whales in the low feeding season would be particularly valuable. Estimating relative feeding rates in the field may be easier than absolute values (based for example on prey availability and proportion of time spent feeding).

In terms of predicting food intake, it is the total energy requirement that is of interest and hence FMR is more relevant than BMR. Thus the question of the relationship between BMR and FMR in relation to body size must also be considered. Koteja (1991) found that FMR scaled as body mass to the power 0.61 compared to BMR which

Table 1

Estimates of FMR based on stored energy assuming *f* = 0.7.

Species	Body mass (kg)	Total energy stored during high feeding period (*S*) MJ	High feeding days (*D*)	Low feeding days (*L*)	Mean low feeding/high feeding intake (*r*)	FMR MJ/day	FMR/ Kleiber BMR	*r* required for 80 kJ kg^{-1} in minke whale
Antarctic minke - immature male[1]	2,900	13,216	90	275	0	48	0.4	
	2,900	13,216	90	275	0.1	77	0.7	
	2,900	13,216	90	275	0.5	306	2.6	0.42
Antarctic minke - mature male[1]	6,800	32,815	90	275	0	119	0.5	
	6,800	32,815	90	275	0.1	190	0.9	
	6,800	32,815	90	275	0.5	760	3.5	0.40
Antarctic minke - immature female[1]	3,800	22,141	90	275	0	81	0.6	
	3,800	22,141	90	275	0.1	129	0.9	
	3,800	22,141	90	275	0.5	512	3.6	0.34
North Atlantic minke whale - mature[2]	5,900	17,589	182.5	182.5	0	96	0.5	
	5,900	17,589	182.5	182.5	0.1	122	0.6	
	5,900	17,589	182.5	182.5	0.5	330	1.7	0.62
North Atlantic minke whale - immature[2]	3,800	11,745	182.5	182.5	0	64	0.5	
	3,800	11,745	182.5	182.5	0.1	82	0.6	
	3,800	11,745	182.5	182.5	0.5	221	1.6	0.61
Antarctic fin whale[3]	48,000	131,341	120	245	0	536	0.6	
	48,000	131,341	120	245	0.1	769	0.8	
	48,000	131,341	120	245	0.5	2,636	2.8	
Antarctic fin whale [4]	47,500	344,400	120	245	0	1,405	1.6	
	47,500	344,400	120	245	0.1	2,016	2.1	
	47,500	344,400	120	245	0.5	6,912	7.3	
North Pacific fin whale[3]	37,000	80,197	182.5	182.5	0	439	0.6	
	37,000	80,197	182.5	182.5	0.1	558	0.7	
	37,000	80,197	182.5	182.5	0.5	1,507	1.9	

[1]Data from Tamura and Konishi (2006). [2]Data from Folkow *et al.* (2000). [3]Data from Brodie (1975). [4]Data from Lockyer (1981) for female fin whale at puberty.

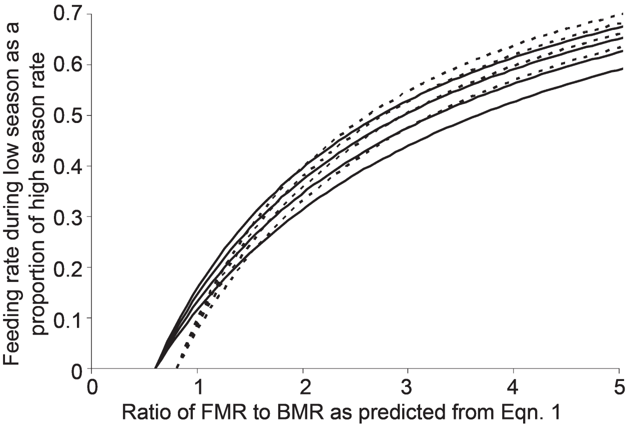

Fig. 2. Sensitivity of relationship between ratio of FMR to BMR as predicted by the Kleiber formula and ratio of feeding during low rate periods to high rate periods for *D*=120 (solid lines), *D*=182.5 (dotted lines) for *f*=0.5-0.8. Based on data for Antarctic fin whales from Brodie (1975).

scaled as body mass to the power 0.71 in his sample of mammal species. Although that study did not include marine mammals and considered mainly smaller species such as rodents, the qualitative result that FMR and BMR tend to converge with increasing body size is supported by Boyd (2002). Boyd suggests that the relationship between the energy cost of locomotion and body size could be one explanation for this. Passive drag is closely related to wetted area of non-propulsive body parts that will scale approximately to body mass to the power 0.67. When this is coupled with other effects such as the reduction in wave-making resistance with body size for a whale swimming at a given speed at the surface, the overall costs of travelling a certain distance at a given speed will scale to body mass raised to something less than 0.67. Locomotion may account for a substantial proportion of energy expenditure in marine mammals. For example Boyd *et al.* (1994) calculated that locomotion costs were 40 to 60% of total energy expenditure in southern elephant seals. Boyd (2002) did note some caveats to his regression analysis that gave a value of *B* of 0.52 for FMR in marine mammals, the main concern being that measurements had been made using a number of different techniques. If only measurements of FMR using doubly-labelled water were considered then the slope (*B* value) was 0.81, although in that case the regression itself was not significant. Excluding the two species with the largest body mass (fin and minke whales) or excluding measurements with doubly-labelled water did not however, change the result. Nagy (2005) also reviewed FMR in relation to body size across a number of taxa. For mammals, there were no significant differences between the slope (*B* value) for BMR or FMR which both lay between 0.67 and 0.75. There is an ongoing debate about whether the value of *B* should be closer to 0.67 which would be expected from Euclidean scaling (White and Seymour, 2003;2005) or closer to 0.75 based on theories predicting quarter-power scaling (Savage *et al*., 2004). However, none of these extensive reviews suggest values outside of the range 0.67-0.75. Thus we conclude that both theoretical and empirical evidence indicate that values of *B* greater than 0.75 are not appropriate for large whales. Nevertheless, the possibility that large whales might be an exception and scale to a value of less than smaller species that dominate the published data also cannot be rejected.

An additional factor that may contribute to larger whales having relatively lower average metabolic rates than might be predicted from extrapolation from smaller cetacean species may be related to the periods of fasting which tend to be longer for larger species. Periods of fasting are often accompanied by metabolic depression (Markussen *et al*., 1992; Rea and Costa, 1992). Lockyer (1981) reviewed weight loss in other long fasting mammals (particularly during hibernation) and found most species tended to lose 0.2-0.3% of body mass per day. If this rate of loss was sustained over an eight month fasting period then total weight loss would be around 50%.

Despite a total lack of theoretical or empirical evidence to support an exponent of 1 when scaling to body mass this value has nevertheless been used in some recent studies. For example, Murase *et al.* (2006) used the estimate of 80kJ kg^{-1} per day from Blix and Folkow (1995) and apply it to humpback and fin whales to estimate the amount of krill consumed in sectors of the Southern Ocean. Inter-specific extrapolations were particularly important for that analysis which attempted to investigate inter-specific competition. The conclusion that 'humpback whales consumed about twice the amount of krill as Antarctic minke whales in Area IV' was largely the result of the choice of B=1. This resulted in estimates of consumption by humpback whales that were more than 50% greater than would have resulted from assuming B=0.67.

It is likely that neither population energy budgets nor consumption rates will be the greatest source of uncertainty in modelling interactions in complex ecosystems. Nevertheless it is important to understand the sensitivity of any model predictions to uncertainty in consumption rates. The values for food intake in large whales used in many models to date would appear to be at the high end of the likely range and model runs should be considered using lower values. As an extreme case, the parameterisation used by Tamura and Ohsumi (2000), which they describe as Method 3, gives predictions an order of magnitude greater than one of the other studies considered here (Boyd, 2002). With this level of uncertainty, comparisons of consumption by cetaceans with fisheries catches, which then may be used out of context, are clearly inappropriate and potentially misleading.

One issue not addressed in detail in this review is variation in the energy density of prey. This is clearly critical to calculating mass of prey consumed from estimates of energy requirements and annual and seasonal variation across trophic levels may also be important from a modelling perspective. Although most studies have used average values, several studies have highlighted the high level of variability in prey energy density (De Lorenzo Costa *et al.*, 2006; Mårtensson *et al.*, 1996; Winship and Trites, 2003).

Winship *et al.* (2002) attempted to quantify some of the uncertainties surrounding estimates of food requirements of Steller sealions (*Eumetopias jubatus*). Their conclusion was that 'uncertainty in diet and bioenergetic parameters resulted in the largest variation in model predictions'. Boyd (2002) also examined the sensitivity of estimates of consumption to input variables for a study of Antarctic fur seals (*Arctocephalus gazella*) and macaroni penguins (*Eudyptes chrysolophus*). In these studies, the body mass of the species in question was within the range that allows interpolation rather than extrapolation of bioenergetic parameters and also where there is least discrepancy between the various studies considered here. Unfortunately, due to the need for extrapolation, it is not possible to quantify the uncertainties in predicting food requirements of large whales using similar approaches. While data on feeding rates of small cetaceans and pinnipeds may allow for improved estimates it seems unlikely that reliable estimates of the feeding rates of large whales will become available in the near future. To date, lethal research programmes based on weighing stomach contents have been able to add little to such estimates. For example, Leaper (2007) found that the data used by Tamura and Konishi (2006) to estimate consumption of krill by Antarctic minke whales were consistent with a range of mean daily consumption on the feeding grounds of 1.5-7% of whale body mass per day. This range covers what might be considered plausible values including all but the maximum two of the lines shown in Fig. 1 over the range of minke whale body mass, and is thus not inconsistent with allometric comparisons. However, despite large sample sizes of 6,777 whale stomachs, the data were not able to narrow the range of values. The IWC Scientific Committee concluded that until questions related to the length of the feeding season, digestion rates and the extent of feeding at night could be resolved 'it would not be possible to move beyond only broad estimates' (IWC, 2008).

In addition to incorporating uncertainty, all studies need to provide a clear justification for the methods and assumptions on which estimates are based. In particular, certain values for some parameters have obtained a status through common usage rather than carefully analysed data. These include ratios of FMR to BMR, digestion rates, the length of time spent on high latitude feeding grounds, the proportion of total annual consumption on these feeding grounds and assimilation efficiency. All these need careful consideration when generating estimates. A constant assimilation efficiency of 80% was used in this paper to allow comparisons between studies (some of which used this value) but this will clearly vary with prey condition, size and species.

In addition to uncertainty in the energy requirements of individuals, estimating numbers of whales in an area is an obvious source of uncertainty in estimating overall prey consumption, although quantifying uncertainties in numbers has received far more attention than most of the other aspects considered here. Estimating the numbers at age and body mass at age of individuals within the population is also challenging. Trites and Pauly (1998) suggest a general relationship for mean mass across the whole population based on maximum length, but such methods may not be appropriate where the population is segregated by age or sex.

Another factor that will affect energy requirements of mature females is the investment in rearing a calf. In terms of population energy budgets this requires data on the number of calves successfully reared until weaning since the energy requirements of lactation are the dominant component associated with reproduction.

Estimates of energy requirements are not just of interest for ecological models, but may also be used to examine the implications of disturbance and changes in behaviour. For example Williams *et al.* (2006) used estimates of energy requirements to estimate the potential impacts of human disturbance on killer whales (*Orcinus orca*). Uncertainties in basic energy requirements may have a substantial impact on the conclusions of such studies.

Resolving the uncertainty in how much large whales eat will not be easy. Our review has concentrated on the implications for Eqn 1 of the value of the exponent (B) rather than the intercept (A). Nevertheless the estimate of the intercept can have a substantial effect. The estimates reviewed were most consistent for body masses between 200 and 1,000kg where the ratio between highest and lowest was around two. This range includes the body masses for which there are most direct data for cetaceans.

From an ecological modelling perspective, tightening the bounds on a range of plausible values may be a useful step, especially given that marine ecological models face so much uncertainty in other regards. We believe the evidence from this review is sufficient to put upper bounds on the mean daily energy requirements of large whales indicating that studies based on Eqn 10 or the mean of 8, 9 and 10 appear to have overestimated the quantity of prey consumed. Specifically, all of the individual data points reviewed in Fig. 1 fall below a mean annual FMR of four times BMR as predicted by the Kleiber equation. Setting lower bounds is more difficult and will probably have to rely on further bioenergetic models, but at the present time mean annual FMRs close to or even slightly below those predicted by the Kleiber equation for BMR, cannot be ruled out. A parameter space for average energy intake for large whales, bounded at the high end by Eqn 8 and at the low end by Eqn 6 (adjusted upwards for assimilation efficiency) might currently be an appropriate choice. This would cover the individual estimates derived from a number of different methods, with the commonly used estimate of FMR from Blix and Folkow (1995) falling roughly in the middle.

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Recent harbour porpoise bycatch in gillnet fisheries in Newfoundland and Labrador, Canada

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ABSTRACT

Despite reduced fishing effort in many North Atlantic fisheries following collapse of fish stocks, concerns remain about levels of direct mortality of harbour porpoise (*Phocoena phocoena*), primarily through incidental catches in fishing gear. Although harbour porpoise incidental catch is known to occur in several fisheries along the coast of Newfoundland and Labrador, Canada, there are no reliable quantitative estimates for the last decade when the commercial fisheries have undergone major changes in effort and target species. Based on incidental catch rates derived using different reporting methods, with net-days as measures of effort and fishing trips as sampling units, the potential number of incidental catches of harbour porpoises in several gillnet fisheries in Newfoundland waters was estimated for the years 2001, 2002 and 2003. Confidence intervals were calculated using re-sampling techniques.

Incidental catches of small cetaceans were estimated to be 862 in 2001, 1,428 in 2002 and 2,228 in 2003 in Newfoundland gillnet fisheries; virtually all cetaceans reported were harbour porpoises. Annual estimates of incidental catch of small cetaceans varied greatly between fisheries and areas. Confidence intervals were large due to variation in reported incidental catch rates among individual fishers and geographic areas. Most small cetaceans were reported in the nearshore cod fishery, although there were also numerous reports of catches in nearshore fisheries for lumpfish, herring and Greenland halibut. Incidental catch of small cetaceans was also identified in offshore fisheries for monkfish, white hake and Greenland halibut. Most incidental catch events occurred during the third quarter of the year (July-September) along the south coast, although catches of harbour porpoises were also reported during the second and fourth quarters.

Several strategies could be implemented to better monitor small cetacean incidental catch in Newfoundland and Labrador waters. However, harbour porpoise population estimates are required before it can be determined if this fisheries-related mortality occurring in Newfoundland is sustainable.

KEYWORDS: HARBOUR PORPOISE; INCIDENTAL CATCHES; GILLNETS; NORTH ATLANTIC; FISHERIES; NORTHERN HEMISPHERE

INTRODUCTION

Despite reduced fishing effort in many North Atlantic fisheries following the collapse of groundfish stocks in the early 1990s, concerns remain about the sustainability of a number of harbour porpoise (*Phocoena phocoena*) populations (e.g. Stenson, 2003). Although potential limiting factors for these populations include habitat change, changes in prey abundance or distribution, marine pollutants and global warming (Aguilar and Borrell, 1995; Anon., 1999; Brodie, 1995; Donovan and Bjørge, 1995; Hutchinson, 1996; Koschinski, 2002; Teilmann and Lowry, 1996); direct mortality, primarily through incidental catches in fishing gear, remains the primary concern. The harbour porpoise is known to be particularly vulnerable to incidental catches in fishing gear; they are most often caught in bottom-set gillnets and to a lesser extent fish weirs and traps (Berggren *et al*., 2002; Gaskin, 1984; IWC, 1994; Larrivée, 1996; Lesage *et al*., 2006; Read and Gaskin, 1988; Smith *et al*., 1993; Stenson, 2003; Trippel *et al*., 1996).

A number of reviews (Anon., 1998; CEC, 2002; Donovan and Bjørge, 1995; Jefferson and Curry, 1994; Read, 1994; Stenson, 2003) have concluded that large numbers of porpoises are caught in commercial fishing gear throughout their range. Based upon declining sightings and/or the perceived impacts of incidental catches, many porpoise populations have been classified as being at risk by either national or international groups responsible for assessing the status of such populations. In Atlantic Canada, harbour porpoises are currently listed as of 'special concern' by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC, 2003a; 2003b).

Although incidental catches of harbour porpoises are known to occur in a number of fisheries in Newfoundland and Labrador, Canada, there are few reliable estimates of such catches (DFO, 2001; Lien, 2001; Lien *et al*., 1988). Substantial harbour porpoise catches are thought to have occurred in the past, since this region has traditionally supported large gillnet fisheries (mainly for Atlantic cod, *Gadus morhua*). Previous information on cetacean incidental catch in Newfoundland fisheries was summarised by Lien *et al.* (1988) and subsequently by the Canadian Department of Fisheries and Oceans (DFO) (DFO, 2001; Stenson, 2003). Based on logbooks and interviews, Lien estimated that the incidental catch of harbour porpoises was likely in the low thousands during the 1980s and early 1990s (Bjørge *et al*., 1994; DFO, 2001; Lien, 2001; Lien *et al*., 1994). Unfortunately, given the limitations of the available data these estimates were extrapolated from reported catches by a limited number of fishermen, often in restricted areas of the province. In addition, none of the estimates had detailed fishing effort data associated with them, mainly because the scale of the fishery (large numbers of small vessels fishing in often-remote locations) has historically made total fishing effort in Newfoundland and Labrador difficult to determine. Therefore, these previous estimates of incidental catch in Newfoundland are biased to an unknown extent, and should only serve as a first indication of the magnitude of incidental catch (DFO, 2001).

As in most areas of the Northwest Atlantic, total landings in the Newfoundland and Labrador cod fishery have been reduced significantly since the 1980s (DFO, 2006b; 2006c; Hutchings and Myers, 1995; Shelton *et al*., 2006). As an example, catches of northern cod in Northwest Atlantic

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Fisheries Organization (NAFO) Divisions 2J+3KL dropped from approximately 240,000mt in 1988 to 2,300mt in 2006 (DFO, 2006a; 2006b); catches in other areas suffered similar declines. Because of this, the fishery, which accounted for the majority of harbour porpoises caught in this region (DFO, 2001; Lien *et al*., 1994; Read, 1994), was closed off the northeast coast of Newfoundland in 1992 and off the south and west coasts in 1993. Cod gillnet fisheries have reopened since 1997, but at much reduced levels. The fishery off the northeast and western coasts of Newfoundland was closed again in 2003, but a limited fishery reopened in 2006. Incidental catches of harbour porpoises were probably significantly reduced during these moratoria and may continue to be less than prior to 1992 (DFO, 2001). Evidence of such reductions in incidental catch due to reductions in fishing effort is available for the Bay of Fundy/Gulf of Maine population (Rossman and Merrick, 1999; Trippel and Shepherd, 2004; Waring *et al*., 2001). However, recent reports from both the industry and Fishery Observers indicate that porpoises continue to be caught regularly despite reduced fishing effort since the early 1990s.

Historically, there has been relatively little effort to monitor marine mammal incidental catch in fisheries in Newfoundland and Labrador. Data are available through a fishery logbook programme, combined with directed phone surveys and interviews (DFO, 2001; Lien, 2001; Lien *et al*., 1994; 1988) but they are limited in time or geographic coverage. Independent incidental catch observers have been recommended as the best means to monitor incidental catches (IWC, 1994), but these proposals have not been widely implemented in Newfoundland and Labrador because much of the local fishery is conducted using small vessels (<10m). Fishery Observers are present aboard some larger fishing vessels, but they provide limited coverage of most fleets, and their primary duty is to document catch levels of directed fish species rather than identifying marine mammal incidental catch. Since 1989, DFO has maintained a network of commercial fishermen throughout the province (hereafter referred to as Bycatch Collectors), who collect and report marine mammal incidental catch as well as detailed fishing effort data. In addition, fishermen involved with the scientifically-managed Sentinel fishery for Atlantic cod were asked to retain and report small cetacean catches.

All available data on fishing effort and catches were reviewed in order to gain a better understanding of recent levels of small cetacean incidental catch in Newfoundland and Labrador, Canada. This paper presents the results of incidental catch analyses of the nearshore gillnet fisheries for Atlantic cod, lumpfish (*Cyclopterus lumpus*), Atlantic herring (*Clupea harengus*) and Greenland halibut (*Reinhardtius hippoglossoides*), as well as the offshore gillnet fisheries for monkfish (*Lophius americanus*), skates (*Rajidae*), white hake (*Urophycis tenuis*) and Greenland halibut, for the years 2001-2003. These fisheries were considered to be the most likely to take harbour porpoises in Newfoundland and Labrador waters based on previous reports of incidental catch.

METHODS

Estimates of harbour porpoise incidental catch were obtained using combinations of fishing effort and incidental catch rate multipliers derived from bycaught porpoises reported by Bycatch Collectors, the Sentinel fishery and/or Fishery Observers. The focus of this study was on gillnet fisheries, since these were assumed to pose the greatest risk for incidental entanglement of small cetaceans in the current Newfoundland fisheries. All data were grouped geographically according to NAFO divisions of Newfoundland and Labrador waters (Fig. 1).

Databases used to estimate incidental catch in this study included a catch-effort database for vessels ≥35ft long (10.7m, hereafter quoted in feet), a fish landings database for vessels <35ft, a Fishery Observer database, a Sentinel Fishery database and a Marine Mammal Bycatch Collector database (see descriptions below). These databases contained records from all types of gillnet fisheries, with the greatest geographical and temporal effort being in the Atlantic cod fisheries. This fishery is of great importance because of the large number of fishers that participate in it, as well as the relatively large amount of data available for this fishery.

Fishing effort data

Catch-effort database for vessels greater than or equal to 35 feet long

The Policy and Economics Branch at DFO in St. John's maintains a catch-effort database for vessels ⩾35ft. This database contains detailed information on total fish landings, general species composition and landed catch by individual species (both gutted and round weight). However, its usefulness in estimating fishing effort was reduced because total soak time and amount of gear deployed were not always reliably recorded by all fishers. When possible, data from the Fishery Observer database (see below) were used in combination with the landed catch data to better calculate total fishing duration, or total amount of gear deployed.

Fish landings database for vessels less than 35 feet long

The landings database maintained by the Policy and Economics Branch at DFO in St. John's contained detailed information on commercial fish landings for small vessels (<35ft). These were often the only data available for these vessels and contained the total landed catch for all trips for every vessel, both in gutted and round weight, for individual species. However, this database suffers from both a lack of effort information (no data on either the duration of the trip, or the number of nets deployed by a vessel) and the lack of any detailed geographical information as to where the fish were caught. Given the small vessel size and likelihood that fishing occurred near to their point of departure, catches are assumed to have been taken in the NAFO unit of the home port.

An additional, separate logbook database for the nearshore fishery for Atlantic cod and associated groundfish was set up by researchers in the Groundfish Section at DFO in St. John's in 1997, to address perceived deficiencies in the existing catch/effort and landings databases. This database contained detailed fishing effort data on a per-day basis, and was only used to derive a corroborative measure of net-days for all vessels. Unfortunately, this database did not contain all fishing effort as not all vessels submitted their logbooks.

Incidental catch data

Marine Mammal Bycatch Collector database

The Marine Mammal Bycatch Collector Programme database consisted of extremely detailed reports on a variety of fisheries since its inception in 1989. Fishermen recorded, for all their commercial gillnet fishing effort, location of sets, water depth, net characteristics, the number of nets hauled daily, soak time, catch (fish, seabirds and marine

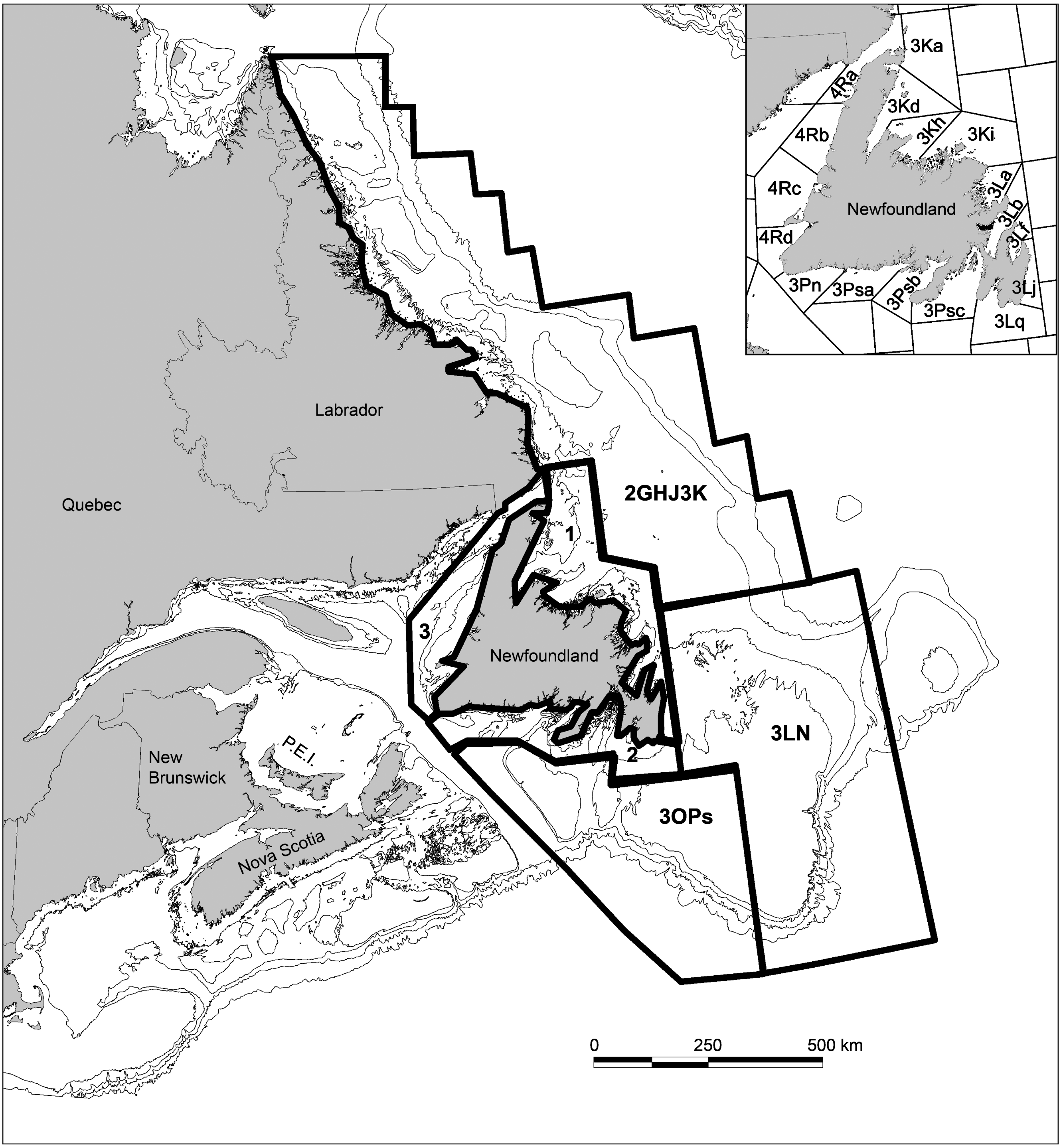

Fig. 1. An overview of Newfoundland and Labrador waters, showing geographical units used to aggregate fishing effort and incidental catch data. 1=Northeast coast; 2=South coast; 3=West coast. Individual nearshore NAFO units, as referred to in the text, are described in the inset. 100m, 200m, 1,000m and 2,000m depth increments are indicated.

mammals) and discards. In many cases, information on location of catches was limited (usually identified by a local landmark) but the boats employed were small (<35ft), so it is assumed that the majority of catches were made close to the home port. Vessels in this programme were most active in the gillnet fisheries for Atlantic cod, lumpfish and other species such as winter flounder (*Pseudopleuronectes americanus*), but other fisheries were less well covered by the present Collector Programme.

DFO selected these vessels because they participated in fisheries that were known to have high incidental catches of seals (e.g. the lumpfish fishery). However, small cetaceans, especially harbour porpoises, were also reported regularly. In 2001, efforts to collect data on small cetacean incidental catches were increased by specifically asking participating vessels to record the capture of each individual. The number of participating vessels that sent in forms varied from year to year (*n*=47 in 2001, *n*=45 in 2002, and *n*=29 in 2003), depending on individual decisions on what fishery to prosecute. Over 80% of vessels who initially agreed to collect the requested information sent in their forms the same year, although this rate declined slightly in following years. Most fishermen who participated in the programme had been doing so for many years, and were familiar with the data requirements; those who did not return the proper information were subsequently excluded from the programme.

Sentinel Fishery database

The Sentinel Fishery database consisted of detailed fisheries data collected from the scientifically-managed Sentinel Fishery for Atlantic cod (*n*=81 nearshore vessels in 2001 and 2002, *n*=58 in 2003). This fishery was established in 1995 after the introduction of the groundfish moratorium to enable a continued monitoring of the cod stocks in nearshore waters in the absence of data from the commercial fleet by fishing under scientifically designed protocols. Vessels involved are almost all <35ft, and their effort is limited (normally up to six nets, set for short periods), but the fishery is considered to be generally comparable in geographic range to the commercial nearshore cod fishery, which uses the same range of vessel sizes. As such the Sentinel Fishery data offers an opportunity to obtain measures of catch per unit effort for small-boat, nearshore fisheries. However, there may be differences in terms of the location and soak times of the nets, which may not correspond exactly to the commercial fishery and lead to divergent catch rates per unit effort.

Fishers participating in the Sentinel Fishery reported incidental catches of marine mammals to DFO's Marine Mammal Section in St. John's. They were asked to report incidental captures in their cod fishery only, unless they were recruited to the Bycatch Collector programme separately. Sentinel Fishery catch per unit effort (net-day) data were compared with Bycatch Collector data from the same time and area to determine if datasets could be combined, using resampling methodology (Blank *et al*., 2001). Where data did not differ significantly, Sentinel catch reports were incorporated into the total catch estimates for that particular area and period of the year. In cases where Sentinel cod catch rates differed significantly from Bycatch Collector rates, Sentinel data were not used.

Fishery Observer database

The database associated with the DFO-managed Fishery Observer Programme provided an independent estimate of fishing effort and records of small cetacean incidental catch events, primarily in large (⩾35ft) vessels. Observers recorded, among other things, the exact amounts of catch and discards, exact geographical fishing location, depth, duration of haul, number and length of nets. This database is biased towards certain fisheries and vessel sizes, as over 80% of observing effort for gillnet fisheries currently takes place on vessels targeting deepwater species such as Greenland halibut and monkfish. In practical terms, there is only limited opportunity for Fishery Observers to board small vessels (<35ft long), and there is no protocol in place to ensure randomised deployment of observers on these vessels (J. Firth, DFO-NL, pers. comm.; NMFS, 2003). Therefore, observer coverage was not directly related to fishing effort (D. Kulka, DFO-NL, pers. comm.). In addition, documenting marine mammal bycatch is not the primary focus of most observers, so events may go unreported. For this reason, it was decided to use the Fishery Observer database only to study incidental catch in offshore fisheries, particularly the gillnet fisheries for monkfish, skates, white hake and Greenland halibut, where Bycatch Collector data were limited or absent. In cases where records of the same trip were available from two or more sources, data from trips monitored by a Fishery Observer were used to correct for reporting errors.

Unfortunately, it is uncertain as to how many animals were involved in a given incidental capture event recorded in this database. Fishery Observers reported the total discarded weight of the small cetaceans of each individual capture event without recording the number of animals, and this, combined with occasional uncertainty in species identification, made it difficult to estimate total numbers of cetaceans caught incidentally in these fisheries. Minimum numbers caught were estimated based on average weights reported in the literature.

Deriving estimates of small cetacean incidental catch

Small cetacean incidental catch events were recorded through the data collection programmes described above. Rates of bycaught small cetaceans per unit effort obtained from the Sentinel and Bycatch Collector logbooks were extrapolated to the entire fishery based on data from the fish landings database and groundfish logbook data. The unit of effort used in these calculations was the number of net-days (number of nets set, multiplied by the total number of days fished).

Gillnet fisheries catch/effort and incidental catch data were organised based on time of year (divided into four quarters where relevant: January-March, April-June, July-September and October-December) and area (based on NAFO units). Nearshore fisheries around the island of Newfoundland were defined as those fisheries occurring in NAFO units immediately adjacent to land, while offshore fisheries occurred outside these waters. Nearshore fisheries were geographically aggregated to correspond to the three coastlines surrounding the island of Newfoundland (northeast coast: NAFO units 3KadhiLabfj; south coast: 3LqPnPsabc; and west coast: 4Rabcd; Fig. 1) and analysed for all three coasts separately. Incidental catch estimation analyses were performed at the geographic scale of coastlines, because it appeared unlikely that porpoises either restricted themselves to a single NAFO unit or were distributed uniformly around the island of Newfoundland (Johnston *et al*., 2005). For logistical reasons, no data on bycatch of small cetaceans could be collected in the nearshore fisheries for cod and lumpfish that were conducted along the southeastern coast of Labrador (NAFO unit 2Jm), and this region has been excluded from further analysis. However, fishing effort has been limited in this area, and it is unlikely that large numbers of small cetaceans would have been captured here. Offshore fisheries were analysed at larger geographic scales, based on a combination of oceanographic and jurisdictional boundaries (NAFO Divisions 2GHJ3K, 3LN and 3OPs; Fig. 1).

In many cases, only landed catch was available as a measure of effort, and it was necessary to estimate the number of net-days of effort for these fishers. These estimates were based on the relationships between landed catch and net-day that were derived from the groundfish logbook database. For each fishing trip, the ratio of kg landed catch per single net-day was calculated. These ratios were averaged over the area and period in question, and the resulting average (kg landed catch/net-day) ratio was then applied to the total amount of landed catch to estimate the equivalent numbers of net-days.

Small cetacean incidental catch rates were calculated using fishing trips of individual fishers as sampling units. When deriving a small cetacean incidental catch estimate, effort and incidental capture data from Marine Mammal Bycatch Collectors (and Sentinel fishers, in the case of the Atlantic cod fishery) were used to calculate an estimated incidental catch rate per net-day of effort. The incidental catch rates for all trips were averaged to obtain the estimated incidental catch rate for a particular time of year, in a particular area.

Sample sizes were frequently small and difficult to analyse with conventional statistics (Efron and Tibshirani, 1993; Simon, 1997). Therefore, the uncertainty associated with estimates of incidental capture was assessed using a resampling procedure (Blank *et al*., 2001). Unlike conventional statistics, resampling methodology does not require assumptions about the distribution of the dataset, and can be used with comparatively small samples.

These incidental catch rate values were resampled 10,000 times, with replacement. This generated a population of 10,000 averages based on individually-resampled incidental catch estimates from all individual fishers, for the relevant geographical scale. The overall mean incidental catch rate per unit effort, and the 2.5th and 97.5th percentile rates from this population, were then used to estimate mean catches as well as upper and lower limits of a 95% confidence interval around the mean. These estimated incidental catch rates were multiplied by fishing effort data for the entire fishery for that area and time of year to estimate total incidental catches of small cetaceans.

RESULTS

Records of incidental capture of small cetaceans in 2001-03

Bycatch Collector reports and Sentinel programme data

Totals of 39, 64 and 35 reports of incidental catch of small cetaceans were received through the Bycatch Collector programme and the Sentinel programme in 2001, 2002 and 2003, respectively, totalling 138 records (Table 1). Of these, 33, 44 and 31 specimens, respectively, were collected and identified by DFO technicians (108 specimens, or an average of 81%). All were harbour porpoises, and there was no apparent deviation from a 50:50 sex ratio (53 females vs. 55 males). The remainder of the bycaught small cetaceans (6, 20 and 4 specimens in 2001, 2002 and 2003, respectively) were not collected and therefore species identification could not be independently verified. However, based on discussions with Bycatch Collectors, most unidentified small cetaceans were probably harbour porpoises, although some may have been Atlantic white-sided dolphins (*Lagenorhynchus acutus*), whitebeaked dolphins (*L. albirostris*) or common dolphins (*Delphinus delphis*).

Most of the reported bycatch events occurred in the nearshore cod gillnet fishery (28 reports out of a combined total of 2.17×10^4 net-days for Bycatch Collectors and 63 reports out of 2.95×10^4 net-days for Sentinel fishery, for all years combined). The remainder of catches were reported in the nearshore fisheries for lumpfish roe (25 reports out of 5.09×10^4 net-days), herring (six reports out of 2.38×10^3 net-days) and Greenland halibut (three reports out of 1.04×10^4 net-days), as well as the offshore fishery for monkfish and skate (three reports out of 5.18×10^3 net-days). Most of the recorded catches (101 out of 138) occurred in July and August, whereas 34 captures were recorded in the second quarter, three took place in the fourth quarter and none were reported in the first quarter, when there is limited fishing activity. The majority of catches involved single animals, although multiple captures of up to four animals (including cow-calf pairs) were occasionally reported (nine times over three years).

There was considerable intra-annual variation in bycatch rates (number of small cetaceans/net-day) among fishers within the same area, as well as variation in bycatch rates from the same fishers in consecutive years. In any given year, most fishers did not capture any small cetaceans, but some captured up to eight animals. During 2001-2003, high porpoise catches were reported from several areas, including waters around Fogo Island (NAFO unit 3Ki), in Conception Bay (NAFO unit 3Lf), St. Mary's Bay (NAFO unit 3Lq) and Bay St. Georges (NAFO unit 4Rd; Fig. 1).

Fishery Observer Programme data

A total of 10, 24 and 3 records of cetacean incidental catch events were recorded by the Fishery Observer Programme in 2001, 2002 and 2003, respectively (Table 1). Bycatches

Table 1

An overview of the incidental catch events of small cetaceans recorded by the Bycatch Observer and Sentinel programme, and the Bycatch Observer programme, during 2001-03.

	Number of bycaught small cetaceans per year, reported by Bycatch Collectors (and Sentinel fishers for cod fishery)			Number of small cetacean catch events per year, reported by Fishery Observers[2]		
Fishery	2001	2002	2003	2001	2002	2003
Cod (nearshore)	23	47	21	8	2	0
Cod (offshore)	0	0	0	0	0	0
Lumpfish (nearshore)	11	0	13	0	0	0
Herring (nearshore)	5	0	1	0	0	0
Monkfish/skate (offshore)	0	3	0	1	21	3
White hake (offshore)	0	0	0	0	1	0
Greenland halibut (nearshore)	0	3	0	0	0	0
Greenland halibut (offshore)	0	0	0	1[3]	0	0
Total	39	53[1]	35	10	24	3

[1] The total number of small cetaceans reported to DFO in 2002 was 64. Eleven of these were brought in by fishers who had no affiliation with either the Sentinel fishery, or the Bycatch Collector programme, but who had become aware of DFO's collection efforts through word of mouth. Ten of these porpoises had been caught in the nearshore cod fishery, while a single porpoise was caught in a lumpfish gillnet. Since these porpoises did not have any netday-effort associated with them, they were not used in further analyses. This problem did not occur in other years.

[2] Fishery Observers did not specifically record the numbers of individuals involved in an incidental catch event, only total weight. Minimum numbers of animals were estimated based on average weights reported in the literature.

[3] This incidental catch event involved at least one long-finned pilot whale, as mentioned in the text.

were associated with the offshore monkfish and skate fishery (*n*=25), the nearshore cod fishery (*n*=10), the offshore white hake fishery (*n*=1) and the offshore Greenland halibut fishery (*n*=1).

The first records of incidental catch events in the fishery for monkfish and skates occurred in 2001 (one report) and then increased dramatically in 2002 (21 reports), before dropping again in 2003 (three reports). In the nearshore cod fishery, a total of eight records were reported in 2001, two events in 2002 and none in 2003; most of these catches were recorded on board small vessels (<35ft). There was a single report of small cetacean bycatch in the offshore gillnet fishery for white hake, in 2002 and another one in the offshore fishery for Greenland halibut in 2001. All these reports referred to various species of dolphins as well as harbour porpoises. Since Observer coverage levels in the nearshore cod fishery were low compared to Bycatch Collector and Sentinel datasets, it was decided to not use these data to estimate incidental catches of small cetaceans in this fishery.

Fishing effort and associated bycatches in Newfoundland and Labrador

Atlantic cod

The number of vessels participating in the Atlantic cod fishery varied from 3,126 in 2001, to 2,708 in 2002, to 962 in 2003 (Table 2). This included small-boat, nearshore operations as well as larger vessels capable of going further offshore. Nets used in this fishery typically have a 14cm mesh size. In 2001 and 2002, most cod fishing effort occurred in nearshore waters along the south and west coasts of Newfoundland; there was relatively little effort offshore off the south coast. In 2003, the cod fishery along the east/northeast and west coasts of Newfoundland was closed for conservation purposes, limiting the directed cod fishery to the Sentinel fishery in those areas and reducing the total number of vessels to 962, fishing mainly off the south coast where a commercial fishery for cod continued on a limited basis (DFO, 2006b; 2006c; Table 2). Landings were highest in July-September (third quarter) of each year, but considerable amounts were also landed in the fourth quarter (Fig. 2). Observer coverage for this fishery was relatively low – an observer was present on less than 10% of trips.

There were no reports of any incidental catches in the only currently operating offshore fishery for cod, off the south coast of Newfoundland. Therefore, incidental catch estimates were only calculated for the nearshore fishery in waters around the island and are presented for each quarter

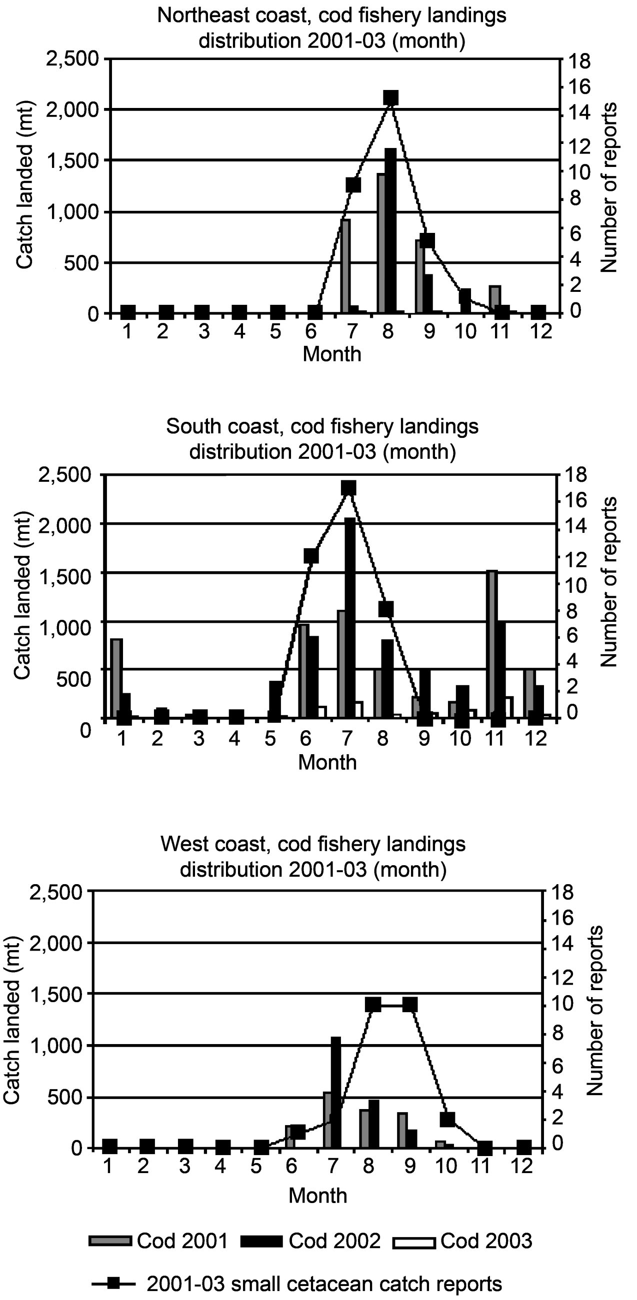

Fig. 2. Distribution of fishing effort and number of recorded small cetacean bycatch reports in the nearshore cod gillnet fishery, for Northeast, South and West coast, for 2001, 2002 and 2003. Small cetacean catch reports are combined for the three years.

Table 2

An overview of landings and effort data for the gillnet fisheries during 2001-03 that were used in this study.

	Number of vessels active in the fishery, per year			Total Catch (mt) per year			Fishing effort (net-days, estimated) per year		
Fishery	2001	2002	2003	2001	2002	2003	2001	2002	2003
Cod (nearshore)	3,126	2,708	962	10,264	10,233	6,284	907,309	1,073,606	793,147
Cod (offshore)	119	147	136	1,394	1,913	1,780	14,299	22,256	17,546
Lumpfish (nearshore)	1,528	811	1,009	872	171	554	218,263	123,315	126,353
Herring (nearshore)	207	196	97	1,430	1,660	1,025	32,073	23,052	14,140
Monkfish/skate (offshore)	36	58	90	942	3,027	2,659	154,467	251,575	211,549
White hake (offshore)	38	24	22	305	345	278	5,907	12,371	9,989
Greenland halibut (nearshore)	273	104	115	1,687	868	1,321	416,933	315,928	1,695,817
Greenland halibut (offshore)	112	96	49	7,237	5,277	3,517	2,563,700	2,135,685	6,674,892

of the year (Table 3). Based on recovered carcasses, all of these animals were probably harbour porpoises. The average annual incidental catch estimates were 688 animals (95% CI: 102-1,715) in 2001, 1,296 animals (95% CI: 365-2,632) in 2002 and 2,001 animals (95% CI: 295-4,678) in 2003. In 2001 and 2002, the majority of estimated catches (77% and 61% respectively) occurred in July-September (third quarter) but in 2003, 73% of all estimated catches occurred in April-June (second quarter). There were very few reports of incidental catches during October-December and none during January-March (Table 4; Fig. 2). The seasonal presence of harbour porpoises in waters around Newfoundland is apparent from the distribution of incidental catch reports, relative to the monthly amount of fish landed (Fig. 2).

Lumpfish

The lumpfish fishery is a relatively small-scale fishery, mainly prosecuted with small vessels in shallow nearshore waters on all coasts of the island. The number of participating vessels varied from 1,528 in 2001, to 811 in 2002 and 1,009 in 2003. Nets used in this fishery typically have a 25cm mesh size. There have been substantial fluctuations in landings in recent years (Table 2). The season for the lumpfish fishery is short when compared to other species, with the majority of catches being landed in May and June. For this reason, all landings in a given year were analysed together. Fishery Observer coverage in this fishery was low (an observer was present on less than 1% of trips).

