Line transects, environmental data and GIS: Cetacean distribution, habitat and prey selection along the Barents Sea shelf edge

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ABSTRACT

Cetacean observations obtained during sighting surveys for abundance estimation can also be used to investigate cetacean habitat and prey selection, the principal processes underlying cetacean distributions. In this paper, we investigate habitat and prey selection of minke (*Balaenoptera acutorostrata*), fin (*B. physalus*) and sperm (*Physeter macrocephalus*) whales and *Lagenorhynchus* (Atlantic white-sided *L. acutus* and white-beaked *L. albirostris*) dolphins observed along predetermined cruise tracks along the Barents Sea shelf edge in 2000, 2001 and 2002. The observations were combined with simultaneously collected data on habitat (depth, sea surface temperature, and temperature gradients) and prey (plankton, 0-group fish, capelin and herring) distributions in a Geographic Information System (GIS) to investigate habitat and prey selection. Minke whales were associated with cold waters and herring, and capelin in years with low herring abundance. Fin whales were mainly associated with northern cold and deep waters, as well as capelin, 0-group fish and plankton. *Lagenorhynchus* dolphins were associated with capelin. Finally, sperm whales were associated with deep waters and 0-group fish. Sperm whales were probably indirectly attracted to 0-group fish through preying on predatory fish such as *Sebastes* spp. and the squid *Gonatus* spp. The cetacean species responded differently to annual variation in habitat and prey distributions. Minke and fin whale distributions and abundances remained similar between years within the study area, suggesting that these species are generalists responding to environmental changes by switching between prey species. Conversely, *Lagenorhynchus* dolphins shifted northwards, likely due to tracking the shifting capelin distributions. The results are discussed in light of how such cetacean habitat and cetacean prey relationships can be valuable for the proper assessment of population sizes and trends, both through guiding the design of sighting surveys and assessing whether changes in abundances within fixed surveyed areas are due to distribution shifts or changes in population sizes.

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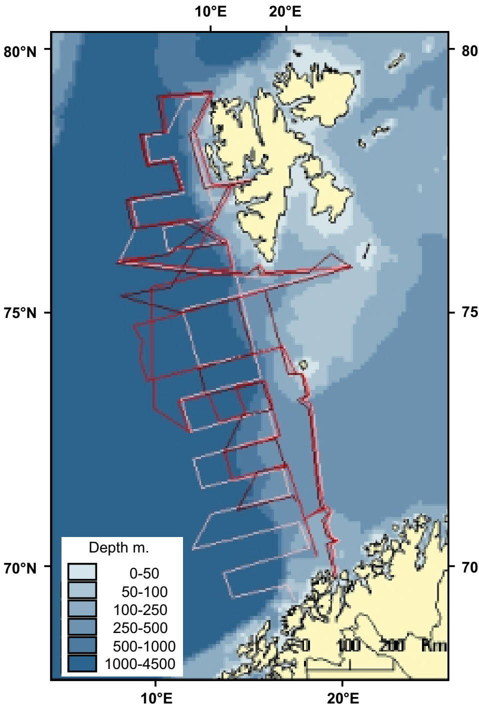
INTRODUCTION

Sighting surveys, like the North Atlantic Sightings Surveys (NASS), are primarily performed for assessing abundance and distribution of cetacean species, and when repeated over time, for assessing temporal trends in cetacean abundance and distribution. Habitat and prey selection, evolved in response to prey availability and competition, are the principal processes underlying cetacean distribution, shaping both the cetacean–prey interactions and the cetacean community (*e.g.* Piatt and Methven 1992, Jaquet and Whitehead 1996, Stern 1998, Hamazaki 2002, Whitehead and Rendell 2004). Inhabiting dynamic marine systems, cetaceans experience shifting habitat and prey distributions. Therefore, cetacean habitat and prey selection should be dynamic behavioural processes responding to environmental changes rather than static behavioural rules. The responses of cetaceans to environmental changes differ between generalists and specialists. Generalists may switch between prey types within the area depending on relative prey availability, while specialists may track changing distributions of their preferred prey into new areas or habitats, resulting in changes in their distributions (*e.g.* Haug *et al.* 1995, Whitehead 1996, Forney 2000). Thus, when combined with information on habitat and prey distributions, cetacean distributions as observed on sighting surveys may provide valuable input to investigations of cetacean habitat and prey selection, and increase our understanding of the processes underlying and causing variation in cetacean distributions. Such information also allows evaluation of whether changes in abundance within repeatedly surveyed areas are due to changes in abundance or in distributions (Forney 2000). Here we present a study combining cetacean distributions, habitat and prey to investigate cetacean habitat and prey selection along the Barents Sea shelf edge.