Based on collected specimens, all of which were harbour porpoises, it is assumed that most bycaught small cetaceans in the nearshore lumpfish fishery were of this species. In 2001, the total average incidental catch estimate for the nearshore lumpfish fishery was 84 small cetaceans (95% CI: 2-240; Table 3). Bycatch Collectors did not report any incidental catch of small cetaceans in 2002, when poor catches were reported in the lumpfish fishery (Table 2). A specimen collected by a fisher not affiliated with the Bycatch Collector programme indicated that despite reduced fishing effort, harbour porpoises were still captured in lumpfish nets in 2002. For 2003, the average incidental catch estimate was 211 small cetaceans (95% CI: 20-499).

Table 4

Monthly distribution of incidental catch reports of small cetaceans in the nearshore cod fishery during 2001-03 around the island of Newfoundland, separated by coastline. Reports originated from Bycatch Collectors and Sentinel fishers, and include records of animals that were not collected for independent identification.

	2001			2002			2003		
Month	East coast	South coast	West coast	East coast	South coast	West coast	East coast	South coast	West coast
Jan.	-	-	-	-	-	-	-	-	-
Feb.	-	-	-	-	-	-	-	-	-
Mar.	-	-	-	-	-	-	-	-	-
Apr.	-	-	-	-	-	-	-	-	-
May	-	-	-	-	-	-	-	-	-
Jun.	-	3	-	-	3	1	-	6	-
Jul.	3	1	1	3	9	1	3	7	-
Aug.	7	-	3	6	8	7	2	-	-
Sep.	1	-	2	3	-	4	1	-	4
Oct.	-	-	1	1	-	1	-	-	-
Nov.	-	-	-	-	-	-	-	-	-
Dec.	-	-	-	-	-	-	-	-	-

Atlantic herring

The nearshore gillnet fishery for Atlantic herring is practiced on a small scale in various parts of the province. The greatest concentration of participants occurs along the west coast of the island, particularly in NAFO unit 4Ra (the Strait of Belle Isle). Nets used in this fishery typically have a 6cm mesh size. Numbers of participating vessels declined from 207 in 2001 and 196 in 2002, to 97 in 2003. Total landed catches were variable during this time (Table 2). There are several clearly defined substocks of herring in these waters, each fished in either the spring or the fall. For this reason, data were separated by quarter (Table 3). There was virtually no Fishery Observer coverage of this fishery.

All incidental catches in this fishery occurred during July-September. Based on collected specimens, all of which were harbour porpoises, it is assumed that the small cetaceans caught in the nearshore herring fishery were porpoises. In 2001, the average incidental catch estimate for the nearshore herring fishery was 89 harbour porpoises (95% CI: 26-176; Table 3). Bycatch Collectors did not report any incidental

Table 3

Estimated catches of small cetaceans (the vast majority are likely to be harbour porpoise) in nearshore and offshore gillnet fisheries in all areas of the island of Newfoundland, based on net-days, for 2001-03. 'N/A' indicates that no 95% confidence interval could be calculated due to small sample size.

			2001		2002		2003	
Fishery	Scale	Quarter	Estimate	95% CI	Estimate	95% CI	Estimate	95% CI
Cod nearshore	Coastline	1	0	0-0	0	0-0	0	0-0
		2	119	0-273	181	0-551	1,467	286-3,149
		3	570	102-1,442	1,088	365-1,997	534	9-1,529
		4	0	0-0	28	0-84	0	0-0
Cod total			688	102-1,715	1,296	365-2,632	2,001	295-4,678
Lumpfish nearshore	Coastline	Whole year	84	2-240	0[1]	0[1]	211	20-499
Herring nearshore	Coastline	3	89	26-176	0	0	10	0-29
Greenland halibut nearshore	Coastline	2	0	0	1	N/A	0	0
		3	0	0	28	0-78	0	0
Greenland halibut total					29	N/A		
Monkfish and skate offshore	3OPs offshore	Whole year	1	0-4	60	32-92	6	0-17
White hake offshore	3OPs offshore	Whole year	0	0	43	N/A	0	0
Grand total			862	130-2,135	1,428	N/A	2,228	315-5,223

[1] No Bycatch Collectors reported harbour porpoise incidental catch in their 2002 lumpfish fishery; however, a single animal was reported by a fisher who was unaffiliated with the programme, and identified as a harbour porpoise.

catch of small cetaceans in 2002. In 2003, the total average incidental catch estimate for the nearshore herring fishery was 10 small cetaceans (95% CI: 0-29).

Monkfish and skates

The monkfish and skate fishery has been prosecuted over the last decade in offshore waters along the southern edge of the Grand Banks (NAFO Divisions 3O and 3Ps), primarily along the shelf edge between 100 and 1,000m (DFO, 2000); (Fig. 1). Only large vessels (⩾35ft) participated in this fishery. Nets used in this fishery have a 30cm mesh size. The number of participating vessels has increased over time, with 36 vessels in 2001, 58 in 2002 and 90 vessels in 2003. Total landed catches of monkfish and skate also increased significantly in recent years although fishing effort peaked in 2002 (Table 2). Incidental catch estimates were calculated for a single area (the continental shelf break in NAFO Divisions OPs). All fishing effort was concentrated in one relatively short period during the summer months; for this reason, all landings in any given year were analysed as one set of data. Fishery Observer coverage in this fishery was relatively high, with observers being present on approx 30% of trips.

Various pelagic dolphins, as well as harbour porpoises, were reported as catch in this fishery by Fishery Observers. For 2001, the average annual incidental catch estimates for the offshore monkfish and skate fishery was found to be one small cetacean (95% CI: 0-4), based on net-days (Table 3). By 2002, these estimates had increased to an annual average of 60 small cetaceans (95% CI: 33-92), of which approximately six animals may have been harbour porpoises, based on the fraction of animals identified as such by Fishery Observers. In this season, 21 incidental capture events were reported, of which two were identified as harbour porpoises, six as common dolphins, six as Atlantic white-sided dolphins and seven as unspecified dolphins or porpoises. This would imply a harbour porpoise bycatch estimate of approximately six animals. In 2003, annual rates of incidental catch had again declined to approximately five small cetaceans (95% CI: 0-12).

White hake

The majority of the gillnet fishery for white hake takes place in offshore waters along the southern edge of the Grand Banks (NAFO Divisions 3O and 3Ps), where the species reaches its northernmost distribution (Fig. 1). Only large vessels (⩾35ft) participated in this offshore fishery, although small catches were also made in nearshore waters along the south coast by some small-boat fishers. Nets used in this fishery typically have a 14cm mesh size. The number of participating vessels decreased from 38 vessels in 2001, to 24 in 2002 and 22 in 2003. Total landed catches and fishing effort varied considerably among years (Table 2). All fishing effort was concentrated in one relatively short period during the summer months; for this reason, all landings in any given year of the offshore component of this fishery (the continental shelf break in NAFO Divisions OPs) were analysed as one set of data. There was no Fishery Observer coverage of the nearshore component of this fishery. Fishery Observer coverage in the offshore fishery ranged between 4 and 14% of trips.

For 2001 and 2003, no incidental catch events were reported. In 2002, the total average incidental catch estimate was 29 porpoises (not resampled; Table 3). This was based on one bycatch event of a harbour porpoise (Table 1).

Greenland halibut

The Greenland halibut fishery is conducted mainly in offshore waters along the edge of the Newfoundland and Labrador continental shelf between 600 and 1,400m, with concentrations in NAFO Divisions 0B, 2J3KL and 3O (Fig. 1). A limited nearshore fishery also takes place wherever deep waters occur close to shore, such as in NAFO units 3Ki, 3Lb, 3Psb and particularly 4Rb (Fig. 1). Vessels fishing offshore were all large (⩾35ft), but in the nearshore areas, smaller vessels also participated. Greenland halibut nets normally have a 19cm mesh size. The number of vessels involved in this fishery has fluctuated, from 317 in 2001, to 178 in 2002 and 183 in 2003. Total landed catches of Greenland halibut have declined in recent years while fishing effort increased significantly in 2003 (Table 2). Incidental catch estimates for the nearshore fishery were calculated for each quarter of the year. The majority of fishing effort was concentrated in the summer months, during the second and third quarters of the year. Fishery Observers were present on approximately 5 to 10% of offshore trips and approximately 1% of nearshore trips.

All incidental catches occurred in the second and third quarter of the year, and all reported small cetaceans were harbour porpoises. It is therefore assumed that the small cetaceans caught incidentally in this fishery were probably harbour porpoises. For 2001 and 2003, no incidental catches were reported in the nearshore fishery. In 2002, the total average incidental catch estimate was 29 small cetaceans (95% CI: 0-78; Table 3). No small cetaceans were reported in the offshore fishery, apart from a single long-finned pilot whale that was reported caught in waters of NAFO Division 3L by a Fishery Observer in 2001.

Total incidental catch

Average incidental catch estimates for small cetaceans (most of which were probably harbour porpoises) ranged from 862 in 2001, to 1,428 in 2002 and 2,228 in 2003. The nearshore cod gillnet fishery accounted for 3,985 incidental catches for the three-year period of 2001-03, or an average of 1,328 catches per year. If this estimate is combined with the annual mean incidental catch estimates for small cetaceans in the nearshore lumpfish fishery (98), the nearshore herring fishery (33) and the nearshore Greenland halibut fishery (9), approximately 1,469 small cetaceans have been incidentally caught annually in these nearshore gillnet fisheries in Newfoundland in 2001-2003 (Table 3). Annual mean incidental capture estimates of small cetaceans in the offshore fishery for monkfish are probably in the low tens to low hundreds, and probably involve common and Atlantic white-sided dolphins, although small numbers of harbour porpoises are thought to have been captured as well. In the offshore white hake fishery, harbour porpoises has been reported bycaught, although it would seem that other small cetaceans are also at risk. The annual mean incidental capture estimate of small cetaceans in the offshore fishery for white hake is approximately 10 animals. The single long-finned pilot whale capture event in the offshore Greenland halibut fishery was not used to estimate catch for the entire fishery, since it is widely distributed along the continental shelf break and the areas where it overlaps with pilot whales are unknown.

DISCUSSION

Estimated small cetacean incidental catch in 2001-03

Based on data presented here, annual mean incidental catch estimates of small cetaceans, the majority of which are probably harbour porpoises, in Newfoundland fisheries were approximately 1,469 animals per year, with the vast majority of these occurring in nearshore fisheries around the island of Newfoundland.

In the late 1980s, a total of 2,242 harbour porpoises were estimated to have been caught in Newfoundland, based on a telephone survey of fishermen (DFO, 2001; Lien, 2001). At the very least, this estimate provides an indication of the level of incidental catches that may have been taking place at the time. Although the current estimate is lower, the confidence limits derived in the present study are large, and thus it is difficult to determine if the new estimates represent a change in incidental catches since the onset of the 1992 moratoria. However, the reduction in fishing effort has probably led to a decrease in catches of harbour porpoises. In the Gulf of Maine, fish stock conservation measures to reduce fishing effort from 1999 onward were partially responsible for a subsequent decrease in incidental catches of harbour porpoises in US waters (DFO, 2001; Rossman and Merrick, 1999; Trippel and Shepherd, 2004; Waring *et al*., 2001).

The overall increase in estimated catches from 2001-03 is principally driven by an increase in catch rates in the nearshore cod fishery, particularly in 2003. The cause for these fluctuations in harbour porpoise catch rates is presently unknown; however, in 2003, one participating Sentinel fishermen reported especially high porpoise catches per net-day during most of his fishing season, which has likely led to a positive bias in the overall estimate. However, this apparent increase may also have been driven by underlying variability in harbour porpoise abundance in nearshore Newfoundland waters.

The wide confidence intervals associated with these estimates are indicative of the variability associated with incidental catches of small cetaceans. Catches occur only during a low number of fishing trips, but when they happen, a large number of animals may be caught. As a result, individual catch rates include a large number of zeroes with only a few catch rates greater than zero, and sometimes quite large. While the number of nets that fishers can use is limited by their license conditions, the soak time can vary considerably due to weather conditions and other logistical factors, leading to a wide range of incidental catch rates (expressed as number of small cetaceans per net-day). This results in highly variable estimates of incidental catch.

The fisheries discussed here represent the vast majority of current gillnet fishing effort in Newfoundland and Labrador. Several other fisheries targeting species such as haddock (*Melanogrammus aeglefinus*), are currently active at very low levels, particularly off the south coast. No reports of incidental catch in these fisheries have been received, but it is likely that they experience catch rates similar to the cod fishery since these species occur in the same areas and seasons, and are fished with nets of comparable mesh sizes. However, the current low level of fishing effort (due to low fish stock sizes) would suggest that levels of incidental catch in these fisheries are not large.

There may be several reasons why there is such variation in reported incidental catch, with some vessels having larger harbour porpoise catches than others. Perhaps some are operating in harbour porpoise 'hotspots' where there is an overlap of harbour porpoises and their prey, or simply areas of higher harbour porpoise density. There were not enough data in this study to provide strong evidence of such 'hotspots' around the island of Newfoundland, although there is a suggestion of this for the Fogo Island area (NAFO unit 3Ki), Conception Bay (NAFO unit 3Lf), St. Mary's Bay (NAFO unit 3Lq), Placentia Bay (NAFO unit 3Psc) and the Strait of Belle Isle (NAFO unit 4Ra; Fig. 1), based on the repeated occurrence of captured porpoises in these areas. Unfortunately, our understanding of the relationship between harbour porpoise abundance and incidental catches, as well as the influence of other factors such as prey abundance and distribution, is limited. Harbour porpoises are known to use oceanographic features such as fronts and island wakes while foraging, and it is possible that a detailed analysis of where these features co-occur with gillnet fisheries, taking into account the geographical location of incidental catch reports, might allow the identification of harbour porpoise 'high-risk zones' in Newfoundland and Labrador (Johnston *et al*., 2005).

The distribution of catch reports confirms that harbour porpoises are only present during the summer and fall months in waters around the island of Newfoundland (Richardson, 1992; Fig. 2). Generally speaking, porpoises are captured from May-October, initially in the lumpfish fishery, and subsequently in other fisheries such as the cod fishery. Frequency of catches appeared to change from coast to coast: there were no catch reports available from the south coast after August despite continued fishing activity, while catches were reported along both the northeast and west coasts of the island through September and into October. It is possible that harbour porpoises along the south coast of Newfoundland are more migratory than those along the other coasts, and leave for presumed wintering grounds off the eastern coast of the United States at an earlier date (Rosel *et al*., 1999). Alternatively, they could move into nearshore waters along the south coast during early summer, and then move northward on both sides of Newfoundland as the season progresses, possibly in search of food. Further research is required to determine how harbour porpoises utilise the nearshore environment around Newfoundland through the entire year.

It is presently unknown exactly how the fisheries for monkfish, skates and white hake capture pelagic dolphins such as common and Atlantic white-sided dolphins, since these species are not generally considered to be benthic foragers. Dolphins may be attracted to sounds of gillnets being set and hauled, as well as to bright lights when fishing at night, potentially leading to entanglement (Tregenza *et al*., 1997). Further research is required to test this hypothesis. It is also unclear why the incidental catch estimates in the monkfish fishery are so variable from year to year, as there is no evidence for a geographical redistribution of fishing effort over this period. Possible reasons might include an increased focus among some Fishery Observers on documenting small cetacean incidental catch, or an influx of pelagic dolphins in response to temporarily favourable conditions in 2002. Both common and Atlantic white-sided dolphins are known to range widely over large areas, and their occurrence is strongly linked to patchily distributed pelagic food resources (NMFS, 2005a;2005b; Reeves *et al*., 2002). Stochastic fluctuations in prey availability may have led to a periodically higher abundance of these species in areas targeted by the monkfish and skate fishery in 2002.

Caveats for incidental catch estimation and means to improve incidental catch monitoring in Newfoundland and Labrador

In recent years, there have been many changes to the gillnet fisheries in Newfoundland and Labrador which may have reduced the effectiveness of existing incidental catch monitoring programmes. Most contributors to the Bycatch

Collector programme target nearshore groundfish species (particularly cod and lumpfish), but coverage is limited in small pelagic species such as herring, or offshore fisheries (particularly for monkfish and skates). The subsample of vessels used to derive incidental catch multipliers could also be unrepresentative of the entire fleet e.g. the Sentinel fishery may cover other areas than the commercial fishery where the density of harbour porpoises might be different; or fishermen change their fishing behaviour when a Fishery Observer is present (Lesage *et al*., 2006). The Sentinel fishery reported more incidental catches of harbour porpoises per net-day than Bycatch Collectors; however the extent of spatial overlap between Sentinel and commercial fisheries could not be investigated due to widespread lack of information on the geographical location of Bycatch Collectors' fishing gear. A more detailed comparison between adjacent Sentinel and commercial gillnets might uncover subtle differences in fishing methodology that influence catch rates of harbour porpoises, as described by Lesage *et al*. (2006).

Inaccurate reporting may occur due to difficulties in correct cetacean species identification by some participants or under-reporting. In this study, it is unlikely that Bycatch Collectors would underreport their incidental catches given their skill and motivation (most have a long working relationship with DFO's Marine Mammals Section). Additional training in cetacean identification, as well as reporting actual numbers of animals involved, might reduce the uncertainty in incidental catch reports by Bycatch Collectors and Fishery Observers, in cases where animals could not be collected. Further improvements in fishing effort data collection could be achieved through stricter adherence to the requirement that fishers complete their logbooks accurately and submit them following each season.

Deploying dedicated observers on every boat has been suggested as the ideal way to improve incidental catch reporting (IWC, 1994). However, this is impractical for many nearshore Newfoundland fisheries as most vessels are small and the cost of such a programme would be prohibitive. The Fishery Observer programme could be expanded to include more trips in nearshore fisheries, such as those for cod, lumpfish and herring, to provide an independent indication of incidental catch. However, concerns remain about placing observers on small boats with regards to observer safety and the potential impact of their presence on fishing operations (Lesage *et al*., 2006; NMFS, 2003).

CONCLUSIONS

As of yet, population sizes for most cetacean species in this part of the Northwestern Atlantic remain unknown, so the potential threat to the existence of these populations arising from this incidental catch is also unknown. Harbour porpoises in eastern Canadian waters are currently managed as three subpopulations, in the Gulf of Maine/Bay of Fundy area, the Gulf of St. Lawrence (including the west coast of Newfoundland) and around the south and east coasts of Newfoundland and northwards along the coast of Labrador (Gaskin, 1984;1992; IWC, 1996). It is unclear to what extent the various fisheries discussed here affect the different subpopulations around Newfoundland and Labrador, since porpoises are thought to seasonally migrate in and out of these waters, bringing them into contact with a variety of fisheries (COSEWIC, 2003a). In addition, there is evidence for long-range movements between porpoise subpopulations, indicating that fisheries may affect more than one local subpopulation (Read and Westgate, 1997; Rosel *et al*., 1999; Westgate and Tolley, 1999).

Means to improve the quality of data collected by deploying dedicated observers on every boat are unfeasible here, although a greater focus of the existing Fishery Observer programme on larger vessels active in these fisheries is possible. At the moment, fostering a long-term, trusting relationship with a number of representative fishers appears to be the best strategy to limit under-reporting of incidental catch.

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Time allocation and diving behaviour of harbour porpoises (*Phocoena phocoena*) in Danish and adjacent waters

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ABSTRACT

To gain insight into the time allocation and diving behaviour of harbour porpoises in Danish and adjacent waters, satellite linked dive recorders were mounted on 14 harbour porpoises. The animals were incidentally caught alive by fishermen using pound nets during 1997-99 in the Danish Belt seas. Information on diving behaviour was collected from April to November. Contact with individual porpoises remained for up to 130 days. The average number of dives per hour was 29 during April-August and 43 during October-November. Daily maximum dive depth corresponds to the depth of the Belt seas and Kattegat where depth generally does not exceed 50m. Maximum dive depth recorded was 132m from animals moving north into Skagerrak. Dives were frequently recorded in the category 10-15min, but could potentially be an artefact of the sampling regime. The diurnal pattern shows that harbour porpoises dive continuously both day and night, but with peak activity during daylight hours. On average they spent 55% of their time in the upper 2m during April-August. These values have implications for aerial abundance surveys when correcting for animals not visible. A mature female and its approximately 10 months old calf were both tagged and swam together for 43 days until contact was lost. The calf made more frequent but shorter dives than the mature female. The number of dives per hour decreased, while the dive depth and duration increased for both animals from May to June, suggesting a change in feeding behaviour. It is not known whether the female and calf synchronised their dives, but the diurnal dive pattern shows a correlated dive rhythm in May, but not in June. This change in mother-calf behaviour suggests that the calf foraged more independently, corresponding to the time of year when porpoise calves leave their mother.

KEYWORDS: SATELLITE TAGGING; TELEMETRY, DIURNAL; BEHAVIOUR; DIVING; HARBOUR PORPOISE; NORTHERN HEMISPHERE; ATLANTIC OCEAN

INTRODUCTION

The diving behaviour of cetaceans is almost impossible to study without the aid of electronic devices. Compared to other marine endotherms like seals and birds, for which the fur and feathers can be used as a base for attachment, the skin of cetaceans consist of live cells that are constantly being replaced, making gluing impossible. For short-term deployments (up to two days) suction cup tags have been used (e.g. Schneider *et al*., 1998) but to follow animals for days or months the tag needs to be attached more permanently to the animal. On large cetaceans this is done by shooting the tag into the tissue (e.g. Heide-Jørgensen *et al*., 2001). For small cetaceans, the animals may be caught and the tag attached by means of pins through the dorsal fin or dorsal ridge (e.g. Read and Westgate, 1997; Wells *et al*., 1999). The latter method has proven to be the most successful in terms of contact duration, with contact remaining for up to 349 days for a harbour porpoise (Teilmann *et al*., 2004).

Two different approaches for gathering dive data have been used in previous studies, one which requires recovery of the device and one in which data are transmitted electronically. Data loggers (e.g. Time-Depth-Recorders, TDRs), which store high resolution data, have only been used to a limited extent on free-living cetaceans. These instruments need to be recovered, as the quantity of data is too large to transmit via satellite and is thus stored in the memory onboard the tag. Difficulties in retrieving the tag have prevented the wide use of this technique. In order to circumvent this, satellite transmitters that store and transmit information have been developed (Satellite-Dive-Recorders, SDRs). This method secures long-term data retrieval as long as contact remains with the satellite. However, the method is limited by the data receiving capacity of the satellite, with the result being lower resolution data organised in bins over several hours unlike the individual readings every few seconds yielded by TDRs. Burns and Castellini (1998) monitored the behaviour of individual Weddell seal pups using both TDRs and SDRs. They found that although the data loggers gave a full record of all dives, while only half of the dives were represented in the data received by the satellite, on average the data from the SDRs gave an accurate representation of the diving behaviour.

The high mortality of harbour porpoises (*Phocoena phocoena*) taken as bycatch in gillnet fisheries throughout the Northern Hemisphere requires mitigation and management (e.g. Lowry and Teilmann, 1994; Vinther, 1999). Better guidance may be given if knowledge on the diurnal and seasonal movements and diving behaviour of these animals is taken into account.

The diving behaviour of harbour porpoises has previously been studied by Westgate *et al*. (1995), Otani *et al*. (2000; 1998) and Teilmann (2000). These studies all used data loggers deployed for up to 12 days.

The present study describes the diurnal and seasonal time allocation and diving behaviour of harbour porpoises over much longer periods than previously. Data are presented on 14 harbour porpoises monitored by SDRs for up to 130 days in Danish and adjacent waters.

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MATERIALS AND METHODS

The area

The tagged harbour porpoises remained primarily in the relatively shallow waters around the islands of Denmark (Fig. 1). The water depth only exceeds 50m along the Swedish west coast north of about 57°N. The bottom is generally comprised of sand, gravel or stone reefs, except for the Swedish westcoast where a rock bottom is found. These waters connect the Baltic to the ocean and have a very complex oceanography with low saline Baltic surface water (<10 psu) and heavy North Sea bottom water (about 30 psu) often forming a pronounced halocline. Although the tide is limited (<0.5m), strong currents are found in the narrow straits between the islands due to fresh water from the Baltic rivers and wind moving the water around.

Availability of the harbour porpoises

The porpoises tagged in this study were all incidentally trapped in pound nets in the Danish Belts (Fig. 1). Pound nets are used all around Denmark (except for the North Sea) in the spring to catch primarily herring (*Clupea harengus*), mackerel (*Scomber scombrus*) and garfish (*Belone belone*) and in autumn to catch eel (*Anguilla anguilla*). Often the porpoises are caught in nets together with herring. Herring may therefore 'guide' the porpoises along the pound net, into the trap. A pound net consists of a lead net that extends from the beach up to 1km ending in a trap. Several traps may follow spaced with another lead net. The trap consists of a wide opening that guide the fish into the final trap, which is a bag net open at the surface. The circumference of the bag is 40-80m with a mesh size of about 2cm. The meshes are too small for entanglement and the harbour porpoises are rarely injured and can swim around freely and dive to depths of 5-10m.

A network of pound net fishermen was established who reported when they observed a live porpoise in their nets. The fishermen were instructed to close the entrance to the net when a porpoise was found, to prevent the animal from escaping before the field team arrived, normally within a few hours. Compensation was paid to the fishermen for assistance with animal handling and for keeping the net closed until the porpoise was tagged and released.

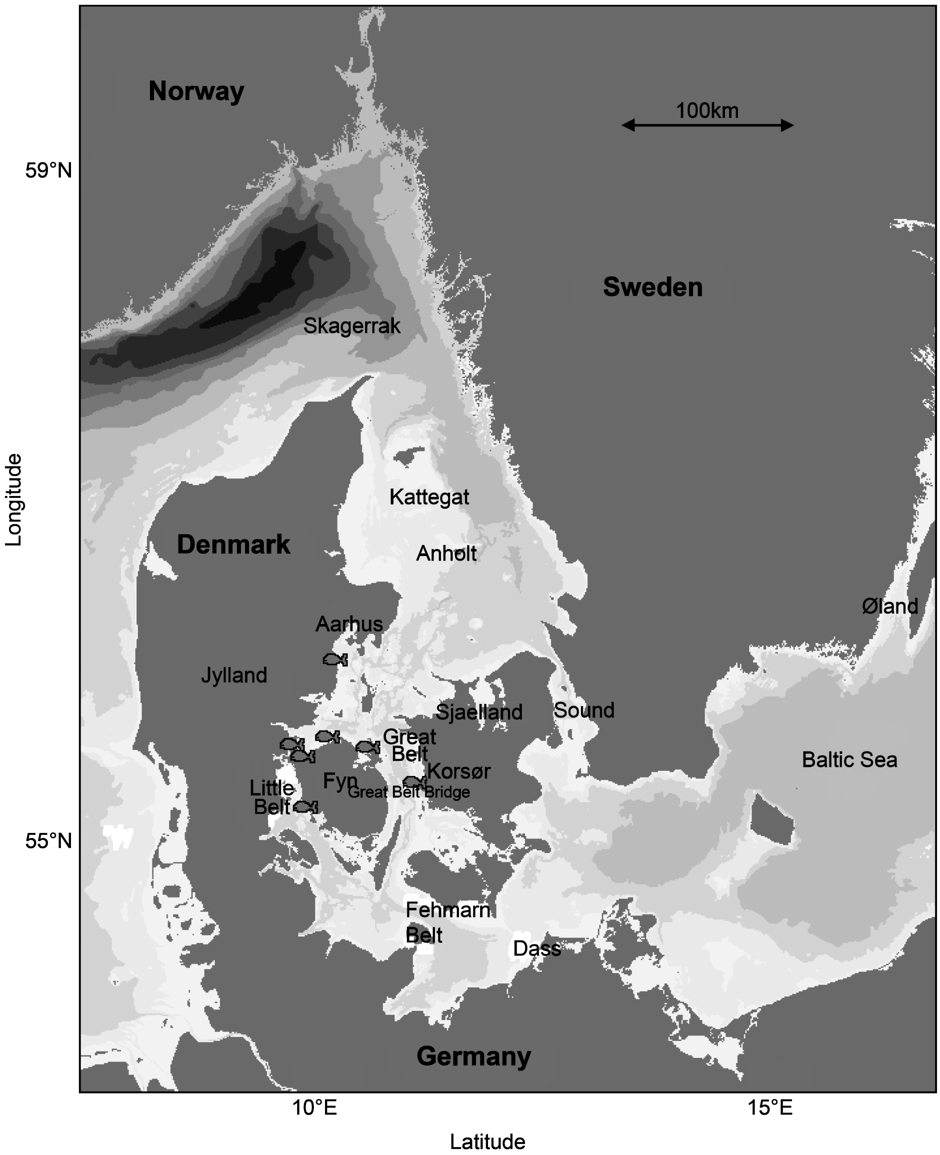

Fig. 1. Map of the study area with bathymetry and names mentioned in the text indicated. The locations of the pound nets where the harbour porpoises were caught are indicated with 'fish' symbols.

Handling and tag attachment

Fourteen harbour porpoises (Table 1) were equipped with SDRs (SDR-T10 with two 2/3 A-cells or two flat 3V lithium batteries (Wildlife Computers, Seattle, USA)). The SDR-T10 transmitters, which were cast in epoxy, weighed 130-240g in air and 10-20g in seawater. Each unit had a transmission power output of 0.25-0.5W, and a potential of around 12,500 transmissions. The transmitters were programmed to give a maximum of 100-500 transmissions per day depending on tag programming (see Table 1) giving an expected battery life of 25-125 days. All tags had a transmission repetition rate of 45s. A saltwater switch (SWS) ensured that transmissions would occur only when the animal was at the surface. Three front-mount and one side-mount designs were used (Table 1). The front-mount transmitters were glued (Flexane or Loctite 414) onto a saddle made from 2mm conveyor belt rubber material, which wrapped around the leading edge of the dorsal fin and was cut into shape for each individual animal to fit the dorsal fin. Side-mount transmitters were also glued (Loctite 414) onto a piece of conveyor belt somewhat larger than the transmitter housing, allowing the belt material to be cut into shape to fit the individual dorsal fin. A backing plate of the same material and shape was made for the side-mount tags. The inside of all ‘saddles’ was lined with 3mm neoprene to reduce abrasion of the skin of the dorsal fin. For all attachments three holes, forming a triangle, were used. Two holes about 2cm from the leading edge of the dorsal fin and one near the trailing edge.

Only animals considered to be in good health (no abnormalities and with a normal blubber layer, see Lockyer *et al*., 2003) were equipped with a satellite tag. After application of local anaesthesia (Lidocain 5% ointment), three holes were made in the dorsal fin by means of a 5mm stainless steel cork borer-type utensil. The best result was obtained if the cork borer was freshly sharpened around the inside of the hole, that the steel wall was as thin as possible and that a slow speed battery drill was used. Five millimetre threaded POM (polyoxymethylen or polyacetal) pins coated with polyester tubing (Sulzer Vascutek, Renfrewshire, Scotland) or silicone tubes as used in human surgery, to protect the tissue, were fitted through the saddle and the dorsal fin and fastened using nylon or iron nuts in both ends. Before inserting the pins they were coated with antiseptic ointment (Betadine). The manufacturer of the pins specified that POM, would degrade under UV light and detach the tag from the animal after some months, similarly the iron nuts would rust away and the tag fall off within an estimated one year period. The tissue samples inside the cork borer were saved for genetic analyses. Full data and sample sets for health check, body condition and reproductive status were taken when possible, including total length, girths, blubber thickness, full blood, serum and plasma, blood cytology, vaginal and blow cytology and bacteriology (Teilmann *et al*., 2004). The animals were handled on the boat for about 20-30 minutes until release.

Time and pressure (depth) were sampled at a default rate of every 10s. These data were stored in three types of 6hr summary histograms and then relayed to the satellite during the following 24hr (see below). In addition, status messages (every 15th transmission) and timelines (every 48th transmission) were transmitted in separate messages. The status messages included the maximum dive depth during the previous 24hr; status of the sensors, total number of transmissions and battery voltage. Timelines were recorded over 24hr and divided into 72 20min periods. Based on the depth sampled every 10s, the tag records whether the animal spends the majority of time (>50%) above or below 1m depth for each 20min period.

Three types of 6hr histograms were sampled: (1) maximum depth for each dive (limit of tags was 250m); (2) duration of each dive; and (3) time spent in each depth interval (TAD). Data from these three categories were sampled and stored in 14 user-defined intervals. Intervals for type 1 were set to 25m, then 5m bins up to 30m, 10m bins up to 100m and then >100m. Intervals for type 2 were one minute up to 10 minutes, 5 minute bins up to 25 minutes and then >25 minutes. Intervals for type 3 were 0-2m, 35m, then 5m bins up to 30m, 10m bins up to 90m and >90m (except for 6172_97, 6173_97, 6171_98 and 6173_98 for which the first bin was 0-5m). The pressure transducer had a resolution of ±1m and an accuracy of ±1% of the depth reading.

Data analysis

Data on movements, diving behaviour and transmitter status were collected via the Argos Location Service Plus system and received online over the Internet and on CD-ROMs. The software program *Satpak* 3.0 (Wildlife Computers) was used for validating dive data received from Argos and transforming data into an ASCII format. *Excel* and *SAS* were used for data analysis.

Table 1

Basic data for the tagged harbour porpoises.

ID no.	Sex	STD length (cm)	Body mass (kg)	Deployment period	Days of contact	Expected lifetime	No. of daily uplinks	Tag configuration
6171_97	F	110	27	14 Apr.-9 May 1997	26	25	500	SDR-T10 frontmount type 1
6170_97	F**	164	63	16 Apr.-23 May 1997	38	25	500	SDR-T10 frontmount type 1
6172_97	M	138	37	27 Oct.-6 Dec. 1997	41	31	400	SDR-T10 frontmount type 2
6173_97	M	114	24	1 Nov.-14 Nov. 1997	14	31	400	SDR-T10 frontmount type 2
6171_98	F**	166	58	11 May-24 Jun. 1998	45	50	250	SDR-T10 frontmount type 3
6173_98	F#	110	26	11 May-22 Jun. 1998	43	50	250	SDR-T10 frontmount type 3
6420_98	M	116	32	19 May-14 Jul. 1998	57	50	250	SDR-T10 frontmount type 3
6172_99	F*	138	45	30 Mar.-16 Jul. 1999	109	125	100	SDR-T10 frontmount type 3
6421_99	F	127	37	13 Apr.-20 Jul. 1999	99	125	100	SDR-T10 frontmount type 3
6422_99	M	120	31	13 Apr.-2 Aug. 1999	112	125	100	SDR-T10 frontmount type 3
6174_99	F'	112	30	25 Apr.-17 Aug. 1999	115	125	100	SDR-T10 sidemount type 2
6173_99	F#	144	65	25 Apr.-17 Aug. 1999	115	125	100	SDR-T10 sidemount type 2
6171_99	F	116	30	26 Apr.-4 Aug. 1999	101	125	100	SDR-T10 sidemount type 2
6170_99	M	118	37	27 Apr.-3 Sep. 1999	130	125	100	SDR-T10 sidemount type 2

**=Lactating female accompanied by calf. *=Female accompanied by calf. #=Calf accompanied by large female.

A dive was defined as deeper than 2m and lasting at least 10s. Surface time (breathing, resting or swimming at the surface), based on the timelines, was defined as the time spent above 1m depth. For each hour of the day, a monthly average value was used for comparison between months. Only for April-August and November were enough data available for this exercise.

RESULTS

System performance

From the 14 porpoises, 7,210 histograms were received (depth=2,341, duration=2,697, TAD=2,172), each representing a complete record of the diving behaviour during a 6hr period. This corresponds to 543-674 days of diving behaviour from each of the three histogram types received. The dive data collected represents on average 58% of the contact duration with the porpoises. The contact duration lasted from 14-130 days, depending on the daily allowance of transmission. On average the contact duration was within 96% of the expected lifetime based on battery capacity, indicating that the battery was the limiting factor in contact duration rather than tag attachment.

Frequency of dives

The overall average number of dives below 2m hr^{-1} was 34, with monthly means from 28 to 46 dives hr^{-1} (April-August, October-November, Fig. 2). The dive rate was not significantly different from April to August (mean=29 dives hr^{-1}, Analysis of Variance (ANOVA), $p>0.05$). Dive rates in October and November (mean=43 dives hr^{-1}) were significantly higher than in the April-August (ANOVA, $p<0.05$).

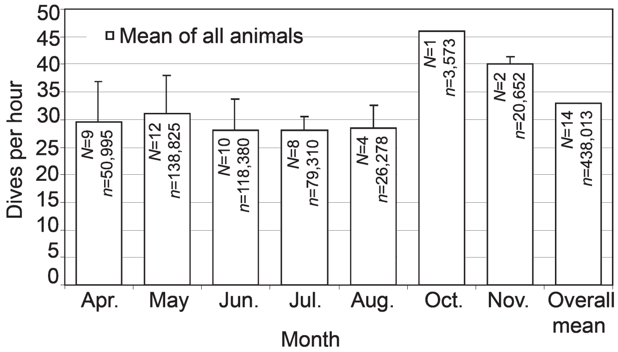

Fig. 2. Number of dives per hour by month. Bars indicate the average of individual means in the particular month and overall mean of animal means. Standard deviation is given above the bars for months where data from more than one animal exists. *N*=number of animals, *n*=number of dives.

Maximum dive depth

The status messages provided a daily exact maximum dive depth and 450 such values were received from the 14 animals (Fig. 3). They ranged from 6-132m, with median and mean values of 26m and 30m (Standard Deviation (SD)=17.8), respectively. The most frequent depths were 14-32m and represented 64% of all daily maximum dive depth values.

Diurnal and seasonal dive patterns

The time spent at the surface varied from 45-63% (mean 55%) in the 0-2m interval depending on the time of the day and month (Fig. 4). Although there was 18% difference in surface time during evening (15:00-21:00) from April to August, no significant differences were found between months or time of day (ANOVA, $p>0.05$).

As seen in Fig. 5, the time spent diving during May, June and July showed a similar pattern. The dive time was rather stable for most of the day, except between 15:00-20:00 when diving activity increase dramatically with peaks between 16:00-17:00. The same general pattern was seen for April and August, however, in April the dive time was lower than in May-July. In August, there was lower activity during 1:00-2:00 and a peak around 7:00 in the morning. In November a different pattern was seen with increased activity from 5:00 to 16:00, followed by a decrease over two hours where it remained until the morning. In early April and late August the sun rises at 6:00 and goes down around 20:00 in the study area. During the longest day (21 June) the sun is up from 4:30-22:00. In mid-November, the sun is up from about 7:30-16:00. There is no obvious correlation between daylight and diving activity during April-August, but in November the peak diving activity corresponds with daylight hours. Statistical correlation showed that May had the same diurnal fluctuations as April, August and November, while June correlated with November and August correlated significantly with July and November (Spearman Rank correlation, $p<0.05$). These correlations show that the diurnal dive patterns for all months correlate with other months, suggesting that abiotic parameters such as light may control the diurnal dive intensity. All the peak activity fell within the daylight hours. No obvious resting periods were found and a high level of diving activity was found throughout day and night in all months.

Time at depth

Generally, the majority of time was spent in the uppermost 5m with progressively less time spent in the deeper intervals. In October-November more time was spend at depths below 10m, compared to the spring and summer months. The overall TAD average for the whole study period shows that harbour porpoises in Danish waters spend about 68% of their time at 0-5m depth, 17% at 5-10m, 8% at 10-15m, 5% at 15-20m and 2% at depths deeper than 20m (Fig. 6).

Female/calf pair

The four adult females tagged in this study were all accompanied by a young animal and in two of the pairs both the female and calf were tagged (Table 1). The relationships between these two pairs were tested genetically (17 DNA microsatellite makers, see Teilmann *et al*. (2004) for details) and the results showed that one pair was a mother and calf (6171_98 and 6173_98) while the other was closely related as half siblings or cousins (6173_99 and 6174_99). In the latter case, the animals were seen swimming away close together after tagging, but the tracks separated the following day. The mother and calf swam close together until contact was lost after 45 (female) and 43 days (calf) due to low battery voltage (Fig. 7). Dive data were collected for 66% (female) and 52% (calf) of the total contact time. The time spent in the first 10m of the surface by the calf was 7% and 6% more than for the female in May and June, respectively (Table 2). From May to June there was an increase of 7% for the female and 4% for the calf in the time spent at greater depth than 10m (Table 2). At the same time the percentage of dives below 10m decreased by 3% and 9% for the female and calf, respectively. Thus, both animals made relatively fewer but longer duration dives from May to June (Fig. 8).

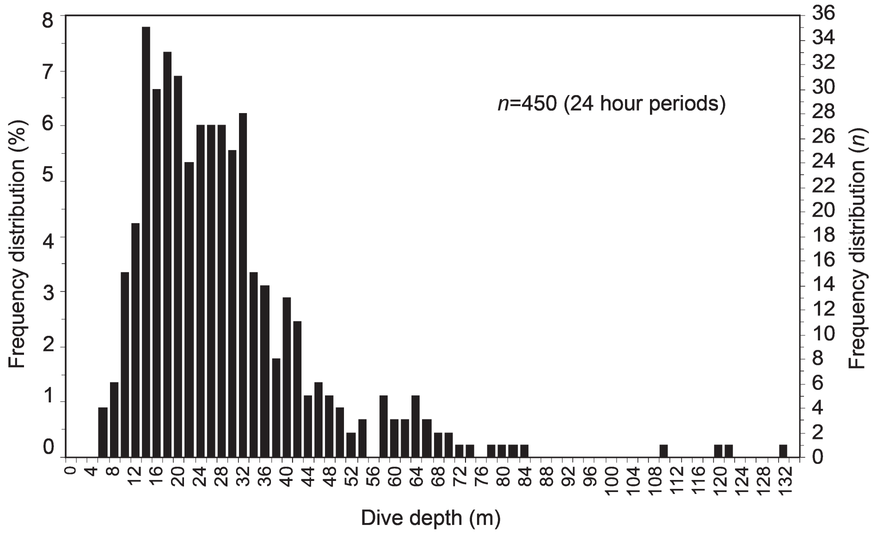

Fig. 3. Maximum dive depth for all animals recorded over 24hr periods. Note that both frequency in percent (left *y*-axis) and frequency in numbers (right *y*-axis) is given. *n*=number of 24-hour periods included.

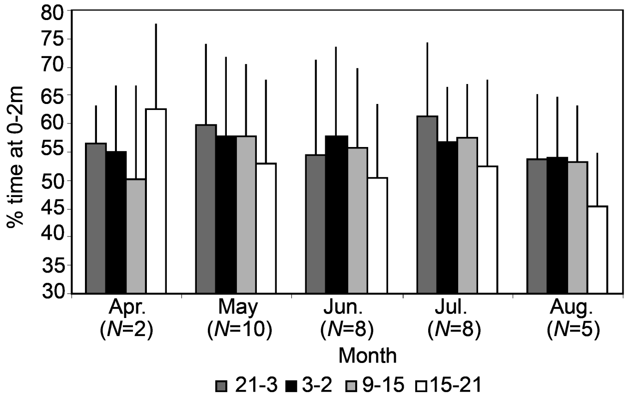

Fig. 4. Average time spent near the surface (0-2m) by month and time of day (night=21-3, morning=3-9, day=9-15, evening=15-21). Data obtained from the first histogram bin in TAD. *N*=number of animals included.

Dive durations up to 5min were recorded daily for both animals, while longer duration dives were recorded occasionally.

The diurnal dive patterns of the two animals, as expressed by the timeline data, were significantly correlated in May (Spearman Rank correlation, $p<0.05$), but not in June ($p>0.05$, Fig. 9). The calf spent significantly less time diving than the adult female during almost any time of the day in May (t-test, $p<0.05$), while this was less pronounced in June. In May, higher diving activity was seen around 4:00 in the morning and between 9:00 and 22:00. This period is mainly within daylight hours as the sun comes up around 5:00 and goes down around 21:15 in mid-May. The dive time below 1m based on timelines increased significantly from May to June for the adult female and the calf, respectively (*t*-test, $p>0.0001$). In June, both animals showed high diving activity in the early morning hours and

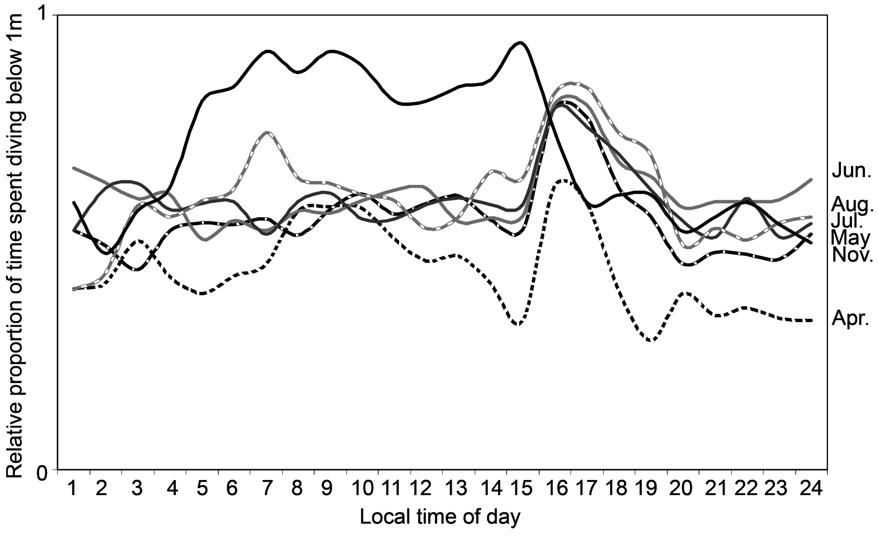

Fig. 5. Relative diving activity below 1m during the day (1 hour increments). *N*=number of animals, *n*=number of 20-minute 'timeline' periods included for each hour per month.

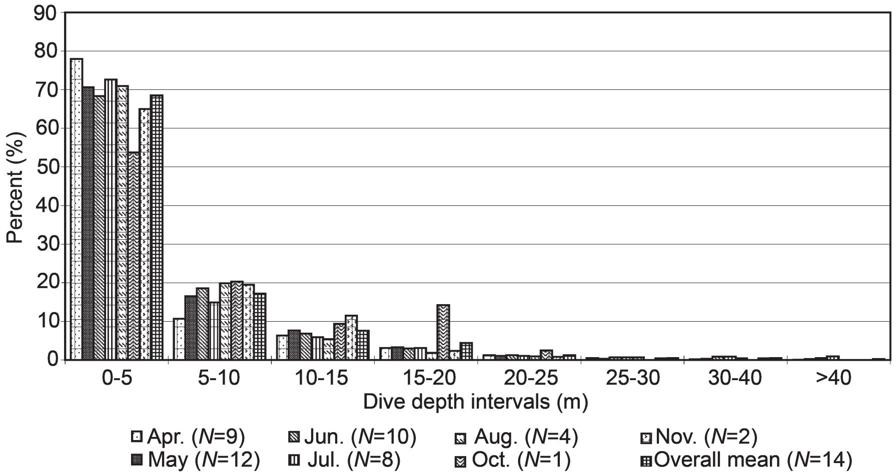

Fig. 6. Average time spent at the different depth intervals for all animals grouped by month. *N*=the number of animals.

from 15:00 to 21:00. Although less pronounced, the latter generally corresponds to the overall peak diving activity in Fig. 5.

The dive depth by the female-calf pair shows that 2-5m and 5-10m were about equally often used, followed by dives to 10-15m and 15-20m (Table 2). The total number of dives per hour decreased significantly for both the female (38 to 34) and the calf (42 to 38) from May to June (t-test, $p>0.01$). The deepest dives were recorded in the 30-40m category, which is consistent with the water depths of the geographical area utilised, which do not exceed 50m (Fig. 7).

DISCUSSION

Effect of tagging

In the present study dive data were collected from 14 harbour porpoises providing dive information for seven months of the year. Following tagged animals for longer periods such as this has the advantage of providing information well past the stressful experience of the tagging situation, thereby providing more reliable data on natural diving behaviour. A study on the effect of a captive porpoise carrying a satellite tag identical to those used in the present study (Geertsen *et al*., 2004) showed a significant behavioural response during the first day after tagging but thereafter no alteration in behaviour was detected during the following month. However, this porpoise was sedated with valium before tagging which may have caused the observed behavioural change during the first day rather than the handling procedure or the tag itself.

The increase in drag due to tag attachment has been measured on porpoise models in wind and water tunnels and these experiments indicate that a tag may substantially increase drag (Bannasch *et al*., 1994; Hanson, 2001). Therefore the possibility cannot be excluded that drag from tags may have a long-term effect by causing an increase in the energetic cost of swimming and diving, as was indicated for fur seals by Walker and Boveng (1995). However, the fact that two harbour porpoises carrying satellite tags caught by fishermen after 3 and 11 months, had full stomachs and their length and weight corresponded to natural growth suggests no strong influence from the tags on the behaviour of harbour porpoises (Teilman, unpubl. data).

Dive frequency

Three studies have described the diving behaviour of harbour porpoises using TDRs over a few hours or days. Westgate *et al*. (1995) recorded diving behaviour of seven harbour porpoises in the western Atlantic at the border between Canada and USA (animal lengths: 114-161cm; deployment duration 10-106 hours in August/September); Otani *et al*. (2000; 1998) presented diving data on three harbour porpoises in Japanese waters (animal lengths: 134-166cm; deployment duration 23-100 hours in April, May, and July); and Teilmann (2000) provided dive data on an immature harbour porpoise followed for 12 days in May in Danish waters. These studies yielded detailed data on individual dives but the duration of the recordings and the small sample size preclude general conclusions being made on diurnal, seasonal and individual variation in harbour porpoise diving behaviour.

In the present study a mean dive rate was found of 29 dives hr^{-1} in April-August and 43 dives hr^{-1} in October-November. The average number of dives per hour was 48 in May in Denmark (Teilmann, 2000), 28-35 in April-July in Japan (Otani *et al*., 1998), and an average of 30 (range=12-109) in eastern USA in August-September (Westgate *et al*., 1995). Although some variations occur between animals, it seems that independent of area, the average dive rate for harbour porpoises during the spring and summer months is around 30 dives hr^{-1} below 2m. The higher dive rate found during October-November may reflect an increased foraging activity, compensating for higher energy requirements as the water temperature decreases at this time of year. This is supported by the fact that the weight of captive harbour porpoises kept under semi-natural conditions has been shown to increase dramatically in October, peaking in January and decreasing again in the spring, with increase in food intake preceding the increase in weight of one-two months (Lockyer *et al*., 2003).

Maximum dive depth

All of the tagged animals dived to 30-50m, resembling the depths in the Danish Belt seas, suggesting that the porpoises regularly explore the seafloor (Figs 7 and 10). Two animals (6171_97 and 6421_99) swam north along the Swedish west coast to Southeast Norway, where water depths of several hundred meters occur. The deepest dives (84 and 132m) were recorded from these two animals. The maximum dive

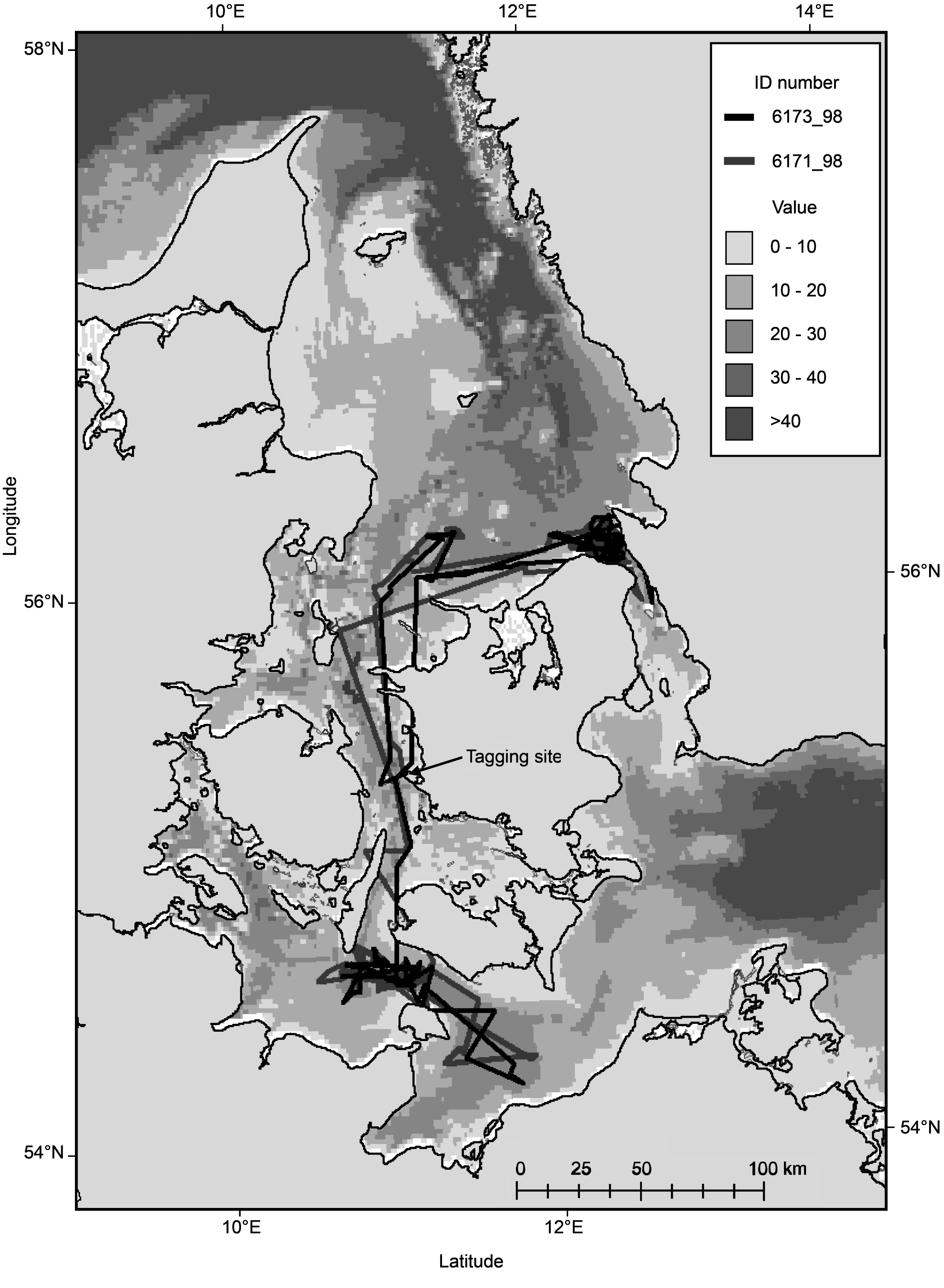

Fig. 7. Movements of mother (6171_98) and calf (6173_98) pair tracked for 45 and 43 days, respectively. The two animals were incidentally caught in the same pound net 11 May 1998 and contact was lost with the mother 24 June 1998 and two days later with the calf.

depths recorded for seven porpoises in the northwest Atlantic were 83, 119, 131, 136, 152, 207 and 226m, respectively (Westgate *et al*., 1995), whereas the three porpoises tagged in the eastern Pacific attained maximum dive depths of 65, 71 and 99m, respectively (Otani *et al*., 2000; 1998). This shows that harbour porpoises are capable of diving to depths of more than 200m and that water depth rather than diving ability is the limiting factor in dive depth within the continental shelf waters where harbour porpoises are mostly found.

An average dive depth represents both shallow resting and travelling dives, deep exploratory dives and feeding dives at various depths. Although deeper water was available in the northwest Atlantic and in the

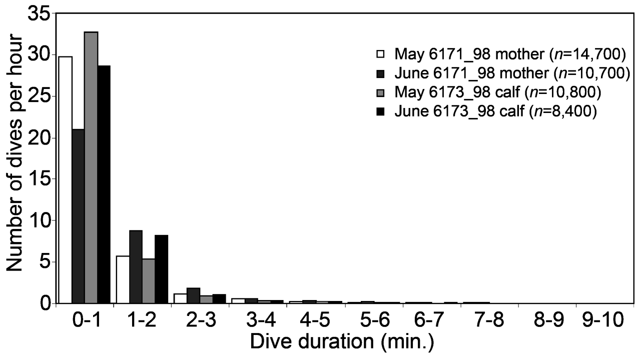

Fig. 8. Duration of dives in 1min intervals and number of dives per hour within each duration interval is indicated for the female (6171_98) and the calf (6173_98) in May and June 1998. *n*=total number of dives recorded by month for each animal.

Table 2

Time spent at depth intervals and the depth of dives for mother-calf pair (6171_98 and 6173_98). Note that the first interval is different between time at depth (0-5m) and depth of dives (2-5m). *n*=the number of hours where 'time at depth' was recorded. *N*=the total number of dives recorded for each animal.

	May		June	
Diving interval (m)	Mother	Calf	Mother	Calf
Time at depth (%) ***n*=540 *n*=678**				
0-5	52.9	60.6	46.7	50.6
5-10	19.7	19.0	17.7	19.6
10-15	20.5	16.6	23.2	22.0
15-20	6.0	3.3	10.3	6.7
20-25	0.8	0.4	1.7	1.0
25-30	0.0	0.1	0.0	0.2
30-40	0.0	0.1	0.0	0.0
>40	0.0	0.0	0.0	0.0
Depth of dives (%) ***N*=27,100 *N*=28,800**				
2-5	40.4	33.1	43.9	38.7
5-10	44.2	40.4	43.6	43.8
10-15	13.5	20.9	11.3	14.0
15-20	1.8	4.4	1.1	3.0
20-25	0.1	1.0	0.1	0.5
25-30	0.0	0.2	0.0	0.1
30-40	0.0	0.1	0.0	0.1
>40	0.0	0.0	0.0	0.0

eastern Pacific, the average depth of dives was 25m (Westgate *et al.*, 1995) and 12m (Otani *et al.*, 2000; 1998), respectively. Teilmann (2000) also found a mean dive depth of 12m. These values are similar to the findings in the present study. The shallow waters around Denmark may therefore represent an ideal habitat for harbour porpoises; high abundance of harbour porpoises is found in most areas around Denmark (Hammond *et al.*, 2002; Teilmann, 2003).

Diurnal dive patterns

Westgate *et al.* (1995) found that the proportion of time spent in the upper 2m varied from 33% to 60%, with a mean of 43% for the seven animals in their study. The range found in the present study is averaged over seven months and 14 animals and varied between 45% and 63% with an average of 55%. The lower proportion of time spent at the surface by the western Atlantic porpoises is probably due to the deeper water depth for this area and the deeper dive depth for these animals. Seasonal energetic requirements, depth dependent food availability and dive depth probably control the time spent at the surface layer.

The proportion of time when animals are visible to aerial observers is an important factor for correcting abundance estimates based on aerial surveys (e.g. Heide-Jørgensen *et al.*, 1992). The depth at which harbour porpoises can be seen depends on several factors including sea state, glare and clarity of the water. This study provides estimates of the proportion of time spent by porpoises in 0-2m by month from April to August. From 9:00-21:00 when most surveys are conducted, the time that porpoises are present at 0-2m varies from 50% during 9:00-15:00 to 63% during 15:00-21:00 in April, with less variation and the opposite dive pattern (more surface time during the morning-midday hours) for May-August. The availability of harbour porpoises to visual observers is therefore an important issue both diurnally and seasonally and may bias abundance estimates significantly if not taken into account.

The present and previous studies demonstrate that harbour porpoises dive continuously, both day and night (Otani *et al.*, 2000; Otani *et al.*, 1998; Teilmann, 2000; Westgate *et al.*, 1995). In the present study, porpoises were

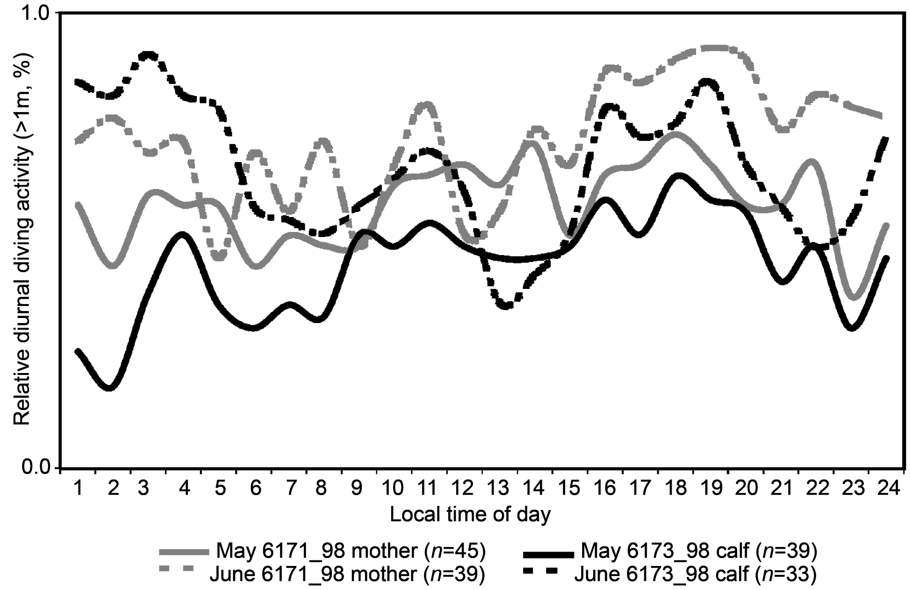

Fig. 9. Relative diving activity below 1m during the day (1 hour increments) for the female (light lines) and the calf (dark lines) in May (solid lines) and June (broken lines). *n*=number of 20-minute 'timeline' periods included for each hour per month.

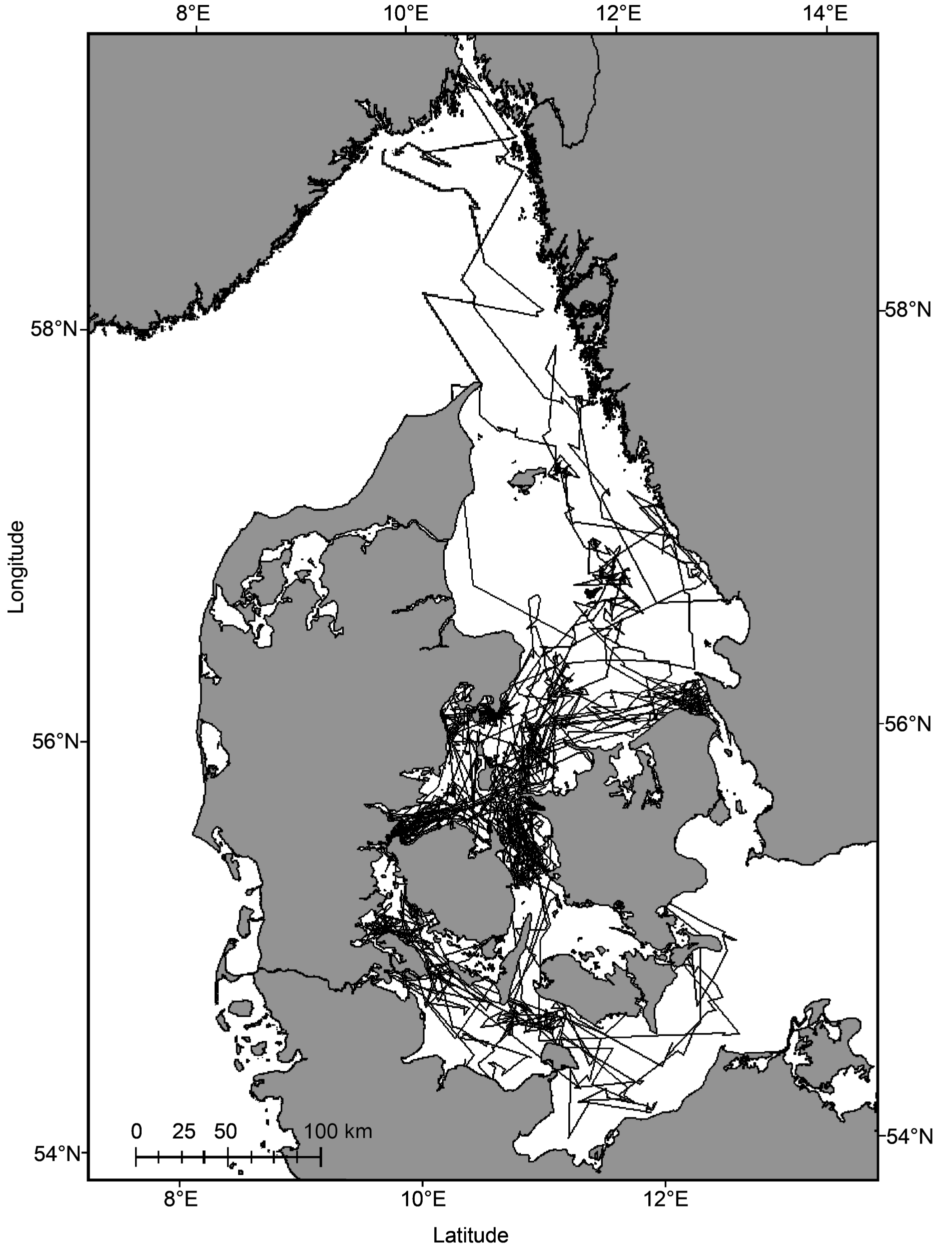

Fig. 10. Movements of 14 harbour porpoises tracked for 14-130 days.

found to dive more within daylight hours, in particular, in November. This is probably linked to prey behaviour or the use of vision to catch prey.

Female-calf pair

Following the movements and diving behaviour of a female-calf pair provided a unique insight into the behaviour of two closely related animals of different sizes, exploiting the same waters and food resources. Harbour porpoises give birth around July in Danish waters (Sørensen and Kinze, 1994), therefore the calf would have been some 10 months old when it was tagged in May and 11 months old when contact was lost. With a pregnancy rate of 0.61-0.73, most females give birth every year (Sørensen and Kinze, 1994). If females abandon their calves before giving birth to the next, these porpoises may have been tracked in the final stage of their time together.

The female spent more time diving than the calf, which made more frequent but shorter duration dives. This probably reflects size-related physiological constraints in breath-holding capacity (Schreer and Kovacs, 1997). Larger body size (both within and between species) generally allows longer and deeper dives due to the increase in the aerobic dive limit. This has for example been shown for white whales of various sizes (Martin and Smith, 1999). The female probably also had higher energy needs as she was lactating and possibly also pregnant. The number of dives per hour decreased for both animals from May to June and both animals dived deeper and for longer in June. This corresponds to the animals staying at the entrance of the Sound in May and moving to the Fehmarn Belt in June (Fig. 7). As the depths in the two areas exploited in May and June were similar, it could indicate that both animals increased their foraging time by 8-10%, as a response to sparse food resources, a change in prey species or increased energy requirements. Lockyer *et al.* (2003) showed that two porpoises kept in an outdoor enclosure lost up to 20% of their weight every summer, which correlated with a rise in water temperature. This however does not support an increase in energy requirements from May to June in the tagged porpoises.

It is not known whether the female and calf synchronised their dives, but the diurnal dive pattern showed a correlated dive rhythm in May. In June there were some similarities in the dive pattern during the day, but the diurnal dive pattern in June was not significantly correlated. This change in diurnal diving behaviour could indicate that the calf gradually became more independent, possibly foraging for its own food and also corresponding to the time of year when it leaves its mother.

Dive duration

The dive duration of the female-calf pair seems to fall within previously reported average dive durations (26-103s) given for harbour porpoises (Otani *et al*., 2000; Otani *et al*., 1998; Westgate *et al*., 1995), although the exact value cannot be calculated in the present study as the resolution of the duration intervals were 1min. The longest dive duration reported previously is 6.3min (Teilmann, 2000). Westgate *et al*. (1995) found dive durations up to 5.4min and Otani *et al*. (1998) recorded dive durations up to 4.7min. In this study significantly longer dive durations were recorded, with dives in the interval 10-15min, from both the female and its calf. An error in the dive duration data could arise if an animal, after a dive, swims to the surface breathes and dives again (to >2m) within 10s (sampling rate of the satellite transmitter), and thereby adding the dive durations of two or more dives together. To avoid this problem the depth limit for dive/surface separation was increased to 4m for some tags; this did not change the distribution of dive duration. In theory a harbour porpoise may still be able to move from 4m depth to the surface, take a breath and move down below 4m again within 10s. Since this cannot be ruled out, it still remains uncertain if harbour porpoises really are capable of diving for more than 10min.

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A note on cue rates for common minke, fin and humpback whales off West Greenland

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ABSTRACT

Field observations of cue rates for common minke whales, fin whales and humpback whales were conducted in July 1996 and May-September 2006. The cue for minke whales was usually the dorsal ridge breaking the water surface. A total of 295min of surfacings of five minke whales ranging 27-106min were observed and the simple mean was 46.1 surfacings per hour (CV=0.11). The cue for fin and humpback whale surfacings was sometimes the head breaking the surface but most often a blow. Twenty-three trials of fin whale groups ranging 1-4 individuals provided 620min of observations. The simple mean of all the trials was 52 blows hr^{-1} (CV=0.06). When trials <10min were excluded the surfacing rate remained unchanged, but when trials <30min were excluded the surfacing decreased to 50 blows hr^{-1} (CV=0.07, *n*=8 trials). A total of 860min (*n*=39 trials) and 1,232 blows from surfacing humpback whales were collected from groups of 1-4 individuals. The simple mean of all trials was 71 blows hr^{-1} (CV=0.07). The minke, fin and humpback whale cue rate estimates are close to values obtained from other studies, but they are the first that are specific to West Greenland and it is suggested that they should be used for correcting abundance estimates obtained from the aerial cue counting method.

KEYWORDS: COMMON MINKE WHALE; FIN WHALE; HUMPBACK WHALE; CUE RATES; WEST GREENLAND; NORTHERN HEMISPHERE; SURVEY-VESSEL; SURVEY-AERIAL; NORTH ATLANTIC

INTRODUCTION

Frequent surveys of common minke whales (*Balaenoptera acutorostrata*), fin whales (*B. physalus*) and humpback whales (*Megaptera novaeangliae*) in West Greenland are an important part of the scientific background for developing advice on the sustainable utilisation of whales in West Greenland. Several types of sighting surveys of cetaceans have been undertaken in West Greenland. Ship-based surveys were conducted in 1982, 1983 and 2005, aerial line-transect surveys were conducted in 1984-85, aerial cue-counting surveys were conducted in 1987-89, 1993 and 2005 and aerial photographic surveys were attempted in 2002 and 2004. Of the four different types of surveys, aerial cue-counting surveys show the best performance, at least for common minke whales. Aerial surveys have the advantage that large areas can be covered during the relatively short windows, with optimal sighting conditions in West Greenland in summer. The cue-counting method (see review in Hiby, 1992) has the advantage of utilising an independent cue rate as a means to correct for whales that are submerged during the passage of the plane. However, estimates of cue rates for the target species have to be developed based on observations, preferably over long periods in the same time period and area as the survey is covering. Various compromises have of course to be implemented to meet these ideal conditions, but it is evident that area-specific cue rate estimates are necessary since diving patterns of whales vary with behaviour, depth, prey and season (cf. Kopelman and Sadove, 1995; Laidre *et al*., 2003); thus cue rate estimates from one area are not necessarily applicable to a survey in a different area.

In order to develop cue rate estimates for minke, fin and humpback whales that are specific to the West Greenland survey area, field observations of diving patterns of whales were conducted at two sites in West Greenland.

METHODS

A cruise targeting common minke whales was conducted on 7-8 July 1996 in Nuuk fjord, West Greenland, with the research vessel *Adolf Jensen* and four trained whale observers (Fig. 1). Observations were conducted using binoculars (Leitz 7×42). Observations of diving patterns of fin and humpback whales were made from 15 to 27 August 2006 in Disko Bay (Fig. 1) from a dinghy with two observers following similar procedures as for the minke whales. Additional observations of humpback whales were made from land-based lookout points and from boats with binoculars (Optimic 10×42) in Nuuk fjord from May to September 2006.

When a whale was located during ship-based observations the boat was directed towards the area. If the whale was resting in the area the engine was shut down at distances >250m from the whale and it was followed visually for as long as possible. If the whale was travelling the engine was kept running and the boat followed at a distance of >250m and at a slow speed. Data were continuously recorded by two observers that recorded time stamps for each event with precision to the nearest second on dictaphones. Observations were initiated when the first cue was observed and only terminated when the whale was lost or weather or light conditions did not allow for reliable sightings.

Cues for minke whale surfacings were defined as: (1) the dorsal ridge breaking the surface; (2) the dorsal fin; or (3) a blow from the whale.

The cue for fin and humpback whales was almost always a blow, however in a few instances the rostrum broke the surface and no blow was seen. Both fin and humpback whales often travelled in pods of 1-4 whales and it was not possible to determine blows from the same individuals. Instead the pod size was determined and the number of

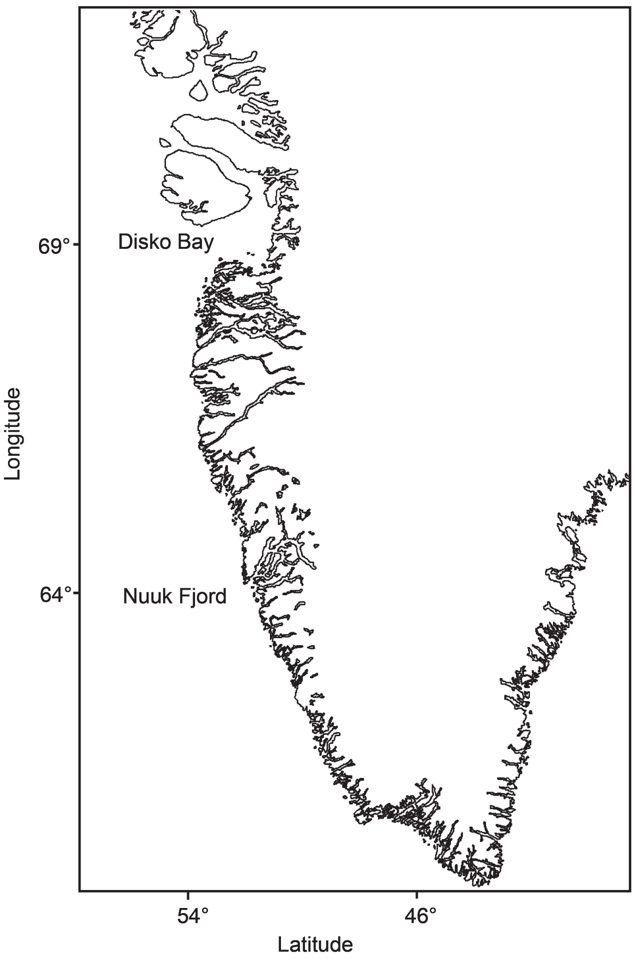


Fig. 1. Map of West Greenland.

blows per individual as a fraction of the pod size was calculated.

It could not be assessed if the minke whales were feeding or travelling, but for the observations of fin and humpback whales it is likely that they were feeding on capelin (*Mallotus villosus*) based on their relatively stationary occurrence during the observation periods.

RESULTS AND DISCUSSION

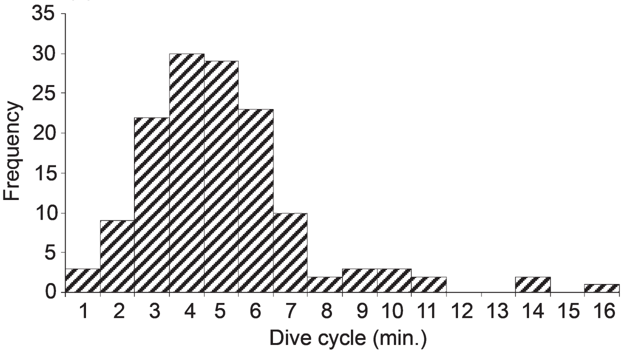
A total of five surfacing sequences of common minke whales ranging 27-106min were obtained in the Nuuk area in 1996 (Table 1). All dive cycles lasted <5min. A simple mean of the five sequences gives 46.1 cues per hour (Coefficient of Variation CV=0.11). Dive cycles for fin and humpback whales lasted up to 19 and 16min, respectively (Fig. 2). There was a slight tendency for lower cue rates for longer observation periods for humpback whales (r^2=0.08, p=0.09) and similarly for longer cue rates for fin (r^2=0.003, p=0.79) and minke whales (r^2=0.294, p=0.35). The lower cue rates for humpback whales could be a result of the increased risk of missed surfacings during longer observation periods. The weakly positive correlation between cueing rate and observation duration for minke and fin whales is far from being statistically significant. Thus no clear indication of the effect of observation duration was provided and it was decided to use a simple mean rather than a mean weighted by the observation period.

Table 1

Duration of trials and cue rates from common minke whales from Nuuk, West Greenland, July 1996.

Trial	Duration (min)	Number of cues	Cue rate (cues/whale/hr)	Time at surface (s)		
				Mean	Min.	Max.
1	107	101	56.92	4.48	2.9	7.4
2	49	26	32.08	3.35	2.0	4.7
3	50	50	60.67	2.97	2.0	4.5
4	64	47	44.27	3.93	2.7	5.7
5	27	17	37.62	2.78	1.7	4.6

(a) Fin whale



(b) Humpback whale

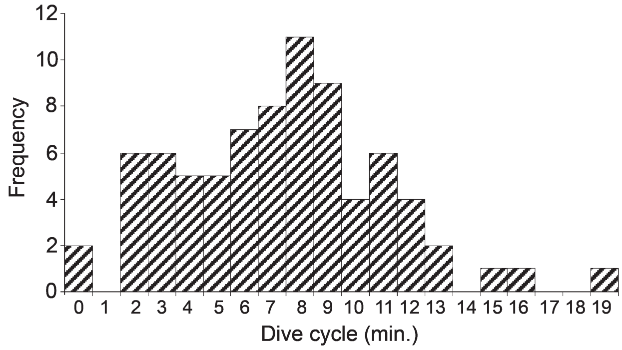


Fig.. 2. Frequency distribution of dive cycles for fin and humpback whales.

Several studies have addressed cue rates for common minke whales in other parts of the North Atlantic (see review in IWC, 2006). Gunnlaugsson (1989) reported an overall average cue rate of one per 52.7s (CV=0.06) from 16 series of visual observations, totalling 501 surfacings mostly collected from presumably feeding minke whales in Icelandic waters in July and August 1987. From the Norwegian Sea, Joyce *et al.* (1989) reported a mean rate of 52.4 cues hr^{-1} (SE=9.4) from four trials. However, this sample size was augmented by a study by Øien *et al.* (1990) that gave a time-weighted average of 36.7 cues hr^{-1} for over 1,000min observations from five vessels in the Norwegian Sea and along the Norwegian coast.

Surfacing rates of minke whales have also been estimated from VHF radio tracking of instrumented whales and Joyce *et al.* (1990) obtained an average day time rate of 60.35 surfacings hr^{-1} (CV=0.43) from one minke whale in Faxaflói, Iceland. Øien *et al.* (2003) summarised Norwegian data on surfacings based on VHF tracking of 14 whales in the North Sea, the Norwegian Sea and off Lofoten and the simple mean of all the whales was 48.1 surfacings hr^{-1} (SD=9.5).

Visual observations and VHF tracking may not be entirely compatible in estimating surfacing rates. Both methods may miss surfacings but depending on the position of the transmitter on the whale, VHF tracking may also give false positive surfacing indications when the antenna is close to the surface but without the whale actually breaking the surface. Independent of this there seems to be generally good agreement between surfacing estimates derived for a variety of studies in very different parts of the North Atlantic thus it seems reasonable to assume that the surfacing rate is a robust parameter with limited population-wide variability.

Witting and Kingsley (2004) used sequences of images of surfacing common minke whales taken during an aerial photographic survey in Faxaflói, Iceland, in 2003 to estimate the average time period during which a surfacing common minke whale can be identified on an image. They estimated this to be 7.2sec (SE=0.07), which is twice as much as that estimated from the visual observations in this study (mean=3.5, SE=0.31). The difference is probably due to the fact that a whale can be seen on aerial photos for some time when the whale is submerged but close to the surface in addition to the time it is breaking the surface.

Data on surfacing from 23 trials of fin whales were collected comprising a total period of 620min and more than 1,000 blows (Table 2 and 3). The simple mean of all the trials was 52 blows hr^{-1} (CV=0.06). If only trials <10min are excluded the surfacing rate remains unchanged, but if trials <30min are excluded the cue rate decreases to 50 blows hr^{-1} (CV=0.07) based on only eight trials. None of these values are significantly different from the value of 52.4 blows hr^{-1} (Hiby, 1992) that has been used as the cue rate for fin whales in West Greenland in past aerial cue counting surveys (Larsen, 1995). However, the present estimate of the blow rate has an associated estimate of the variance and it is specific to whales in West Greenland and must therefore be considered a more realistic value for correcting surveys of fin whales.

Table 2

Duration of trials and cue rates defined as blows per whale from fin whales from Disko Bay, West Greenland, September 2006.

Trial	Duration (min)	Number of blows	Number of whales	Blows/hour	Cue rate (blows/whale/hr)
1	14	21	1	90	90.0
2	7	9	1	77	77.1
3	43	80	2	112	55.8
4	32	78	3	146	48.8
5	9	14	2	93	46.7
6	114	246	2	129	64.7
7	12	11	1	55	55.0
8	49	155	3	190	63.3
9	40	142	4	213	53.3
10	24	79	4	198	49.4
11	12	10	1	50	50.0
12	23	40	2	104	52.2
13	6	4	2	40	20.0
14	20	46	3	138	46.0
15	31	27	3	52	17.4
16	5	13	3	156	52.0
17	9	31	3	207	68.9
18	18	41	2	137	68.3
19	11	17	2	93	46.4
20	11	17	2	93	46.4
21	64	100	2	94	46.9
22	19	28	2	88	44.2
23	47	64	2	82	40.9

Table 3

Duration of trials and cue rates defined as blows per whale from humpback whales from Disko Bay and Nuuk Fjord, West Greenland, May-September 2006.

Trial	Location	Duration (min)	Number of blows	Number of whales	Blows/hr	Cue rate (Blows/whale/hr)
1	Disko	7	16	1	137	137.1
2	Disko	24	53	1	133	132.5
3	Disko	25	43	1	103	103.2
4	Disko	5	10	1	120	120.0
5	Disko	8	12	2	90	45.0
6	Disko	16	18	1	68	67.5
7	Disko	5	13	1	156	156.0
8	Disko	7	9	1	77	77.1
9	Disko	5	13	2	156	78.0
10	Disko	23	27	1	70	70.4
11	Disko	12	7	1	35	35.0
12	Disko	27	36	1	80	80.0
13	Disko	8	14	2	105	52.5
14	Disko	6	46	4	460	115.0
15	Disko	34	83	2	146	73.2
16	Disko	19	119	3	376	125.3
17	Disko	11	44	4	240	60.0
18	Disko	11	42	2	229	114.5
19	Disko	24	19	1	48	47.5
20	Nuuk	9	4	1	27	26.7
21	Nuuk	49	48	1	59	58.8
22	Nuuk	22	28	1	76	76.4
23	Nuuk	20	20	1	60	60.0
24	Nuuk	19	14	2	44	22.1
25	Nuuk	16	18	1	68	67.5
26	Nuuk	29	37	2	77	38.3
27	Nuuk	65	75	1	69	69.2
28	Nuuk	15	20	1	80	80.0
29	Nuuk	16	13	1	49	48.8
30	Nuuk	27	19	1	42	42.2
31	Nuuk	28	27	1	58	57.9
32	Nuuk	7	7	1	60	60.0
33	Nuuk	39	33	1	51	50.8
34	Nuuk	61	77	2	76	37.9
35	Nuuk	32	39	1	73	73.1
36	Nuuk	22	16	1	44	43.6
37	Nuuk	28	18	1	39	38.6
38	Nuuk	48	59	1	74	73.8
39	Nuuk	31	36	1	70	69.7

Data from 39 trials, from 5 to 65min duration, on surfacing humpback whales (19 trials from Disko Bay and 20 trials from Nuuk fjord) were collected, comprising a total period of 860min and 1,232 blows. The simple mean of all trials was 71 blows hr^{-1} (CV=0.07). This value is close to the mean blow rate estimates of 72 blows hr^{-1} obtained from humpback whales in Fredericks Sound, Alaska (Dolphin, 1987).

Time spent at the surface was determined for 436 fin whale surfacings and had a mean of 4s (SD=2) with a range from 2-11s and for 479 humpback whale surfacings in Disko Bay and had a mean of 4s (SD=2) with a range of 1-18s.

The present study provides the first cue rates with associated variances for common minke, fin and humpback whales for West Greenland and it is therefore suggested that these estimates can appropriately be deployed to reduce the availability bias in visual aerial cue-counting surveys of these whales in West Greenland (see Heide-Jørgensen *et al*., 2007).

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Use of videogrammetry to estimate length to provide population demographics of dwarf minke whales in the northern Great Barrier Reef

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ABSTRACT

Commercial swim-with-whale programmes, based on the dwarf minke whale (*Balaenoptera acutorostrata*), have been conducted in Great Barrier Reef waters since 1996 and under permit since 2003. Evaluating the effectiveness of management requires information on the biology of the whales, including possible impacts on their critical life stages, such as mating or calving. In this study, length measurements have been used as the best available proxy for age and thus state of sexual maturity. Underwater videogrammetry was used to estimate the lengths of dwarf minke whales interacting with boats and swimmers during June/July 2003 and 2004. The calibrations used to correct systematic biases in distance and length estimates are presented and other sources of error associated with the methodology and the behaviour of the whales are discussed.

Mean lengths (from replicate measurements of individually identified whales) ranged 4.82-6.61m in 2003 (*n*=23, from five encounters) and 4.48-7.18m in 2004 (*n*=56, from 29 encounters). The overall mean length (2003: 5.90m; 2004: 5.73m) did not differ significantly between years. In both years, the mean lengths of the majority of whales (2003: 57%; 2004: 59%) were less than 6m, which is regarded as sexually immature based on available life history data. The size ranges within a single encounter were broad; no encounter was dominated by one size class. Segregation by size was not observed.

This paper presents the first field measurements of dwarf minke whales on their tropical wintering grounds. While most whales interacting with vessels or swimmers were immature, adult whales, including cow-calf pairs, also were involved. More information, especially on cumulative effects, is needed to assess the impact of these swim-with programmes.

KEYWORDS: AGE DISTRIBUTION; AUSTRALASIA; DWARF MINKE WHALE; MONITORING; PHOTOGRAMMETRY; PHOTO-ID; SEGREGATION; SOCIAL; WHALEWATCHING; SOUTHERN HEMISPHERE; SURVEY-VESSEL

INTRODUCTION

The dwarf minke whale, generally considered to be a subspecies of the common minke whale, *Balaenoptera acutorostrata* (Rice, 1998), has approached vessels and divers on the northern Great Barrier Reef at least since the early 1980s (Arnold, 1997). Advertised commercial swim-with-whales activities have occurred since 1996. From 2003, only operators with a specific swim-with-whales permit from the Great Barrier Reef Marine Park Authority can conduct such advertised activities, although extensive 'incidental' encounters occur from other tourist and recreational vessels. A management programme, including a code of conduct (*www.gbrmpa.gov.au*) is in place.

Swim-with programmes are a contentious issue. A review by the Scientific Committee of the International Whaling Commission (IWC) noted that 'available evidence indicated that swim-with programmes in the wild could be considered as being highly invasive' (IWC, 2001, p.57). However they further noted that impacts will vary between species and locations, thus requiring an assessment on a case by case basis. To conduct such an assessment for the dwarf minke whale swims, and to evaluate the effectiveness of management options, biological information on the target population is required.

One concern is the possible impact on critical life history stages. The swim-with programmes are conducted at low latitudes during the austral winter months. Based on life history knowledge of other Southern Hemisphere baleen whale stocks and the limited life history data on dwarf minke whales, swim-with programmes may occur at the time of mating and/or calving. In order to assess the possible impact on critical life history stages it becomes important to know to what extent mature (and thus potentially breeding) whales are involved in the programmes. Field measurements of lengths can serve as an indicator of maturity state.

The underwater videogrammetry technique developed by Spitz *et al*. (2000) was modified so that it could be combined with routine photo-identification studies that were also conducted. In this paper, the modified technique is outlined, sources of error are assessed and length data are presented from encounters with dwarf minke whales on a commercial dive vessel during the 2003 and 2004 seasons. Finally, the implications for management are discussed.

METHODS

Data were collected from *Undersea Explorer* in JuneJuly 2003 and 2004, during trips offering commercial swim-with-whale programmes along the Ribbon Reefs between Port Douglas and Lizard Island (14°39'-16°03'S and 145°35'-145°39'E). Expeditions were of six days and nights duration, departed on Saturday evenings and followed a similar cruise pattern.

Field procedures

General field procedures were as outlined in Birtles *et al*. (2002) and Valentine *et al*. (2004), which can be consulted for more details. Videogrammetry procedures are presented

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in greater detail in Sobtzick (2005) and are further refined in this paper.

Encounters depended on the initial approaches of whales. In open water, as soon as the whales approached the vessel (within approximately 30-40m) and were usually beginning to circle it in close proximity, 50m ropes were deployed from both the stern and bow, engines were turned off and the vessel was allowed to drift. Initially researchers and then passengers entered the water, hanging on to the ropes or to uninflated rubber inner tubes attached to each rope. A similar procedure occurred during reef encounters, except that often only a single rope was run from the stern if the boat was moored by the bow.

During an encounter, there was a researcher positioned at the end of each of the two ropes (usually AB and SS). They were equipped with a wetsuit, mask, snorkel and fins, and additional gear such as a digital video camera in a waterproof housing and an underwater slate for the length estimation studies.

Measurements were made during five encounters in 2003 and 29 encounters in 2004, during which whales interacted with the vessel for an average period of 148min. Many of the animals made repeated passes within the range of 5-16m from the videographer, which provided the opportunity for multiple independent size measurements to be taken. The whales' approaches and passes were below the surface, which resulted in filming of the whales at an angle ranging from approximately 15° from the surface to 90° (vertically beneath the videographer).

The videographer spent as much time as possible in the water, filming the whales with a *Sony* DCR VX 1000E digital camera in an Amphibico VH-1000 underwater housing. An underwater portable sonar rangefinder (*Hondex* PS7 from Speedtech Instruments) was attached to the camera housing to measure the distance between the camera and whale. In addition to the length estimation measurements, the videographer tried to film as many whales as possible, recording features that could be used to identify individual whales. For this it was necessary to use the zoom option on the camera to provide the clearest records of specific features like scars or colour patterns. A requirement for the size estimation method is that the field of view (FOV) of the camera is always consistent. The videographer ensured that for every length measurement the camera was zoomed out to the maximum angle of view.

This often created a problem for encounters with a large number of whales present or when the whales stayed with the boat only for a short period of time. Since it was necessary to obtain the identification footage first, and this way of filming differed from the way of filming for the length estimations, it was almost impossible to obtain length measurements for every whale present in the encounter.

The passes chosen to activate the sonar were when the videographer was perpendicular to the whale's longitudinal axis, the entire length of the whale was visible in the viewfinder and the clarity of the image was sufficient to suggest identification would be possible. The distance between the camera and whale was measured with the sonar at the moment the whale's midline passed the camera. Depending on the size of the whale, this was possible from a distance of 5m or more.

If there was relative movement between the whale and videographer between measurements, then these were regarded as independent measurements. Relative movement was assessed from the video footage by monitoring whale movement and also changes in sonar distance measurements.

The sonar reading of the distance was transcribed onto an underwater slate, which was then filmed to create a permanent record of the measurement on the digital video tape. Depending on the nature of the interaction, it was nearly always possible to capture several shots of the same whale at varying distances as the whales usually made repeated passes.

In 2003, the percentage of measured whales/identified whales in an encounter ranged from 33.3-69.2% (a total of 23 whales were measured over five encounters), whereas in 2004 up to 100% of identified whales were measured (range 18.8-100%, total of 56 whales measured over 29 encounters).

The sonar has a range of 79m, a 24° beam angle and a working frequency of 200kHz (*www.speedtech.com*). Previous research on minke whale vocalisation showed that the highest frequency sound produced by dwarf minke whales had a maximum frequency of 9.4kHz (Gedamke *et al*., 2001). Hearing would be expected to be within this low frequency range from 50Hz-9.4kHz. The anatomy of mysticete whale ears also suggests that their hearing range is low frequency (Wartzok and Ketten, 1999), well below the working frequency of the sonar. The sonar should not be audible to the whales and no reaction of the whales towards the sonar was observed.

Image extraction and analysis

The video images were reviewed on a computer with speakers using the video editing software Adobe *Premiere* 6.0. An audible click sound is made by the sonar enabling the exact frame corresponding to sonar activation to be captured. Individual frames were captured with this software and then edited with Adobe *Photoshop* 5.0 LE.

The following criteria were used to ensure the identified errors (detailed below) were minimised or eliminated: (1) the picture was in focus; (2) the camera was on full wide angle; (3) the whole body length of the whale was visible; (4) the whale's midline was perpendicular to the camera axis; and (5) the body of the whale was fully extended, without the tail being bent up or down.

To estimate the size of an animal in a suitable image, the researcher first enhanced the picture if necessary by changing brightness, contrast and colour balance of the image using Adobe *Photoshop* software. Then, the size of the whale image from the tip of its rostrum to the anterior point of the notch at the centre of the tail fluke (X-Y coordinates) was marked using the Adobe *Photoshop* 'Measure Tool' as shown in Fig. 1. The ratio of the whale image length in pixels (%FOV) to the total image width in pixels (total FOV) was calculated (Eqn 2). Together with the sonar distance and the subtended camera lens angle, this enabled whale length to be calculated.