Cetaceans are mobile predators that often undertake extensive seasonal migrations from tropical breeding areas in winter to boreal and arctic foraging areas in summer. Tracking prey concentrations within foraging areas yields a positive spatial correlation between predators and their prey, termed the predator's aggregative response (Hassel and May 1974). Hence, cetacean prey selection may be inferred from significant positive correlations between cetacean and prey distributions. Prey may congregate in specific physical habitats, recognised by certain physical features such as depth, bottom topography, temperature, eddies, thermoclines or fronts. Prey tracking may thus result in selective habitat use, defined as significant correlations between cetacean distributions and physical habitat measures (*e.g.* Kasamatsu *et al.* 2000, Gregr and Trites 2001, Waring *et al.* 2001, Davis *et al.* 2002). Alternatively, cetaceans may also selectively use specific habitats to increase the probability of encountering prey.



Synoptic cruises, simultaneously recording physical habitat, prey and cetacean distributions, allow investigations of cetacean habitat and prey selection. In July August 2000, 2001 and 2002, synoptic cruises were conducted along the Barents Sea shelf edge where cetaceans are commonly observed (Fig. 1). A total number of 12 marine mammal species were observed. Here we report on the distribution and habitat and prey selection of the most frequently observed cetaceans; minke whales, fin whales, *Lagenorhynchus* dolphins (Atlantic white-sided and white-beaked dolphins) and sperm whales. The synoptic data were incorporated into a GIS (Geographic Information System), and used for investigating the following hypotheses: i) Do the selected cetacean species demonstrate habitat and prey selection? and ii) do cetaceans respond to inter annual environmental variation by a) changing their distribution relative to alterations in habitat or prey distributions, maintaining similar habitat and prey selection across years? or b) altering habitat or prey selection? Our results are discussed in light of how sighting survey data can be used in similar approaches to habitat selection modelling, to increase our understanding of marine mammal ecology and possibly increase precision of abundance estimates and population trends.

Fig. 1. *Study area and cruise lines from the cruises in 2000 (light red), 2001 (red) and 2002 (dark red).*

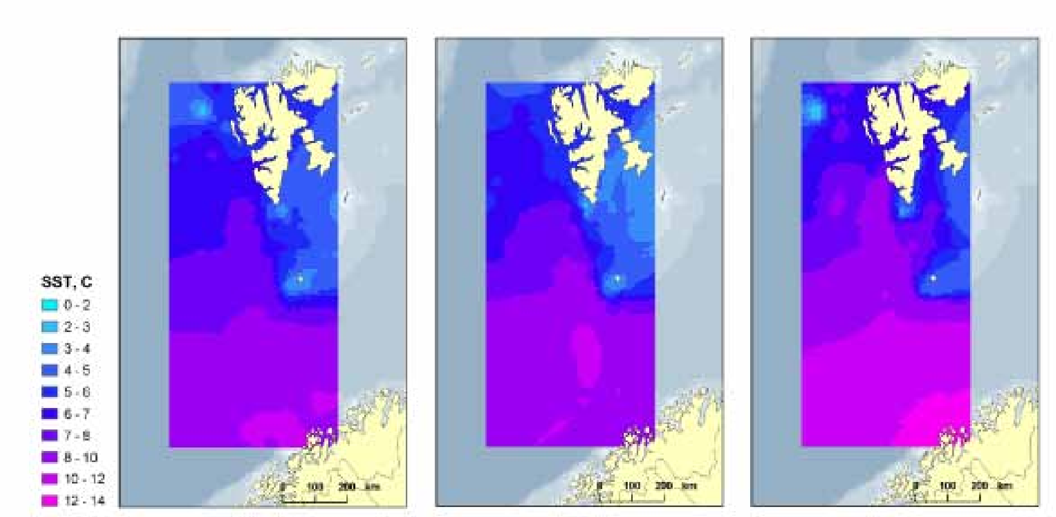


Fig. 2. *Interpolated raster map of sea surface temperature (°C) in 2000, 2001 and 2002.*

MATERIALS AND METHODS

Study area

The cruises were conducted in August September in 2000 (18 August 6 September), 2001 (20 August-8 September) and 2002 (23 August-7 September) following predetermined transects at 12 knots along the Barents Sea shelf edge (Fig. 1). The shelf edge defines the border between the shallow Barents Sea (depths <400 m) and the deep Norwegian Sea (depths >1000 m, Fig. 1). Warm Atlantic water masses flow north along the shelf break and along the west coast of Spitsbergen, and eastwards into the Barents Sea (Fig. 2). Cold Arctic water masses flow southwards through the Barents Sea and the Greenland Strait (Fig. 2). These water masses meet and create the highly productive polar front, recognised in the northern part of the study area and between the Svalbard south end and Bear Island as steep temperature gradients (Fig. 2). Both the Barents Sea and north eastern Norwegian Sea serve as nursery areas for several species spawning off the Norwegian coast, such as herring (*Clupea harengus*), cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*) and saithe (*Pollachius virens*; Bergstad *et al.* 1987, Gjøsæter 1995, Dragesund *et al.* 1997). In the warmer Atlantic water masses the zooplankton community mainly consists of krill (*Euphausiids*) and copepods (*Calanus finmarchichus*), in colder Arctic water masses of copepods (*C. glacialis*, *C. hyperboreus*) and amphipods (*e.g. Themisto libellula*) (Dalpadado *et al.* 1998, Tande *et al.* 2000). Capelin (*Mallotus villosus*) and juvenile herring are the dominant planktivorous fish in Atlantic waters in the Barents Sea, whereas polar cod (*Boreogadus saida*) dominate in Arctic waters (Nilssen and Hopkins 1992). In the deeper Norwegian Sea, adult herring are a dominant planktivorous fish, together with blue whiting (*Micromesistius poutassou*) and mackerel (*Scomber scombrus*).