From selected images, individual whales were identified using scar and colour patterns (Arnold *et al*., 2005; Birtles *et al*., 2002). Animals were initially identified in the field. Later, the tapes for each encounter were reviewed to catalogue each time a whale was filmed in an encounter. Replicate images for individual whales were extracted using this shot list. While reviewing the video tapes, at least two researchers were present to confirm individual whale identification.

Individual whale identification codes were named in chronological order of length measurement L1, L2, L3 and onwards. An encounter code was used to identify each whale encounter (year.day.month. no. of encounter within that day). For example, 03.06.26.3 is the 3rd separate whale encounter on 26th of June 2003. There were numerous

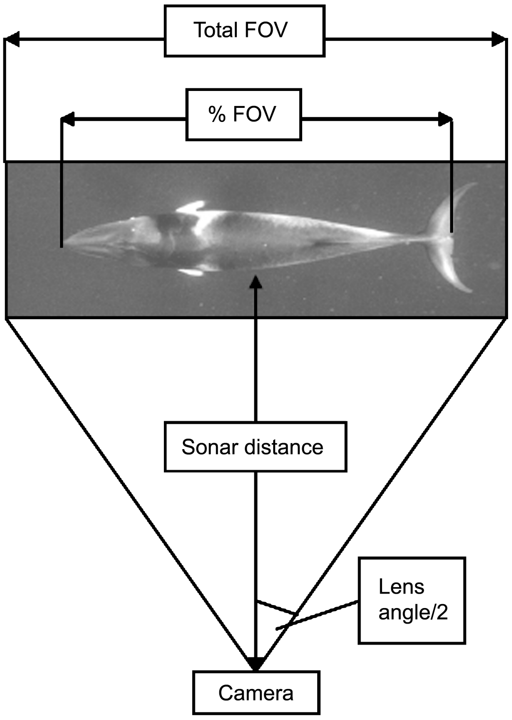

Fig. 1. Whale length determination and trigonometric background for the calculations. Dorsal shot of a dwarf minke whale with the length of the animal marked from the tip of its rostrum to the anterior point of the notch at the centre of the tail fluke

resightings of individual whales during separate encounters, however, only two resightings have resulted in length measurements. Whale L43 was measured during encounters 04.06.30.1 and 04.07.04.3 and whale L65 was measured during encounters 04.07.12.1 and 04.07.12.2 (Table 1).

The mean number of length estimation measurements per whale varied considerably between individual encounters on different days (e.g. mean of 6.2 and 2.7 shots per measured whale in encounters 04.06.30.1 and 04.07.06.2 respectively) (Table 1). However, the overall mean number of measurements per whale was 4.6 in 2003 (23 whales measured) and 5.3 in 2004 (56 whales measured).

Camera lens angle determination

A 6.0m long white polyvinylchloride (PVC) pipe with a diameter of 90mm was placed on a flat sandy bottom on a sheltered dive site. To ensure minimal water movements, calm days were picked and locations that were mostly protected from currents. The PVC pipe was marked in 1m intervals with black PVC tape. From the centre of the pipe a measuring tape and a rope were attached that were both suspended vertically by a float to a few metres below the surface while the pipe was weighted down with dive weights.

Five consecutive measurements were taken at each metre interval, 5-10m from the pipe. This range covered the distances to the whales for most measurements taken in previous years. Measurements from both the sonar and tape measure were recorded by an observer as the videographer recorded images. This process was done twice, while divers were ascending and descending.

The sonar activation frames were captured using the same method as for the whale images (see later). Out of the five measurements per distance, the three best images were selected, i.e. where the pipe was clearly visible, not angled and the picture was in focus; these images were used for further calculations.

From these frames individual images of the pipe in 1m increments were cropped, starting at 4m (smaller than smallest whale in the sample). The size of the pipe segment was measured using the Adobe *Photoshop* 'Measure Tool'. The %FOV of these pipe segments was calculated and was used, together with their known true length to calculate the full field of view at this sonar distance. This FOV measure was used to calculate the subtended angle of the camera lens when zoomed out to its widest angle.

Length determination theory

The sonar distance and the widest angle of view of the camera lens provide the trigonometric values necessary to calculate the length of individual whales. Sonar ranges were determined to be synonymous with range to the object. The errors pertaining to this assumption are dealt with in the treatment of sonar calibration errors.

The camera lens angle was calculated through field calibrations based on previous underwater videogrammetry studies (Spitz *et al*., 2000). In this case a pipe of known length marked in metre increments was filmed from a range of known distances. The resulting linear relationship between camera field of view (FOV) and sonar distance allowed the lens angle to be calculated as 54.25°.

Using this lens angle ($\acute{\varnothing}$) enabled the field of view to be calculated in metres for each sonar distance measurement (SD),

$$\text{FOV(metres)} = 2 \times \tan\acute{\varnothing} \times \text{SD}$$

As $\acute{\varnothing} = 54.25°$ then

$$\text{FOV(metres)} = 1.019 \times \text{SD} \qquad (1)$$

Through analysis of images in Adobe *Photoshop* it was possible to calculate the %FOV taken up by the whale as described in the section on image extraction and analysis and hence to calculate the length of the whale (Fig. 1).

$$L = 1.019 \times \text{SD} \times \text{\%FOV of whale} \qquad (2)$$

Treatment of errors

Image selection and whale body flexure

Body flexure can result in underestimates of length measurement. Minke whales flex dorsoventrally much more than laterally as this is their main locomotory movement. Within an individual frame it is possible to assess the level of dorsoventral flexure from the side orientation (dvfS) and level of lateral flexure from a top orientation (latfT). It is not possible to assess dorsoventral flex from the top (dvfT) nor is it possible to assess lateral flex from the side (latfS) in a still image. Using the video footage, head and tail movement were obvious if the whale was actively swimming (dorsoventral flex) or changing direction (lateral flex). It was possible to assess levels of body flexure in these orientations in the period before, during and after the captured frame.

To quantify error levels, only high quality still images were used and classified as: (1) straight; (2) minor flex; or (3) major flex. The whales in these images were measured in two ways: (1) in a straight midline from snout to tail notch; and (2) following the convex outline of the body. This procedure was carried out for the two orientations where this was possible, to quantify both dorsoventral and lateral flexure. For dvfS, the ratio of straight line to outline was, straight = 0.99, minor flex = 0.95 and major flex = 0.92. LatfT ratios were straight = 0.98, minor flex = 0.95. Whale flexure in this orientation is restricted so major flex was not an issue.

Table 1

Summary of dwarf minke whale encounters and length data taken during 2003 and 2004.

Encounter	No. of measured whales/no. of whales present	Whale ID	Calculated length (m)			Stdev. (m)	Whale ID	Calculated length (m)			Stdev. (m)
			Mean	Range	Rep.			Mean	Range	Rep.	
2003											
03.06.26.3	1/3 (33%)	L1	6.28	5.86-6.52	3	0.368	L2	6.39	6.00-6.82	6	0.329
03.07.07.2	1/3 (33%)	L3	5.6	5.52-5.68	2						
03.07.08.2	9/13 (69%)	L4	6.17	5.94-6.45	4	0.239	L5	5.67	5.45-5.83	4	0.181
		L6	5.62	5.35-5.85	6	0.212	L7	6.02	5.73-6.53	5	0.301
		L8	5.8	5.67-5.94	3	0.139	L9	4.82	4.80-4.83	2	
		L10	5.9	5.54-6.25	5	0.293	L11	5.2	5.15-5.27	3	0.063
		L12	5.87	5.66-6.22	3	0.306					
03.07.09.2	5/10 (50%)	L13	5.68	5.50-5.94	6	0.156	L14	6.18	6.15-6.22	2	
		L15	6.4	6.37-6.44	2		L16	5.77	5.72-5.89	5	0.074
		L17	6.03	5.94-6.11	2		L18	6.55	6.37-6.82	5	0.171
03.07.10.2	5/10 (50%)	L19	6.11	5.87-6.42	6	0.262	L20	6.61	6.30-6.85	14	0.18
		L21	5.56	5.41-5.71	2		L22	5.68	5.58-5.80	7	0.08
		L23	5.66	5.35-5.97	8	0.19					
2004											
04.06.07.1	1/1 (100%)	L24	6.09	5.81-6.26	4	0.195					
04.06.09.1	2/3 (66.7%)	L25	5.68	5.36-6.04	34	0.204	L26	7.18	7.07-7.36	7	0.127
04.06.15.2	1/1 (100%)	L27	6.17	6.02-6.35	7	0.127					
04.06.15.3	1/3 (33.3%)	L28	6.34	6.23-6.52	4	0.125					
04.06.20.2	2/10 (20%)	L29	5.44	5.25-5.68	4	0.18	L30	5.07	4.95-5.13	4	0.086
04.06.21.1	1/1 (100%)	L31	6.13	5.96-6.35	9	0.117					
04.06.21.2	1/1 (100%)	L32	6.59	6.40-6.70	6	0.115					
04.06.22.1	3/16 (18.8%)	L33	4.98	4.91-5.06	2		L34	5.88	5.82-5.95	3	0.065
		L35	5.86	5.81-5.92	2						
04.06.23.2	2/4 (50%)	L36	5.27	5.20-5.34	2		L37	6.23	5.97-6.36	8	0.137
04.06.25.2	1/2 (50%)	L38	6.72	6.54-6.83	7	0.129					
04.06.27.1	3/3 (100%)	L39	6.18	6.03-6.39	5	0.144	L40	5.95	5.92-5.99	2	
		L41	5.44	5.26-5.56	3	0.154					
04.06.30.1	5/7 (71.4%)	L42	4.79	4.58-4.98	12	0.134	L43	6.22	6.19-6.25	2	
		L44	6.36	6.21-6.57	6	0.123	L45	5.89	5.64-6.08	5	0.191
		L46	6.52	6.16-6.71	6	0.216					
04.07.01.1	2/2 (100%)	L47	6	5.84-6.14	6	0.11	L48	5.15	5.06-5.25	2	
04.07.01.2	3/3 (100%)	L49	4.76	4.63-4.83	3	0.108	L50	6.61	6.49-6.87	7	0.147
		L51	5.54	5.52-5.56	2						
04.07.02.1	2/3 (66.7%)	L52	6.18	6.06-6.30	3	0.123	L53	5.58	5.50-5.79	4	0.142
04.07.04.2	2/2 (100%)	L54	5.3	5.07-5.53	7	0.148	L55	5.69	5.40-5.97	6	0.229
04.07.04.3	3/8 (39.5%)	L43	5.99	5.80-6.14	4	0.152	L56	4.97	4.83-5.03	4	0.093
		L57	4.48	4.43-4.53	3	0.052					
04.07.06.1	1/3 (33.3%)	L58	6.13	5.90-6.25	3	0.198					
04.07.06.2	3/6 (50%)	L59	5.56	5.49-5.66	4	0.071	L60	6.1	6.07-6.14	2	
		L61	5.87	5.84-5.89	2						
04.07.11.1	1/2 (50%)	L62	4.89	4.77-5.24	7	0.164					
04.07.11.2	2/3 (66.7%)	L63	4.67	4.57-4.75	6	0.075	L64	6.19	6.00-6.44	8	0.144
04.07.12.1	2/4 (50%)	L65	5.63	5.48-5.74	7	0.107	L66	6.65	6.42-6.84	3	0.215
04.07.12.2	4/11 (36.4%)	L65	5.41	5.32-5.51	8	0.091	L67	5.15	4.94-5.30	7	0.125
		L68	4.74	4.66-4.80	3	0.072	L69	6.1	5.99-6.21	4	0.104
04.07.14.1	1/3 (33.3%)	L70	6.25	6.24-6.27	3	0.015					
04.07.14.2	1/2 (50%)	L71	6.03	5.85-6.20	2						
04.07.15.2	1/1 (100%)	L72	5.04	4.94-5.23	4	0.138					
04.07.21.1	3/3 (100%)	L73	5.62	5.55-5.67	5	0.056	L74	5.35	5.27-5.43	2	
		L75	4.99	4.94-5.05	2						
04.07.23.1	1/4 (25%)	L76	5.68	5.56-5.81	9	0.093					
04.07.30.1	3/3 (100%)	L77	4.78	4.73-4.83	2		L78	5.33	5.23-5.45	4	0.102
		L79	7.11	7.08-7.14	2						

Maximum errors arise from image angles where the flexure is not easily identified (dvfT and latfS). In a top shot major dorsoventral flex is obvious from the video footage and such images were rejected. This leaves the maximum error as being -5% for both images of laterally flexed animals viewed from the side and also images of dorsoventrally flexed animals viewed from the top.

Image selection and whale perpendicularity

Accurate length determination requires that the whale axis is perpendicular to the camera. To quantify the angle of images accepted or rejected, a 3D minke whale model was rotated on a protractor template. Both videographers (SS and AD) were asked to class the angle of the whale as perpendicular (1), slightly off (2) or greatly off perpendicular (3). This test showed situations where the angle was greater than 10° were classed as (3) and were rejected on all occasions. At a 10° angle (the greatest angle of acceptance) this equates to a length estimation error of −1.5%.

Whale pixel measurement (%FOV)

Whales were measured (pixel count) using the Adobe *Photoshop* 'Measure Tool'. Two factors contributed to errors in these measurements: (1) low image resolution blurring the accurate identification of the extreme ends of the measure, snout and tail notch; and (2) inaccurate placement of the end cursor of the 'Measure Tool'. To quantify this error the two main videographers independently measured 10 separate images to compare results. Applying the Mann-Whitney test showed no significant difference between videographer's results at the 95% confidence level.

Sonar calibration

The sonar measurement was consistently less than the tape measurement by a mean of 2.2%. The ratio was consistent across the different distances and the standard deviations were also sufficiently small (<0.022) to indicate that this difference is a systematic error. Underestimation could be a precautionary safety feature in the design of the sonar device. It could also be an overestimate in the tape measurements as a result of slight tape curvature due to water movement. In 2004 a second sonar unit was also used which showed a variation of 0.5% in measurements.

While the sonar has a consistent error related to 'real distance' this did not affect the accuracy of whale length determination. The camera lens angle determination and subsequent whale length calculations relied solely on sonar distance readings and known pipe lengths for calibration. These are consistent and show a linear relationship between distance to object and %FOV.

Sonar error and depth

The depth of the whale at the time it was filmed could potentially produce errors due to difference in sound (sonar) transmission speeds at different depths. Transmission speed varies due to effects of changes in salinity, temperature or pressure with depth. In the outer reef areas of this study the water is well mixed and temperature and salinity are constant across the range of depths (3-16m) where whale measurements were taken. Maximum pressure effects over this 13m depth variation are approximately 0.2m sec^{-1}, or a 0.013% difference in speed of sound transmission (Jensen *et al*., 1994) and therefore sonar error.

Curvature of the lens

The effects of the curvature of the wide angle lens with regards to a possible distortion existing at the edges of the field of view was examined. A black and white grid (40×56cm) consisting of 2cm squares was filmed underwater at a set distance (38.85cm) from the nodal point of the camera's wide angle lens, as in Spitz *et al*. (2000).

Each square within the grid was measured using the Adobe *Photoshop* 'Measure Tool'. This produced a pixel count per square (observed) which could be graphed against mean pixel count per square (expected) across the full field of view to show lens distortion. The general principles and calculation of the curvature regression equation are the same as used in Spitz *et al*. (2000) and produced the quadratic regression equation (r^2=1.000).

$$y = 0.00007x^2 + 1.0532x - 2.002.$$

This equation was applied to all whale pixel measurements (%FOV) to eliminate error due to lens curvature.

The same camera and underwater housing were used in each field season; therefore it was not necessary to retest the curvature of the lens or the lens subtended angle.

RESULTS

Summary of encounters during 2003 and 2004

Overview of length estimations 2003 and 2004

Fig. 2 shows the mean body lengths and standard deviation of all whales measured in 2003 and 2004 for which replicates were available. This shows there is no discontinuity in size and also demonstrates the variation in measurements in relation to the size of the whole group.

In 2003, the mean lengths of whales varied from 4.82m to 6.61m (n=23, from five encounters). In 2004, the sample size (n=56, from 29 encounters) was larger and the size range (4.48m-7.18m) was greater (Fig. 3).

The overall mean size of all whales measured was 5.90m in 2003 and 5.73m in 2004. Testing the data for normal distribution by applying the Levene's Test for Equality of Variances indicated that the data were normally distributed (F=6.064, p=0.016). Therefore a parametric t-test was used; which showed that the mean lengths of the whales in 2003 and 2004 were not significantly different (p=0.243). All statistical analyses were conducted with *SPSS* for Windows, version 14.0.1.

Kato and Fujise (2000) suggested that females were likely to attain maturity at a length of 6-6.5m; the smallest mature female in their study was 6.6m in length. A study of 13 whales by Best (1985) showed the smallest mature female was 6.4m. Male baleen whales are generally about 5% smaller than females (Boyd *et al*., 1999) suggesting that males ⩾6m would also be mature. As the gender of many of the measured animals was not able to be determined, all animals <6m were assumed to be definitely immature and all those ⩾6m as mature or maturing.

In both 2003 and 2004 most of the whales measured were smaller than 6m (2003: 13/23=56.5%; 2004: 33/56=58.9%) and can therefore be regarded as sexually immature (see Discussion).

The size classes 5.50-5.99m and 6.00-6.49m were the most frequent classes in both years with the difference that in 2003 47.8% of the measured whales belonged to the 5.50-5.99m class, whereas in 2004 only 23.2% of the examined animals belonged to that group. Mature or maturing whales (6m or more in length) comprised a sizable proportion of the total in both years (43.5% in 2003, 41.1 % in 2004).

Size classes in individual encounters for 2003 and 2004

To examine whether the size structure of whales in individual encounters varied between years, all encounters from 2003 (Fig. 4) were compared with encounters in 2004 with three or more whales (Fig. 5). The encounters were in weeks 3-5 in 2003 and 4-8 in 2004.

The group composition was similar in both years. The size range covered in all of the encounters was similar and included the size classes '<6m' and '≥6m' whales. No encounter was clearly dominated by one size class.

Size segregation within season

To examine whether dwarf minke whales show a size segregation over the season, the length data were grouped into the two size classes '<6m' and '≥6m' by week for 2004 (Fig. 6). Data from 2003 were excluded because they were taken in only three weeks of the eight week season.

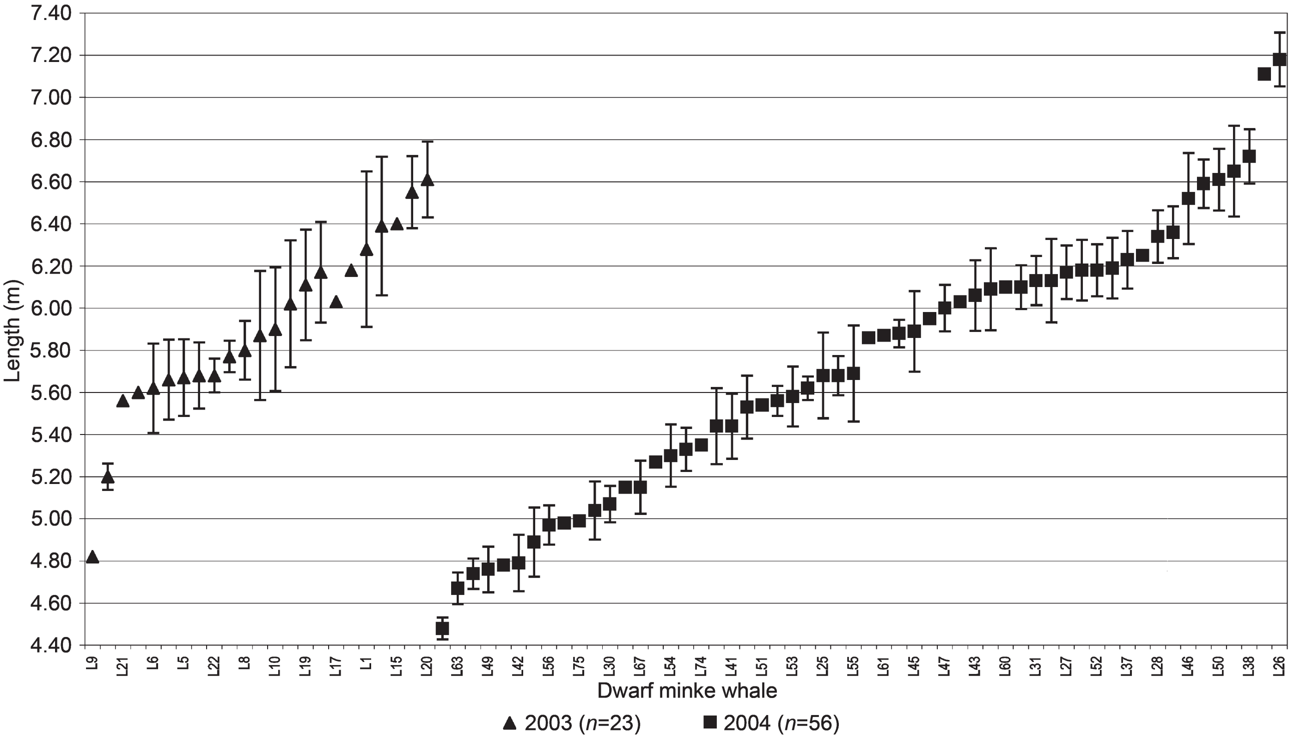

Fig. 2. Mean body length and standard deviation of 79 whales measured in 2003 and 2004.

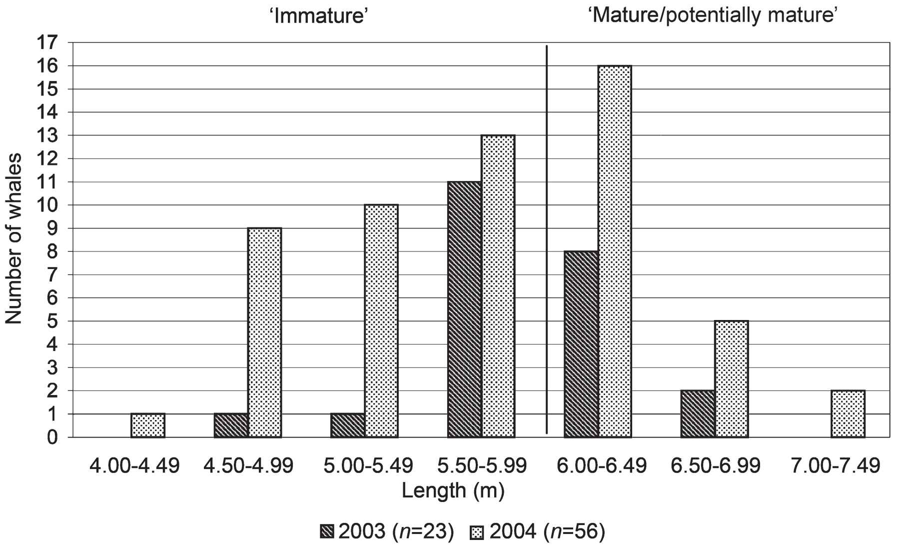

Fig. 3. Number of individual whales in half metre size classes in 2003 and 2004. The thick black line separates the immature whales (<6m), from the mature or potentially mature whales in Figs 3, 4 and 5.

Fig. 6 clearly shows that dwarf minke whales approaching the boat over the period of eight weeks were not clearly segregated by size. In weeks 3-6, which were the ones best sampled, both size classes were present. Both size classes were not represented in weeks 2 and 7, which could have been caused by the small sample size.

DISCUSSION

Sources of error

Underwater videogrammetry has proved to be a relatively robust method to measure dwarf minke whales. There are systematic errors, resulting especially from inaccuracies in the distance measured by sonar and with different sonar units, which emphasises the need for routine calibration. There was no correlation between extent of variation in size measurements and distance to the whale, nor was precision increased with a larger sample size within the range of our measurements. The major sources of error may thus be non-systematic and attention should be directed at more rigorous identification of flexure and perpendicularity of whales in the image selection process. Improving clarity of images to more accurately identify the snout and tail notch for pixel measurement should be possible with future use of high definition video for this procedure.

Overview of data

Only 50 size measurements of dwarf minke whales have been published (Table 2), with an additional eight whales from the sub-Antarctic reported by Kato and Fujise (2000).

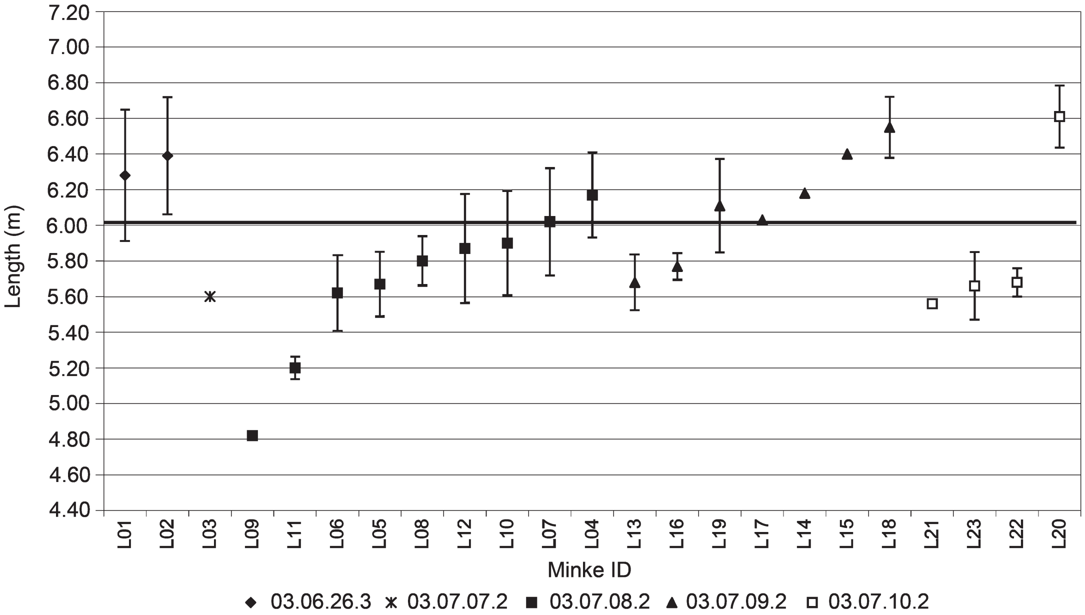

Fig. 4. Mean lengths (plus standard deviation) of minke whales in 2003 grouped by encounter.

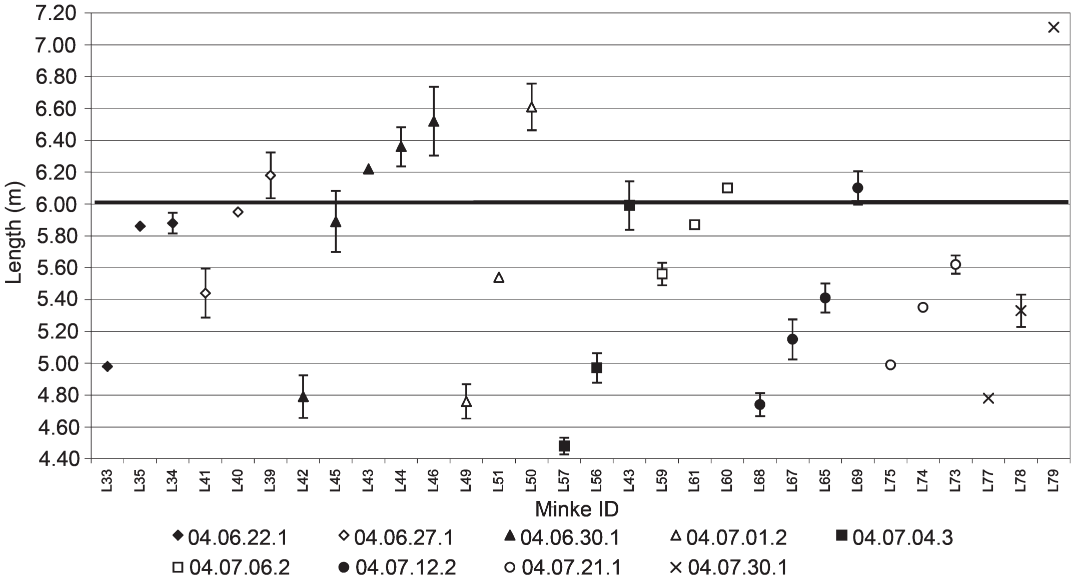

Fig. 5. Mean lengths (plus standard deviation) of minke whales from nine selected encounters in 2004 grouped by encounter.

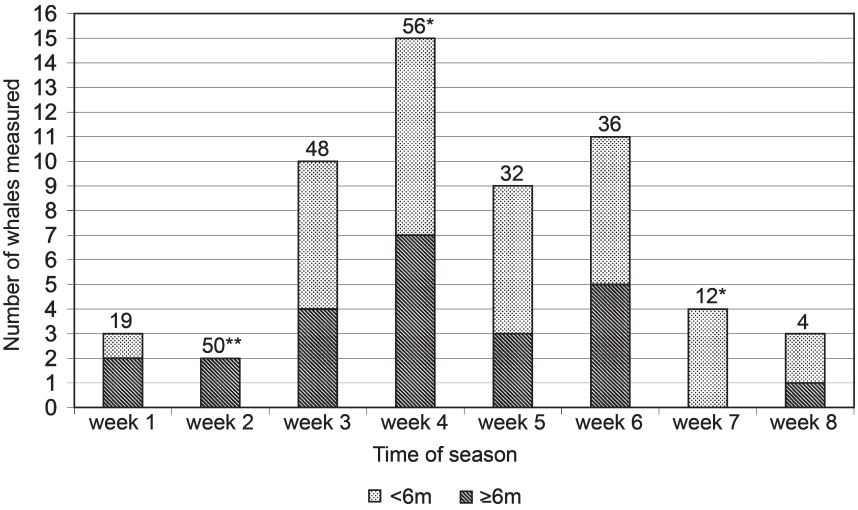

Fig. 6. Number of whales in the size classes '<6m' and '⩾6m' over the length of the field season 2004 and occurrence of cow and calf pairs (asterisk). The total sample size is 57, since one whale appears twice in the figure (L43 was allocated to two different size classes). (See text for details).

The length estimates of 79 dwarf minke whales presented in this paper thus considerably extends the sample size of length measurements; moreover they are the first data from the low latitude wintering grounds where mating and reproduction may take place and they were obtained by non-lethal methods.

Each data set has biases. The mean length of dwarf minke whales taken by commercial whalers (Best, 1985) was 6.9m, however Best (1982) noted that small whales were generally avoided by whalers. The mean length of dwarf minke whales taken in the sub-Antarctic during the Japanese scientific whaling programme (Table 2), in which there was no such selection against smaller whales, was 5.2m. The mean lengths of stranded dwarf minke whales from South Africa, eastern Australia and New Zealand, and eastern South America were 2.9m, 4.4m and 3.9m respectively, suggesting a bias towards younger animals.

Table 2
Previously published size measurements of dwarf minke whales.

Size range, sample size	Location	Sources
1.9 -7.8, *n*=17	South Africa	Best (1985)
2.2 -7.1, *n*=11	E Australia, New Zealand	Arnold *et al.* (1987); Dawson and Slooten (1990); Arnold (1997); Paterson *et al.* (2000)
2.6 -7.0, *n*=14	Brazil	Zerbini *et al.* (1997)
3.8 -7.0, *n*=8	Sub Antarctic	Kato *et al.* (1990); Kasamatsu *et al.* (1993)
4.5 -7.2, *n*=79	Northern GBR, Australia	This paper

The data set obtained represents animals that interact with vessels and swimmers during commercial swim-with-whales programmes. It is possible that those animals that approached closely enough underwater to be filmed repeatedly were not representative of the whole group around the vessel. However there were no indications from continuous surface observations (by PA) maintained throughout the encounters of any whales remaining at a distance from the vessel. The data set was dominated by animals under 6m in length (mean length 5.66m in 2003, 5.73m in 2004). Although calves estimated as being 2-3m were seen (during three encounters in 2003 and four encounters in 2004), none were measured. Thus the smallest whales are under-represented in the data set and larger whales may also have been, although the largest length estimate (7.18m) was comparable to the largest measured animals reported in the literature (7.0-7.8m) (Table 2). Despite all the biases noted here, a wide range of sizes (4.82-6.61m in 2003, 4.48-7.18m in 2004) were recorded throughout the season and within individual encounters in both 2003 and 2004 (Figs 4 and 5).

As discussed previously the selection of 6m as the length of maturity is based on low sample numbers in studies by Best (1985) and Kato and Fujise (2000). There will not be an absolute separation of mature and immature animals at 6m; males, which mature at a smaller length than females in baleen whales (Boyd *et al*., 1999), in particular might be mature at under 6m. There is a marked lack of animals >6.5m in the data set while Best and Kato and Fujise both reported a number of whales exceeding 6.5m and even 7m in their small datasets. This may indicate a lack of interaction by larger animals in this study. It could also signify a smaller mean size (and therefore size at maturity) of individuals within this population. So little is known about dwarf minke whales that this must be considered, with observed courtship and previously identified females returning with calves as evidence of mature animals within the observed population. Moreover, the error margin within the mean estimates of lengths could lead to an inconsistent classification as potentially mature/mature or immature. This happened in one case in which the mean estimate for the same whale was 6.22m and 5.99m (L43 in encounter 04.06.30.1 and 04.07.04.3, respectively) (see Table 1). Despite such sources of error, there was a similar pattern for 2003 and 2004, with 56.5% and 58.9% of the whales having a mean length under 6m and thus probably being immature.

Northern Hemisphere minke whales have been reported to segregate by age and gender (e.g. Jonsgård, 1951; Omura and Sakiura, 1956; Williamson, 1975). There was no evidence of segregation by length during the eight week field season in 2004, however no length measurements were taken when whales were first seen (April-May) or later in the season (September-October).

Management implications

Assessment of the structure of whale populations is difficult. Often juveniles interact with vessels (Constantine, 2001) and commercial whaling selects for larger animals. An even more marked factor is the depletion of populations by whaling and lack of ‘normal’ whale populations. These factors along with the inherent data deficiency have a significant effect on the ability for population structure to be accurately determined.

Although it is possible that the data set presented here may not fully represent the larger population of dwarf minke whales present in the region during the winter months, the length estimates do reflect those animals that most regularly interact with vessels and swimmers during commercial swim-with-whales activities. These whales thus represent the segment of the population that is most subject to potential impacts from such swim-with programmes and are the management unit that the Great Barrier Reef Marine Park Authority is most concerned with.

In both years, more than half of the whales measured had a mean length of under 6m and thus were probably immature. This is similar to the situation with bottlenose dolphins subject to swim-with activities in the Bay of Islands, New Zealand (Constantine, 2001). As noted by that author, the interactions may represent play activity of younger animals as part of developing their social and behavioural skills. In both years, the whales from 5.0-5.9m were the dominant size class (58% in 2003, 45% in 2004) and were probably immature.

Constantine (2001) reported that, on average, only 19.3% of the dolphins in an encounter interacted directly with swimmers. There was no such apparent segregation noted in dwarf minke whale interactions, with a size range from 4.79-6.52m in single encounters (Fig. 5). The measured animals (79) represented 51.3% of the 154 whales which approached the boat and were identified as individuals. The latter represented 87.5% of the total number of whales seen anywhere around the boat either underwater or from the constant surface watch (*n*=176). From 9-13% of the measured whales exceeded a mean length of 6.5m in 2003 and 2004 and thus were most probably mature; less than half of the interacting whales were 6m or above in length and thus were likely to be mature or maturing. Only a small number of cow-calf pairs were encountered (see Fig. 6), however mature animals may have been engaged in socialising activities associated with mating. The presence of mixed gender groups, observed courtship behaviour (Birtles, unpubl. data) and recordings of vocalisations that may act as reproductive advertisement displays (Gedamke *et al*., 2001) all suggest that mating activities occur on these wintering grounds. Individual whales return to the same area from year to year (Birtles *et al*., 2002); (Birtles, unpubl. data), underlining the need for more data on cumulative impacts, particularly on mature whales which may be engaged in courtship or nursing behaviour.

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Sadly, Dr Peter Arnold passed away suddenly while this paper was in its review stages. His guidance, invaluable knowledge, enthusiasm and motivation will be greatly missed by all associated with the Minke Whale Project.

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Occurrence and distribution of cetaceans off northern Angola, 2004/05

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ABSTRACT

The occurrence and distribution of cetacean species off northern Angola was examined using dedicated survey data and incidental sighting records. Dedicated surveys for cetaceans were carried out during two geophysical seismic surveys off northern Angola between August 2004 and September 2005. A total of 3,268hr of survey effort data were collected, resulting in 779 on-effort cetacean sightings. There were 263 sightings reported off-effort and incidentally from other platforms and sports fishermen. With 21 cetacean species confirmed, the cetacean community off northern Angola is diverse and primarily tropical in characteristic, comprising four species of baleen whale, two sperm whale species, at least two beaked whale species, and 13 species of delphinid. Humpback and sperm whales were the most frequently recorded cetaceans. The occurrence of humpback whales was significantly higher within neritic waters, and during the winter and spring months in association with seasonal occupancy of their West African breeding grounds. Sperm whales were recorded in water depths exceeding 1,000m and demonstrated significant seasonality, with peak occurrence during the summer and autumn. Atlantic spotted dolphins and common dolphins (*Delphinus* sp.) were the most numerous delphinids recorded, with spotted dolphins showing a significant seasonal peak during the spring and summer, and common dolphins in the winter. Other species recorded included fin whale, sei whale, Bryde's whale, dwarf sperm whale, Cuvier's and *Mesoplodon* beaked whales, killer whale, short-finned pilot whale, false killer whale, melon-headed whale, Atlantic humpback dolphin, rough-toothed dolphin, Risso's dolphin, bottlenose dolphin, Pantropical spotted dolphin, spinner dolphin, Clymene dolphin and striped dolphin. Further research is required to document the cetacean community in Angola, particularly given the unknown threat from fishery bycatch and the increasing level of oil and gas exploration in the region.

KEYWORDS: CETACEANS; DISTRIBUTION; HABITAT; SCHOOL SIZE; ANGOLA; ATLANTIC OCEAN; SURVEY-VESSEL; INCIDENTAL SIGHTINGS; FIN WHALE; SEI WHALE; BRYDE'S WHALE, DWARF SPERM WHALE; HUMPBACK WHALE; COMMON DOLPHIN; CUVIER'S BEAKED WHALE; KILLER WHALE; SHORT-FINNED PILOT WHALE; FALSE KILLER WHALE; MELON-HEADED WHALE; ATLANTIC HUMPBACK DOLPHIN; ROUGH-TOOTHED DOLPHIN; RISSO'S DOLPHIN; BOTTLENOSE DOLPHIN; PANTROPICAL SPOTTED DOLPHIN; SPINNER DOLPHIN; CLYMENE DOLPHIN; STRIPED DOLPHIN

INTRODUCTION

There is a paucity of information on the occurrence of cetaceans off Angola, located on the west coast of Africa in the southeastern Atlantic Ocean (Fig. 1). The historical occurrence of large whales off Angola is documented via whaling records (Best, 1994; De Figueiredo, 1958; Townsend, 1935). Rigorous exploitation of whales on the west coast of Africa commenced towards the end of the 18th century, with whalers working in the Gulf of Guinea during 1763 and arriving at Angola before 1770 (Best, 1981). Between 1909 and 1916 modern shore-based and floating whaling stations were established at Lobito, Baia dos Elefantes, Mossamedes, Porto Alexandre and Baia dos Tigres (Best and Ross, 1986; De Figueiredo, 1958). The whaling charts of Townsend (1935) show large catches of sperm whales (*Physeter macrocephalus*) and humpback whales (*Megaptera novaeangliae*) off the coast of Angola between 1761 and 1920, while the review by Best (1994) also indicates catches of blue (*Balaenoptera musculus*), fin (*B. physalus*), sei (*B. borealis*) and Bryde's whales (*B. edeni*)[1] off Angola between 1909 and 1928. Whaling records from nearby waters in Gabon, extending to 5°S also testify to the frequent occurrence of large rorquals and sperm whales in the region (Budker, 1952;1953; Budker and Collignon, 1952; Budker and Roux, 1968), and a traditional hunt of humpback whales continued at Annobon Island off central Gabon into at least the 1970s (Aguilar, 1985). Current knowledge of large whales off Angola is limited to the humpback whale, which was the focus of a 12-day study in coastal waters off northern Angola during September 1998 (Best *et al*., 1999) and this species is also the subject of a long-term photo-identification and genetic capture-recapture study in nearby Gabon (Rosenbaum *et al*., 2002).

In contrast to large whales, the distribution of smaller cetaceans off Angola remains almost completely unknown. A review of small odontocetes off West Africa by Jefferson *et al*. (1997) did not include Angolan waters and the scarce literature available comprises only opportunistic sightings (Morzer Bruyns, 1968; Perrin *et al*., 1994b; van Waerebeek *et al*., 2004; Weir, 2006a;2006b).

There is growing interest in the cetacean fauna inhabiting the waters off Angola, where industrial activity including geophysical seismic surveys is increasing. The planning of industrial activities and the mitigation of potential effects from anthropogenic sound sources upon cetaceans requires an understanding of the occurrence of species within the region. This paper presents results from dedicated cetacean survey work carried out off northern Angola during 2004 and 2005.

METHODS

Study area

The topography of the marine environment off Angola differs between the northern and southern regions (Fig. 1). In the north, the continental shelf is wide extending around 50km from the coast, with water depths of 1,000m generally occurring around 90km offshore. The shelf is much narrower (8km) to the west of Luanda and also in the region of the Congo Canyon off Soyo where water depths of over 1,000m occur around 50km from the coast. The southern

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[1] Bryde's whale off Angola are likely to be *B. brydei* rather than *B. edeni* (IUCN, 2006).

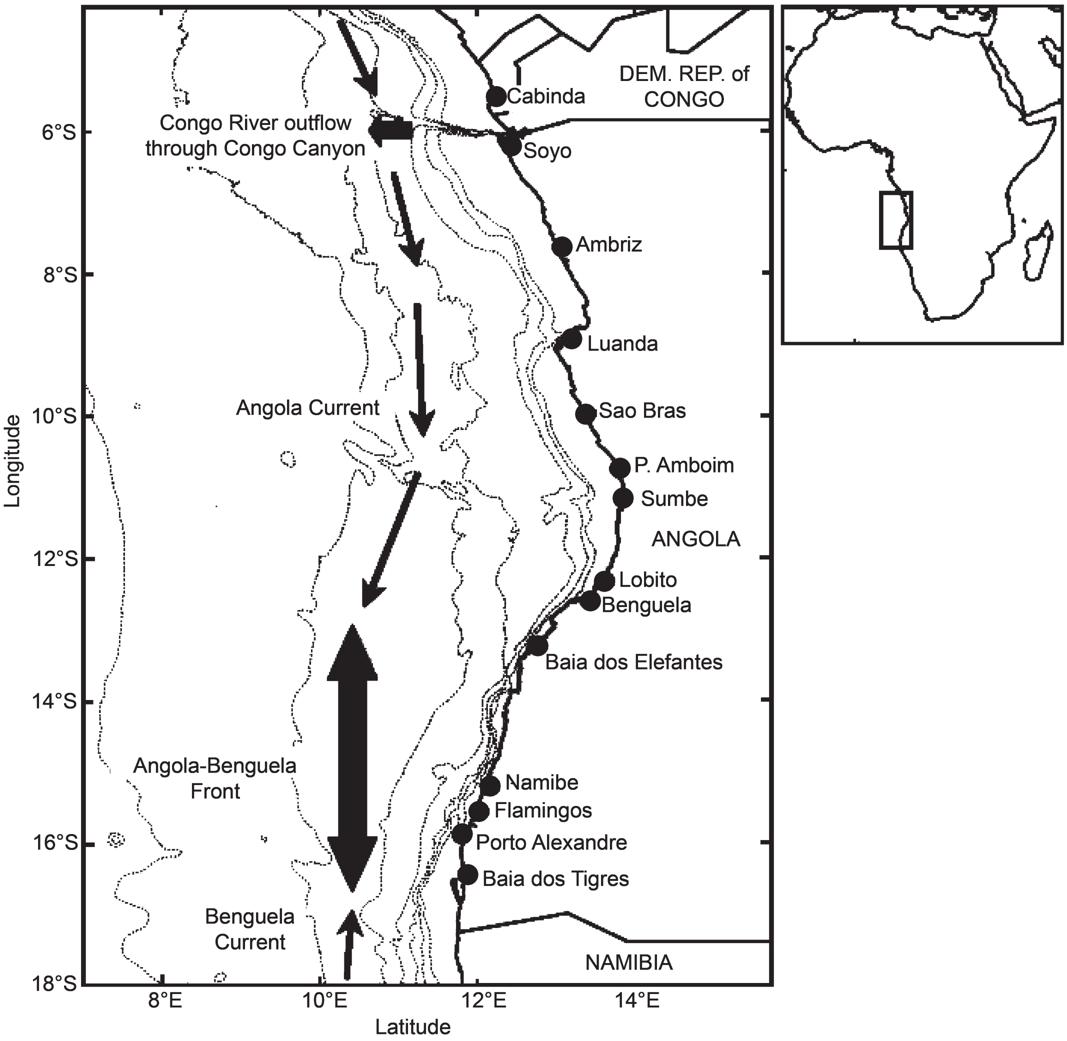

Fig. 1. Location, bathymetry and principal oceanographic features of the study area.

portion of Angola from Benguela south to Tombwa is characterised by a very narrow continental shelf (<10km) which slopes steeply into 1,000m only around 15km from the coast. Offshore, the seabed slopes gradually to water depths exceeding 5,000m in the Angola Basin.

There is also oceanographic variation between northern and southern Angola due to the influence of two large marine ecosystems (LMEs): the Benguela Current LME; and the Gulf of Guinea LME (Fig. 1). The cold-water Benguela Current is the primary oceanographic influence in Angola's marine environment, being one of the strongest locally wind-driven coastal upwellings in the world (Hardman-Mountford *et al*., 2003). This current extends northwards along the west coast of southern Africa, bringing colder, nutrient-rich water from the south. Off Namibia the current diverges, with the smaller branch continuing to flow northwards along the coast and into southern Angola (Hardman-Mountford *et al*., 2003). In northern Angola, warm water flows southwards from the Gulf of Guinea as the Angola Current, a fast and narrow band of warm water that extends along the Angolan coast between 9°S and 16°S (Hardman-Mountford *et al*., 2003; Moroshkin *et al*., 1970). The coastal northward-flowing cold Benguela Current and the southward-flowing warm Angola Current dominate the eastern Angola Basin, converging at latitudes of between 17°S and 13°S (depending on season) to form the Angola-Benguela front (Moroshkin *et al*., 1970).

The Congo River is the largest freshwater input to any worldwide eastern ocean boundary (Hardman-Mountford *et al*., 2003) and has a significant impact on Angola's marine environment. Freshwater outflow (the 'Congo River Plume') extends as a sediment-laden surface current primarily in the upper 5-15m of the water column (Eisma and van Bennekom, 1978). This outflow of turbid freshwater is detectable at ranges of 800km offshore during the monsoon months between November and April (Eisma and van Bennekom, 1978; Van Bennekom and Berger, 1984), causing peaks in primary productivity around 150-200km from the river mouth (Van Bennekom and Berger, 1984).

Survey methodology

Two categories of data were used to examine the distribution of cetaceans in the region: (1) dedicated survey data; and (2) incidental sighting records.

Dedicated surveys

Cetacean data were collected during two geophysical seismic surveys between August 2004 and September 2005. These surveys comprised dedicated cetacean watches where an associated measure of effort was recorded. Most marine mammal data were collected from the *Geco Triton* at 18.5m eye height (1 August 2004 to 15 May 2005), which conducted two consecutive large-scale 3D seismic surveys using airgun arrays of 5,085 and 3,147cu. in. respectively. The *Sea Trident* at 10.75m eye height (10 August to 27 September 2005) conducted a high-resolution seismic survey that utilised a low volume airgun array of 70cu. in. Most data were collected at survey speed (4-5 knots or 8km hr^{-1}), with a small portion of data collected during transits between survey sites (7 knots or 13km hr^{-1}).

Dedicated watches for marine mammals were carried out throughout daylight hours and in all weather conditions on each day at sea. During 'search mode' a single dedicated observer scanned 360° around the vessel using the unaided eye and 8-10× binoculars. Effort logs (comprising the position, time, water depth and environmental data including Beaufort sea state, swell height and visibility) were completed for every watch. Whenever a cetacean was sighted, the species, number (and age class where possible) of animals, behaviour, position, distance from the vessel, water depth and associated environmental data were recorded. While subject to some error, the two experienced observers recorded a 'best estimate' of cetacean group size by eye, a method often relied upon during cetacean field surveys (Moreno *et al*., 2005). Where possible, animals were photographed in the field to confirm identification using a Canon Single Lens Reflex (SLR) camera and a 100-400mm Canon zoom lens. However the nature of the survey meant that animals could not often be approached to confirm species identification or group size.

Cetacean data were collected in a non-random manner, with the distribution of the survey effort determined by the geophysical survey work. Most of the survey work was concentrated over two deep-water areas: 120km off the Congo River mouth in water depths of 1,400-2,700m; and 150km north-west of Luanda in water depths of 1,200-1,500m. Limited survey data were also collected over the continental shelf and slope. The northern limit for data presented here is 5°S at the northern edge of the Angolan province of Cabinda and some data offshore Democratic Republic of Congo (DRC) are therefore also included. A total of 779 cetacean sightings were recorded during the dedicated survey work.

Incidental sightings

Cetacean sightings were classified as 'incidental' if no measure of effort was recorded. This category contained records reported 'off effort' during dedicated surveys (e.g. sightings at night) and records from several marine mammal surveys where the data collection methods were not rigorous enough for inclusion as dedicated surveys (e.g. no record of vessel position, incomplete data forms). A total of 264 incidental cetacean sightings were reported from a range of offshore platforms including seismic survey, guard, underwater vehicle, benthic and electromagnetic survey vessels, sports fishing trips operating out of Luanda (1991-2006), and during a kayak trip along the coast from the Cunene River to Luanda during 2004. Incidental records were only included in the analyses when the species identification could be confirmed via adequate descriptions on the data form, during discussion with the author, or from submitted photographs.

Data analysis

Prior to analysis, the effort, dedicated sightings and incidental sightings data were combined into single standardised databases. For a small number of incidental sightings a GPS position was not available, and these data were looked up from an electronic nautical chart (*C-Map World* for Windows, Version 3) according to descriptions of sighting locations provided by the observers. Where necessary, water depths were also looked up from a nautical chart. The depths recorded at the start and end of each dedicated watch were averaged to produce a mean water depth for each watch. Intermediate sea states (e.g. Beaufort 2-3) recorded in the field were rounded up to the higher value for analysis. The species identification provided by observers was checked and verified using written descriptions and photographs. In the majority of cases (*n*=39) the verification process involved downgrading sightings from a specific species to a category (e.g. 'dolphin species'). This occurred where the animals were judged to be too distant from the vessel to allow definite identification (>2km for *Stenella*/*Delphinus* dolphins), where an inadequate species description was provided, where the description/behaviour/location seemed inconsistent with the stated species, or where a sighting of an uncommon/rare species was not supported by adequate information. In limited cases sightings were 'upgraded' to species level (*n*=9), usually where photographs existed. Where mixed-species schools of cetaceans were encountered, data for each species were analysed as separate sightings.

The water depth distribution of cetacean species was described using the following terms: coastal (marine waters immediately adjacent to land, usually <20m depth); continental shelf (waters less than 200m depth); slope (200-1,000m); and deep oceanic (seaward of 1,000m). The terms 'neritic' and 'pelagic' were used to refer to areas over and seaward of the continental shelf respectively. For the four cetacean species for which sample size exceeded 15 dedicated survey sightings the relative abundance (Beaufort sea state 0-4) was examined in four water depth categories (<200m, 200-999m, 1,000-2,000m, >2,000m). Due to low sample size in several of the depth categories, statistical analysis of cetacean occurrence related to depth categories was not feasible.

The seasonal occurrence of each species was examined as relative rather than absolute abundance (using only 'on effort' sightings recorded during dedicated surveys) since the survey effort was spatially uneven, an effective strip width method was not used, sample size was small for many species, and there was an unknown potential influence from the airguns. The relative abundance was calculated as $(N/E)\times 100$, where N is the number of animals recorded and E is the total survey effort (min), and only effort and sightings recorded in Beaufort sea states ≤ 4 (Beaufort ≤ 2 for beaked and *Kogia* whales) were used. Seasonal analysis was carried out according to: spring (Sep-Nov); summer (Dec-Feb); autumn (Mar-May); and winter (Jun-Aug). For humpback and sperm whales (with over 100 dedicated survey sightings in Beaufort sea states 0-4), a Chi-squared Goodness of Fit test was used to determine whether the number of encounters recorded differed from that expected in each season.

There is relatively little published information on the responses of cetaceans to open-water seismic exploration and most published studies have examined responses to airgun arrays of much lower volume than those utilised during actual geophysical seismic surveys (e.g. 20 cu. in. used during playback experiments on humpback whales by McCauley *et al*. (2000)). The exact effects of seismic survey upon cetaceans are unknown, but potentially include masking of communication signals and echolocation, altered behaviour, temporary or permanent hearing/tissue damage, stress and displacement from habitat (Gordon *et al*., 2003; Richardson *et al*., 1995). The data presented here are therefore potentially influenced by unknown reactions of each cetacean species to airgun sound produced during the survey, and such impacts should be borne in mind when considering spatio-temporal trends within the dataset.

RESULTS AND DISCUSSION

A total of 3,268hr (196,063min) survey effort data were collected during dedicated survey work in 2004 and 2005. Effort occurred in all survey months except for June and July, with the largest amount occurring during August and September (Table 1). While the summer and autumn seasons received similar amounts of survey coverage, the spring months received 38% of the total effort and the winter only 17% (Table 1). Survey coverage occurred over a greater spatial scale during the spring and summer, with effort as far south as Porto Amboim (Fig. 2). Most effort occurred in pelagic slope and oceanic waters, with the percentage of total effort distributed as: <200m (0.6%); 200-999m (1.7%); 1,000-1,499m (5.8%); 1,500-1,999m (46.5%); 2,000-2,499m (37.6%); and >2,499m (7.8%). Some 26% (50,520min) of effort occurred in Beaufort sea state 0-2, 45% (88,154min) during Beaufort 3, 26% (51,298min) during Beaufort 4, and 3% (6,091min) during Beaufort 5-6. Daily water temperature data collected between August 2004 and May 2005 varied between 21.8°C and 30.3°C (Weir, 2006d).

Table 1

Seasonal distribution of dedicated survey effort, 2004/05.

Month/season	Survey effort (min)	Percentage of total effort
Sep.	36,035	18.4
Oct.	19,691	10
Nov.	18,420	9.4
Spring total	*74,146*	*37.8*
Dec.	13,855	7.1
Jan.	17,037	8.7
Feb.	17,600	9
Summer total	*48,492*	*24.7*
Mar.	16,070	8.2
Apr.	16,935	8.6
May	8,080	4.1
Autumn total	*41,085*	*21.0*
Jun.	0	0
Jul.	0	0
Aug.	32,340	16.5
Winter total	*32,340*	*16.5*
Survey total	**196,063**	**100**

A total of 1,042 dedicated and incidental cetacean sightings were recorded off Angola, comprising at least 39,883 animals. Of these, 779 sightings occurred during the dedicated survey work. The cetacean community off Angola was diverse with at least 21 species recorded (Table 2), comprising four species of baleen whale, two sperm whale species, at least two beaked whale species, and 13 species of delphinid. A large number of animals, particularly dolphins, remained unidentified at sea due to a combination of distance from the vessel, adverse weather (choppy sea state and sun glare), brevity of the sighting, uncertainty over mixed-species groups, and the close similarity in external appearance of many species within the region (particularly *Balaenoptera* and *Stenella* species). Much of the data within the following species accounts are summarised in Tables 2 and 3, with an overview of the seasonal occurrence of each species in Angolan waters presented in Fig. 3.

Fin whale (*Balaenoptera physalus*)

Conclusively separating between fin, sei and Bryde's whales proved difficult at sea, and a total of 21 encounters were logged as being one of these three species. There were four confirmed sightings of fin whales between 2003 and 2006, comprising two on-effort and two incidental sightings (Table 2). All records involved single or pairs of animals, distributed in deep water pelagic areas of 1,500-1,739m depth (Table 2, Fig. 4). Fin whales were sighted only in August (3) and September (1) during the winter and spring, which is consistent with the theory of a seasonal migration of this species between summer Antarctic feeding areas and winter low-latitude breeding grounds (Gambell, 1985).

Sei whale (*Balaenoptera borealis*)

Only one sighting was positively identified as sei whale during the survey work, a pair of animals recorded in 1,691m water during August 2004 (Fig. 4). The seasonality of this record agrees with the proposed southward seasonal migration towards summer feeding grounds (Best and Lockyer, 2002). The status of this species off Angola remains unclear.

Bryde's whale (*Balaenoptera edeni*)

Bryde's whales were the most numerous of the *Balaenoptera* species recorded off Angola, with a total of 19 sightings (Table 2). However, group size was small (mean ($\bar{\chi}$)=1.3 animals) and the overall relative abundance of this species off Angola was low (Table 3). Bryde's whales occurred in distinctly separate habitats, with 42% of sightings in waters of <100m depth and the remaining 58% of sightings in deep oceanic waters exceeding 1,600m depth (Figs 5 and 11). The apparent divide in Bryde's whale distribution between neritic and pelagic habitat is consistent with Best's (2001) proposal of distinct 'offshore' and 'inshore' forms off the west coast of Africa.

There was some suggestion of seasonality in Bryde's whale occurrence off Angola, with most sightings recorded between June and November (Fig. 3). Observations from sports fishermen suggest that Bryde's whales are seen most frequently inshore off Luanda during August and September (Ian Austin, pers. comm.). However, three incidental sightings of Bryde's whale from coastal waters in southern Angola during January 2004 testify to some presence of this species in Angolan waters during other seasons. While it is generally considered that inshore Bryde's whales inhabit the west coast throughout the year, the offshore form is thought to make extensive migrations between South Africa (Jan-Feb) and Gabon (May-Jul) (Best, 1996; Best, 2001). More work is required to determine the exact status of Bryde's whales off Angola; however, it seems reasonable to conclude that this species is reasonably common within the region and may occur year-round.

Humpback whale (*Megaptera novaeangliae*)

The whaling charts of Townsend (1935) show a distinct area of humpback whale abundance off West Africa extending primarily from northern Angola to Gabon. The present-day occurrence of humpback whales in this region has been confirmed via short surveys in northern Angola (Best *et al*., 1999), Congo (Weir, 2006d), São Tomé and Príncipe (Carvalho *et al*., 2003) and Gabon (Walsh *et al*., 2000; Weir, 2006d), and by a long-term population study off Gabon since 1997 (Rosenbaum *et al*., 2002). Humpback whales were the most frequently recorded cetacean species during survey work in 2004/05, with a total of 205 sightings

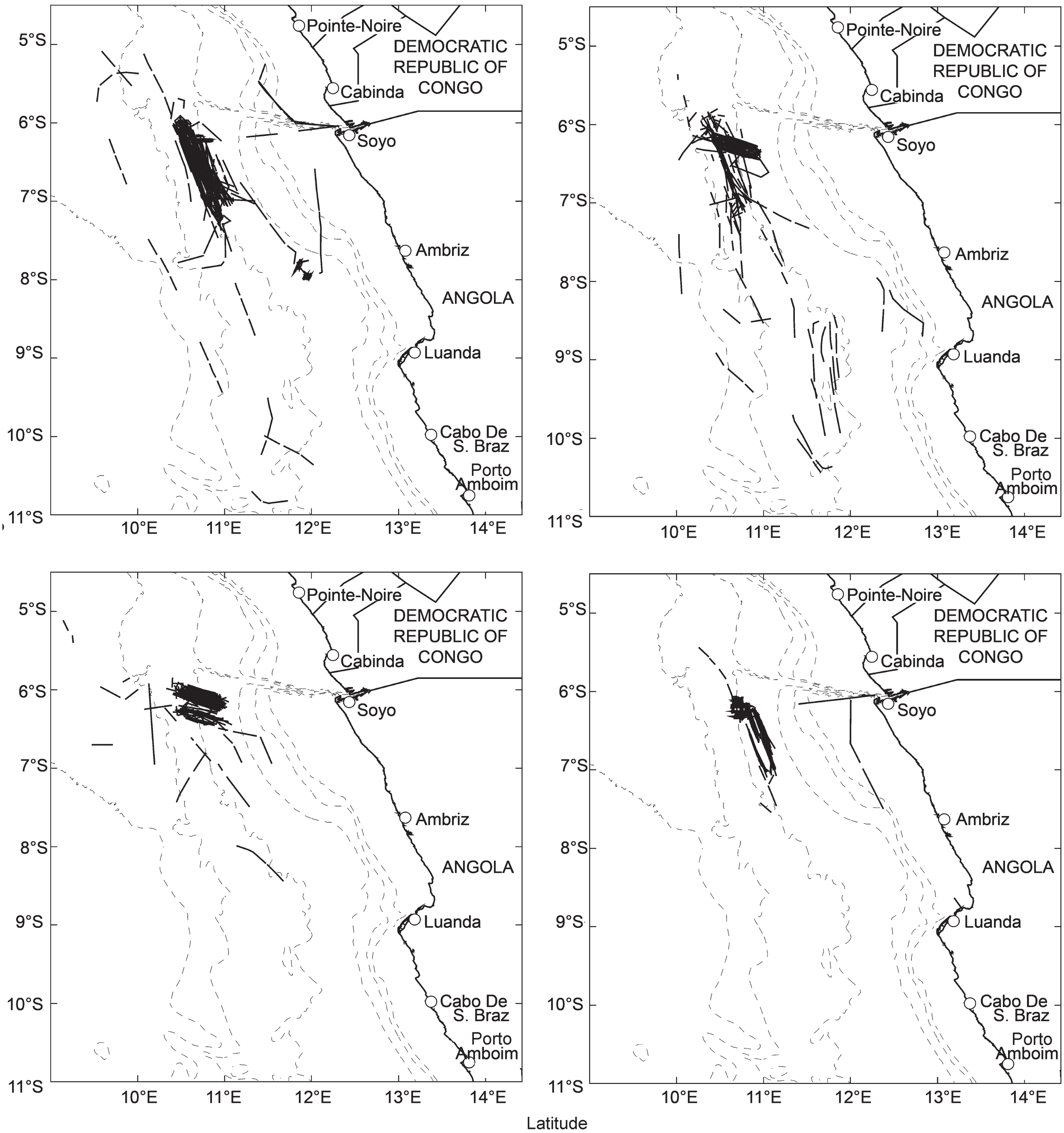

Fig. 2. Seasonal distribution of survey effort in (A) spring, (B) summer, (C) autumn and (D) winter.

including 157 on-effort records (Table 2). The majority of sightings were recorded off northern Angola (Fig. 6), with clusters of records over both of the deep-water study sites and in the vicinity of the Congo Canyon. Relative abundance of humpback whales was five times higher in depths of <200m (5.09 animals $100min^{-1}$) than over the shelf edge (1.07 animals $100min^{-1}$) or in depths >1,000m (0.08 animals $100min^{-1}$).

There was a significant difference in the number of humpback whale encounters (χ^2=141.6, d.f.=3, *p*=<0.001) recorded according to season. Significantly more humpback whales were recorded during the winter and spring, and significantly fewer during the summer and autumn (Table 3). The earliest seasonal record was an individual sighted on 7 May. Although there was no dedicated survey effort during June and July, incidental sightings over this period testified to the occurrence of humpback whales. Moderate densities remained into October, but then decreased sharply with few sightings recorded in November (2), December (1) and January (3). The seasonality of humpback whales in Africa is also apparent from the mid-May to October timing of whaling catches off Gabon (Budker and Roux, 1968), although most modern whaling activities in West Africa were anyway confined to the June-November period (Best and Ross, 1986). The seasonal pattern relates to their use of the region as a calving and mating ground during the winter months (Best *et al*., 1999), as indicated by sightings of surface-active whale groups and mother-calf pairs in Angolan waters. Of 157 groups of humpback whales where age composition was recorded, single (*n*=62) and pairs

Table 2

Cetacean species recorded in Angola (listed in decreasing order of number of dedicated survey sightings) showing group size and water depth.

Species	Dedicated surveys		Incidental sightings		School size			Water depth (m)		
	Sightings	Animals	Sightings	Animals	Mean	SD	Range	Mean	SD	Range
Unid. dolphin	293	21,426	75	6,296	75.3	91.8	1–500	1,845	420.5	10–3,300
Humpback whale	157	289	48	85	1.8	0.9	1–6	1,464	810.5	40–4,036
Sperm whale	126	1,219	13	53	9.2	8.8	1–65	1,977	327.7	1,349–2,917
Unid. whale	39	68	14	23	1.7	2.7	1–20	1,928	479.8	61–3,578
Unid. baleen whale	27	28	11	18	1.2	1	1–7	1,853	411.8	183–2,693
Atlantic spotted dolphin	20	2803	18	1,146	103.9	125.1	1–500	1,633	329.6	1,000–2,266
Common dolphin sp.	19	1,172	19	2,165	87.8	109.7	1–500	1,601	627.0	74–2,385
Dwarf sperm whale	14	23	0	0	1.6	0.6	1–3	1,760	199.7	1,290–2,009
Fin/sei/Bryde's whale	13	16	8	9	1.2	0.4	1–2	1,815	695.1	77–2,795
Pilot whale sp.	11	216	11	603	37.2	56	4–200	2,014	606.9	1,206–3,400
Bryde's whale	11	13	8	12	1.3	0.7	1–4	1,246	1,103.0	15–1,903
Bottlenose dolphin	8	96	7	128	14.9	9.3	1–30	1,187	1,018.8	10–2,585
Striped dolphin	7	309	2	225	59.3	62.9	8–200	1,785	229.2	1,612–2,385
False killer whale	5	82	4	30	12.4	11.4	1–35	1,930	327.9	1,467–2,561
Killer whale	5	32	2	7	5.6	2.5	3–9	1,714	1,067.5	20–2,609
Unid. beaked whale	5	9	1	1	1.7	0.5	1–2	1,870	218	1,477–2,091
Spinner/Clymene dolphin	5	310	0	0	62	51.7	20–150	2,101	446.4	1,614–2,809
Risso's dolphin	4	36	3	22	8.3	3.9	4–15	1,770	374.9	1,391–2,375
Unid. cetacean	2	2	10	49	4.3	5.7	1–20	1,601	429.9	1,240–1,834
Fin whale	2	2	2	3	1.3	0.5	1–2	1,611	99.7	1,500–1,739
Melon-headed whale	2	350	1	300	216.7	104.1	100–300	1,915	509.6	1,330–2,265
Cuvier's beaked whale	2	6	0	0	3.0	0	3	1,984	376.9	1,717–2,250
Rough-toothed dolphin	1	25	1	10	17.5	10.6	10–25	2,095	62.9	2,050–2,139
Sei whale	1	2	0	0	2	0	2	1,691	0	1,691
Atlantic humpback dolphin	0	0	4	14	3.5	0.5	2–4	11	2.5	10-15
Pantropical spotted dolphin	0	0	2	170	85.0	49.5	50–120	1,900	0	1,900

Table 3

Relative abundance (individuals/100min) of cetacean species according to season (Beaufort 0–4), listed in decreasing order of overall abundance.

Species	On effort (Beaufort 0–4)*		Total relative abundance*	Seasonal relative abundance (effort (min))			
	Sightings	Animals		Spring (72,766)	Summer (47,412)	Autumn (37,454)	Winter (32,340)
Unid. dolphin	288	21,101	11.107	10.708	5.336	8.749	23.197
Atlantic spotted dolphin	19	2,768	1.457	1.568	2.130	1.354	0.340
Common dolphin sp.	19	1,172	0.617	0.449	0.348	0.000	2.103
Sperm whale	118	1,167	0.614	0.054	0.584	2.179	0.108
Melon-headed whale	2	350	0.184	0.344	0.211	0.000	0
Spinner/Clymene dolphin	5	310	0.163	0.082	0.380	0.053	0.155
Striped dolphin	6	301	0.158	0.240	0	0.120	0.250
Humpback whale	155	285	0.150	0.210	0.015	0.003	0.383
Pilot whale sp.	11	216	0.114	0.103	0.287	0.013	0
Bottlenose dolphin	8	96	0.051	0.080	0.042	0.000	0.056
False killer whale	5	82	0.043	0.071	0	0.021	0.068
Dwarf sperm whale*	13	21	0.042	0.022	0	0	0.117
Unid. whale	35	64	0.034	0.038	0.006	0.024	0.074
Risso's dolphin	4	36	0.019	0.026	0	0.000	0.053
Killer whale	5	32	0.017	0.021	0.036	0.000	0
Unid. baleen whale	27	28	0.015	0.023	0	0.016	0.015
Rough-toothed dolphin	1	25	0.013	0.034	0	0.000	0
Unid. beaked whale*	3	6	0.012	0	0.018	0	0.026
Fin/sei/Bryde's whale	13	16	0.008	0.010	0.013	0.008	0
Bryde's whale	11	13	0.007	0.014	0.002	0.000	0.006
Cuvier's beaked whale*	1	3	0.006	0	0	0.029	0
Fin whale	2	2	0.001	0	0	0.000	0.006
Sei whale	1	2	0.001	0	0	0.000	0.006

*Beaked and *Kogia* whales calculated at sea state Beaufort 0-2, total effort = 50,520min

(*n*=41) of adult animals were most frequently observed. Forty-eight groups (31%) contained immature animals of which 28 (18%) groups included calves, a similar proportion to the 21% of groups containing calves recorded by Best *et al.* (1999) in this area. However, it is likely that the proportion of groups containing calves was greatly underestimated during the current survey work due to the distance of many sightings from the survey vessel.

Sperm whale (*Physeter macrocephalus*)

Townsend's (1935) charts show a significant year-round sperm whale ground off Angola, and sperm whales were by far the most numerous large whale species recorded in Angolan waters, with a minimum of 1,219 individuals recorded during survey work (Table 2). This is partly a facet of their large group size ($\bar{\chi}$=9.2 animals), since the total number of sightings was slightly lower than for humpback

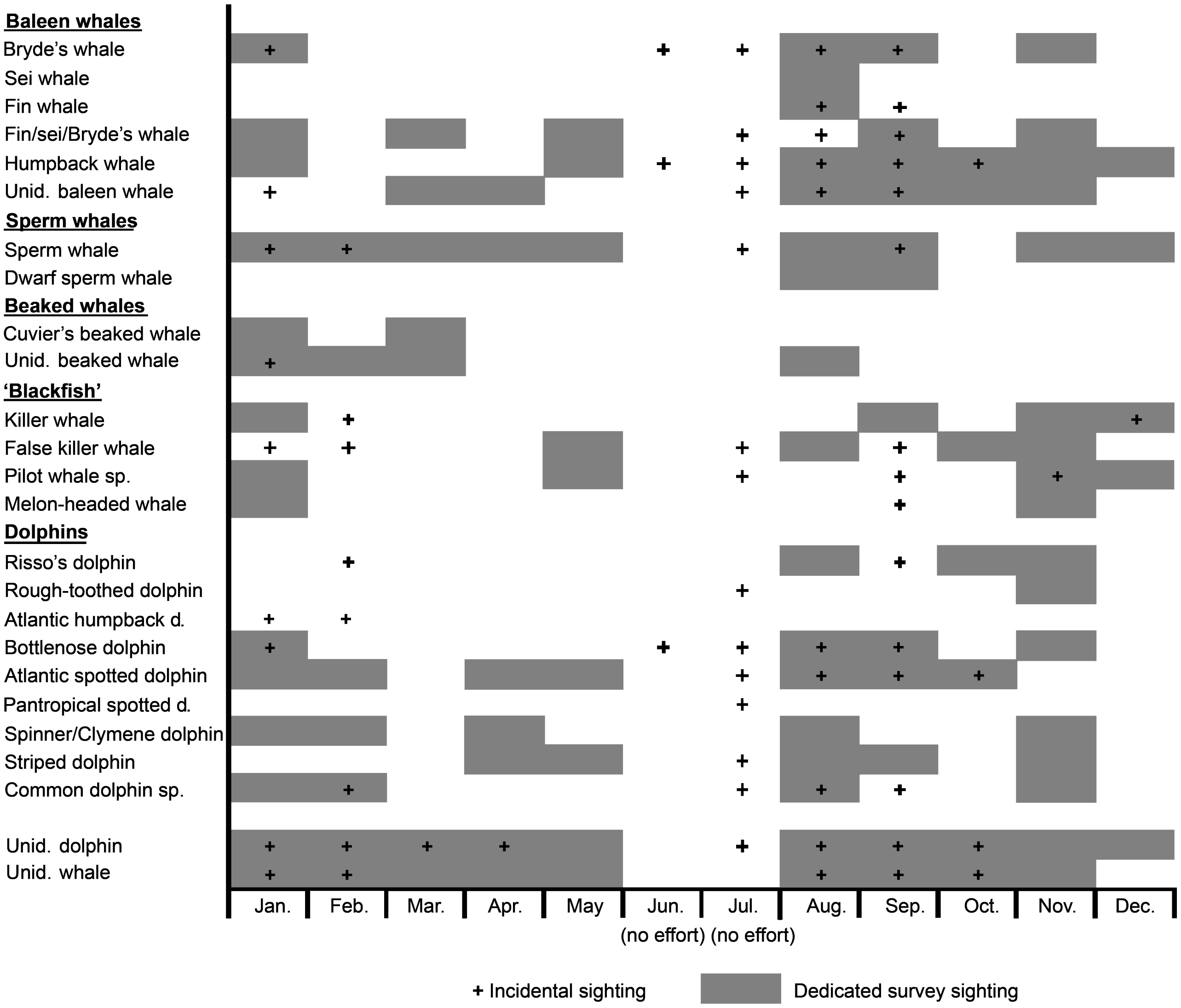

Fig. 3. Seasonal occurrence of cetaceans in Angolan waters.

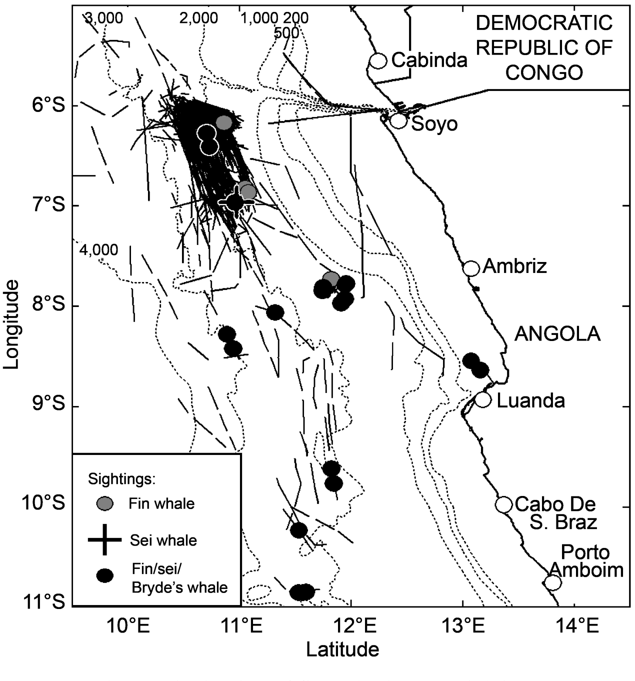

Fig. 4. Distribution of fin and sei whale sightings

whales. The overall relative abundance of sperm whales was 0.6 individuals/100min, making it the third most abundant cetacean species off Angola (Table 3). Sperm whales were sighted exclusively seaward of the shelf break (Table 2), which is consistent with their known preference for deep-water habitat and their relative abundance was similar (0.41-0.72 animals/100 min) across all depth categories exceeding 1,000m. Sightings were clustered particularly in the northeast region of the study area to the west of the Congo River mouth (Fig. 7), with a smaller number of sightings further south off central Angola.

The occurrence of sperm whales within the study area peaked between January and May, and there was a significant difference in the number of encounters (χ^2=198.8, d.f.=3, p=<0.001) recorded according to season (Table 3). Significantly more encounters than expected were recorded during the autumn, and significantly fewer during the winter and spring. There was no significant difference between the number of observed and expected sperm whale encounters during the summer. It is currently unclear whether this seasonality represents animals moving into Angolan waters from elsewhere, or a more localised movement of sperm whales within Angola. The timing of peak seasonal abundance of sperm whales in the study area

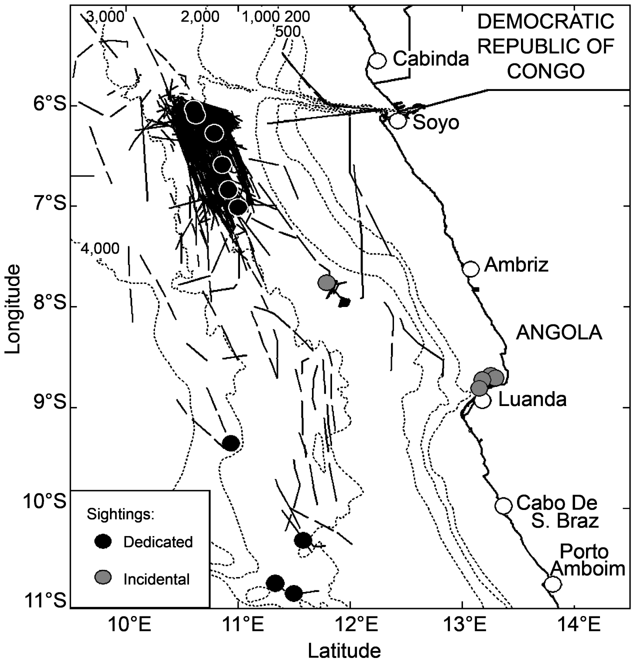

Fig. 5. Distribution of dedicated and incidental Bryde's whale sightings.

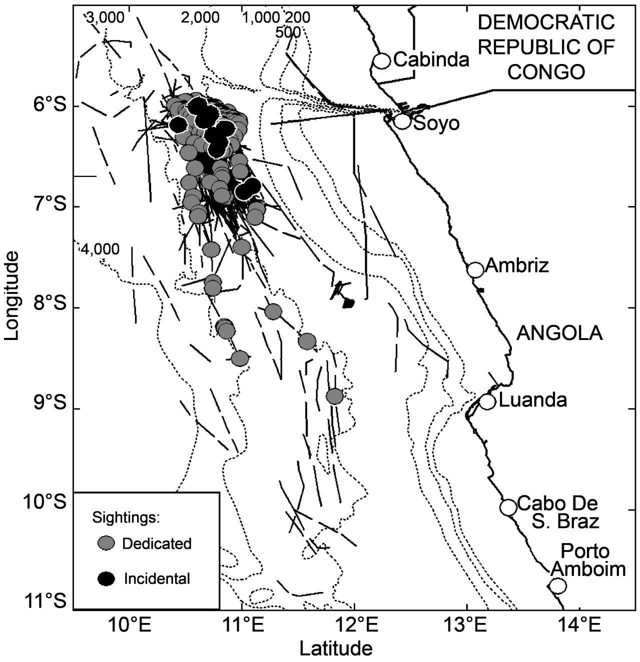

Fig. 7. Distribution of dedicated and incidental sperm whale sightings.

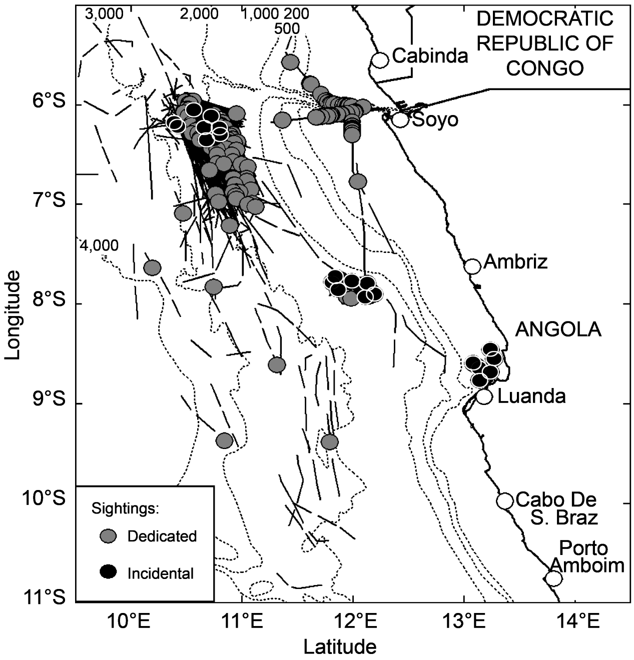

Fig. 6. Distribution of dedicated and incidental humpback whale sightings.

correlates with the monsoon season (Nov-Apr), and may be related to increased outflow and productivity from the Congo River. Large-scale correlations between sperm whales and productivity occur worldwide, and this association off Angola (based on Townsend's 1935 charts) has been previously inferred (Jaquet, 1996).

Sperm whales were often sighted at long range from the survey vessel, and age composition could only be confirmed in 47 of the encounters. Of these, 21 comprised adult-only groups, while 26 groups contained juveniles and/or calves. Mature bulls were seen on very limited occasions, with most pods comprising smaller animals considered to be females or immature males. The dorsal calluses often indicative of mature females (Kasuya and Ohsumi, 1966) were observed on some closer animals. These data confirm that sperm whale nursery groups regularly use Angolan waters on at least a seasonal basis.

Dwarf sperm whale (*Kogia sima*)

Kogia whales comprising the closely related dwarf (*K. sima*) and pygmy sperm whale (*K. breviceps*) inhabit tropical and warm temperate regions worldwide (Caldwell and Caldwell, 1989). There were 14 on-effort sightings of *Kogia* within the Angolan study area, comprising small groups of 1-3 animals (Table 2). One of these animals was identified simply as '*Kogia* sp.', but the remaining sightings were all positively identified as dwarf sperm whales based on the proportion and position of their dorsal fins, and verified from photographs taken in the field. This species was the fifth most commonly sighted cetacean in Angolan waters despite its detection being severely hindered by weather conditions (93% of sightings occurred in Beaufort sea state 0-2). Dwarf sperm whales were recorded only in deep oceanic waters ranging from 1,290-2,009m depth (Table 2). A cluster of sightings occurred in the north-east of the survey area offshore from the Congo River mouth (Fig. 8). Dwarf sperm whales were recorded only during August and September (Fig. 3), although this also corresponds with the period of greatest survey effort and calmest weather conditions. Although Maigret (1994) suggests that *Kogia* species are migratory off West Africa, sightings of dwarf sperm whales have also occurred off Angola during January (pers. obs.), and more year-round survey effort in suitable weather conditions is required prior to drawing conclusions on seasonality.

Cuvier's beaked whale (*Ziphius cavirostris*)

There were two confirmed sightings of Cuvier's beaked whales during dedicated survey work, and these are described in detail elsewhere (Weir, 2006b). Both encounters involved groups of three animals, located over deep water ($\overline{\chi}$=1,984m) in northern and central Angola (Fig. 8). The sightings occurred during January and March.

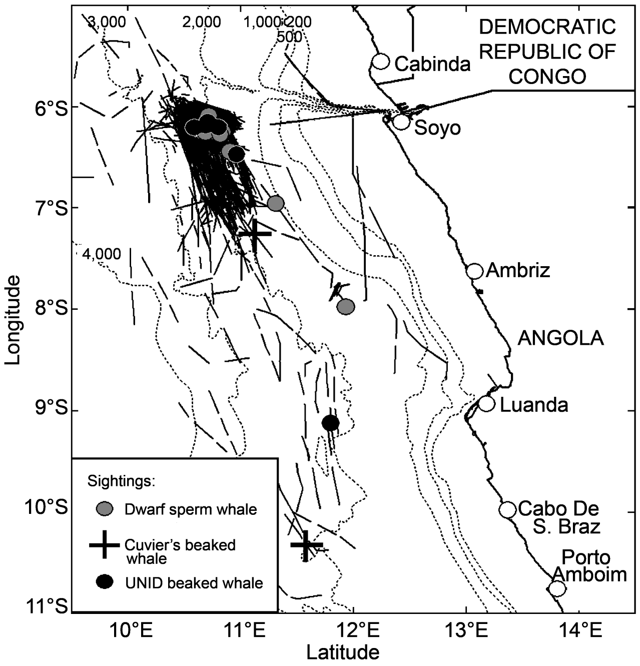

Fig. 8. Distribution of all dwarf sperm whale and beaked whale sightings.

Unidentified beaked whales

The worldwide distribution of many beaked whale species has been determined primarily from strandings, since these species are elusive, difficult to distinguish between at sea and inhabit only deep-water areas (Mead, 1989). Records of beaked whales off the west coast of Africa have been summarised by Weir (2006b), with Cuvier's, Blainville's (*Mesoplodon densirostris*) and Gervais' (*M. europaeus*) beaked whales considered the most likely species to occur off Angola. Previous records off Angola include a sighting of three unidentified *Mesoplodon* whales reported in July 1966 (Morzer Bruyns, 1968), and an unidentified breaching *Mesoplodon* observed in March 2004 (Weir, 2006b).

A total of six sightings of unidentified beaked whales (either *Ziphius* or *Mesoplodon* sp.) were recorded (Table 2), comprising five on-effort records (Weir, 2006a) and one incidental sighting of an unidentified beaked whale during January 2006. All beaked whale sightings occurred over deep-water oceanic habitat ($\bar{x}$=1,870m). Most sightings occurred in the northern portion of the study area offshore from the Congo River mouth, with a single record west of Luanda (Fig. 8). Beaked whales were recorded between January and March, and in August (Fig. 3). The detection of beaked whales at sea is limited by increasing sea state, and it is likely that these species are more numerous off Angola than indicated by the dataset.

Killer whale (*Orcinus orca*)

There were seven sightings of killer whales during the survey, of which five were on-effort (Table 2). Sightings were recorded in coastal waters (*n*=1), over the slope (*n*=1) and in deep oceanic habitat (*n*=5) (Fig. 9). All on-effort sightings involved groups of four to nine animals off northern Angola over water depths exceeding 2,000m. It was notable that the five killer whale sightings recorded from the seismic vessel occurred only during periods of airgun inactivity, and possible avoidance of the sound source by this species may have resulted in under-recording. The incidental records comprised three animals observed north of Luanda during December 1991, and a pod of four approximately 40km west of Luanda during February 1992 (Iain Nicolson, pers. comm.). At least three inshore sightings have been observed between Tombwa and Namibe (Bruce Bennett, pers. comm.), also testifying to the occurrence of this species in southern Angola.

Killer whales were recorded during five months of the year and there was a suggestion of seasonality in the offshore sightings with most records occurring between November and January (Fig. 3, Table 3). This corresponds with the timing of killer whale sightings off Angola in the 1960s/70s by Mikhalev *et al*. (1981) and with the migratory occurrence noted by Maigret (1994) for this species off West Africa.

The external appearance of killer whales off Angola is consistent with the Type A whales documented by Pitman and Ensor (2003). Killer whales in offshore waters were noted in proximity to sperm whales on three occasions, including observations of an apparent predatory attack upon sperm whales in January 2005.

Pilot whales (*Globicephala macrorhynchus* and *G. melas*)

The distribution of the short-finned pilot whale (*G. macrorhynchus*) is assumed to be continuous along the west coast of Africa (Jefferson *et al*., 1997), although it is replaced off the coast of Namibia and South Africa by the closely related long-finned pilot whale (*G. melas*), which inhabits cold temperate and subpolar regions (Bernard and Reilly, 2000; Findlay *et al*., 1992). The exact distribution of these two species off the west coast of Africa is unclear (due to lack of previous survey effort, and difficulties in distinguishing between them at sea), and it is possible that some records off Angola might relate to long-finned pilot whales, particularly in southern areas and years when the cool Benguela Current pushes further northwards. However close views allowed some groups to be positively identified as short-finned pilot whales, and the tropical location of most sightings is strongly suggestive of this species.

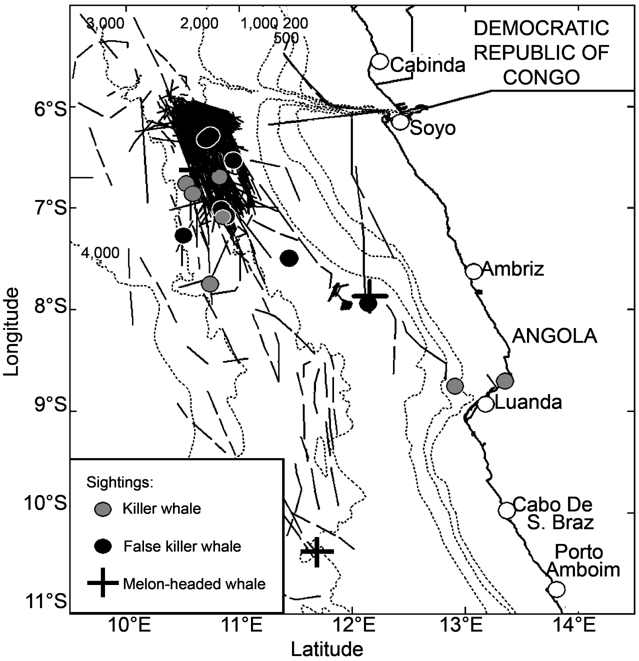

Fig. 9. Distribution of all killer, false killer and melon-headed whale sightings.

There were a total of 22 pilot whale sightings, that were evenly split between on-effort and incidental sightings (Table 2). The relatively large group size ($\bar{\chi}$=37.2 animals) resulted in a relative abundance of 0.1 animals/100min (Table 3), and pilot whales are therefore one of the more commonly occurring cetaceans off Angola. Pilot whale sightings were located exclusively seaward of the 1,000m isobath, with a mean water depth of 2,014m (Table 2). The majority of pilot whale sightings were recorded south of the main survey area with a relatively high number of sightings occurring west of Luanda (Fig. 10). In contrast only five pilot whale groups were observed within the area of prime survey effort off the Congo River mouth where they appeared to be comparatively scarce.

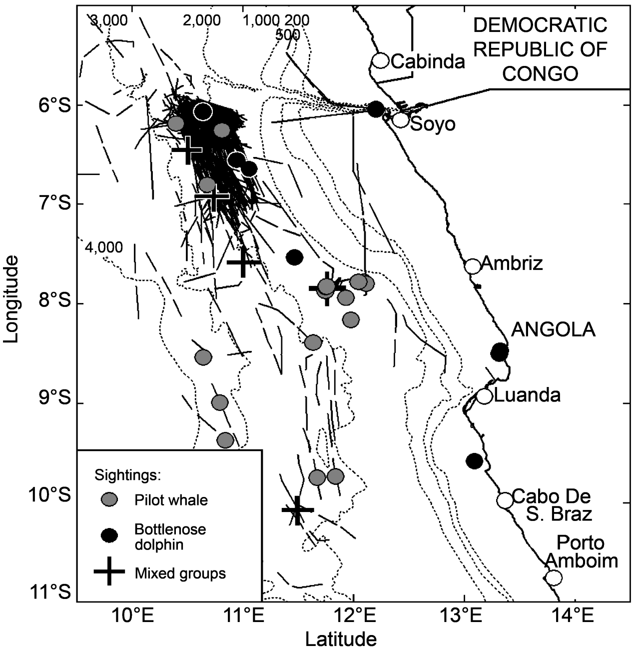

Fig. 10. Distribution of all pilot whale and bottlenose dolphin sightings.

Pilot whales were recorded during only four of the ten dedicated survey months (Fig. 3), but incidental sightings occurred during two other months and this species likely occurs year-round in Angolan waters. Groups consisted of four to 200 animals (Table 2), with the largest groups reported during incidental sightings to the west of Ambriz (Fig. 10). As is commonly observed in other areas (Bernard and Reilly, 2000), five of the sightings involved mixed-species assemblages with common bottlenose dolphins, and pilot whales have also been observed travelling with rough-toothed dolphins off Angola and Gabon (pers. obs.).

False killer whale (*Pseudorca crassidens*)

There were nine sightings of false killer whales off Angola, including five on-effort records (Table 2). The sightings were all located over deep-water areas seaward of 1,467m, with a mean water depth of 1,930m. False killer whales were sighted in eight months of the year (Fig. 3), and can be considered resident in deep, warm Angolan waters. The mean school size of false killer whales in Angolan waters was 12.4 animals (Table 2), and both calves and juveniles were recorded. All sightings occurred in single-species schools. Although unconfirmed (and not included in the analysis), a group of three to five large animals almost certainly of this species was observed feeding on a manta ray (*Manta birostris*) in deep water west of Luanda during the summer of 1990/91 (Iain Nicolson, pers. comm.).

Melon-headed whale (*Peponocephala electra*)

There were three confirmed records of melon-headed whales, and several additional sightings that were strongly suspected to be this species but could not be conclusively separated from the very similar pygmy killer whale (*Feresa attenuata*) which is also expected to occur throughout tropical West Africa (Caldwell and Caldwell, 1971; Jefferson *et al*., 1997). All sightings were recorded in deep oceanic water (Fig. 9), over depths of 1,330-2,265m (Table 2). Although there were only a small number of records, the large group size of this species (Table 2) made it one of the more abundant species recorded during the survey work (Table 3). Sightings occurred during January, September and November (Fig. 3).