Physical habitat variables

Depth was measured acoustically along predetermined transects every 5 nautical miles (nm). For graphic representation of the study area we have used a bathymetric map obtained from the GEBCO 97 Digital Atlas from the British Oceanographic Data Centre. Sea surface temperature (SST) was measured using a CTD probe at stations approximately 35 nm apart, except the stretch from the Norwegian mainland to Bear Island, where sampling stations were 15 nm apart. An SST raster map with pixel size 5 nm was produced using 2nd order inverse distance weighted interpolation (with 5 influencing neighbours). To identify the steep temperature gradients formed by ocean fronts we calculated the standard deviation of SST within a circle with radius 15 nm using the SST raster maps. The resulting raster maps (sdSST) contained high values where the temperature gradients were steep and low values where the temperature gradients were flat.

Prey variables

Data on prey distribution and abundance were recorded along the transects using standard acoustic survey methods, including a Simrad EK-500 split beam echo sounding system and a Bergen Echo Integrator post processing system (Knudsen 1990, MacLennan and Simmonds 1992). The echo integrator measures the intensity of returned echoes which are transformed to S_A values (area back scattering coefficient) by a specific target strength function (MacLennan and Simmonds 1992). S_A values were allocated to different species (capelin and herring) or groups (plankton and 0-group fish (4-6 months old fish)) according to standard methods, using the integrated information from the echo sounder and pelagic trawl and net (MOCNESS and WP2, mesh size 180 μm) hauls at stations approximately 35 nm apart (MacLennan and Simmonds 1992, Nakken and Raknes 1996, Dalpadado *et al.* 2003). S_A values were used as a relative measure of prey availability in our analyses.

Cetacean observations

Cetacean observations were made by 2 dedicated observers from the wheelhouse onboard the survey vessels with 1 observer scanning starboard side and the other the port side. This corresponds to eye heights of about 10-12 m above sea level. Only the first blow or sight of animals was recorded with species, pod size, angle and radial distance from the trackline and apparent swim direction. For all observations time (UTC) and position of sighting were recorded. Activity and covariates were recorded on an hourly basis and comprised vessel speed and course, weather, wind direction, Beaufort Sea State (BSS) and meteorological visibility. Primary search activity was conducted when the survey vessel steamed between stations and when BSS was 3 or less and visibility more than 1,000 m.

The focal species in this work are minke, fin and sperm whales and *Lagenorhynchus* dolphins. Whereas minke whales, fin whales, and *Lagenorhynchus* dolphins are generally associated with the pelagic prey sampled in this study (Haug *et al.* 1995, Hai *et al.* 1996, Lindstrøm *et al.* 2002, Kinze *et al.* 1997), sperm whales are generally associated with meso and bathypelagic prey not sampled by us (Sarvas 1999, Flinn *et al.* 2002). Therefore, analyses of sperm whale prey selection may not be appropriate in this study. However, as general distribution and habitat selection were of interest we chose to include sperm whales in this study.

Due to the similar appearances of Atlantic white-sided and white-beaked dolphins in the field, few observations of *Lagenorhynchus* dolphins were determined to species. We therefore analysed habitat and prey selection for the 2 species combined. However, all species determined observations of *Lagenorhynchus* dolphins were of white-beaked dolphins (n=18), suggesting that white-beaked dolphins are the dominant *Lagenorhynchus* dolphin species in this area.

Data treatment and analyses

All data were projected in a polar stereographic projection, using 15° E and 75° N as the point of tangency. SST and sdSST were assigned to each 5 nm cruise line segment defined by the prey recordings as the values of the 5x5 nm pixel which contained the central coordinate of each 5 nm cruise line segment. To enable comparison between cetacean distribution and habitat and prey distribution, cetacean observations were assigned to each 5 nm cruise line segment. The number of minutes the observers were active in each 5 nm segment was assigned to each segment as a measure of observer effort.

We applied log linear analyses to model the relationship between cetacean observations

Table 1. Mean (minimum-maximum) values of habitat and prey variables of cruise line segments with observer activity >0.