Atlantic humpback dolphin (*Sousa teuszii*)

The Atlantic humpback dolphin is endemic to tropical and subtropical West Africa, where it occupies shallow, coastal waters from Morocco south to Angola (Jefferson *et al*., 1997; van Waerebeek *et al*., 2004). This species was not recorded during dedicated survey work, no doubt due to the predominantly offshore distribution of the survey effort. However, at least three Atlantic humpback dolphin groups are thought to be resident along the coast of Namibe Province, including two groups inhabiting the area between Namibe and Flamingos, and a third group off Inamagando located 130km north of Namibe (Bruce Bennett, pers. comm.). These dolphins are typically observed in groups of 4-6 animals (including calves), with sightings located in shallow water (<5m) over, or in close proximity to, rock reefs. Details were kept of four incidental sightings that occurred between 29 January and 7 February 2004 during a kayak trip through this region (Alex Vogel, pers. comm.) (Table 2). Three sightings (each of four animals) occurred off Flamingos to the south of Namibe, including one group that contained a calf. A single sighting of two animals was reported 2km south of Flamingos (Fig. 11).

The sightings of Atlantic humpback dolphins in southern Angola imply a potential occurrence off both central and northern Angola. The author carried out watches specifically for this species during several port calls to Luanda and Soyo in Angola, and Pointe Noire in Congo, but no dolphins were recorded. Further coastal survey work is required to establish this species' exact distribution within Angola and adjacent waters.

Rough-toothed dolphin (*Steno bredanensis*)

Two sightings of rough-toothed dolphins were reported in Angola, of which one was on-effort (Table 2). A group of 25 animals was seen in a mixed-species assemblage with unidentified blackfish (melon-headed or pygmy killer whales) in November 2004, and a pod of ten was observed in July 2005. Both sightings were recorded in over 2,000m water (Table 2) in the northern portion of the study area (Fig. 12). Additional records of this species in Angola include a group of 12 animals photographed west of Luanda during March 2004, and 11 observed in a mixed-species school with bottlenose dolphins and pilot whales off Gabon during September 2005 (Weir, 2006c). All sightings of this species have occurred in shelf edge or oceanic waters.

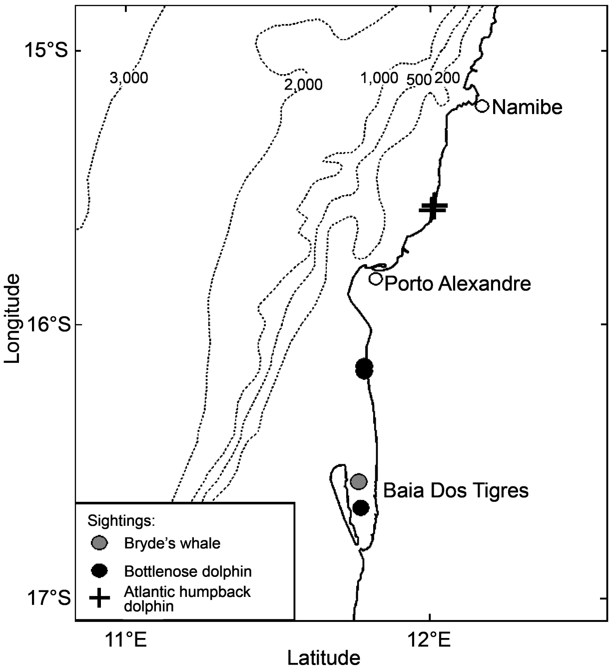

Fig. 11. Distribution of incidental cetacean sightings in southern Angola.

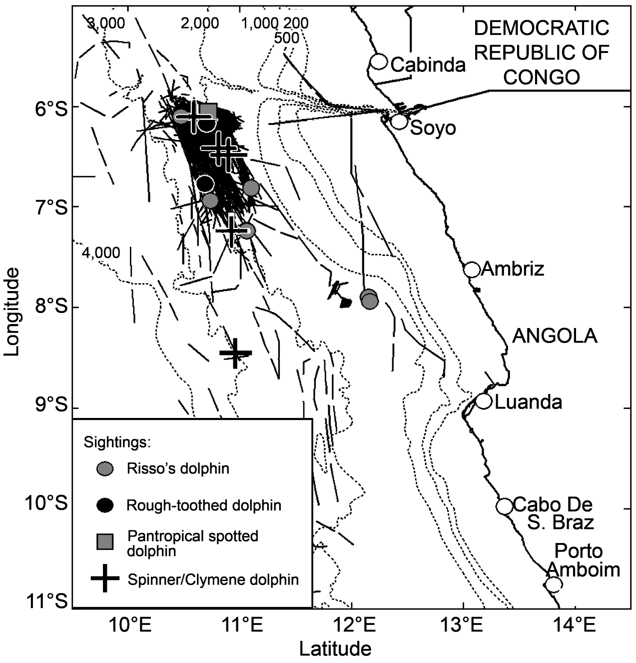

Fig. 12. Distribution of all Risso's, rough-toothed, Pantropical spotted and Spinner/Clymene dolphin sightings.

Risso's dolphin (*Grampus griseus*)

There were a total of seven sightings of Risso's dolphins, four of which were on-effort (Table 2). This species showed a deep-water pelagic distribution off Angola, with all sightings occurring in water depths exceeding 1,300m (Table 2). However a sighting of this species over the Gabon shelf in April 2004 (pers. obs.) suggests that Risso's dolphins might also occasionally occur in shallower habitat in Angola. Five of the sightings were located in the northern study area, while two occurred north-west of Luanda in around 1,400m water (Fig. 12). Risso's dolphins were observed in small groups of 15 or fewer animals (Table 2). Sightings occurred in five of the survey months and it has additionally been recorded during January (pers. obs.), indicating a likely year-round occurrence off Angola.

Common Bottlenose dolphin (*Tursiops truncatus*)

Although there were only eight sightings during dedicated survey work, a further seven sightings of this species were recorded incidentally making it the third most frequently sighted dolphin species in Angola (Table 2). Sightings were distributed throughout northern, central and southern Angola (Figs 10 and 11) and occurred in both neritic and oceanic waters (Table 2). This species has also been recorded inside Luanda harbour (pers. obs.). Sightings were divided into those distributed in depths of <100m ($\bar{\chi}=30.8$m, $n=6$) and those in waters exceeding 1,000m depth ($\bar{\chi}=1957.9$m, $n=9$). Genetic studies have distinguished separate 'inshore' and 'offshore' populations of bottlenose dolphins in many areas worldwide (Duffield *et al*., 1983; Hoelzel *et al*., 1998) and this may also be the case in Angola.

Bottlenose dolphins are a year-round inhabitant of Angolan waters, being sighted in six of the survey months (Fig. 3, Table 3), and also recorded during other surveys in March and April (pers. obs.). Group size ranged from one to 30 animals (Table 2). A third of the sightings in Angola comprised mixed-species schools with pilot whales. The mean group size of bottlenose dolphins was higher within mixed-species ($\bar{\chi}=19.0$, $n=5$) rather than dolphin-only ($\bar{\chi}=12.9$, $n=10$) schools, and total group size (including pilot whales) was almost four times higher ($\bar{\chi}=51.4$, $n=5$) than that of dolphin-only ($\bar{\chi}=12.9$, $n=10$) groups. Although some dolphin-only groups were observed in deep water, the mean water depth of mixed-species associations was three times higher ($\bar{\chi}=2{,}174$m, $n=5$) than that of bottlenose dolphin-only ($\bar{\chi}=694$m, $n=10$) sightings. Rough-toothed dolphins were also present in one mixed-species group off Gabon during September 2005. The tendency for bottlenose dolphins to occur in mixed-species schools with increasing distance from shore has also been recorded in the eastern tropical Pacific Ocean, where pilot whales again form the majority of associations (Scott and Chivers, 1990).

Other notable observations of bottlenose dolphins in Angolan waters include a white (albino or leucistic) bottlenose dolphin sighted amongst a mixed bottlenose dolphin/pilot whale group west of Luanda on 27 December 2001 (photographed by Iain Nicolson), and the several-month residence of a sociable adult female bottlenose dolphin in Mussulo Bay, Luanda during late 2004 (photographed by Iain Nicolson), which frequently interacted with swimmers before eventually being killed.

Pantropical spotted dolphin (*Stenella attenuata*)

Although some sightings of unidentified *Stenella* dolphins recorded during dedicated surveys were strongly suspected to be pantropical spotted dolphins, none of these records could be confirmed. However, two incidental sightings were reported during July 2005, involving bow-riding groups seen at close range. The sightings occurred in close proximity in the north of the study area, over water depths of around 1,900m (Table 2). Three sightings were also recorded over the shelf edge off northern Angola during the autumn of 2004 (pers. obs.). The status of this species in Angola remains unclear.

Atlantic spotted dolphin (*Stenella frontalis*)

Gabon is currently recognised as the southern distributional limit of Atlantic spotted dolphins in the eastern Atlantic Ocean (Perrin *et al*., 1994a; Perrin *et al*., 1987). However, Atlantic spotted dolphins were one of the most frequently sighted dolphin species in Angolan waters during survey work, with a total of 38 sightings including 20 on-effort records (Table 2). This species was also numerous, and at 1.5 individuals/100min^{-1}, the relative abundance of Atlantic spotted dolphins was more than double that of any other species in Angola (Table 3). The tendency of this species to approach survey vessels to bow-ride may have resulted in an over-recording of its frequency relative to other less interactive dolphin species. However, sightings of this species during the seismic surveys may also have been under-recorded, since Atlantic spotted dolphins appeared to show avoidance of active large-volume airgun arrays and only approached the vessel to bow-ride outside of periods of airgun use.

Although most numerous over continental shelf waters in the western Atlantic (Davis *et al*., 2002; Herzing, 1997; Moreno *et al*., 2005), this species clearly inhabits slope and oceanic waters seaward of the shelf break in Angola (Fig. 13, Table 2). Relative abundance was highest over depths of 1,000-1,499m (4.95 animals/100min^{-1}). Although no sightings were recorded over the slope (200-999m) during dedicated surveys, this depth category received rather little effort and opportunistic sightings pertain to the occurrence of this species over slope regions in both Angola and Gabon. Atlantic spotted dolphins were recorded in most months of the year (Fig. 3) and are likely to be year-round residents in Angolan waters. However, their relative abundance showed a clear peak during the summer months (Table 3).

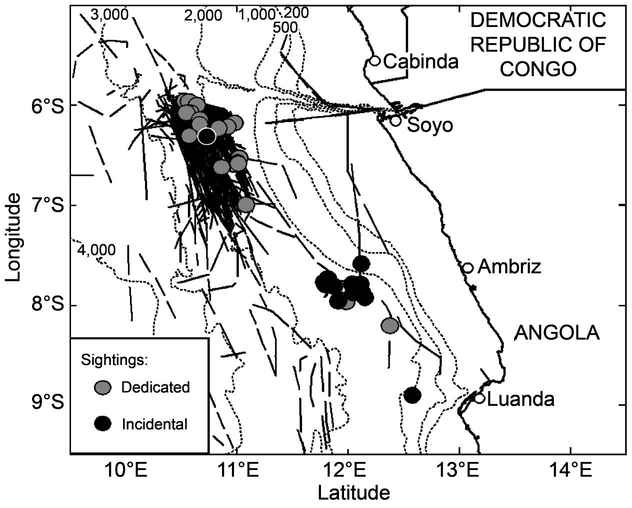

Fig. 13. Distribution of dedicated and incidental Atlantic spotted dolphin sightings.

Group size ranged from one to 500 individuals (Table 2), with pods of over 100 animals recorded on 12 occasions. This group size is notably higher than that reported in the western Atlantic (Davis *et al*., 2002; Herzing, 1997; Moreno *et al*., 2005), which together with the difference in habitat type is suggestive of a different ecology of this species in the south-east Atlantic compared to other parts of its range.

Spinner dolphin (*Stenella longirostris*) and Clymene dolphin (*Stenella clymene*)

Although no sightings of spinner or Clymene dolphins were confirmed during the survey work reported here, both species are known to occur in Angola (pers. obs.); (Weir, 2006a). In addition, five on-effort sightings were recorded as either spinner or Clymene dolphins (Table 2), since their characteristic behaviour of leaping from the water and spinning repeatedly around their longitudinal axis (Perrin and Gilpatrick, 1994; Perrin and Mead, 1994) was observed. The records were distributed over deep pelagic waters with a mean depth of 2,101m (Table 2). The status of spinner and Clymene dolphins in Angola is currently uncertain due to the low number of confirmed sightings, confusion with other species, and frequent observations that some of the smaller dolphin species (particularly *Stenella* sp.) exhibited avoidance and detoured around the survey vessel resulting in under-recording.

Striped dolphin (*Stenella coeruleoalba*)

The striped dolphin inhabits warm temperate and tropical waters worldwide, and there are two previous records from offshore Angola (Perrin *et al*., 1994b). Striped dolphins were recorded on nine occasions during the survey work, including seven on-effort sightings (Table 2). This species had one of the higher relative abundance values in Angola (Table 3), due to its occurrence in fairly large schools of up to 200 animals (Table 2). Striped dolphins were observed only in deep, oceanic waters (Fig. 14), over a mean water depth of 1,785m. Sightings occurred in six of the survey months (Fig. 3), and the species is potentially resident year-round in most of Angola's deep-water areas.

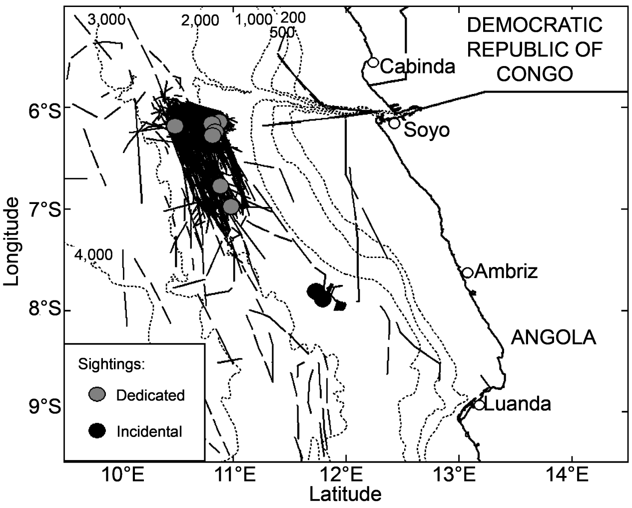

Fig. 14. Distribution of dedicated and incidental striped dolphin sightings.

Common dolphins (*Delphinus delphis* and *D. capensis*)

Together, the short-beaked (*D. delphis*) and long-beaked common dolphin (*D. capensis*) (Heyning and Perrin, 1994) are abundant throughout temperate and tropical areas worldwide. Jefferson *et al*. (1997) consider these to be the most common offshore delphinids in West Africa, while Van Waerebeek (1997) confirmed that both species occur off Gabon and Angola. However, they are analysed together here since most observers did not distinguish between the two species during the survey work, and due to uncertainties regarding their external appearance off Angola (Fig. 15). A total of 38 sightings of common dolphins (*Delphinus* sp.) were recorded, of which 19 were on-effort and 19 were incidental (Table 2). The overall relative abundance of 0.6 individuals 100min^{-1} (Table 3) was lower than that of Atlantic spotted dolphins. However, 13 of the 16 groups that comprised over 80 animals occurred as incidental sightings and were not included in the calculation of relative abundance. The mean group size of common dolphins was significantly higher in water depths of <1,000m ($\bar{\chi}$=231, standard deviation (SD)=204, *n*=5) compared with >1,000m ($\bar{\chi}$=66, SD=71, *n*=33) (Mann-Whitney *U*=26, *n*=38, *p*=<0.05), which suggests that this species may be more numerous in Angolan waters than indicated by the predominantly deep-water survey effort.

Fig. 15. External appearance of common dolphin (*Delphinus* sp.) photographed off Angola, showing shorter beak length than typically observed in *D. capensis* but colouration pattern more comparable to *D. capensis* than *D. delphis*.

Common dolphin sightings were recorded in all habitat types, including neritic (*n*=4), slope (*n*=1) and deep oceanic waters (*n*=33) (Fig. 16). However, although most sightings were recorded over deep water, when corrected for effort the relative abundance was much higher at depths <200m (33.89 animals/100min^{-1}) than over the shelf edge (1.63 animals/100min^{-1}) or in depths >1,000m (0.53 animals/100min^{-1}).

Relative abundance peaked during the winter months (Table 3) probably due to the relatively large number of sightings recorded during August 2005. Common dolphins are likely to be numerous year-round residents throughout Angolan waters, although clarification is needed on the relative occurrence of the two species in the region.

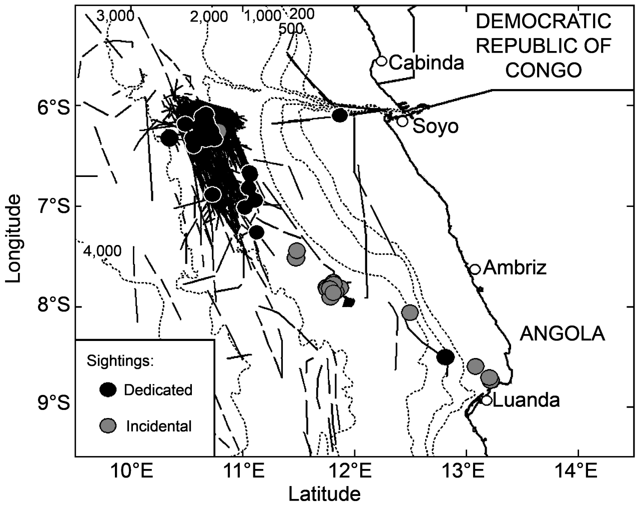

Fig. 16. Distribution of dedicated and incidental common dolphin (*Delphinus* sp.) sightings.

CONCLUSIONS

These data provide preliminary information on the occurrence, habitat preferences and seasonality of cetaceans in Angolan waters, particularly in providing novel information on small odontocetes in the region. However, most data were collected from a seismic survey vessel and the potential reaction of particular individuals and/or species to airgun sound must be considered when describing the species' distribution.

Although most of the recorded species were previously unconfirmed in Angola, all were expected to occur based on their worldwide distribution. The cetacean community off northern Angola is similar to other tropical areas such as the eastern tropical Pacific, the Indian Ocean and the Gulf of Mexico (Anderson, 2005; Ballance and Pitman, 1998; Davis *et al*., 2002), containing both cosmopolitan species such as bottlenose dolphins, killer whales and sperm whales, and species restricted to warm temperate and tropical waters such as Pantropical spotted dolphin, rough-toothed dolphin and Bryde's whale. However it is important to note that variation in oceanographic conditions within Angola, and particularly the presence of the cold-water Benguela Current, is likely to result in a rather different species composition in southern Angola. Survey work is required in this area to properly document cetacean occurrence. Since the cetacean community recorded in Namibia comprises predominantly cold water and temperate species (Findlay *et al*., 1992), it is likely that many of the tropical cetaceans recorded off northern Angola will have their southernmost distributional limits somewhere in central or southern Angola.

The data revealed trends in both the seasonal occurrence and depth-related distribution of cetacean species in Angola. Although survey data were lacking for June and July, cetaceans were present in the region throughout the year and trends in seasonality were apparent for the most numerous species. Notable concentrations of sperm (summer and autumn) and humpback (winter and spring) whales occur on a seasonal basis, and the contrasting seasonal occurrence of these two species means that Angolan waters are of year-round importance for breeding whales. As noted in other areas (Davis *et al*., 1998; Moreno *et al*., 2005), water depth is a major factor influencing cetacean occurrence off Angola. The cetacean fauna can be broadly divided into separate neritic and deep-water communities. Humpback whale, Bryde's whale, killer whale, bottlenose dolphin and common dolphin were present in both communities; however there may be distinct inshore and offshore populations of the latter four species. Although survey effort was biased towards slope and deep oceanic waters, the highest diversity of cetaceans in Angola does appear to occur over deep water habitat with sperm whales, baleen whales, *Stenella* dolphins and large delphinids such as pilot whales and false killer whale all occurring exclusively seaward of the shelf break.

Owing to a lack of previous studies, the conservation status of cetacean species in Angola is unclear. Maigret (1981; 1994) reports the presence of purse seine fisheries in West Africa at artisanal, national and foreign commercial scales, and these fisheries are known to catch dolphins. Coastal West African species such as bottlenose and Atlantic humpback dolphins are particularly vulnerable to artisanal fisheries (Jefferson *et al*., 1997; van Waerebeek *et al*., 2000), while commercial purse seine fisheries are capable of causing mass mortality of pelagic species, for example at least 125 Atlantic spotted dolphins killed in a purse seine operation off Mauritania in 1995 (Nieri *et al*., 1999).

Information on the occurrence and status of marine mammals in Angola is important for environmental impact assessments and mitigation of airgun sound by the oil and gas industry, and also for potential future development of whale-watching ecotourism in Angolan waters. Long-term monitoring throughout the region and the establishment of a proper stranding recording scheme are required to ensure conservation and management of cetaceans in Angola.

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Mother and calf humpback whale responses to vessels around the Abrolhos Archipelago, Bahia, Brazil

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ABSTRACT

As the humpback whale population spreads along the Brazilian coast, whalewatching activities are becoming more frequent especially along the coast of the state of Bahia. In order to evaluate the appropriateness of the Brazilian legislation that regulates vessel approaches to cetaceans, the behaviour of humpback whale mothers and calves was studied around the Abrolhos Archipelago, an area with a high concentration of tourism vessels. Mother and calf groups were observed by means of continuous sampling and tracked along with vessels using a theodolite. Three whale-vessel categories of distances were analysed: closer than 100m (category 1); between 100-300m (category 2); and further than 300m (category 3). Rates of behavioural events and time spent in particular behavioural states of mothers and calves were compared separately in the three categories to observations of randomly selected mother and calf groups not involved in an interaction with a vessel (category 0). A total effort of 39hr was analysed including observations in each of the four categories. The results showed that differences in humpback whale mother and calf behaviour occurred mostly in the presence of vessels within distances of 100-300m. Mothers increased linearity and mean speed of movement, decreased blow intervals and time spent resting. Calves exhibited less rolling, fluke-ups and others active behavioural events, as well as diminished resting time. During interaction with vessels, the frequency of potentially important behaviours, both for mothers and calves, reduced, probably as a response to the approaching whalewatching vessels. Repeated short-term behavioural disturbances might lead to cumulative effects that may result in risks for species conservation. It is recommended that the Brazilian legislation should include a 300m-radius restrictive zone around mother and calf groups or include a 300m caution zone, where boats should reduce speed and avoid sudden changes in engine status and direction. The environmental education work with local communities along the coast must be continued and constant.

KEYWORDS: HUMPBACK WHALE; WHALEWATCHING; SHORT-TERM CHANGE; SHORE-BASED; BRAZIL; REGULATIONS; BEHAVIOUR; SOUTHERN HEMISPHERE; ENERGETICS

INTRODUCTION

For many years, Abrolhos Bank was considered the only known breeding and calving ground for humpback whales (*Megaptera novaeangliae*) in the western South Atlantic, however there is evidence that the population that winters off the Brazilian coast has increased in recent years (Freitas *et al*., 2004) and humpback whales are now being encountered along the entire coast (Andriolo *et al*., 2006; Martins, 2004; Pizzorno *et al*., 1998; Zerbini *et al*., 2004). Nevertheless, the area surrounding the Abrolhos Archipelago is still considered unique because of the high concentration of whale groups with calves (Martins *et al*., 2001; Morete *et al*., 2007; Morete *et al*., 2003b).

Accompanying this increased occurrence of humpback whales along the Brazilian coast are whalewatching activities which are becoming more frequent, not only around the Abrolhos Archipelago, but in other sites along the coast of Bahia (Cipolotti *et al*., 2005). Whalewatching is a particularly lucrative industry in many parts of the world and is often seen as an economic alternative to whaling (e.g. Hoyt, 1995). However, several studies worldwide suggest that whalewatching can cause short and long-term adverse reactions by humpback whales, perhaps affecting them at the population level. Short-term reactions include changes in respiration, diving and swimming patterns, and/or exhibitions of particular behaviours (breaching, head slap). These changes may be correlated with vessel numbers, proximity, speed and direction changes and depend on the composition of the group of whales present (Baker *et al*., 1983; Baker *et al*., 1982; Bauer, 1986). Longer-term reactions such as cow-calf pairs becoming less frequent close to shore with increasing numbers of recreational boats have been suggested by Glockner-Ferrari and Ferrari (1985; 1990) and Salden (1988). However, the number of whales in Hawaiian waters seems to be increasing despite continuous exposure to human activities (Bauer *et al*., 1993). Similarly, humpback whales still use the waters off Cape Cod, Massachusetts, USA as an annual feeding ground, despite exposure to many kinds of vessels (Clapham *et al*., 1993). Watkins (1986) noted that humpback whales off Massachusetts have gradually changed their reactions towards whalewatching boats, suggesting a positive habituation. However, a long-term study (by Bejder *et al*., 2006a) on Indo-pacific bottlenose dolphins (*Tursiops* sp.) suggested that although one could think of dolphin moderate short-term behavioural responses towards whalewatching vessels as a process of habituation, it might be a process of displacement of those individuals more sensitive to dolphin-watching tourism, resulting in a decline in relative abundance (Bejder *et al*., 2006b). Gill *et al*. (2001) proposed that the decision of whether or not to move away from disturbed areas is determined by other factors such as the quality of the site being occupied, so animals with no suitable habitat nearby may be forced to remain despite disturbance, regardless of whether or not this will affect their survival or reproductive success.

Scheidat *et al.* (2004) suggested that mother-calf humpback whale pairs may be especially vulnerable to whalewatching disturbance since some potential avoidance responses (for example, increased swim speed and longer dives) may be beyond the physiological limits of the calf and because calves may have less opportunity to nurse if the mother is forced to increase her speed or change her

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300m before arriving at the group and not leaving the group after interaction.

behaviour from resting to swimming. Lien (2001) suggested that mother and calf groups are especially vulnerable to human presence, and so they should receive more strict protection under regulations.

Baker and Herman (1989) reported that most behavioural changes of humpback whales on the Alaskan feeding ground were caused by vessels within 400m of a group. However, behaviour could be affected by vessels up to 4km distant. Watkins (1986) shows that whales can have negative reactions (i.e. changes from activity to inactivity, usually suspending vocal activity, startle responses including sharply turning away or diving quickly, persistent movement away from the sources of stimuli) when within 100m of sound sources (sudden and loud sounds such as engine start up, ships' close approaches, propeller cavitation during reverse or sharp turns). Most whalewatching guidelines and/or legislation worldwide suggests a 300m radius from a whale group as a caution area, from which the speed of the vessel should be decreased and the closest approach of a vessel towards a whale group is normally 100m. The Brazilian legislation (117/1996) concerning whalewatching activities states that boats cannot go closer than within 100m of a whale group, but does not consider any caution zone before this minimum distance. Stimulated by this legislation, the objective of this study was to evaluate the responses of mother and calf groups to vessels in three distances categories, based on 100m and 300m limits. Three vessel-whale distance categories were analysed: vessel present further than 300m; vessel within 100 to 300m; and vessels closer than 100m.

The behaviour of humpback whale mothers and calves was studied around the Abrolhos Archipelago, an area of high concentration of tourist vessels, in order to evaluate whether it is necessary to improve Brazilian legislation.

MATERIALS AND METHODS

The Abrolhos Bank (16°40'S to 19°30'S, 37°25'W to 39°45'W) is an extension of the continental shelf on the east coast of Brazil. It is characterised by water that is both warm (winter average temperature =24ºC) and shallow (average depth ≈20m), as well as by an extensive coral reef system. These features are typically associated with breeding grounds for humpback whales in other locations around the world (e.g. Clapham, 1996; Whitehead, 1981; Whitehead and Moore, 1982). The land-based observation station (17°57'44"S, 38°42'22"W) was located 37.8m above highest sea level, on the top of the western portion of the Santa Barbara Island, in the Abrolhos Archipelago. The height of the land-station was measured using a 'total station' (a device which may produce an error of 3cm in the height being measured at a distance of 10km). The measurements were made from Siriba and Redonda Islands (both less than 500m from the land station) so this error was unlikely to be problematic. The study area encompassed a radius of 9.3km around the land-station (Fig.1), however to reduce measurement error of the whale's position, intrinsic in theodolite tracking approach (see Würsig *et al*., 1991), only those whale and boat interactions that occurred within 3.5km radius of the land-station were considered for this study. At 3.5km from the land-station, a 10cm error in the instrument's height-above-sea-level would produce an error of 10m in the whale or boat position, a 50cm error in instrument's height could produce an error of 48m. Unfortunately, the measurement of swell height is very difficult from the land-station, and it has been assumed that some uncertainties may have been introduced in the whale position due to swell. Limiting observations to good weather and sea-state conditions minimised these errors. In addition, the maximum error of measured distance between interacting whales is much less than the error of range from the distant land-station, making the errors in relative position much smaller (Tyack, 1981).

Field observations

Every morning, weather permitting, a one-hour scan was conducted. After the scan, a group of humpback whales would be chosen (normally one of the closer groups) for continuous sampling behavioural observations (Mann, 1999), which involved collection of behavioural data (events and states, see Altman (1974)) on a whale or group of whales containing a maximum of two adults and one calf, as recommend by Altmann (1974) for obtaining reliable data. Sampling continued until the group either moved out of the study area or until sighting conditions reduced observation quality (rain or Beaufort Sea state >4 and glare). Observations of mother-calf groups approached by vessels were collected opportunistically (i.e. when the group under observation was approached by a tourist vessel, or in some instances when our research vessel was in the vicinity and was contacted by radio to approach the group). These data were collected from 1998 to 2003, during the months of July to November, using a *Sokkia* DT5 30-power digital theodolite and *Tasco* 7×50 binoculars. The position of an object relative to the land-based observation station was obtained by measuring the angles of depression (or vertical deviation) and angles of horizontal deviation to the object. This method allows one to follow the movements of whales and boats in detail (Tyack, 1981).

The land-based station team consisted of three people: the theodolite operator, who was the principal observer; the binoculars observer; and the computer operator. The theodolite observer communicated all whale behaviour to the computer operator, who entered the data in real-time on a *Macintosh* Powerbook computer running the time-synchronised data-collection program *Aardvark* (Mills, 1996), designed for land-based cetacean studies (Frankel and Clark, 1998; Frankel *et al*., 1995). The theodolite operator also gave vocal commands for the computer operator to record the theodolite readings (position) of the target whale (or vessel) when this was possible. The theodolite operator also recorded positions of the vessel as often as possible without compromising the whale observations and took a mean of one whale position for each 1.5min of observation. The binoculars observer served as a 'back-up' since binoculars have a broader range of view than the theodolite. This observer alerted the principal observer of the approach of vessels, other whale groups in the vicinity and would check if the principal observer (theodolite operator) had missed any behavioural events.

Tide variations were entered into *Aardvark* hourly for correction of the eyepiece height of the theodolite above the surface of the water. *Aardvark* statistical outputs were used to estimate the mean whale speed and direction for each distance category.

Definitions

A calf was defined as an animal in close proximity to an adult whale, estimated to be less than 50% of the length of the accompanying animal (Chittleborough, 1965) and presumably born during the current season. A whale was considered to be a mother when it had a calf by its side. The variables used for behavioural events and states are listed and described in Table 1.

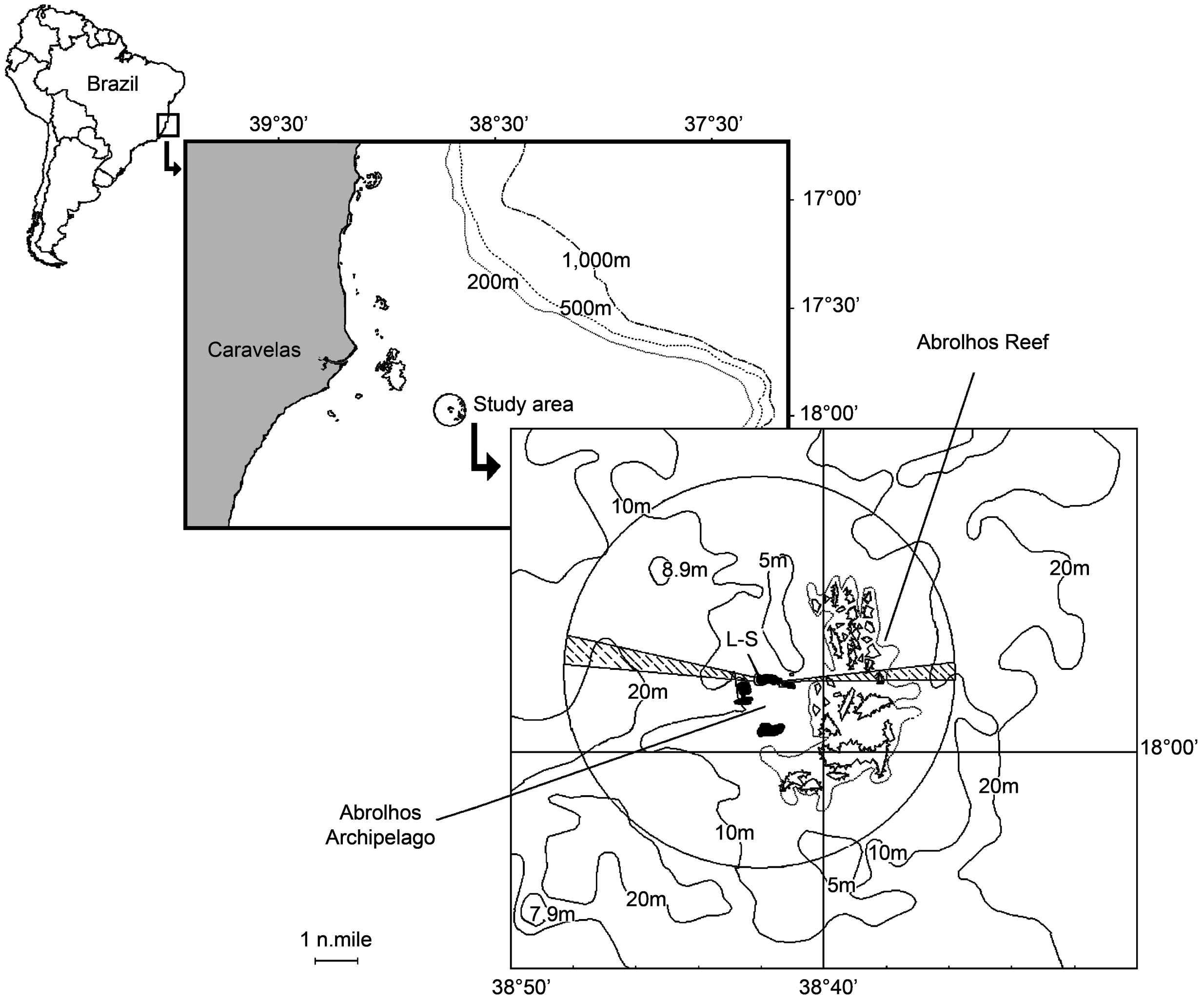

Fig. 1. The study area encompasses 9.3km (5 n.miles) radius excluding the two blind areas (to east and west) from the land-based observation station (L-S) at Santa Barbara Island in the Abrolhos Archipelago, east coast of Brazil.

Analyses

In order to evaluate the behaviour of mothers and calves in the presence of the vessel, three distances categories were created: (1) the presence of the vessel closer than 100m (category 1); (2) between 100-300m (category 2); and (3) further away than 300m[1] (category 3). Some whale groups were approached and re-approached by whalewatching or research vessels within the same continuous sampling period (e.g. a boat entered a 300m radius of a whale, spent some time with the group, left, then re-approached). In such cases, only one period of sampling in each distance category was considered for the analyses. In other words, for each continuous sampling, only one set of data from each distance category was included. Due to the opportunistic nature of this study, not all observations contained the three distance categories. Some observations commenced when the boats were already closer than 300m and fewer observations were carried out in category 1. This would be expected because in Brazilian waters, tourism boats theoretically cannot approach a whale closer than 100m (ordinance 117/1996) and in fact, all observations made in category 1 were of research vessels. This ordinance stipulates that tourism boats cannot stay longer than 30min watching a group, resulting in short periods of observations in categories 1 and 2. These shorter interactions (less than 10min in each category) were excluded from the analyses in order to reduce bias. Fifteen continuous samplings of mother and calf groups that were not approached by vessels were chosen randomly to serve as a control. This set of data was entered into the analysis as category 0.

The variables analysed for the mothers and calves are listed in Table 1. For the calves, blow rate was not taken into consideration because of the potential error of counts due to the small size of the blow which easily could be missed by the observer if the calf was 'behind' the mother (in relation to the theodolite observer), or if glare or wind were strong. Three mutually exclusive and cumulative inclusive behavioural states were considered for the mothers (swimming, tail-up and resting) and for calves (swimming, resting and milling). Calves do not perform tail-up behaviour (Morete *et al*., 2003a). Behavioural states were checked every time the whale surfaced. As positions of the mothers were obtained the variable linearity was used as an indirect measure of their milling. For behavioural states, the proportion of time the whale spent in each state was calculated.

Data from the three distance categories for mother and calf behaviours (separately) were compared to data from category 0, using a non-parametric Mann-Whitney test for two independent samples. All statistical analyses were run in the software *STATISTICA* 6.0 (Statsoft Inc, 2001).

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[1] 300m before arriving at the group and not leaving the group after interaction.

Table 1

Variables including behavioural events and states to evaluate the behaviour of mothers and calves in the presence of a vessel in three distance categories and in the absence of the vessel.

Variables	Definitions
Linearity*	Calculated by dividing the distance between the first and last position of the whale by the cumulative distance covered between all recorded positions.
Mean speed*	Total distance covered divided by total time of observation.
Blow interval*	Elapse time between blows.
Blow*	Exhalation above the surface of the water.
No blow*	Surfacing with no evidence of exhalation.
Fluke up	Submerging, lifting the flukes so that the ventral side of the fluke can be exposed.
Active	Including breaches, pectoral fin slap, tail and peduncle slap, tail slashes, tail breach and head slap.
Rolling**	Including exposition of pectoral fins, movement showing the ventral part of the body, exposition of half of the fluke and belly-up.
Lap**	The calf goes on top of the mother's rostrum while the mother is resting, and almost its whole body can be observed out of the water.
Head exposition**	When the calf moves its head above the surface at an angle less than 60°.
Spyhop**	Lifting the head vertically above the surface of the water (90° angle).
Tail-up*	Behavioural state: maintaining fluke above the water for some period – see Morete *et al.* (2003a).
Swimming	Behavioural state: movement in a fixed direction (for calves) and/or in varying direction (for mothers) when the whale shows the dorsal part of the body intermittently, sometimes interspersed by diving.
Resting	Behavioural state: floating motionless, lying at the surface exposing the dorsal part of the body.
Milling**	Behavioural state: as swimming, however varying direction, within a small area – for a calf also when it swims circling the mother.

*Variables calculated just for mothers. **Variables calculated just for calves.

RESULTS

Due to the opportunistic nature of data collection, a balanced design was impossible to achieve. Excluding other humpback whale groups categories, groups observed further than 3.5km from the land station, periods of the sampling where boats re-approached the same group and observations of known individual whales that were already part of the dataset, 23 mother-calf groups observations were analysed, summing 17.2h of continuous observations of whales in the presence of vessels. Among these, 1.6hr (*n*=6; mean=0.26hr; SE=0.025) in category 1; 4.26hr (*n*=14; mean=0.3hr; SE=0.028) in category 2 and 11.33hr (*n*=14; mean=0.81h; SE=0.144) in category 3. A total of 22.1hr (*n*=15; mean=1.47hr; SE=0.198) of observations of mother and calf groups was used as control for the analyses (category 0). In all 23 whale-vessel interactions never more than one boat was present. Mean values for the rates of occurrence of behavioural events and states for mother and calf are listed in Table 2.

Mothers

The comparison of all variables for mothers, between category 0 and category 3 revealed no significant difference. Mothers' mean speed in the presence of vessels within 100m (3.98km hr^{-1}) was significantly faster when compared to the control (1.99km hr^{-1}). Between categories 0 and 2 there were statistically significant differences in linearity, mean speed, blow interval and resting state (Table 3). When compared to the absence of boats, mothers tended to move in a more straightforward manner and faster when vessels were between 100 to 300m away (category 2). Additionally, mothers' blow intervals were smaller in the presence of vessels (100-300m), leading to an increase blow rate that was not statistically different from when boats were absent. The proportion of time spent in the resting behavioural state reduced by 54%, from 27.02% (category 0-control) to 12.49% when vessels were present between 100-300m (category 2).

Calves

The comparison of all variables for calves between category 0 and category 3 resulted in no significant difference; however a significant difference was found between categories 0 and 1 and between 0 and 2 (Table 3). In the presence of boats within a radius of 300m of the calf (both categories 1 and 2), the number of rolling events decreased. When boats were between 100 and 300m away they exhibited less active events, less fluke-ups and reduced the time spent resting. When boats were closer than 100m, calves decreased the amount of time spent milling. Although the lap event was not significantly different between categories 0 and 1, it is important to note that it did not occur while boats were within 100m of the group (Table 2).

DISCUSSION

Land-based research platforms for studying cetacean behaviour, especially when the objective is to evaluate whale responses to human activities, have been used worldwide (Bauer, 1986; Frankel and Clark, 1998; Frankel *et al*., 1995; Heckel *et al*., 2001; Scheidat *et al*., 2004; Williams *et al*., 2002) because they offer the advantage of being non-intrusive, when compared to research vessels that can influence the measured response.

Many studies have shown that the responses of humpback whales to whalewatching vessels can occur at distances further than the 300m (the distance stipulated for this research). Bauer (1986) shows that several behaviours appear to be affected by the presence of a vessel within 500m and/or between 500 to 1,000m; Baker and Herman (1989) observed that humpback whale behaviour on the Alaskan feeding grounds could be affected by vessels up to 4km away, but most changes were caused by vessels within 400m.

Motivated by whalewatching guidelines and legislation around the world and especially by the Brazilian legislation, which stipulates 100m as the minimum distance of a whalewatching vessel to a group of whales, this study focussed on the presence of vessels further away than 300m, between 300 – 100m and within 100m.

Corkeron (1995) found significant differences in some humpback whale behaviours when exposed to boats within 300m. The results presented here mainly show differences in humpback whale mother and calf behaviour in the presence of vessels within a distance of 300 to 100m, when compared to the control situation (category 0: continuous sampling

Table 2

Mean values and standard deviation (SD) of rates of occurrence of behavioural events, proportion of time in behavioural states of humpback whale mothers and calves in the absence of vessels (Cat 0) and in the presence of vessels in three categories of distance: category 1 (Cat 1), category 2 (Cat 2) and category 3 (Cat 3).

	Cat 0 (no vessel)		Cat 1 (0-100m)		Cat 2 (100-300m)		Cat 3 (+300m)	
	N = 15		*N* = 6		*N* = 14		*N* = 14	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Mothers								
Linearity	0.66	0.23	0.79	0.20	0.83	0.17	0.63	0.26
Means speed (km hr^{-1})	1.99	1.65	3.98	2.71	4.18	2.83	2.38	1.39
Blow interval (min)	1.70	0.68	1.54	0.31	1.21	0.63	1.47	0.67
Blow hr^{-1}	38.59	11.85	30.82	10.94	49.84	21.63	42.11	13.77
No blow hr^{-1}	7.24	5.17	14.13	21.21	13.69	13.21	8.28	9.47
Fluke up hr^{-1}	0.53	0.87	0	0	9.05	15.88	1.30	1.99
Active hr^{-1}	0.89	1.52	0.71	1.74	0.95	1.95	0.30	0.54
Tail-up duration (min)	7.25	0.38	4.58	1.84	8.16	3.92	7.00	3.42
%tail-up	8.15	21.5	25.9	31.4	17.4	23.9	19.6	26.92
%swimming	64.83	35.60	57.45	49.38	70.13	35.43	47.42	36.40
%resting	27.02	27.77	16.67	22.21	12.49	21.29	32.94	30.67
Calf								
Fluke up hr^{-1}	1.06	2.10	0.71	1.74	0.00	0.00	0.53	1.21
Rolling hr^{-1}	7.72	13.44	0.71	1.74	3.65	12.54	9.15	13.47
Active hr^{-1}	8.15	19.10	4.27	10.45	0.15	0.55	4.16	8.19
Lap hr^{-1}	0.76	1.44	0.00	0.00	0.68	1.80	1.08	1.86
Head exposition hr^{-1}	1.45	3.43	0.71	1.74	0.76	2.24	2.17	4.83
Spyhop hr^{-1}	0.09	0.20	0.00	0.00	0.00	0.00	0.54	1.41
%swimming	53.04	36.43	54.40	50.87	70.13	35.44	42.39	35.46
%resting	15.20	19.56	40.33	45.46	5.50	14.07	18.41	18.34
%milling	31.76	32.81	5.26	12.89	24.37	28.64	39.20	27.70

Table 3

Values of Mann-Whitney test (U) and respective *p* value of rates of occurrence of behavioural events, proportion of time in behavioural states of humpback whale mothers and calves in the absence of vessels (Cat 0) and in the presence of vessels in three categories of distances: category 1 (Cat 1), category 2 (Cat 2) and category 3 (Cat 3). *P* significant at level 0.05. Significant differences appear in **bold**.

	Cat 0/Cat 1		Cat 0/Cat 2		Cat 0/Cat 3	
	U	*P*	U	*P*	U	*P*
Mother						
Linearity	30	0.242	55	**0.029**	99	0.793
Mean speed (km hr^{-1})	20	**0.051**	57	**0.036**	84	0.359
Blow interval (min)	43	0.876	50	**0.016**	78	0.238
Blow hr^{-1}	25	0.119	76	0.206	92	0.57
No blow hr^{-1}	32	0.31	82	0.315	91	0.54
Fluke up hr^{-1}	27	0.078	84	0.305	97.5	0.707
Active hr^{-1}	36.5	0.43	92.5	0.506	88	0.381
Tail-up duration (min)	0	0.083	4	0.505	5	0.738
%tail-up	29.5	0.106	78	0.134	76	0.108
%swimming	44	0.937	84	0.354	73	0.161
%resting	31	0.272	59	**0.04**	87.5	0.444
Calf						
Fluke up hr^{-1}	31.5	0.24	49	**0.001**	76.5	0.15
Rolling hr^{-1}	16.5	**0.02**	41	**0.002**	104	0.96
Active hr^{-1}	29	0.18	47	**0.002**	94	0.61
Lap hr^{-1}	27	0.08	82	0.2	102.5	0.9
Head exposition hr^{-1}	33	0.29	75	0.11	95	0.62
Spyhop hr^{-1}	36	0.25	84	0.08	100	0.76
%swimming	43.5	0.91	75.5	0.19	86.5	0.42
%resting	37.5	0.55	62.5	**0.049**	81	0.29
%milling	16.5	**0.02**	85.5	0.38	82	0.31

with no whale-vessel interaction). Mother and calf groups increased their mean speed and presented more direct displacement and the mothers decreased their blow intervals. The increase of speed in the presence of boats has been observed in other humpback whale studies (Au and Green, 2001; Bauer, 1986; Scheidat *et al*., 2004). Bauer (1986) and Baker *et al.* (1982) found that the closer the vessel, the smaller the mean blow interval and Baker (1988) stated that within 400m whales responded to close proximity of vessels by decreasing their blow intervals, as was observed for the mothers in category 2 of this study. Additionally, it was observed that mothers and calves reduced their time spent resting. Additionally, calves significantly reduced their activities above the surface (i.e. fluke-up, rolling and other active behavioural events).