	2000		2001		2002	
Depth, m	504	(54-2993)	783	(37-3232)	613	(21-1583)
SST, C°	6.7	(3.3-10.2)	7.2	(3.1-10.4)	8.2	(2.2-13.5)
sdSST	0.23	(0.01-0.96)	0.20	(0.02-1.05)	0.24	(0.03-1.40)
Plankton, S_A	95	(0-3354)	32	(0-935)	72	(7-769)
0 group fish, S_A	43	(0-700)	1	(0-73)	24	(0-786)
Herring, S_A	21	(0-1939)	17	(0-1370)	61	(0-742)
Capelin, S_A	0	(0-43)	4	(0-52)	52	(0-413)

and habitat and prey distributions, using the 5 nm cruise line segments as units in the analyses. Only cruise line segments where cetacean observers were active were included in the statistical analyses. In analyses of minke and sperm whale distributions we used number of individuals observed on each segment as the response variable, assuming independence between individuals if observed simultaneously, as both minke and sperm whales are predominantly solitary in these waters (Øien 1990). Fin whales and *Lagenorhynchus* dolphins, on the other hand, are often observed in groups (Øien 1990). For these species we therefore used the number of groups observed per segment as the response variable, assigning individuals observed simultaneously to the same group.

The habitat and prey variables were to some extent correlated and thus confounded (see Results section). The correlation was not sufficiently systematic for variable reduction through *e.g.* principal component analyses, as preliminary analyses demonstrated a need for inclusion of at least 6 components to explain >85% of the variation for each year. All variables were therefore included as predictors in the statistical models.

To identify the best models explaining variation in cetacean distribution relative to habitat and prey, we started with a full model and used a backward selection procedure based on the C_p statistic in an iterative process. Terms reducing the C_p statistic most were deleted from the model (1 at a time) as long as deleting the term reduced the model C_p. The full model included observer effort, and all habitat and prey variables both as main affects and in interaction with year. All habitat and prey variables, except SST and observer effort, were log-transformed to normalise the distributions by reducing effects of extreme observations.

Table 2. Number of cruise line segments with observer activity >0 and prey abundance >0.

	2000	2001	2002
Tot. no. of segments	227	208	271
Plankton	222	193	271
0-group fish	200	143	271
Herring	12	38	220
Capelin	7	23	96

All statistical analyses were performed in S-PLUS 2000, whereas ArcMAP v.8.2 was used for data treatment and visualisation.

RESULTS

Physical habitat and prey distributions

The cruises covered areas with diverse habitats with respect to depth and temperature (Table 1, Figs 1 and 2). Depth ranged from 20 to 3,200 m and SST ranged from 2 to 14°C. In 2001 the cruise covered slightly more of the deeper western areas than in 2000 and 2002, resulting in a greater mean and maximum depth in 2001 than in 2000 and 2002 (Table 1). Temperature increased during the 3 years of surveys due to an increased influx of warm Atlantic water masses (Table 1, Fig. 2). However, an increased mean temperature in 2002 was also due to increased observer effort in the southern part of the study area in 2002 compared to 2000 and 2001 (Table 1, Fig. 1). Prey abundance varied considerably along the transects and between years (Table 1 and 2, Figs 3-6). Both plankton and 0-group fish were most abundant in 2000 and least abundant in 2001, but were present in more segments in 2002 than in other years (Table 2, Figs 3 and 4). Herring was more abundant than capelin (Table 2). Both species were most abundant in 2002 and least abundant in 2000, and were in 2000 observed only on a few segments (Table 2, Figs 5 and 6).

Habitat variables were correlated, although correlations often differed between years (Table 3, a-c). SST decreased with increasing latitude in all years and SST increased with longitude in 2002 only, due to the increased inflow and dispersion of Atlantic water masses in 2002 (Fig. 2). Steepness of temperature gradients, sdSST, increased with decreasing SST, and was in 2000 and 2001 negatively correlated with depth and positively correlated with longitude, demonstrating that fronts generally occurred in the eastern and shallower water masses.

Correlations between prey and physical habitat variables showed few consistent patterns during the 3 years. Plankton was most abundant in northern and colder water masses in 2000 and 2001. In 2002 this pattern reversed, as plankton was most abundant in southern and warmer water masses. In 2001 and 2002 plankton was

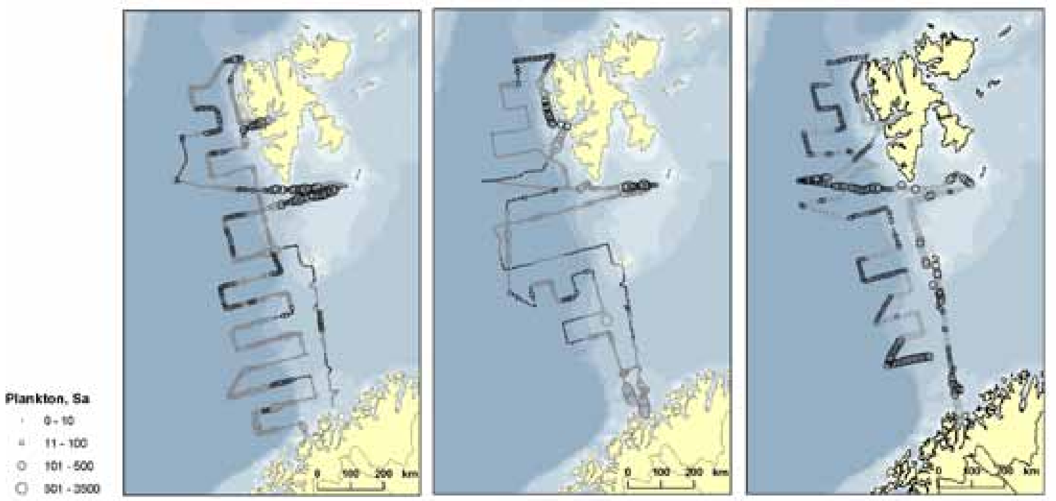


Fig. 3. Distribution of plankton along the cruise lines in 2000, 2001 and 2002. Black cruise line segments indicate segments with observer effort >0 which are included in the statistical analyses of cetacean habitat and prey selection, grey cruise line segments indicate segments with observer effort=0 which are not included in the statistical analyses.

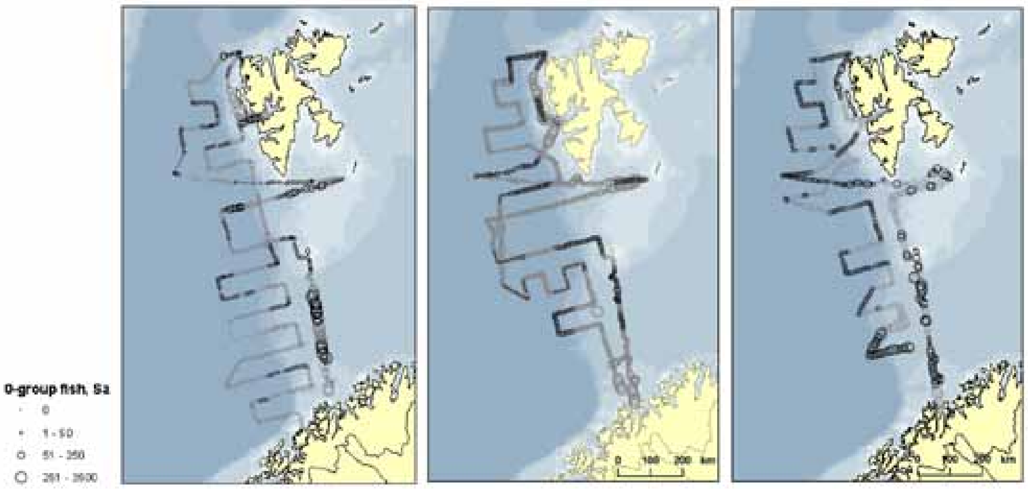


Fig. 4. Distribution of 0-group fish along the cruise lines in 2000, 2001 and 2002. Black cruise line segments indicate segments with observer effort >0 which are included in the statistical analyses of cetacean habitat and prey selection, grey cruise line segments indicate segments with observer effort=0 which are not included in the statistical analyses.

also positively associated with shallower water masses. 0-group fish were generally most abundant in eastern and shallower water masses. In 2000, 0-group fish showed no variation in abundance along the latitudinal axis. In 2001, however, 0-group fish were most abundant in the northern colder water masses, whereas in 2002, 0-group fish were most abundant in the southern warmer water masses. The distribution of pelagic fish correlated with few habitat variables. Herring was positively associated with temperature in 2000 and 2002, and in 2002 herring abundance increased with increasing depth. Capelin was negatively correlated with temperature in 2001 and 2002. In 2001 capelin abundance increased with longitude, and in 2002 capelin abundance increased with increasing latitude.

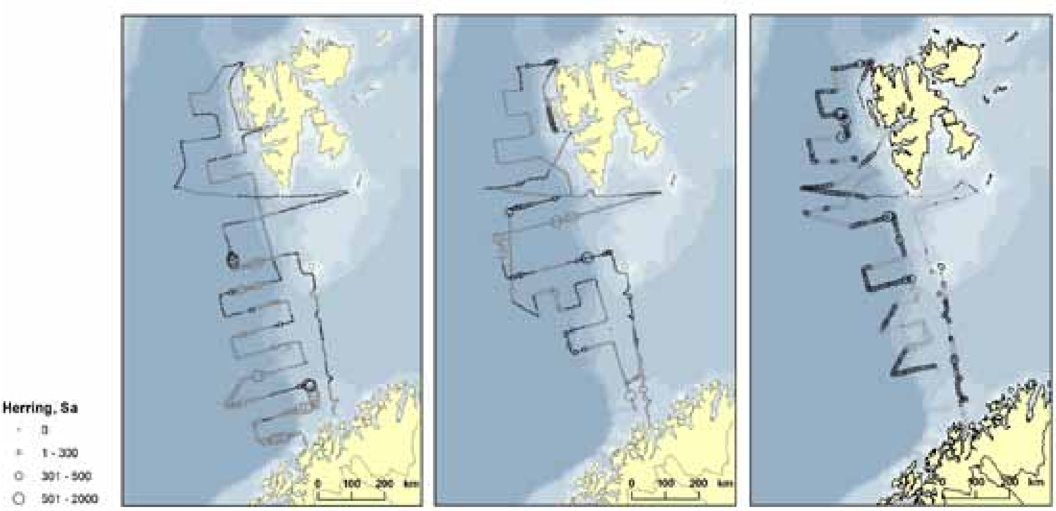


Fig. 5. *Distribution of herring along the cruise lines in 2000, 2001 and 2002. Black cruise line segments indicate segments with observer effort >0 which are included in the statistical analyses of cetacean habitat and prey selection, grey cruise line segments indicate segments with observer effort=0 which are not included in the statistical analyses.*