The results presented here point to significant changes in humpback whale mother-calf pairs behaviour in the presence of vessels and they can be thought of as negative effects. Due to the high energetic cost of lactation (e.g. Lockyer, 1981) and the virtual absence of feeding during the winter season, mothers should theoretically spend more time in the resting state as an energy saving measure. Conversely, calves could benefit from vigorous activity in the form of play (Bisi, 2006; Thomas and Taber, 1984) since exhibiting active behavioural events leads to the development of motor skills and coordination. While mothers rested, calves were frequently observed circling them (milling) and rolling interspersed by dives, which could be related to nursing activity (Bisi, 2006). With the approach of a vessel, these behaviours (resting and presumably suckling), reduced. Normally after a captain had spotted a whale group for the first time and until the final approach, the boat changed speed and direction several times repeatedly to keep following the whale group as close as 100m. Watkins (1986) discussed that whales respond negatively to sudden and loud sounds from nearby sources, such as from an engine starting or propeller cavitation during reverse or sharp turns. However, he noted that the sounds of an engine that had been running at a particular rate for some time generally did not cause a reaction (Watkins, 1986). In fact, although whalewatching vessels usually maintain the 100m minimum distance stipulated by the Brazilian legislation, they do frequently change engine status while the group is underwater and thus generate the sounds discussed by Watkins (1986).

It could thus be expected that mother and calf groups would react most strongly to vessels closer than 100m. However, except for the percentage of time spent milling and the rate of occurrence of rolling by calves, (significantly lower when compared to the control condition) and the increase in swimming speed for mothers, no other alterations were statistically significant. The absence of the occurrence of lap behaviour (calf on top of mothers rostrum) by calves while in the presence of vessels within 100m is a cause for concern and it is thought that the low number of samples in category 1 may have compromised the significance level of the results presented here. The lack of a significant difference in this instance may have been due to a type II statistical error, but in all six cases of vessels present within 100m of a mother and calf the boats were research vessels. Although these approached closer than whalewatching vessels, avoiding abrupt changes in direction and speed, or even keeping the engine in idle most of the time, would have considerably reduced or eliminated noise (Au and Green, 2001).

Whale responses to vessels approaching but still further than 300m, were not different from the behaviour of control whale groups (category 0). Assuming that vessels navigate at a mean speed of 15km hr^{-1}, it would take about 4min to travel 1km, so the duration of time whales were exposed to the vessel in this study was much shorter when compared to the whole period of observation. The mean time of continuous sampling in category 3 was 0.81hr, diluting any behavioural changes that might occur further away than 300m, as found in some other studies (Baker and Herman, 1989; Bauer, 1986; Green and Green, 1990). Nevertheless we believe that at least visually it is not possible to attribute a given reaction from a humpback whale to the presence of a boat that is not nearby, because others factors unrelated to the vessel not under the view/control of the observers may influence that whale group.

Short-term reactions to whalewatching vessels are well documented in the literature and once again were observed here. However, the ultimate question of what may be the long term effects of whalewatching activity is still unanswered. Normal behaviours by mothers and calves were altered in the presence of vessels and that may interfere with how the whales deal with their energetic demands. Repeated short-term behavioural changes such as these may lead to cumulative effects that might prevent animals from carrying out normal life processes. If disruption occurs to a particular segment, or to a significant number of individuals within a population, it follows that conservation of the population may be at risk (Lien, 2001). Whalewatching is spreading along the coast of Brazil (Cipolotti *et al*., 2005), in regions inside and outside protected areas. Although there is no information on the extent to which the total population in the area is affected, it is known that these interactions occur in a great part of its distribution and certainly not all the people conducting this activity have knowledge and/or are conscious of the national regulations.

Whether the short-term behavioural changes described here are accompanied by a long term avoidance of the Abrolhos Archipelago region as a breeding site has not been determined. Abundance estimates in the area suggest that the population is increasing (Andriolo *et al*., 2006; Freitas *et al*., 2004). Indices of abundance around the land-station have shown that sightings of adult whales per scan increased, especially from 2002-04 based on a seven-year study from 1998 to 2004 (Morete *et al*., In press). Gill *et al*. (2001) proposed that the decision of whether or not to move away from disturbed areas is actually determined by other factors such as the quality of the site being occupied, so animals with no suitable habitat nearby may be forced to remain despite disturbance. In addition, for long-lived, slow-breeding species, the long-term effects of reduced resting behaviour on fitness, individual reproductive success and hence population size, would take a long time to detect (e.g. Thompson *et al*., 2000; Wilson *et al*., 1999) and cannot be observed until they have actually occurred (Tyack *et al*., 2004). The acceptable limit of the observed short-term reactions (i.e. decrease of resting, increase of swimming speed, decrease of suckling) that would not trigger long-term effects, as suggested by Lusseau (2003) must now be investigated.

At a practical level, from a precautionary perspective we recommend that Brazilian legislation should be amended to create a 300m radius restrictive zone around mother and calf groups or at least should contain an item about a 300m caution zone, where boats should reduce speed, avoid sudden changes in direction and speed (i.e. reduce noise level) and approach and leave whales cautiously and slowly. In any event, Brazilian whalewatching legislation must be respected by whalewatching vessels and for this to occur, extensive environmental education work with local communities along the coast must be continued. Training of boat captains and effective reinforcement of the guidelines should be done by the appropriate Brazilian authorities.

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Genetic analyses reveal promiscuous mating in female common minke whales, *Balaenoptera acutorostrata*

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ABSTRACT

Based on 25 microsatellites, first order relatedness was established for three dyads of individuals contained in the Norwegian minke whale DNA-register. One large female minke whale was a member of all three dyads. Two competing genealogies were considered and under both of these the quartet contained siblings that with high probability must be half-siblings, as opposed to being full siblings.

KEYWORDS: COMMON MINKE WHALE; DNA FINGERPRINTING; NORTH ATLANTIC OCEAN; REPRODUCTION; GENETICS; NORTHERN HEMISPHERE

INTRODUCTION

Our current knowledge regarding the breeding biology of baleen whales in general and of common minke whales, *Balaenoptera acutorostrata*, in particular is very limited. For many species (or populations) specific breeding ground locations are not known and thus direct observations of mating behaviour are not feasible. For those species for which the breeding grounds are known, behavioural observations thus far strongly indicate the absence of mate-fidelity in either sex. Female right (*Eubalaena spp.*) and gray whales (*Eschrichtius robustus*) have been observed to copulate with multiple males during the course of one bout of mating (Payne *et al*., 1986; Stone *et al*., 1988; Swartz, 1986). For humpback whales, *Megaptera novaeangliae*, behavioural observations of actual mating success are lacking, but observed behaviours involving competitive groups support a mating system that is likely to be promiscuous (Clapham, 1996 and references therein).

Genetic analyses have been employed to investigate the mating system of humpback whales (Cerchio *et al*., 2005; Clapham and Palsbøll, 1997; Nielsen *et al*., 2001). In an analysis of known mothers where samples were available from two or more calves, multi-annual sighting records of individually identified humpback whales were used to confirm that female humpback whales indeed mated promiscuously across seasons (Clapham and Palsbøll, 1997). For males, Nielsen *et al*. (2001) used genetics to determine that some have higher reproductive success than others, and Cerchio *et al*. (2005) showed evidence of polygyny (males mating with multiple females). In species without the extensive multi-year sighting records of individuals that are available for the humpback whale, both maternity and paternity may need to be inferred indirectly. The latter approach is appealing for minke whales, as they occur almost exclusively as solitary individuals. Skaug and Øien (2005) used DNA-profiles from mother-foetus pairs to establish paternity in a database of male minke whales.

Skaug *et al*. (2005) used statistical methods to identify pairs of related individuals in the Norwegian minke whale DNA-register, which contains DNA-profiles from nearly all animals caught by Norway since 1997. Among their findings were three dyads of 1st order relatives having one female individual in common. Two possible genealogies for the four individuals involved in these three dyads are considered in this paper. Given the genealogy and additional biological information, the probability that certain members of the quartet were full siblings, as opposed to being half-siblings was calculated. These findings yield information about minke whale breeding biology that is otherwise difficult to obtain.

MATERIAL AND METHODS

The establishment of the Norwegian minke whale DNA-register ensures that samples (muscle tissue) are taken from each animal caught under the Norwegian catch quota and that a DNA-profile is established from each individual whale and stored in a database (Olaisen, 1997). The DNA-profile consists of 10 microsatellites, mitochondrial (mt) DNA and a sex-marker (Dupuy and Olaisen, 1998). In addition, for each animal the register contains information about the time and geographical location of capture, as well as some biological parameters (length, etc). For the period 1997-2002, the DNA-register contains DNA-profiles for 3,301 individuals. These samples were geographically spread according to the IWC's Small Area delineation of the Northeastern Atlantic (Fig. 1). The best estimate of population size for minke whales in the region is 107,000 animals with a Coefficient of Variation (CV) of 0.14 (Skaug *et al*., 2004).

The present study involves three dyads of individuals, which among other dyads were identified in Skaug *et al*. (2005) as likely relatives based on the 10 microsatellites constituting the DNA-register. These three dyads, all being consistent with a parent-offspring relationship, were brought to special attention due to the fact that they shared a common individual. All four individuals involved were females and the fact that they shared mtDNA haplotype suggested that all three dyads were mother-daughter pairs. To ascertain the estimated degree of relatedness the four individuals were typed at 15 additional microsatellite loci (Table 1). As part of a larger study 439 additional individuals were typed at the same 15 loci, allowing estimates of population allele frequencies to be established.

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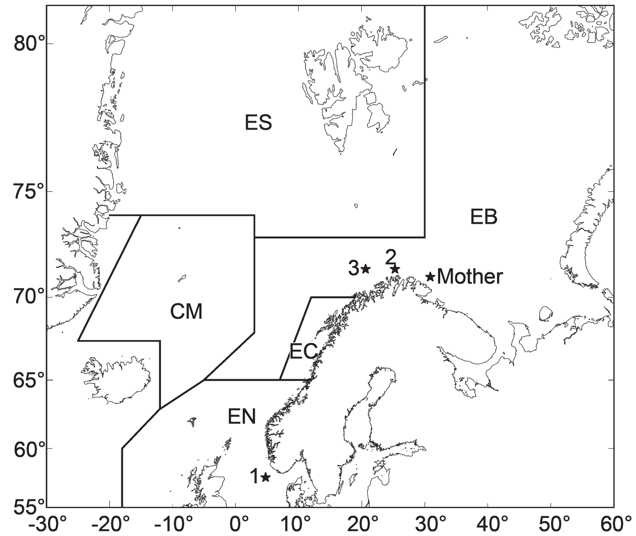

Fig. 1. Capture locations (stars) of the individuals in the quartet of individuals (Table 2). Also shown are (pre-2003) Small Areas to which the minke whale catches were allocated. The 3,301 genetic samples used in the present study were distributed among Small Areas as follows, EN: 634, EC: 69, EB: 1626, ES: 719, CM: 253.

Table 1

Multilocus genotypes for the four individuals involved in the present study. The genotypes consist of 25 microsatellite loci (Tautz, 1989), out of which 10 loci comprise the Norwegian minke whale DNA-register loci (Dupuy and Olaisen, 1999). The 15 additional loci are described in Palsbøll *et al.* (1997) and Bérubé *et al.* (2005). The three 1st order dyads are: (Mother, 1), (Mother, 2), (Mother, 3).

	10 original loci comprising the DNA-register				
	GATA098	**GT509**	**EV1**	**EV37**	**GT310**
Mother	91/95	193/211	153/161	197/201	115/117
1	91/95	193/211	149/161	197/207	115/117
2	91/95	193/193	153/171	199/201	115/117
3	91/95	193/207	155/161	197/199	111/115
	GT211	**GT575**	**GT023**	**GATA028**	**GATA417**
Mother	106/108	162/164	97/105	161/207	213/220
1	102/106	154/164	105/105	161/211	220/228
2	106/106	162/164	97/99	207/211	213/220
3	102/108	154/162	99/105	161/207	217/220
	15 additional loci				
	AC045	**AC087**	**AC137**	**ACCC392**	**CA128**
Mother	182/190	163/167	109/119	246/246	137/139
1	170/182	163/167	117/119	246/246	137/139
2	182/190	163/167	109/121	246/246	137/139
3	182/188	167/167	109/119	246/254	139/143
	CA232	**EV094**	**EV096**	**GT122**	**GT129**
Mother	148/148	212/212	242/252	140/142	103/103
1	148/152	212/212	252/252	138/140	103/103
2	148/152	212/212	242/250	140/142	103/103
3	148/152	212/212	242/252	140/140	103/105
	GT195	**GT307**	**GT541**	**RW26**	**RW4-10**
Mother	162/168	136/140	102/102	169/171	200/204
1	164/168	140/140	102/102	167/169	198/200
2	162/168	136/140	102/102	171/171	204/204
3	162/168	136/136	102/102	167/171	200/204

For each of the three dyads, the computer program *Familias* (Egeland *et al*., 2000) was used to calculate the posterior probability of a parent-offspring relationship, versus unrelatedness. In these calculations, only the 15 new loci were used, to avoid any ascertainment bias that would arise from including the ten original loci. Originally developed for forensic science, *Familias* uses a Bayesian framework to calculate the probability of each candidate pedigree, given DNA-profiles for some or all individuals in the pedigree. In the present application of *Familias* all candidate pedigrees were assumed *a priori* equally likely.

Assuming that all three dyads consist of 1st order relatives, only two individual genealogies were consistent with the data (sex and mtDNA). The four samples are comprised of either: (1) a mother and her three female offspring; or (2) a grandmother, her daughter and her two granddaughters. In case (1) the question of interest is whether any of the three offspring were sired by the same male. In case (2) the two offspring are most likely the two smallest individuals (1 and 3 in Table 1), and the question of interest is whether they have the same father. Both of these hypotheses were tested using *Familias* based on genotype data from all 25 loci.

RESULTS

The 15 loci confirmed 1st order relatedness (probabilities 0.998, 1.000 and 0.999, respectively, for dyads 1, 2 and 3 in Table 2). Additional evidence was provided by the fact that the mtDNA haplotype shared by the four females was rare (population frequency 0.0173). Under genealogy (1) the probability that three different males sired the three offspring was found to be 0.980. It should also be noted that at locus EV1 the three daughters hold as a trio three distinct alleles (149, 155 and 171) not found in the mother (Table 1). This fact excludes the possibility that a single male has sired all three offspring. Under genealogy (2) the probability that two different males sired the two offspring was 0.9998. Even if the grandmother in reality should be 3 (and not 2 as assumed by us), the calculations done under genealogy (1) show that 0.980 is a lower bound on this probability.

Table 2

Summary of non-genetic information about the four individuals (all females) that constitute the three dyads. The column ‘ID’ gives the internal identification numbers in the DNA-register, and ‘length’ is the zoological length (cm) measured on board the catching vessel.

		Time of catch			
Individual	ID	Year	Month	Date	Length (cm)
Mother	9802286	1998	June	2	900
1	0104083	2001	May	12	740
2	0201618	2002	June	5	870
3	0003304	2000	July	21	810

DISCUSSION

The results presented here constitute the first indication of the occurrence of promiscuous mating of female common minke whales. They support the expectation from other baleen whale species that female minke whales mate promiscuously across seasons. The genetic analysis employed in this study revealed that even though only 3% of the population was sampled it is possible to obtain insights into parentage and mating strategies.

The 10 microsatellite loci show very little sign of spatial inhomogeneity in allele frequencies (IWC, 2004). It is not straight forward to check if the same holds true for the additional 15 loci, because the 439 individuals used to estimate allele frequencies were not randomly sampled from the DNA-register. The probabilities presented were all calculated under the assumption that the four individuals comes from a single homogeneous population. Violation of this assumption would make it even more unlikely that the three dyads should match at all 15 loci, and hence is of little concern for the main conclusion regarding relatedness.

The three dyads considered in the present paper are a subset of the dyads detected in Skaug *et al.* (2005). For dyads involving mother and offspring caught in different years, as is the case for the three dyads considered, the capture locations may provide information about maternally-inherited site fidelity. The fact that the mother is caught at the Finnmark coast (Fig. 1), while one daughter (1) was caught in the North Sea, apparently provides evidence against such an hypothesis. This interpretation is however confounded by the fact that minke whales are a migratory species and it is possible that the maternally inherited factor is the whole migratory route and timing. To test this more complicated hypothesis one should also look at date of capture, but a sample of three dyads does not allow such an analysis to be conducted.

Breeding structure is currently not a part of the population dynamics models employed by the IWC, and the findings of the present paper suggest that this practice is appropriate for common minke whales.

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Abundance of Antarctic blue whales south of 60°S from three complete circumpolar sets of surveys

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ABSTRACT

Sightings from the IDCR/SOWER austral summer surveys are analysed to provide abundance estimates for Antarctic (true) blue whales (*Balaenoptera musculus intermedia*) south of 60°S. The IDCR/SOWER ship-borne surveys have completely circled the Antarctic three times: 1978/79-1983/84 (CPI); 1985/86-1990/91 (CPII); and 1991/92-2003/04 (CPIII), covering strata totalling 64.3%, 79.5% and 99.7% of the ocean surface between the pack ice and 60°S. During the surveys, blue whale sightings were rare but were recorded in all regions. Raw sighting rates (schools per 1,000 n.mile of primary search effort) were 0.44 (CPI), 0.67 (CPII) and 1.48 (CPIII). Respective circumpolar abundance estimates were 453 (CV=0.40), 559 (CV=0.47) and 2,280 (CV=0.36), with corresponding mid-years of 1981, 1988 and 1998. The CPIII estimates are the most complete and recent for this subspecies. When adjusted for unsurveyed regions in a simple way, the estimated circumpolar rate of increase is 8.2% (95% CI=1.6–14.8%) per year; nevertheless, Antarctic blue whales still number far less than the estimated 202,000-311,000 that existed before exploitation. These abundance estimates are negatively biased because some Antarctic blue whales may have been north of 60°S or in the pack ice at the time of the surveys and because a small number of blue whales on the trackline were probably missed. Furthermore, a small proportion of pygmy blue whales, probably less than 1%, may have been included in the sightings.

KEYWORDS: BLUE WHALE; SOWER; WHALING-HISTORICAL; ANTARCTIC; SOUTHERN HEMISPHERE; SURVEY-VESSEL; ABUNDANCE ESTIMATE

INTRODUCTION

Whaling reduced the once large numbers of blue whales (*Balaenoptera musculus*) to a small fraction of their original levels (e.g. Clapham *et al*., 1999). Of the three widely recognised subspecies, Antarctic blue whales (*B.m. intermedia*) greatly dominated pre-exploitation abundance and historical catches, while catches and pre-exploitation abundance of northern blue whales (*B.m. musculus*) and pygmy blue whales (*B.m. brevicauda*) were an order of magnitude lower (Branch *et al*., 2004; 2007a). Based on existing estimates of abundance, Antarctic blue whales originally numbered 239,000 (95% CI=202,000-311,000) but whaling from 1905-73 depleted them to a low of 360 (95% CI=150-840); despite statistically significant evidence for a subsequent increase, their numbers are still below 1% of their pre-exploitation level (Branch *et al*., 2004).

This estimated current status of Antarctic blue whales is based largely on abundance estimates from the IWC's International Decade for Cetacean Research (IDCR) and Southern Ocean Whale Ecosystem Research (SOWER) programmes. These ship-based surveys south of 60°S have been conducted annually since the 1978/79 austral summer season (i.e. December 1978 to February 1979). The surveys are conveniently grouped into three circumpolar sets of surveys (CPs), each of which completely encircled Antarctica – from 1978/79-1983/84 (CPI), 1985/86-1990/91 (CPII) and 1991/92-2003/04 (CPIII). The 1984/85 survey and those after 2003/04 were largely devoted to experiments and so are customarily excluded when obtaining abundance estimates (e.g. Branch, 2006a; 2007a; Branch and Butterworth, 2001a; 2001b). The most recent IDCR/SOWER estimates for CPI and CPII were 440 (CV=0.41) and 550 (CV=0.48) respectively (Branch and Butterworth, 2001a), but no estimates have been provided for the complete CPIII set. The CPIII estimate for the proportion of the area which had been covered up to 1997/98 (68%) was 1,100 (CV=0.45) (Branch and Butterworth, 2001a), and for that up to 2001/02 (91%) was 1,700 (CV=0.42) (Branch and Rademeyer, 2003). However, since these estimates were presented, CPIII has been completed, with the most important addition being the resurveying (2001/02-2003/04) of IWC Management Area V (130°E-170°W) from the pack ice northwards to 60°S. When Area V was previously surveyed earlier during the CPIII set in 1991/92, the survey did not include the northernmost area south of 60°S.

For the analyses that follow, blue whale sightings south of 60°S are assumed to be Antarctic blue whales, although some may be pygmy blue whales. The proportion that are pygmy blue whales has previously been assumed to be no more than 7% (IWC, 2003); however, evidence from length frequencies and from ovarian corpora data suggests that for females (and therefore probably also for males) the upper limit is closer to 1% (Branch, 2006b; Branch *et al*., 2007b).

This paper presents updated abundance estimates from the three completed circumpolar sets of surveys. Previous estimates were provided at the circumpolar level only, but here, estimates are also presented for individual surveys and for IWC Management Areas.

METHODS

The analysis methods are presented concisely below as they are only slightly modified from those in Branch and Butterworth (2001a). These minor modifications are listed in detail for humpback whales (Branch, 2007a) and so are only summarised here in Table 1. Data extraction and abundance estimation are mostly automated in the IWC's Database Estimation System Software (DESS 3.42 April 2006; described in Strindberg and Burt (2004)), but substantial post-DESS manipulation is required to divide estimates among the IWC Management Areas (Figs 1 and 2) and to account for multiple surveys of areas during the same CP set.

Table 1

Summary of changes to the analyses compared to those in Branch and Butterworth (2001a).

Topic	Branch and Butterworth (2001a)	This paper	Implications
Activity codes	BA, BB, BC, BL, BR, SE, BH, BI, BO, BP, BQ, BU, BV	BB renamed to BK	None
Duplicates and triplicates	'Definite' and 'possible' duplicates and triplicates treated as multiple records of a single sighting	Only 'definite' duplicates and triplicates treated as multiple records of a single sighting	Increases estimates by about 1%
Survey legs parallel to ice edge in 1988/89 and 1989/90	Included	Excluded	Decreases CPII estimate by 0.4%
Area of ES stratum in 1996/97	67,072 n.mile^2	Corrected to 52,534 n.mile^2	Decreases CPIII estimate by 0.5%
EN2 stratum in 1997/98	Treated as if divided into two separate strata each surveyed by one vessel	Treated as one stratum surveyed by two vessels	No effect
Estimated school size	Either regression method or mean within 1.5 n.miles	Regression method unless positive correlation or school size less than one, then mean within 0.5 n.mile	No effect since regression always positive for blue whales

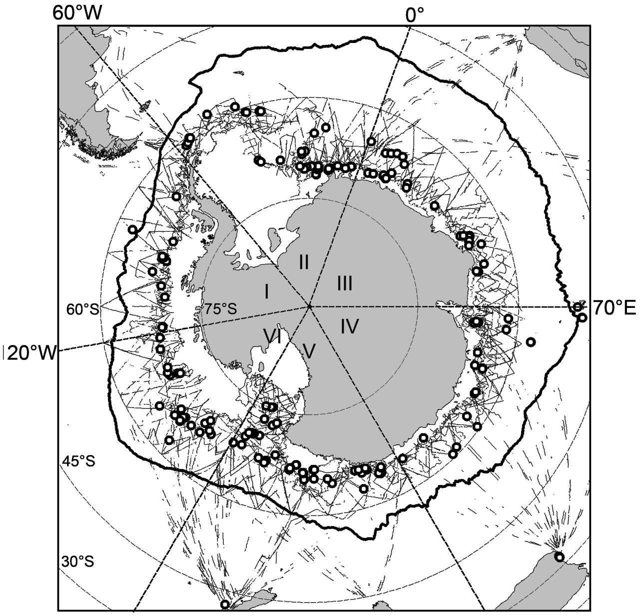

Fig. 1. Primary effort (thin grey lines) and all sightings of blue whales (black circles) from the IDCR/SOWER surveys, 1978/79-2004/05. Plotted survey effort includes transits to and from the survey regions and survey years (1984/85, 2004/05) devoted primarily to experiments that are not included in the abundance estimates. Sightings include those made off effort and during refuelling, but exclude duplicate and triplicate sightings of the same school. The Antarctic Polar Front is represented by a thicker line and is based on data from Moore *et al.* (1999). Dashed lines extending from the South Pole and associated Roman numerals I–VI demarcate the IWC Management Areas.

Survey design

Details of the surveys can be obtained from annual reports (e.g. Ensor *et al.*, 2007), while most of the survey methods are summarised in multi-year reviews (Branch and Butterworth, 2001b; Joyce *et al.*, 1988; Matsuoka *et al.*, 2003). Survey design differed among the three CPs, complicating efforts to compare abundance estimates between CPs (Figs 1-2). In CPI, one vessel generally followed the pack ice while the other surveyed in a rectangular pattern, leaving unsurveyed regions both between the northern and southern strata, and between the northern survey boundary and 60°S. In CPII, the surveys generally followed a zig-zag design with no gap between northern and southern strata, but left unsurveyed regions between the northernmost boundary and 60°S. Finally, the CPIII surveys completely surveyed the region south of 60°S to the ice edge, but had to reduce annual longitudinal coverage to achieve the additional latitudinal coverage, and hence needed 13 years to complete compared to the six years for each of CPI and CPII. Additionally, in CPIII but not in CPI or CPII, some longitudinal regions were surveyed more than once. Survey modes differed among the CPs; in CPI the surveys were conducted in closing mode only, while in the other two CPs the surveys alternated between closing mode and independent observer (IO) mode. IO mode is a form of passing mode where the vessel did not leave the trackline to confirm the species identity and school size of the sighting, and there was an observer in the independent observer barrel on the mast in addition to the observers in the topman platform.

Data selected for analysis

Closing mode and IO mode data are combined for analysis in this paper, due to the low number of blue whale sightings. The raw sighting rates (per 1,000 n.mile) for CPII and CPIII were 0.93 for closing mode and 1.08 for IO mode, based on a small number (82) of sightings. Although the closing mode sighting rate is somewhat smaller, the estimated search half width is expected to be narrower in closing mode (because there is one fewer observer), which would offset this difference. Previous Antarctic analyses have also combined these data and sensitivities to this kind of pooling showed that estimates for other species obtained separately for each mode were similar (Branch and Butterworth, 2001a). Many different effort codes have been recorded over the years as listed in Branch and Butterworth (2001a; 2001b). Primary effort is when the vessels were searching for whales, and excludes, for example, effort spent confirming species identity or school size, refuelling, experiments and drifting during bad weather. In this paper, all primary search effort is included, except for research effort specifically directed towards areas of high expected blue whale density (BB activity code). Sightings were included when calculating the estimates if recorded as code 01 (Antarctic blue whale), code 98 (blue whale, probably Antarctic), or code 99 (blue whale, undetermined subspecies), but were excluded if recorded as code 56 (pygmy blue whale) or code 96 (blue whale, probably pygmy). Where duplicate and triplicate sightings were recorded from multiple platforms during IO mode, those classified as 'definite' duplicates and triplicates were assumed to refer to a single school, while 'possible' and 'remote' duplicates and triplicates were assumed to be sightings of multiple schools. Only 0.3% of sightings of all

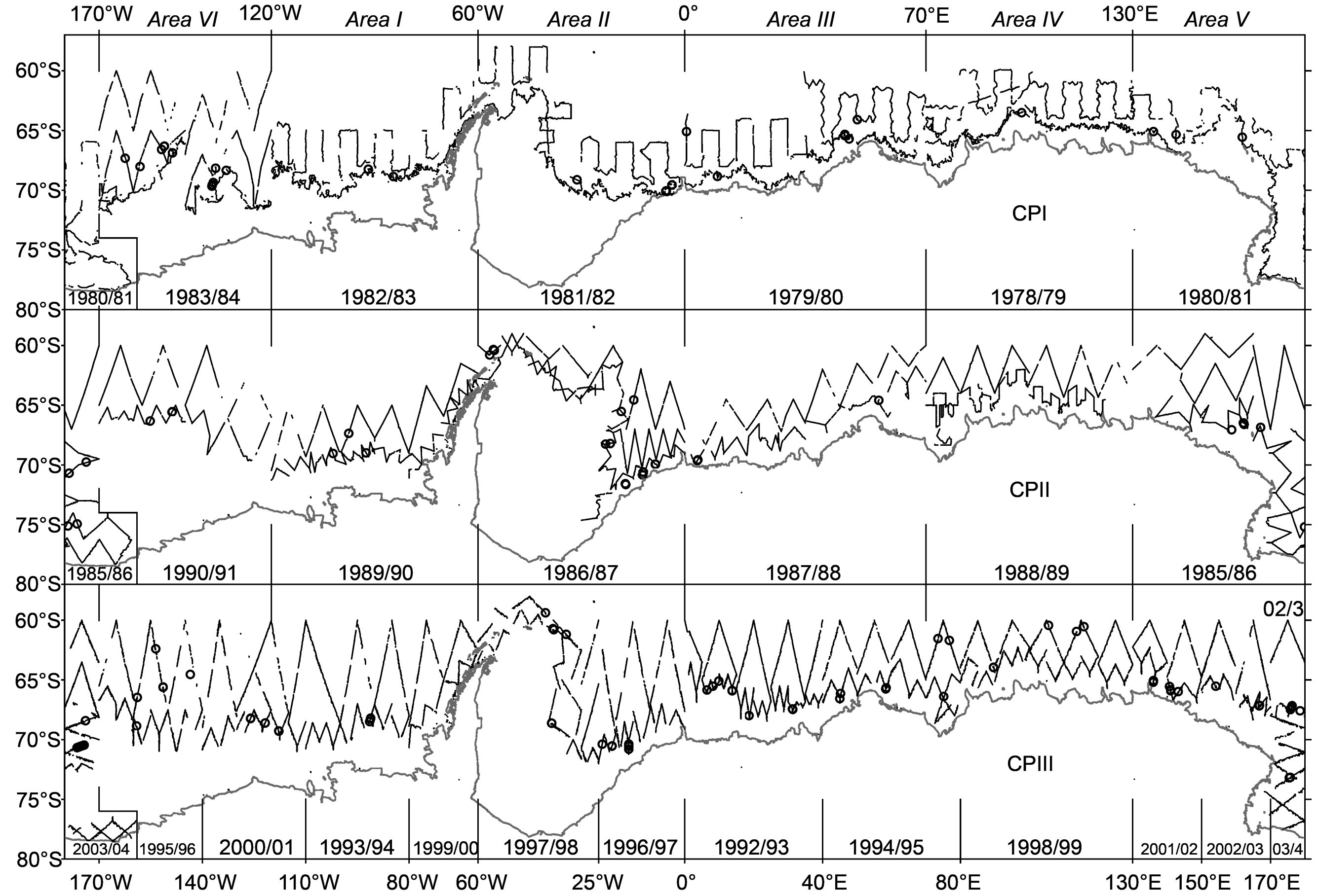

Fig. 2. Primary search effort (solid lines) during each of the surveys included in the first, second and third circumpolar sets of surveys (CPI, CPII and CPIII), and associated sightings of blue whales (circles). Only the effort and sightings used in estimating circumpolar abundances are shown. Vertical lines at the top of each panel indicate the six IWC Management Areas, while vertical lines at the bottom of each panel show the divisions between the surveys.

species were recorded as 'possible' duplicates (Branch and Butterworth, 2001a), thus this decision about duplicates should have negligible impact on the results.

Abundance estimation

Abundance estimates were obtained using the standard line transect formula:

$$N = \frac{A \cdot E[s] \cdot n}{2 \cdot w_s \cdot L} \qquad (1)$$

where:

N = abundance estimate;
A = area of stratum (n.mile^2);
$E[s]$ = mean school size;
n = number of schools sighted during primary search effort;
w_s = effective search half-width for schools (n.mile);
L = primary search effort (n.miles).

The CV for N was calculated from:

$$CV(N) = \sqrt{\left[CV\left(\frac{n}{L}\right)\right]^2 + \left[CV\left(E[s]\right)\right]^2 + \left[CV\left(w_s\right)\right]^2} \qquad (2)$$

Sightings were smeared using Method II of Buckland and Anganuzzi (1988) and then grouped into 0.1 n.mile bins to the truncation distance of 3.0 n.miles, as recommended during analyses by Branch and Butterworth (2001a). In analyses for minke whales and humpback whales, smearing parameters were estimated from the data (Branch, 2006a; 2007a). However, because of the paucity of data for blue whales, smearing parameters could not be estimated reliably from the data and were instead set to 4.0° (angle) and 0.3 n.mile (distance), based on average values for other species and the recommended values used by Branch and Butterworth (2001a). The hazard rate detection function was fitted to the smeared perpendicular distances of the selected sightings:

$$\begin{aligned} f(y) &= f(0)g(y) \\ &= f(0)\left[1-\exp\left(-\left[\frac{y}{a}\right]^{-b}\right)\right] \end{aligned} \qquad (3)$$

where $g(y)$ is the probability that a school at a perpendicular distance y from the trackline will be sighted, and a and b are estimated parameters subject to the constraints that $a \geq 0.0001$ n.mile and $b \geq 1$. For the abundance estimates it was assumed that $g(0)=1$, i.e. that all schools on the trackline were sighted, which seems a reasonable approximation given the highly visible cues produced by blue whales.

School size estimates were obtained from sightings with confirmed school sizes in closing mode only. Large schools are visible at greater distances than small schools and therefore estimates of school size were corrected for bias using the regression method proposed by Buckland *et al.* (1993), which accounts for changes in the detectability of different school sizes with distance from the vessel. Sample sizes were small, requiring sightings to be pooled over all surveys in a CP set to estimate search half-width and mean school size.

Combining estimates

Abundance estimates were obtained for individual surveys, for each IWC Management Area, and for each CP set. For CPI and CPII, the survey design rendered estimates easy to obtain for Management Areas and for circumpolar sets, but during CPIII some surveys repeated longitudinal coverage and others were spread over two Management Areas. Therefore, CPIII Management Area and circumpolar estimates required the splitting of strata and the division of survey effort and sightings between the new substrata as outlined in detail in Branch (2005). Note that circumpolar estimates from CPIII exclude the 1991/92 survey in Area V since this region was more completely covered during 2001/02-2003/04.

The differing nature of the three CPs poses several issues when comparing estimates, including: the different survey design and survey modes; the unsurveyed central regions in CPI; the lack of survey effort northwards to 60°S in most of the CPI and CPII surveys; and the unknown proportion of blue whales north of 60°S during the survey period. The most important of these issues is the unsurveyed northern areas in CPI and CPII, which are taken into account using the simple assumption employed by Branch and Butterworth (2001a; 2001b) and Branch (2006a; 2007b) that the density in the unsurveyed northern areas is the same as in the adjacent northern strata. This assumption will tend to over-estimate the 'comparable-areas' estimates in CPI and CPII because the density in the unsurveyed northern areas is likely lower than in the corresponding northern strata, given that their density declines with increasing distance from the pack ice (Branch *et al*., 2007a; Kasamatsu *et al*., 2000). Following this reasoning, the best estimates for the whole area south of 60°S based on CPI and CPII are likely between the base survey estimates (which assume zero whales in the unsurveyed northern areas) and the 'comparable-areas' estimates, which are 31% (CPI) and 23% (CPII) higher (see Results).

Circumpolar sighting rates

For comparison with other blue whale surveys in the Southern Hemisphere and northern Indian Ocean listed in Branch *et al.* (2007a), the number of schools sighted per 1,000 n.mile of primary effort was calculated for all strata surveyed during 1978/79-1983/84 (CPI), 1985/86-1990/91 (CPII) and 1992/93-2003/04 (CPIII). For these calculations, sighting numbers were neither smeared nor truncated at 3.0 n.mile.

Annual rate of change

The annual rate of increase for the circumpolar comparable-area abundance estimates was estimated by fitting an exponential growth model to the log of the estimates:

$$\ln \hat{N}_t = \ln N_0 + rt$$

where

N_0 is the abundance in the starting year (1981);
$\hat{N}_t$ is the model-estimated abundance t years after the starting year;
r is the annual rate of increase.

For many reasons, the distribution of whales within and also between Management Areas changes from year to year, and this inter-Area variability would not be taken into account if the variance of an abundance estimate obtained by summing over Areas (i.e. the CP abundance estimates) accounted only for the sampling variance estimate from each survey. This missing component of the overall variance is termed 'additional variance'. The variance (in the form of a CV^2) for fitting a growth model to interannual estimates therefore comprises both the variance for each survey, CV_t^2, and the additional variance, CV_{add}^2, which is assumed to be the same for all CP estimates. The resulting negative log likelihood expression for obtaining maximum likelihood estimates of N_0, r, and CV_{add}^2 (ignoring constant terms) is:

$$-\ln L = \sum_t \left[\ln \sqrt{CV_t^2 + CV_{\text{add}}^2} + \frac{\left(\ln N_t - \ln \hat{N}_t\right)^2}{2\left(CV_t^2 + CV_{\text{add}}^2\right)} \right]$$

The 95% confidence intervals for r were obtained by likelihood profiling, i.e. by finding the two values of r for which the negative log likelihood is 1.92 units higher than for the maximum likelihood estimate (MLE) (e.g. Hilborn and Mangel, 1997).

RESULTS

Survey coverage and primary effort distribution

Survey coverage of the ice-free area south of 60°S was most complete in CPIII, when 99.7% of the area was covered, compared to 64.3% (CPI) and 79.5% (CPII) in the earlier surveys (Fig. 2). Blue whales were sighted in all regions of the Antarctic, typically close to the pack ice, and were also sighted occasionally north of the survey region during transits in the southern Indian Ocean and close to New Zealand (Fig. 1). Based on historical catch length frequencies and their current distribution, the northerly sightings were most likely to have been pygmy blue whales (Branch *et al*., 2007a; 2007b).

Abundance estimates

Stratum-specific components of the abundance estimates are presented in Table 2. CP-specific estimates of search half width and mean school size were highest in CPI, but were not significantly different from the CPII and CPIII estimates (Table 3). The detection function fits to the sighting distributions (Fig. 3) appear poor in CPI and CPII, but care must be taken in interpreting the apparent systematic deviations between 'data' and model estimates in these plots, as the 'data' here are smeared, which in conjunction with the small associated sample sizes (Table 3) leads to substantial correlation across neighbouring perpendicular distance bins in the histograms shown. The only 'mis-fit' of potential concern is the large peak for the first 0.1 n.mile bin for CPI, which probably reflects insufficient smearing to account for the relatively large number of angle observations rounded to 0 in the CPI cruises. To test whether this lack of fit to the apparent peak introduced any bias, the data were grouped into 0.5 n.mile bins (instead of 0.1 n.mile bins) and the hazard rate model re-fitted. The estimate of search half width changed from 1.97 to 1.99, indicating that this introduces little bias to the estimates.

Estimated circumpolar abundance increased by a small amount from CPI to CPII but was markedly higher for CPIII, even when each is adjusted simply for unsurveyed areas (Table 4). Abundance estimates were 453 (CV=0.40)

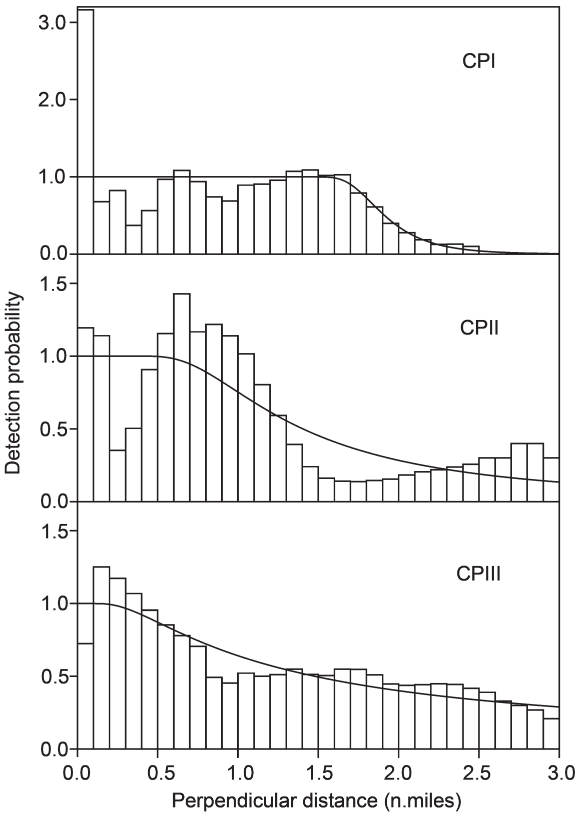

Fig. 3. Detection function fits to the smeared and truncated sightings for the circumpolar abundance estimates based on data from CPI (top panel), CPII (middle panel) and CPIII (bottom panel). Note that a different vertical scale is used for CPI.

for CPI, 559 (CV=0.47) for CPII and 2,280 (CV=0.36) for CPIII. Note that the CPIII circumpolar estimate declined when adjusted for comparable areas because some primary survey effort north of 60°S in Area II was excluded.

Abundance estimates were highest in CPIII for all IWC Management Areas, but when the estimates were adjusted for unsurveyed areas, this pattern did not hold in Areas I and III (Table 5), although the CVs at this fine spatial scale are too large to allow detection of differences of any statistical significance. Area V was consistently estimated to contain the most blue whales.

At least one blue whale was recorded during primary search effort in all surveys except 1988/89 and 1999/00, for which the abundance estimates were zero, while the highest estimated abundance for a single survey was 557 in 2003/04 (Table 6).

Estimated rate of increase

The estimated rate of increase based on ‘comparable-area’ circumpolar abundance estimates was 8.2% per annum (95% CI=1.6-14.8%). Had additional variance been ignored, the 95% CI would have been underestimated as 3.8-12.5%. Overall sighting rates (number of schools per 1,000 n.mile of primary effort) increased over time from 0.44 (CPI) to 0.67 (CPII) to 1.48 (CPIII).

DISCUSSION

The IDCR/SOWER surveys provide the most comprehensive circumpolar abundance estimates to date for Antarctic blue whales. During CPIII, survey coverage was 99.7% of the ice-free area south of 60°S during the austral summer when most Antarctic blue whales are found in the survey region. Estimates are negatively biased to some extent because some Antarctic blue whales do not enter the survey region; 20.2% of the historical catches (some of which were pygmy blue whales) were north of 60°S during the survey months (Horwood, 1986). Furthermore, some Antarctic blue whales do venture into the unsurveyed southern pack ice (Tomilin, 1967; Best, 2007; P. Ensor, pers. comm.), although acoustic evidence suggests they generally avoid areas covered by sea ice (Širovíc *et al*., 2004). Negative bias to the estimates also occurs because it is assumed that all whales on the trackline were sighted, i.e. that $g(0)=1$. The bias resulting from this assumption is probably small because of the great visibility of blue whale cues and their frequency of cue production: $g(0)$ for the surveys is probably between 0.9 and 1 (Best *et al*., 2003; Calambokidis and Barlow, 2004; Kasamatsu, 2000). There is great uncertainty about the magnitude of these factors, but if the estimates above are applicable, the CPIII abundance estimates would be negatively biased by 20-30%.

It has previously been assumed that a small proportion of these estimates (no more than 7%) could be pygmy blue whales (IWC, 2003). However, recent mixture models of ovarian corpora data (Branch, 2006b) and the length frequencies of mature females (Branch *et al*., 2007b) demonstrate that this proportion is no more than 1% for females in the historical catches. There is no obvious reason to suppose that these results might not apply to the present-day population of both sexes: there is no evidence in the corpora data that the proportion of pygmy blue whales south of 60°S increased over time despite substantial depletion of Antarctic blue whales (Branch, 2006b) and the sex ratio in catches was close to the birth sex ratio (Branch *et al*., 2007b).

Estimated sighting rates (schools per 1,000 n.mile of primary effort) increased from 0.44 (CPI) to 0.67 (CPII) to 1.48 (CPIII). These sighting rates are in line with simple estimates from other Antarctic studies listed in Branch *et al.* (2007a), 0.31 from the earlier Japanese Scouting Vessel (JSV) data (1965/66-1988/89) and 0.63 from Japanese Whaling Research Program under Scientific Permit in the Antarctic (JARPA) surveys (1989/90-2004/05), but are substantially lower than sighting rates (3.7-97.0) recorded for other populations of blue whales in the remainder of the Indian Ocean, around southern Australia and in Chilean waters.

Circumpolar estimates for CPI and CPII differ little from previous estimates (Branch and Butterworth, 2001a; Branch and Rademeyer, 2003), but the CPIII estimate of 2,280 (CV=0.36) is substantially larger than the 1,069 (CV=0.45) in Branch and Butterworth (2001a) and the 1,671 (CV=0.42) in Branch and Rademeyer (2003). There are two reasons for the increase: (1) the previous estimates were for areas that covered only 68% (Branch and Butterworth, 2001a) and 91% (Branch and Rademeyer, 2003) of the region south of 60°S; and (2) Area V was resurveyed in 2001/02 to 2003/04 and the new estimate of 765 replaced the previous estimate of 260 from 1991/92.

Antarctic blue whales were sighted throughout the Antarctic, so it is not surprising that the abundance estimates are spread among all of the IWC Management Areas. The highest historical catches were taken from Areas I-III, which have lower current abundances of Antarctic blue whales than Areas IV-VI. This may suggest that the extent of depletion was greater in Areas I-III, but the evidence for this is weak given the great uncertainty around the abundance estimates. JARPA estimates for Areas IV and V are also highly uncertain (Matsuoka *et al*., 2006), (Fig. 4).

Table 2

Components of abundance estimates for each survey. Indicated for each stratum are the stratum name, vessel, area (A), number of transects (N_L), number of schools sighted during primary search effort (n), number of schools sighted after smearing and truncation (n_s), search effort (L), sighting rate (n_s/L), and estimates of abundance in each stratum (N). Strata that were surveyed by more than one vessel have the same number in the 'Ave' column.