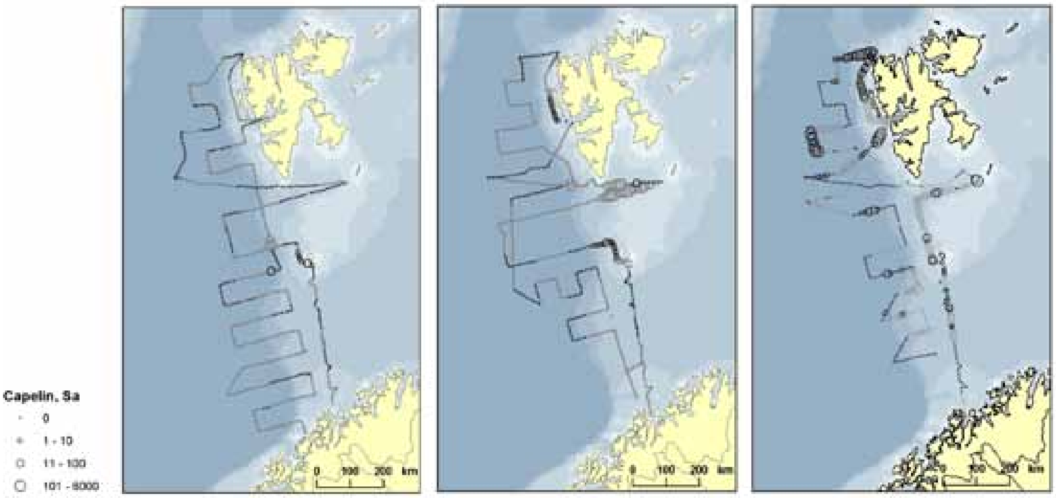


Fig. 6. *Distribution of capelin along the cruise lines in 2000, 2001 and 2002. Black cruise line segments indicate segments with observer effort >0 which are included in the statistical analyses of cetacean habitat and prey selection, grey cruise line segments indicate segments with observer effort=0 which are not included in the statistical analyses.*

Whereas plankton and 0-group fish were found in all parts of the study area in all 3 years, capelin and herring were absent in the northern area in 2000, but increased in the northern areas during 2001 and 2002 (Figs 5 and 6). Plankton and 0-group fish were positively correlated in all 3 years, and capelin and herring were positively correlated in 2001. No other associations between the different prey types were evident.

Cetacean distributions and habitat and prey selection

During the 3 years, 106 observations (107 individuals) of minke whales, 60 observations (79 individuals) of fin whales, 74 observations (870 individuals) of *Lagenorhynchus* dolphins and 47 observations (50 individuals) of sperm whales were recorded (Fig. 7). Whereas minke whales and *Lagenorhynchus* dolphins were observed more or less throughout the study area,

Table 3. Correlations between habitat and prey variables in 2000, 2001 and 2002. Significant correlations ($P \leq 0.05$) are in bold.

a) 2000

	Lat	Lon	Depth	SST	sdSST	Plankton	0-group fish	Herring	Capelin
Lat	1.00								
Lon	**-0.51**	1.00							
Depth	-0.04	**-0.65**	1.00						
SST	**-0.67**	-0.04	0.53	1.00					
SdSST	0.07	**0.40**	**-0.46**	**-0.44**	1.00				
Plankton	0.27	0.04	0.02	**-0.23**	-0.10	1.00			
0-group fish	-0.02	**0.45**	**-0.32**	-0.06	0.00	**0.23**	1.00		
Herring	-0.11	-0.02	0.02	**0.13**	-0.07	-0.02	-0.05	1.00	
Capelin	-0.06	0.07	0.06	-0.07	0.05	-0.03	-0.04	-0.01	1.00

b) 2001

	Lat	Lon	Depth	SST	SdSST	Plankton	0-group fish	Herring	Capelin
Lat	1.00								
Lon	**-0.38**	1.00							
Depth	**-0.15**	**-0.45**	1.00						
SST	**-0.79**	0.03	**0.42**	1.00					
SdSST	0.02	**0.40**	**-0.18**	**-0.18**	1.00				
Plankton	**0.46**	0.13	**-0.31**	**-0.43**	0.09	1.00			
0-group fish	**0.35**	**0.40**	**-0.23**	**-0.39**	**0.33**	**0.30**	1.00		
Herring	-0.03	-0.03	0.07	0.05	0.05	-0.05	-0.04	1.00	
Capelin	0.03	**0.16**	-0.12	**-0.18**	0.09	**0.14**	0.02	-0.02	1.00

c) 2002

	Lat	Lon	Depth	SST	SdSST	Plankton	0-group fish	Herring	Capelin
Lat	1.00								
Lon	**-0.68**	1.00							
Depth	**0.17**	**-0.26**	1.00						
SST	**0.83**	**0.51**	0.03	1.00					
SdSST	0.12	0.02	-0.10	**-0.35**	1.00				
Plankton	**-0.50**	**0.50**	**-0.54**	**0.25**	**0.17**	1.00			
0-group fish	**-0.47**	**0.63**	**-0.46**	**0.31**	0.09	**0.79**	1.00		
Herring	-0.07	0.01	0.26	0.14	-0.06	-0.10	-0.06	1.00	
Capelin	**0.22**	-0.06	0.04	**-0.21**	-0.10	-0.10	-0.13	-0.07	1.00

fin whales were mainly observed in the northern part and sperm whales only in the south western part (Fig. 7). These 2 species therefore seem to have core areas within the study area. Being confined to certain restricted areas within the study area, habitat and prey availability outside these restricted areas may be of less relevance for fin and sperm whales. We therefore defined fin and sperm whale core areas by drawing polygons around the cetacean observations and neighbouring cruise line segments, and repeated the habitat and prey selection analyses using the cruise line segments within the core areas only.

Minke whales

Minke whales occurred throughout the study area, except for the deeper areas in the south western part (Fig. 8). No obvious change in minke whale distribution between years was evident, and the encounter rate was similar all 3

Table 4. Estimates (and SE) of variables in selected model describing minke whale distributions within the study area in 2000, 2001 and 2002. Residual deviance=446.95 (Null deviance=528.19), residual DF=695.

Main effects						
SST	0.34 (0.07)					
Herring	0.16 (0.05)					
Interactions	**2000**		**2001**		**2002**	
Year	0.55	(0.41)	2.46	(0.97)	1.10	(0.64)
SdSST	0.17	(0.71)	6.08	(1.75)	3.78	(1.01)
Capelin	0.48	(0.14)	0.19	(0.08)	0.09	(0.08)

Table 5. Estimates (and SE) of variables in selected model describing fin whale distributions within the study area in 2000, 2001 and 2002. Residual deviance=235.48 (Null deviance=357.20), residual DF=689.

Main effects						
Depth	1.24 (0.23)					
Capelin	0.26 (0.10)					
Interactions	**2000**		**2001**		**2002**	
Year	7.25	(1.95)	5.57	(2.51)	9.03	(1.89)
SST	0.32	(0.21)	1.14	(0.28)	0.24	(0.16)
SdSST	2.91	(0.94)	1.1	(1.72)	0.08	(0.93)
0-group fish	0.21	(0.18)	0.77	(0.32)	0.24	(0.16)
Herring	0.78	(1.36)	0.28	(0.15)	0.36	(0.13)

Table 6. Estimates (and SE) of variables in selected model describing fin whale distributions within the fin whale core area in 2000, 2001 and 2002. Residual deviance=189.17 (Null deviance=262.64), residual DF=314.

Main effects						
Depth	0.96 (0.21)					
sdSST	1.58 (0.57)					
Capelin	0.34 (0.10)					
Interactions	**2000**		**2001**		**2002**	
Year	-6.90	(1.58)	1.92	(1.23)	-2.51	(0.81)
SST	-0.08	(0.32)	-1.05	(0.31)	0.45	(0.26)
0-group fish	-0.16	(0.20)	0.43	(0.25)	0.53	(0.22)
Herring	-*	-	0.34	(0.15)	-0.27	(0.12)

* No herring occurred inside the fin whale core area in 2000

Table 7. Estimates (and SE) of variables in selected model describing *Lagenorhynchus* dolphin distributions in 2000, 2001 and 2002 within the study area. Residual deviance=319.13 (Null deviance=417.25), residual DF=698.

Main effects						
Zooplankton	-0.13 (0.08)					
Capelin	0.33 (0.07)					
Interactions	**2000**		**2001**		**2002**	
Year	-0.52	(0.23)	-2.08	(0.35)	-1.99	(0.44)
SdSST	3.20	(0.57)	3.39	(1.08)	0.90	(0.75)

years. Numbers of minke whales observed in 2000, 2001 and 2002 were 35 (mean 0.15 individuals per cruise segment, SE 0.04), 30 (mean 0.14 individuals, SE 0.04) and 42 (mean 0.15 individuals, SE 0.3), respectively. The selected model, accounting for 15% of the deviance, showed that minke whales were associated with SST and temperature gradients, as well as herring and capelin (Table 4). Independent of year, minke whales were negatively correlated with SST, suggesting a selective use of the colder water masses. In 2000 there was no association between minke whales and sdSST, and in 2001 and 2002, minke whales were negatively correlated with sdSST. Thus, in no year were minke whales attracted to fronts in the study area. Minke whales were positively associated with herring in all 3 years, and with capelin in 2000 and 2001 only (Table 4).