Stratum	IWC Area	Year	Vessel	Stratum	A (n.mile^2)	N_L	n	n_s	L (n.mile)	$n_s/L*10^3$	CV	N	CV	Ave
1	IV	1978/79	T16	EN	156,766	18	0	0.0	2,155.5	0.00	0.00	0	0.00	
2	IV	1978/79	T16	W1N	39,256	2	0	0.0	222.2	0.00	0.00	0	0.00	1
3	IV	1978/79	T16	W1S	20,389	5	0	0.0	200.6	0.00	0.00	0	0.00	
4	IV	1978/79	T16	W2N	153,914	3	0	0.0	384.7	0.00	0.00	0	0.00	2
5	IV	1978/79	T16	W2S	29,600	12	1	1.0	1,073.3	0.93	1.03	13	1.04	3
6	IV	1978/79	T18	ES	27,571	16	0	0.0	1,436.6	0.00	0.00	0	0.00	
7	IV	1978/79	T18	W1N	39,256	6	0	0.0	685.3	0.00	0.00	0	0.00	1
8	IV	1978/79	T18	W2N	153,914	11	0	0.0	1,212.5	0.00	0.00	0	0.00	2
9	IV	1978/79	T18	W2S	29,600	4	0	0.0	393.4	0.00	0.00	0	0.00	3
10	III	1979/80	K27	ES	41,772	20	3	3.0	1,346.5	2.23	0.68	43	0.70	
11	III	1979/80	K27	WN	200,724	16	1	1.0	2,014.9	0.50	1.03	46	1.04	
12	III	1979/80	T11	EN	217,865	20	1	1.0	2,636.7	0.38	0.99	38	1.00	
13	III	1979/80	T11	WS	33,619	19	1	1.0	968.2	1.03	0.82	16	0.84	
14	V	1980/81	K27	EN	208,159	14	0	0.0	877.3	0.00	0.00	0	0.00	
15	V	1980/81	K27	ES	98,766	5	0	0.0	439.6	0.00	0.00	0	0.00	4
16	V	1980/81	K27	WS	34,164	17	0	0.0	698.1	0.00	0.00	0	0.00	
17	V	1980/81	T11	ES	98,766	21	1	1.0	2,133.3	0.47	0.81	21	0.83	4
18	V	1980/81	T11	WN	139,191	15	1	1.0	1,151.6	0.87	0.80	56	0.83	
19	II	1981/82	SM1	ES	29,633	18	1	1.0	1,162.9	0.86	0.99	12	1.01	
20	II	1981/82	SM1	W1N	135,504	10	0	0.0	1,064.9	0.00	0.00	0	0.00	
21	II	1981/82	SM1	W2S	52,096	10	0	0.0	920.6	0.00	0.00	0	0.00	5
22	II	1981/82	SM2	EN	145,063	17	0	0.0	1,748.8	0.00	0.00	0	0.00	
23	II	1981/82	SM2	W1S	35,725	9	0	0.0	872.2	0.00	0.00	0	0.00	
24	II	1981/82	SM2	W2S	52,096	12	1	1.0	812.4	1.23	1.17	30	1.18	5
25	I	1982/83	SM1	ES	33,050	15	1	1.0	928.0	1.08	0.95	16	0.97	
26	I	1982/83	SM1	WN	163,926	15	0	0.0	1,426.1	0.00	0.00	0	0.00	
27	I	1982/83	SM2	EN	149,433	17	0	0.0	1,054.4	0.00	0.00	0	0.00	
28	I	1982/83	SM2	WS	25,596	19	1	1.0	1,414.8	0.71	1.27	8	1.29	
29	VI	1983/84	K27	EMS	158,893	5	1	1.0	1,094.4	0.91	1.67	67	1.68	
30	VI	1983/84	K27	WN	207,721	5	0	0.0	875.6	0.00	0.00	0	0.00	
31	VI	1983/84	SM1	EN	202,108	5	0	0.0	911.6	0.00	0.00	0	0.00	
32	VI	1983/84	SM2	WMS	156,457	5	2	2.0	1,309.0	1.53	0.72	110	0.75	
1	V	1985/86	K27	EN	279,611	16	0	0.0	1,757.7	0.00	0.00	0	0.00	
2	V	1985/86	K27	WS	104,814	28	4	3.9	1,596.8	2.45	1.06	113	1.11	
3	V	1985/86	SM1	EM	165,912	20	2	2.0	1,866.4	1.07	0.83	78	0.90	
4	V	1985/86	SM1	WM	166,349	8	0	0.0	850.0	0.00	0.00	0	0.00	
5	V	1985/86	SM2	ES	107,717	22	3	1.0	1,737.8	0.56	0.74	27	0.81	
6	V	1985/86	SM2	WN	139,065	10	0	0.0	1,121.5	0.00	0.00	0	0.00	
7	II	1986/87	K27	ES1	23,142	8	0	0.0	527.6	0.00	0.00	0	0.00	
8	II	1986/87	K27	WS1	10,270	4	1	1.0	185.5	5.39	1.08	24	0.35	
9	II	1986/87	K27	WS2	21,143	4	0	0.0	239.7	0.00	0.00	0	0.00	6
10	II	1986/87	K27	WS3	79,605	15	0	0.0	1,014.8	0.00	0.00	0	0.00	7
11	II	1986/87	K27	EN	124,057	7	1	1.0	965.9	1.01	0.98	55	1.04	
12	II	1986/87	SM1	EBAY	15,242	7	0	0.0	232.2	0.00	0.00	0	0.00	
13	II	1986/87	SM1	ES2	44,975	29	3	3.0	1,287.8	2.33	0.69	46	0.77	
14	II	1986/87	SM1	WBAY	11,505	3	0	0.0	166.4	0.00	0.00	0	0.00	
15	II	1986/87	SM1	WN	95,361	6	0	0.0	516.6	0.00	0.00	0	0.00	
16	II	1986/87	SM2	EM	69,908	9	0	0.0	1,445.6	0.00	0.00	0	0.00	
17	II	1986/87	SM2	WS2	21,143	3	0	0.0	234.6	0.00	0.00	0	0.00	6
18	II	1986/87	SM2	WS3	79,605	19	0	0.0	1,119.8	0.00	0.00	0	0.00	7
19	III	1987/88	SM1	ES	87,677	15	1	1.0	1,196.0	0.84	0.78	32	0.85	
20	III	1987/88	SM1	WN	148,821	13	0	0.0	857.3	0.00	0.00	0	0.00	
21	III	1987/88	SM2	EN	168,881	14	0	0.0	1,086.7	0.00	0.00	0	0.00	
22	III	1987/88	SM2	WS	74,351	21	3	3.0	1,247.3	2.41	0.88	79	0.94	
23	IV	1988/89	SM1	BS	6,520	4	0	0.0	231.9	0.00	0.00	0	0.00	
24	IV	1988/89	SM1	EN	181,166	12	0	0.0	1,116.3	0.00	0.00	0	0.00	
25	IV	1988/89	SM1	WS	58,693	10	0	0.0	483.5	0.00	0.00	0	0.00	
26	IV	1988/89	SM2	BN	17,486	15	0	0.0	627.7	0.00	0.00	0	0.00	
27	IV	1988/89	SM2	ES	52,441	9	0	0.0	554.3	0.00	0.00	0	0.00	
28	IV	1988/89	SM2	WN	156,617	12	0	0.0	1,431.9	0.00	0.00	0	0.00	
29	I	1989/90	SM1	ESBAY	62,594	24	0	0.0	1,386.7	0.00	0.00	0	0.00	
30	I	1989/90	SM1	WN	168,761	13	1	1.0	1,167.1	0.86	1.03	64	1.09	
31	I	1989/90	SM2	EN	153,029	14	0	0.0	1,429.8	0.00	0.00	0	0.00	
32	I	1989/90	SM2	WS	45,128	30	2	1.5	1,433.1	1.03	0.61	21	0.70	

Cont.

Stratum	IWC Area	Year	Vessel	Stratum	A (n.mile^2)	N_L	n	n_s	L (n.mile)	$n_s/L*10^3$	CV	N	CV	Ave
33	VI	1990/91	SM1	EN	191,954	7	0	0.0	666.6	0.00	0.00	0	0.00	
34	VI	1990/91	SM1	WS	45,414	14	2	1.0	950.1	1.05	0.75	21	0.83	
35	VI	1990/91	SM2	ES	108,268	9	0	0.0	952.9	0.00	0.00	0	0.00	
36	VI	1990/91	SM2	WN	211,788	9	0	0.0	1,043.4	0.00	0.00	0	0.00	
1	V	1991/92	SM1	EN	165,429	17	2	1.7	1,008.8	1.67	0.77	127	0.82	
2	V	1991/92	SM1	WS	58,643	15	1	1.0	748.2	1.34	0.63	36	0.69	
3	V	1991/92	SM2	ES	82,039	22	0	0.0	1,416.4	0.00	0.00	0	0.00	
4	V	1991/92	SM2	WN	137,734	9	1	1.0	655.3	1.53	0.64	97	0.70	
5	III	1992/93	SM1	ES	23,207	23	1	0.0	893.4	0.00	0.00	0	0.00	
6	III	1992/93	SM1	WN	210,035	15	0	0.0	1,404.5	0.00	0.00	0	0.00	8
7	III	1992/93	SM1	WS	61,527	3	0	0.0	143.0	0.00	0.00	0	0.00	9
8	III	1992/93	SM2	EN	150,547	9	0	0.0	1,101.2	0.00	0.00	0	0.00	
9	III	1992/93	SM2	WS	61,527	31	5	5.0	1,774.6	2.82	0.53	80	0.60	9
10	III	1992/93	SM2	WN	210,035	1	0	0.0	134.2	0.00	0.00	0	0.00	8
11	I	1993/94	SM1	WS	50,596	23	3	3.0	1,068.3	2.81	1.02	66	1.06	
12	I	1993/94	SM1	EN	293,196	22	0	0.0	1,581.8	0.00	0.00	0	0.00	
13	I	1993/94	SM2	WN	251,735	16	0	0.0	1,134.0	0.00	0.00	0	0.00	
14	I	1993/94	SM2	ES	72,249	20	0	0.0	1,076.4	0.00	0.00	0	0.00	
15	III	1994/95	SM1	WS	51,938	23	4	3.7	919.6	3.97	0.74	95	0.79	
16	III	1994/95	SM1	EN	146,681	15	2	2.0	1,154.5	1.73	0.69	117	0.75	
17	III	1994/95	SM2	WN	148,803	14	0	0.0	921.6	0.00	0.00	0	0.00	
18	III	1994/95	SM2	ES	60,046	17	1	1.0	899.2	1.11	0.92	31	0.96	
19	III	1994/95	SM2	PRYD	21,096	8	0	0.0	414.2	0.00	0.00	0	0.00	
20	VI	1995/96	SM1	WS	34,051	19	0	0.0	738.9	0.00	0.00	0	0.00	
21	VI	1995/96	SM1	EN	242,073	21	4	4.0	1,045.3	3.83	0.66	427	0.72	
22	VI	1995/96	SM2	WN	97,945	9	0	0.0	528.5	0.00	0.00	0	0.00	
23	VI	1995/96	SM2	ES	72,349	19	1	1.0	1,068.5	0.94	0.88	31	0.92	
24	II	1996/97	SM1	ES	52,534	38	3	2.0	1,229.2	1.63	0.86	39	0.90	
25	II	1996/97	SM1	WN	113,687	10	0	0.0	463.9	0.00	0.00	0	0.00	
26	II	1996/97	SM2	EN	241,928	32	0	0.0	1,260.4	0.00	0.00	0	0.00	
27	II	1996/97	SM2	WS	23,028	15	2	2.0	384.5	5.20	0.37	55	0.46	
28	II	1997/98	SM1	WS	32,620	17	0	0.0	490.3	0.00	0.00	0	0.00	
29	II	1997/98	SM1	EN1	84,726	12	1	1.0	581.1	1.72	0.83	67	0.88	
30	II	1997/98	SM1	ES2	10,451	9	0	0.0	226.3	0.00	0.00	0	0.00	
31	II	1997/98	SM1	EN2	80,013	4	0	0.0	202.1	0.00	0.00	0	0.00	10
32	II	1997/98	SM2	WN	52,135	8	1	1.0	493.3	2.03	0.86	49	0.91	
33	II	1997/98	SM2	ES1	47,036	16	4	4.0	741.5	5.40	0.93	117	0.97	
34	II	1997/98	SM2	EN2	80,013	4	0	0.0	330.8	0.00	0.00	0	0.00	10
35	IV	1998/99	SM1	WS	42,605	26	0	0.0	850.0	0.00	0.00	0	0.00	
36	IV	1998/99	SM1	EN	169,387	25	3	3.0	1,136.1	2.63	0.55	205	0.62	
37	IV	1998/99	SM2	WN	105,396	18	1	1.0	637.2	1.57	0.98	76	1.02	
38	IV	1998/99	SM2	ES	70,193	50	0	0.0	1,241.6	0.00	0.00	0	0.00	
39	IV	1998/99	SM1	ES	70,193	2	0	0.0	52.5	0.00	0.00	0	0.00	
40	I	1999/00	SM1	WS	20,506	13	0	0.0	446.9	0.00	0.00	0	0.00	
41	I	1999/00	SM1	EN	57,309	11	0	0.0	417.7	0.00	0.00	0	0.00	
42	I	1999/00	SM2	WN	110,906	11	0	0.0	664.4	0.00	0.00	0	0.00	
43	I	1999/00	SM2	ES	23,632	11	0	0.0	298.0	0.00	0.00	0	0.00	
44	VI	2000/01	SM1	WN	252,078	12	0	0.0	514.0	0.00	0.00	0	0.00	11
45	VI	2000/01	SM1	WS	43,916	16	0	0.0	446.5	0.00	0.00	0	0.00	12
46	VI	2000/01	SM2	WN	252,078	21	0	0.0	710.3	0.00	0.00	0	0.00	11
47	VI	2000/01	SM2	WS	43,916	16	2	2.0	311.5	6.42	0.38	130	0.47	12
48	I	2000/01	SM1	EN	127,789	19	0	0.0	700.8	0.00	0.00	0	0.00	13
49	I	2000/01	SM2	EN	127,789	2	0	0.0	37.3	0.00	0.00	0	0.28	13
50	I	2000/01	SM2	ES	29,080	20	1	1.0	542.7	1.84	0.66	25	0.72	
51	V	2001/02	SM1	WS	34,886	21	2	2.0	550.4	3.63	0.50	59	0.57	
52	V	2001/02	SM1	ES	26,099	11	5	3.5	292.9	12.08	0.54	146	0.60	14
53	V	2001/02	SM2	WN	46,333	7	0	0.0	438.5	0.00	0.00	0	0.00	
54	V	2001/02	SM2	EN	83,082	8	0	0.0	486.4	0.00	0.00	0	0.00	
55	V	2001/02	SM2	ES	26,099	3	0	0.0	131.2	0.00	0.00	0	0.00	14
56	V	2002/03	SM1	ES	126,870	24	1	1.0	1,018.0	0.98	1.03	58	1.07	
57	V	2002/03	SM1	EN	135,038	6	0	0.0	183.9	0.00	0.00	0	0.00	15
58	V	2002/03	SM1	W2N	101,237	11	0	0.0	459.1	0.00	0.00	0	0.00	16
59	V	2002/03	SM1	W1S	22,128	12	1	1.0	352.0	2.84	1.67	29	1.69	
60	V	2002/03	SM2	EN	135,038	23	0	0.0	861.6	0.00	0.00	0	0.00	15
61	V	2002/03	SM2	W2S	21,327	27	2	2.0	526.0	3.80	0.85	37	0.89	
62	V	2002/03	SM2	W1N	75,395	13	0	0.0	466.0	0.00	0.00	0	0.00	
63	V	2002/03	SM2	W2N	101,237	4	0	0.0	43.8	0.00	0.00	0	0.00	16

Cont.

Stratum	IWC Area	Year	Vessel	Stratum	A (n.mile^2)	N_L	n	n_s	L (n.mile)	$n_s/L*10^3$	CV	N	CV	Ave
64	V	2003/04	SM2	N1	123,227	13	0	0.0	489.1	0.00	0.00	0	0.00	
65	V	2003/04	SM1	N2	95,445	18	0	0.0	587.2	0.00	0.00	0	0.00	
66	V	2003/04	SM1	N3	14,598	4	4	4.0	153.0	26.14	1.13	176	0.28	
67	V	2003/04	SM1	ROSS	56,444	23	0	0.0	544.6	0.00	0.00	0	0.00	17
68	V	2003/04	SM2	ROSS	56,444	15	0	0.0	556.7	0.00	0.00	0	0.00	17
69	V	2003/04	SM1	MID	131,782	18	7	6.9	707.3	9.82	0.73	597	0.78	18
70	V	2003/04	SM2	MID	131,782	23	3	3.0	881.5	3.40	0.51	207	0.58	18

Table 3

Estimates of search half-width (w_s), mean school size ($E[s]$) and their associated CVs for each circumpolar set of surveys. Estimates differ slightly for each category of the CPIII estimates due to slight changes in how the strata were divided and which strata were included to obtain the estimates.

Surveys	w_s	CV	$E[s]$	CV
CPI all	1.966	0.110	1.81	0.149
CPII all	1.624	0.277	1.43	0.208
CPIII circumpolar	1.700	0.286	1.59	0.105
CPIII IWC areas	1.736	0.280	1.57	0.101
CPIII individual surveys	1.854	0.262	1.71	0.102

Comparable abundance estimates are difficult to obtain from the circumpolar sets of surveys, primarily because of differences in percent coverage, but also because of changes in survey design (Branch and Butterworth, 2001b; Matsuoka *et al*., 2003). A simple method was used to account for the unsurveyed areas south of 60°S; it was assumed that unsurveyed northern strata contained the same density of blue whales as in the corresponding northern strata. This method increases the CPI estimate by 31% and the CPII estimate by 23% and has been used in previous IDCR/SOWER assessments for blue and minke whales (Branch and Butterworth, 2001a;2001b; Branch and Rademeyer, 2003). More sophisticated methods of comparing the circumpolar estimates are beyond the scope of this paper, but could include estimating abundance south of a northern boundary common to all CP sets, or fitting a model to the downward trend in density with increasing distance from the ice edge. It is expected that these more sophisticated methods would result in a higher ratio between CPIII abundance estimates and those from CPI or CPII.

The rate of increase from the comparable-areas circumpolar estimates is 8.2% per year, which is significantly greater than zero (95% CI=1.6-14.8%). The validity of this rate of increase is subject to the reasonableness of the comparable-area CP estimates. However, it should be noted that the IWC's in-depth assessments of Antarctic minke whales have highlighted several reasons why the CPIII minke estimates are probably negatively biased compared to the CPII estimates (Branch, 2007b); if they are also applicable to blue whales, they would tend to increase the estimated rate of increase for blue whales if taken into account (Branch *et al*., 2004). The estimated rate of increase is nearly identical to the 8.2% (95% CI=1.9-14.8%) obtained from a Bayesian assessment of Antarctic blue whales based on the IDCR/SOWER, JARPA and JSV data, when the rate of increase was weakly constrained by a Bayesian prior ~ U(-0.3, 0.3). The estimated rate of increase from the JARPA surveys is also similar: 7.4% per annum (CV=1.19) (Matsuoka *et al*., 2006). These rates of increase are close to the maximum biologically possible (10.1-12.6%) for blue whales and humpback whales (Branch *et al*., 2004; Brandao *et al*., 2000; Clapham *et al*., 2001; Clapham *et al*., 2006).

In summary, the updated circumpolar estimate of abundance for Antarctic blue whales, following completion of CPIII, is 2,280 (95% CI=1,160-4,500). This estimate is negatively biased (perhaps by 20-30%) because some Antarctic blue whales remain north of 60°S during the survey time period and because some whales on the trackline are missed. The available evidence continues to support increases in this population, although the population still remains far below the pre-exploitation levels of 202,000-311,000 estimated in Branch *et al*. (2004).

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Table 4

Estimates of abundance obtained from each circumpolar set of surveys, with the associated CVs and 95% confidence intervals obtained using the method of Buckland (1992). CPIII estimates exclude the 1991/92 survey.

		Circumpolar estimates			Adjusted simply for comparable areas		
Circumpolar set	Mid-year	N	CV	95% CI	N	CV	95% CI
CPI	1980/81	453	0.40	(210; 970)	592	0.40	(280; 1,270)
CPII	1987/88	559	0.47	(230; 1,350)	686	0.47	(280; 1,660)
CPIII	1997/98	2,280	0.36	(1,160; 4,500)	2,249	0.36	(1,140; 4,440)

Table 5

Estimates of abundance for each IWC Management Area. Estimates from Area V in CPIII were obtained from complete coverage south of 60°S in 2001/02-2003/04, and were also repeated for the survey with incomplete coverage in 1991/92 (denoted by CPIII*).

					Estimates		Comparable areas	
IWC Area	CP set	Seasons	Long. range	Mid-year	*N*	CV	*N*	CV
Area I	CPI	1982/83	60	1982/83	25	0.80	25	0.80
(120°W-60°W)	CPII	1989/90	60	1989/90	84	0.91	178	1.03
	CPIII	1993/94	30					
		1999/00	20					
		2000/01	10	1997/98	88	0.85	88	0.85
Area II	CPI	1981/82	60	1981/82	26	0.81	26	0.81
(60°W-0°)	CPII	1986/87	60	1986/87	126	0.64	158	0.71
	CPIII	1996/97	25					
		1997/98	35	1997/98	298	0.55	268	0.58
Area III	CPI	1979/80	70	1979/80	143	0.52	219	0.61
(0°-70°E)	CPII	1987/88	70	1987/88	111	0.79	111	0.79
	CPIII	1992/93	40					
		1994/95	30	1993/94	166	0.60	166	0.60
Area IV	CPI	1978/79	60	1978/79	9	1.06	9	1.06
(70°E-130°E)	CPII	1988/89	60	1988/89	0	0.00	0	0.00
	CPIII	1994/95	10					
		1998/99	50	1997/98	419	0.51	419	0.51
Area V	CPI	1980/81	60	1980/81	73	0.68	110	0.73
(130°E-170°W)	CPII	1985/86	60	1985/86	218	0.75	218	0.75
	CPIII*	1991/92	60	1991/92	260	0.56	534	0.61
	CPIII	2001/02	20					
		2002/03	20					
		2003/04	20	2002/03	765	0.43	765	0.43
Area VI	CPI	1983/84	50	1983/84	177	0.81	177	0.81
(170°W-120°W)	CPII	1990/91	50	1990/91	21	0.90	21	0.90
	CPIII	1996/96	30					
		2000/01	20	1998/99	500	0.68	500	0.68

Table 6

Estimates of abundance for each IWC survey.

Year	Area	Longitudes	*N*	CV
1978/79	IV	70°E-130°E	9	1.06
1979/80	III	0-70°E	143	0.52
1980/81	V	130°E-170°W	73	0.68
1981/82	II	60°W-0	26	0.81
1982/83	I	120°W-60°W	25	0.80
1983/84	VI	170°W-120°W	177	0.81
1985/86	V	130°E-170°W	218	0.75
1986/87	II	60°W-0	126	0.64
1987/88	III	0-70°E	111	0.79
1988/89	IV	70°E-130°E	0	0.00
1989/90	I	120°W-60°W	84	0.91
1990/91	VI	170°W-120°W	21	0.90
1991/92	V	130°E-170°W	260	0.56
1992/93	III	0°E-40°E	74	0.66
1993/94	I	110°W-60°W	66	1.09
1994/95	III+IV	40°E-80°E	243	0.56
1995/96	VI	170°W-140°W	459	0.73
1996/97	II	30°W-0	95	0.54
1997/98	II	60°W-25°W	233	0.65
1998/99	IV	80°E-130°E	282	0.60
1999/00	I	80°W-60°W	0	0.00
2000/01	VI+I	140°W-110°W	78	0.49
2001/02	V	130°E-150°E	159	0.52
2002/03	V	150°E-170°W	124	0.74
2003/04	V	170°E-170°W	557	0.49

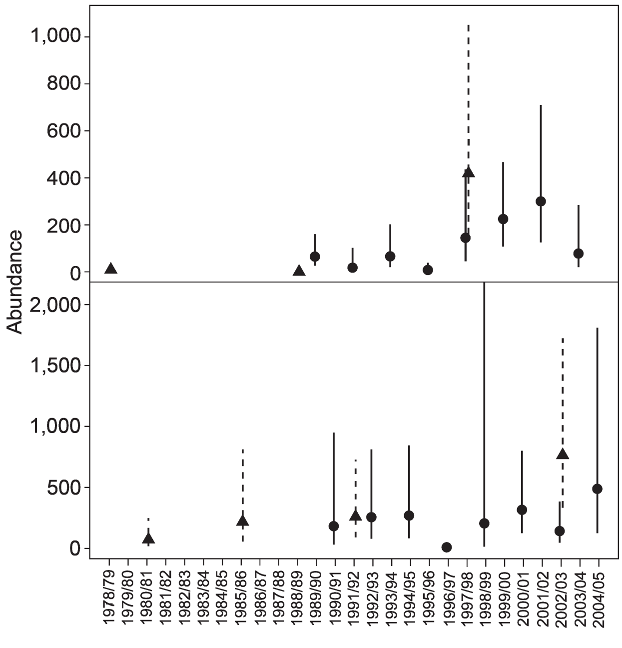

Fig. 4. Comparison of comparable-areas abundance estimates for blue whales from the IDCR/SOWER surveys and those from the JARPA surveys for Area IV (top figure) and Area V (bottom figure). The 95% CIs are shown for both sets of estimates. JARPA estimates are taken from Matsuoka *et al*. (2006).

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A note on observations on cetaceans in the western Indian sector of the Southern Ocean (20-56°S and 45-57°30'E), January to March 2004

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ABSTRACT

A multi-disciplinary and multi-institutional pilot expedition was organised by the National Centre for Antarctic and Ocean Research (NCAOR) to the ice-free areas of the Western Indian Ocean sector of the Southern Ocean onboard *ORV Sagar Kanya* during the austral summer of 2004 (January-March). This survey, conducted by the Central Marine Fisheries Research Institute (CMFRI), is the first Indian attempt to survey for cetacean diversity in the Southern Ocean. The ultimate objective is to determine distribution, relative abundance, migration patterns and critical habitat parameters. 68% of a total of 13 sightings (22 individuals) were positively identified and species observed included Antarctic minke whales (*Balaenoptera bonaerensis*), fin whales (*B. physalus*), sei whales (*B. borealis*) and blue whales (*B. musculus*). The blue whales were not identified to the sub-species level. The highest concentration of cetaceans was between 35° and 37°S (along 45°E) and between 48° and 53°S (along 45°E). Relatively small numbers of cetaceans were observed during the present cruise, possibly because most of the cetacean sighting effort was made during inclement sea conditions. Results on the sighting characteristics and occurrence patterns of the cetaceans in relation to the region and hydrographical parameters are discussed briefly *vis a vis* published information from the Southern Ocean.

KEYWORDS: SOUTHERN OCEAN; CETACEAN SIGHTINGS; ANTARCTIC MINKE WHALE; FIN WHALE; HUMPBACK WHALE; SEI WHALE; BLUE WHALE; SOUTHERN HEMISPHERE; SURVEY-VESSEL; DISTRIBUTION

INTRODUCTION

The Southern Ocean is one of the most dynamic oceans in the world, with a very strong current system and it plays a prominent role in controlling the global ocean-atmospheric climate system (Luis and Pandey, 2004). However, many aspects of its oceanography and the response of the Southern Ocean to climate change remain unknown, primarily due to the lack of high-resolution oceanographic observations, which in the Indian Ocean sector have been limited to the Arabian Sea, Bay of Bengal and Indian Ocean basin (Pandey *et al*., 2006).

In addition, many aspects of the biology of the Southern Ocean, especially in the western Indian Ocean sector remain unknown. Among the living resources of this region are the marine mammals, several species of which (especially the 'Great Whales') have been severely depleted as a result of human activities, including whaling. Species known to have been reduced in number include blue whales (*Balaenoptera musculus*), fin whales (*B. physalus*), sei whales (*B. borealis*) and humpback whales (*Megaptera novaeangliae*). The severe depletion of almost all stocks of 'great whales' in the Southern Hemisphere is well documented (Cherfas, 1989; Clarke and Lamberson, 1982; Laws, 1985). Amongst the efforts of the International Whaling Commission (IWC) to facilitate the recovery of the great whales was the establishment of an Indian Ocean sanctuary in 1979 (Leatherwood and Donovan, 1991). The sanctuary consists of those waters of the Northern Hemisphere from the coast of Africa to 100°E and those waters of the Southern Hemisphere between 20°E and 130°E from the Equator to 55°S. In 1994, the IWC declared the majority of the Southern Ocean a sanctuary from commercial whaling (IWC, 1995). The northern boundary of the Southern Ocean Sanctuary follows the 40°S parallel of latitude, except in the Indian Ocean sector where it joins the southern boundary of the Indian Ocean Sanctuary at 55°S and around South America and into the South Pacific where the boundary is at 60°S.

Despite the fact that the Southern Ocean is one of the most important feeding grounds for cetaceans, including the great whales, relatively little is known about their distribution and relative abundance outside the area south of 60°S during the austral summer and even less is known about their behaviour and ecology (De Boer, 2000a; Leatherwood and Donovan, 1991). Visual surveys of cetaceans can provide valuable baseline information for long-term research and monitoring of their populations and thus identify areas of concern for management of their populations. The present note presents the results of the cetacean sighting survey component of a multidisciplinary cruise (not a dedicated cetacean cruise). It forms the first large scale Indian attempt to investigate the distribution and relative abundance of cetaceans in the Southern Ocean.

The opportunity for this work was attained by the Central Marine Fisheries Research Institute (CMFRI) during a Pilot Expedition (PESO) organised by the National Centre for Antarctic and Ocean Research (NCAOR), Goa, to the ice-free areas of the region onboard *ORV Sagar Kanya* during the austral summer of 2004 (January-March). This expedition, as a prelude to long-term observational programmes in the Southern Ocean, was multi-disciplinary and multi-institutional in nature, involving a dedicated team of 30 scientists drawn from various research and

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development institutions/universities. Information on the major objectives, programmes and brief account of preliminary results of various studies/experiments/ observations of the PESO cruise can be found elsewhere (Pandey *et al*., 2006).

METHODS

Cruise track and sighting schedule

The *ORV Sagar Kanya* left Port Louis (Mauritius; 20°09'S, 57°30'E) on 23 January 2004. The cruise proceeded to 31°S, 45°E and further along the meridian 45°E to 56°S latitude. The return leg was along 57°E, back to Port Louis, where the ship arrived on 4 March 2004 (Fig. 1). Tracklines and procedures followed were not developed to optimise cetacean studies but for other components of the multidisciplinary cruise. As dedicated ship time was not available for the cetacean component, fine-scale work (e.g. prey sampling where cetaceans are known to congregate for feeding) could not be undertaken. Sightings data were thus collected only in 'passing mode' (i.e. the vessel did not deviate from the trackline).

Field identification

Identification in the field was based mainly on Jefferson *et al*. (1993). Cetaceans were identified to the lowest taxonomic level possible. Species identification was not always possible for all sightings due to sea state, time spent at the surface by the cetaceans or distance of sighting from vessel. Species identity (and length estimates) were determined only for animals close to the vessel and in good sea conditions. Sightings were initially identified as 'possible' or 'confirmed' or, usually for animals far from the vessel, 'unidentified'. Photographs and videos were taken of the sightings and later confirmed and identified with the help of appropriate experts. Thus, in this note, 68% of individual cetaceans sighted during the cruise were identified to species level.

Data collection

During each sighting, data on date and time (GMT and local time), place (nearest landmark), latitude and longitude, number of animals, distance from vessel (km), depth of the area (m), movement of the animals and their visible characteristics, as well as weather condition and sea state were recorded. Observation conditions were characterised using sea state (according to the Beaufort scale), swell height, wind direction, wind speed cloud cover and precipitation (e.g. rain, snow, fog, haze, etc).

Beaufort 0-2 was associated with good conditions (although 0 and 1 were never encountered), Beaufort 3-4 with average conditions and Beaufort 5+ with poor conditions. Precipitation at times reduced visibility to less than 100m. At Beaufort 5 and above, cetaceans were difficult to sight and could only be identified with certainty if they were close to the ship (within 200m). The wind force was never below 2 throughout the entire cruise. This information was collected at two hourly intervals and when sightings were made.

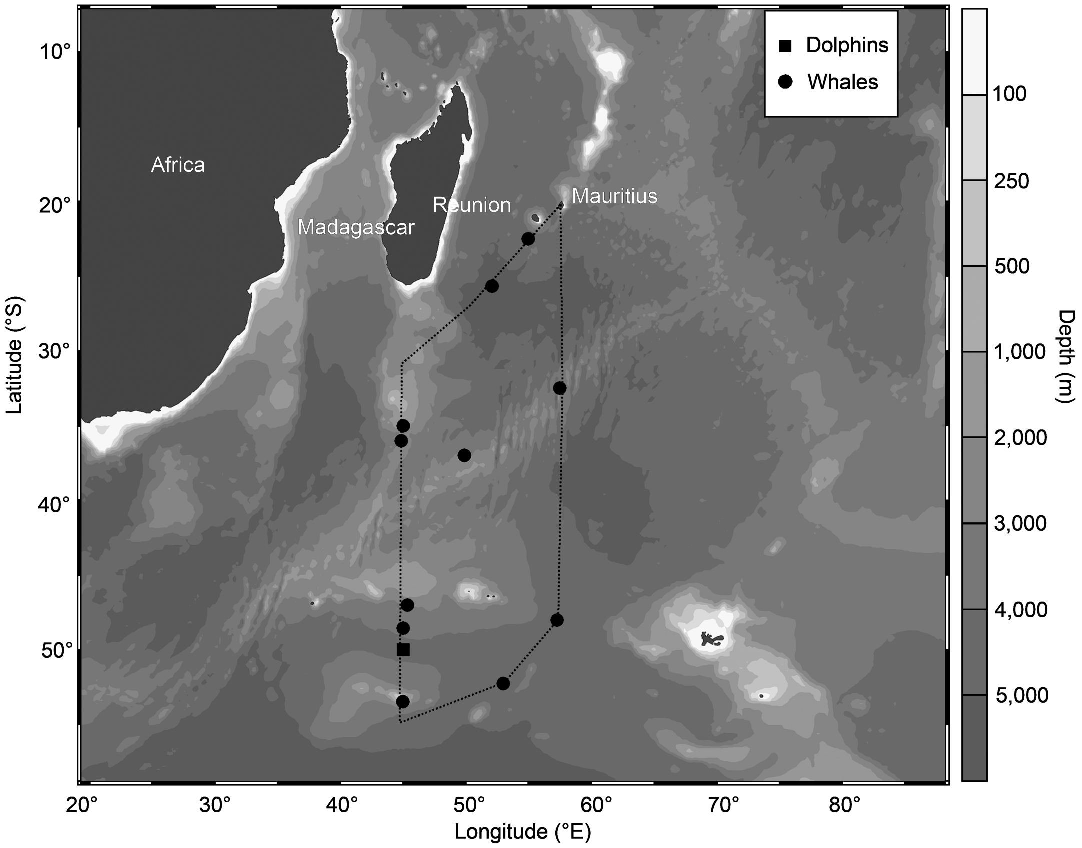

Fig. 1. Track of *ORV Sagar Kanya* pilot cruise to the Western Indian Sector of Southern Ocean and locations of cetacean sightings during the Austral Summer of 2004.

In addition, Sea Surface Temperature (SST) was measured using a Conductivity Temperature and Depth (CTD) system (SBE 9/11, Sea-Bird Electronics, USA; temperature accuracy: +0.001°C and depth +0.005% of the full scale) and salinity was measured using a salinometer (Autosal 8400A, Guildline, Canada), at places where cetaceans were sighted as well as throughout the cruise.

RESULTS

Sea state and sighting frequency

Information on cetacean sightings and hydrographical data is presented in Table 1. Survey effort totalled 415hr (mean= 9.8hr day^{-1}, SE=0.5) and covered approximately 9,260 linear km on effort; 12.9% (53.5hr) at Beaufort 2), 51.6% (214.2hr) at Beaufort 3-4 and 35.5% (146.9hr) at Beaufort ≥5.

Cetaceans were sighted on 12 of the 42 days at sea. Thirteen sightings (22 individuals) were made during the present cruise in the area between 22°S and 53°S latitudes (Fig. 1). The mean number of sightings per day was 0.31 (SE=0.08, range 0-2), number of individuals sighted per day was 0.52 (SE=0.15, range 0-3) and the mean encounter rate for the entire survey was 0.13 sightings per 100 linear km. The highest concentration of cetaceans was between 35° and 37°S (along 45°E), where the mean number of individuals sighted was 0.24 hr^{-1} and between 48° and 53°S (along 45°E), where the mean number of individuals sighted was 0.27hr^{-1}. This indicates their possible abundance around Bob Fischer Ridge, Deacon Seamount and Madagascar basin during the austral summer (Table 2). Cetaceans were also sighted over Mascarene plain, near Prince Edward Islands, the Fracture zone around Crozet Island, Lena Seamount and Marion Dufresne Seamount. The highest number of cetaceans encountered on a single day was three (mean sighting rate of individuals 0.3 hr^{-1}) which occurred on four different days during the voyage between 35°01'S, 44°00'E and 49°59'S, 45°00'E, where depth ranged from 2,245 to 4,000m.

Cetacean species and sighting characteristics

The present survey was aimed at detecting all cetacean species and thus sightings were conducted over the full range of weather conditions at which cues might be visible (most Southern Ocean are medium to large whales with cues that can be detected in relatively high Beaufort sea states). Sixty eight percent of the whales sighted in Beaufort 3-6 were positively identified (Table 3). The relatively large number of unidentified sightings in Beaufort 3-4 reflected the fact that sightings could be made several nautical miles away under those conditions; the confirmed sightings seen in Beaufort 5-6 were close to the ship.

Table 2

Sighting frequencies (all cetaceans combined) in seven regions of the Southern Ocean.

Region	Mean[1]	SD	SE	Range
Madagascar basin	0.16	0.39	0.11	0-1
Bob Fischer Ridge	0.25	0.45	0.13	0-1
Prince Edward Island region	0.08	0.29	0.08	0-1
Deacon seamount	0.25	0.62	0.18	0-2
Lena seamount	0.08	0.29	0.08	0-1
Marion Dufresne seamount	0.08	0.29	0.08	0-1
Southwest Indian Ridge	0.08	0.29	0.08	0-1

[1] Number of sightings/total number of cetacean sightings in the whole cruise

A total of seven baleen whale and dolphin sightings were made that could not be identified to species, mainly due to their great distance from the ship. A total of 68% of sightings were identified to species (Table 4); sightings of the rorquals are summarised below.

Fin whale (Balaenoptera physalus)

Two sightings of fin whales were made, both at station depths of 2,727m: a single animal seen in the Bob Fischer Ridge and Fracture zone (36°07'S, 44°51'E) moving in a south westerly direction; and a group of three at Bob Fischer Ridge (37°01'S, 49°53'E) moving in a southerly direction. SST varied from 5.0-7.0°C and salinity ranged from 34.30-

Table 3

Cetacean sightings in relation to wind strength made on board *ORV Sagar Kanya* in the Southern Ocean.

Beaufort scale	Number of sightings	Number of individuals	Percentage of species identified
3	2	2	50.00
4	6	13	53.85
5	2	4	100.00
6	1	2	100.00
7	0	0	0
8	1	1	0
Total	12	22	45.45

Table 1

Information on cetacean sightings made on board *ORV Sagar Kanya* in the western Indian sector of Southern Ocean during the austral summer 2004.

Date	Species	Number of sightings	Number of individuals	°S	°E	Depth (m)	SST (°C)	Salinity (‰)
24/01/04	Unidentified baleen whale	1	1	22° 30'	54° 58'	4,234	27.1	34.91
26/01/04	Unidentified baleen whale	1	1	25° 39'	52° 04'	5,109	27.3	34.72
02/02/04	Antarctic minke whale	1	3	35° 01'	44°00'	2,245	21.8	35.70
03/02/04	Fin whale	1	1	36° 07'	44° 51'	2,727	21.8	35.62
04/02/04	Fin whale	1	3	37° 01'	49° 53'	2,727	21.0	35.60
11/02/04	Sei whale	1	2	47° 07'	45° 21'	3,301	7.0	34.30
12/02/04	Sei whale	2	3	48° 35'	45° 03'	3,505	5.0	34.38
13/02/04	Unidentified dolphins	1	3	49° 59'	45° 00'	4,000	4.0	34.34
15/02/04	1 blue whale and 1 unidentified baleen whale	1	2	53° 28'	44° 59'	326	2.2	34.52
20/02/04	Blue whale	1	1	52° 14'	52° 58'	4,240	4.8	33.64
22/02/04	Blue whale	1	1	48° 08'	57° 14'	4,500	4.8	33.77
29/02/04	Unidentified baleen whale	1	1	32° 29'	57° 28'	690	23.0	35.67

Table 4

Sighting frequencies of cetaceans encountered in the Southern Ocean cruise.

Species	Mean[1]	SD	SE	Range
Antarctic minke whale	0.08	0.29	0.08	0-1
Fin whale	0.17	0.39	0.11	0-1
Sei whale	0.25	0.62	0.18	0-2
Blue whale	0.25	0.45	0.13	0-1
Unidentified baleen whale	0.33	0.49	0.14	0-1
Unidentified dolphin	0.08	0.29	0.08	0-1

[1]Number of sightings/total number of cetacean sightings in the whole cruise.

34.38%. The estimated lengths of the animals, which were seen about 200m from the vessel, were between 21-23m in length. After the first sighted blow, whales undertook a long slow, fairly shallow roll ending at the surface with the dorsal fin, repeated 4-5 times at intervals of 10-20s; after this, the back was arched more steeply, before a deep dive.

Blue whale (Balaenoptera musculus)
Three blue whale sightings were made: one near Lena seamount (53°28'S, 44°59'E, 326m depth) moving south; one to the southeast of Crozet Island (48°08'S, 57°14'E, 4,500m depth) moving southwest; and one near Marion Dufresne Seamount (52°14'S, 52°58'E, 4,240m depth). SST ranged from 2.20-4.80°C and salinity from 33.64-34.52‰. The animals were estimated at 25-28m in length. After the first blow, the whales undertook several short (*ca* 20s) shallow dives.

Antarctic minke whale (Balaenoptera bonaerensis)
There was one sighting of Antarctic minke whales comprising three individuals (estimated at 8-9m in length) moving northeasterly. This was made at Bob Fisher Ridge (35°01'S, 44°00'E), at a depth of around 2,245m. The SST was 21.80°C and salinity was 35.70%. No flipper patches were seen (a characteristic feature of *B. acutorostrata*).

Sei whale (Balaenoptera borealis)
Three sei whale sightings were made: one comprising two animals between Prince Edward Island and Crozet Island (47°07'S, 45°21'E) moving in a south-easterly direction; and two, both comprising three animals, off Deacon Seamount (48°35'S, 45°03'E). The depths ranged from 3,301-3,510m, SST ranged from 5°-7°C and salinity ranged from 34.30-34.38%.

Unidentified whales
Four sightings (consisting of four individuals) of unidentified whales were made near Madagascar basin, Lena Mount and southwest Indian Ridge. One group of unidentified dolphins (three individuals) was seen moving rapidly 160 n.miles south off Deacon Seamount. The SST, salinity and depth information is given in Table 1.

DISCUSSION

De Boer *et al.* (2003) have made a comprehensive review of the published information relating to the over 40 cetacean species found in the Indian Ocean Sanctuary. Donovan (2007) summarised information on those whale species found in the Antarctic during the austral summer, where they feed.

It is difficult to separate true or normal blue whales (*B. musculus intermedia*) from pygmy blue whales (*B. musculus brevicauda*) at sea (e.g. Williams and Donovan, 2007). Although true/normal blue whales are generally found in more southerly latitudes than pygmy blue whales in the austral summer (e.g. Branch *et al.*, 2007), there was insufficient information to identify the three animals seen during the present study.

Two species of minke whale are found in the Southern Hemisphere; the Antarctic minke whale and the diminutive form of minke whale (Arnold *et al.*, 1987; Best, 1985) which is actually genetically related to the common minke whale found in the Northern Hemisphere. The sighting made at 35°S in February was identified as an Antarctic minke given the absence of the characteristic white flipper band. Kasuya and Wada (1991) found that although the latitudes of highest minke whale densities were south of 60°S during November to March, considerable sightings of minke whales were reported to the north of 55°S in the austral summer, suggesting that in summer not all individuals migrate to waters south of the Antarctic convergence. This is in agreement with the present observation.

Fin whales have been encountered mainly between 40-60°S and 30-90°E in the Indian Ocean sector in recent years (Donovan, 2007). The present sightings of fin whales were between 44° and 49°E but somewhat further north (36°-37°S) than the main concentrations which are between 50 and 65°S.

Sei whales generally have the most northerly austral distribution of the 'Antarctic' whales (Donovan, 2007), with their distribution mainly on or near the Antarctic Convergence (around 40°-50°S). The observation of Kasuya and Wada (1991) that high sei whale densities are encountered between 40° and 55°S in January and between 40° and 50°S in February is in accord with our sightings (Table 1).

Although the sample sizes are small, during the present cruise blue whales were encountered in the lowest SST range, sei whales preferring slightly warmer waters, while fin and minke whales were sighted in much higher SSTs. The results for blue and sei whales are not unexpected and is related to their feeding behaviour (e.g. Donovan, 2007; Kasamatsu *et al.*, 1990; Kawamura, 1994). Fin and minke whales usually feed in colder waters than observed here but have been found in warmer waters. It is not clear whether these were animals that had returned from the Antarctic or animals that not migrated.

Relatively small numbers of cetaceans were observed during the present cruise and this to a great part reflects the fact that almost 90% of the cetacean sighting effort time was made in 'average' to 'poor' conditions. In addition, the survey was generally further north than the expected peak densities in January-February (e.g. De Boer, 2000b; Donovan, 2007) Despite this, the present results show that marine mammal research programnes can be conducted aboard vessels that are not primarily designed for cetacean research. The practicality and possibility of conducting certain kinds of cetacean research aboard such vessels has been reported elsewhere (De Boer *et al.*, 1999; Reid *et al.*, 1999; Thiele and Chester, 2000; Tynan, 1997) although the objectives must be clearly specified.

Considerably more focussed research is required to allow more accurate determination of spatial and temporal changes in distribution. Examining cetacean species diversity and their prey abundance in the Southern Ocean environment in their current state will provide some understanding of the dynamics of recovering populations. The interactions between the greatly depleted species and those that have increased dramatically since commercial whaling ceased should be an important focus for research within this ecosystem (Thiele and Chester, 2000). The present survey can be seen as the first Indian attempt to contribute to the ongoing global effort to collect data on Southern Ocean cetacean species distribution and abundance from platforms of opportunity, ultimately to help determine distribution, migration patterns and critical habitat parameters.

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