Fin whales

Except for 2 observations in the southern part of the study area, all fin whales were observed in the northern part (Fig. 9). No shifts in distribution were evident between years. In 2000, 2001 and 2002, the number of fin whale groups recorded was 20, 18 and 22, respectively. The corresponding numbers of individuals observed were 24, 22 and 33, yielding mean groups sizes of 1.2, 1.2 and 1.5 individuals, respectively. Mean encounter rate per 5 nm segment was similar across years (2000: mean 0.09, SE 0.02, 2001: 0.09, SE 0.03, 2002: 0.08, SE 0.03). The selected model at the study area scale accounted for 34% of the deviance and demonstrated that fin whales were associated with depth, SST, sdSST, 0-group fish, herring and capelin (Table 5). Fin whales were negatively associated with SST and positively associated with depth, suggesting a selection for deeper and colder water masses. Fin whales were positively associated with sdSST in 2000. Among the different prey types fin whales were positively associated with capelin in all 3 years, and a positive association between fin whales and 0-group fish and herring was observed in 2001 (Table 5).

The defined fin whale core area enclosed all fin whale observations except 2 southern observations from 2000 (Fig. 9). Within the fin whale core area, both herring and capelin were absent in 2000 (Figs 5 and 6). Independent of year, fin whales were associated with deeper water masses, steep temperature gradients and with capelin within the core area (Table 6). A positive association with 0-group fish was observed in 2001 and 2002, and with herring in 2001. In 2002 fin whales were negatively associated with herring. The selected model accounted for 28% of the deviance.

Table 8. Estimates (and SE) of variables in selected model describing sperm whale distributions within the in 2000, 2001 and 2002 within the study area Residual deviance=218.20 (Null deviance=317.94), residual DF=690.

Main effects						
SST			0.66	(0.14)		
Interactions	**2000**		**2001**		**2002**	
Year	-27.34	(4.24)	-12.25	(3.62)	-23.98	(6.21)
Depth	2.60	(0.6)	0.57	(0.48)	1.70	(0.82)
SdSST	-4.33	(2.78)	-0.99	(1.81)	-8.69	(2.5)
0-group fish	0.55	(0.14)	-0.04	(0.29)	-0.24	(0.13)
Herring	0.39	(0.13)	-0.15	(0.21)	0.20	(0.15)

Lagenorhynchus dolphins

In 2000, *Lagenorhynchus* dolphins were observed south of Svalbard, mainly on the shelf (Fig. 10). In 2001, a few observations were also recorded west of Svalbard, whereas in 2002 *Lagenorhynchus* dolphins were predominantly observed west of Svalbard. Thus, the *Lagenorhynchus* dolphin distribution shifted northwards during the 3 years. Numbers of groups and individuals observed varied between years. In 2000, 39 groups of a total of 262 *Lagenorhynchus* dolphins were recorded, in 2001 only 9 groups of 186 individuals, and 26 groups of 422 individuals were recorded in 2002. Observation rate was 0.17 groups per segment (SE 0.05) in 2000, 0.04 (SE 0.2) in 2001 and 0.10 (SE 0.02) in 2002. Mean group size in 2000, 2001 and 2002 was 12, 23 and 21 individuals respectively. However, median group size varied little between years (7, 10 and 11 for 2000, 2001 and 2002, respectively) demonstrating that the differences in mean group sizes were mainly due to the sightings of a few large groups with more than 50 individuals in 2001 (1 group of 100 individuals) and 2002 (2 groups of 64 and 69 individuals) but not in 2000.

The selected model accounted for 24% of the deviance and demonstrated that the distribution of *Lagenorhynchus* dolphin groups was associated with sdSST, zooplankton and capelin (Table 7). In 2000 and 2001 *Lagenorhynchus* dolphins were positively associated with sdSST, suggesting a use of the fronts in the study area. Independent of year, *Lagenorhynchus* dolphins were negatively associated with zooplankton and positively associated with capelin.

Sperm whales

Sperm whales were only observed in the deeper areas in the south western part of the study area, and the distribution remained similar across years (Fig. 11). Numbers of sperm whale individuals observed in 2000, 2001 and 2002 were 18, 14 and 18, respectively. Encounter rate per segment differed little between years (in 2000: 0.08, SE 0.03; 2001: 0.07, SE 0.02 and in 2002: 0.07, SE 0.02).

According to the selected model, accounting for 31% of the deviance, sperm whales were associated with depth, SST and sdSST, as well as 0-group fish and herring at the scale of study area (Table 8). Sperm whales were positively correlated with both depth and temperature, suggesting a selection of deeper and warmer water masses. Negative associations with sdSST suggest that sperm whales were not attracted to ocean fronts. Sperm whales were positively associated with 0-group fish and herring in 2000, but in 2001 and 2002 these association were either absent or negative (Table 8).

A simpler model was selected when analyzing sperm whale distribution within the core area. Independent of year, sperm whales were positively associated with depth (est. 1.00, SE 0.07) and 0-group fish (est. 0.28, SE 0.07). The selected model accounted for only 9% of the deviance (residual deviance=181.64, null deviance=198.90, residual DF=216).

DISCUSSION

Cetacean distributions depend on prey distributions, at least in areas in which they feed. The abundance and distribution of prey is in turn dependent on oceanographic processes yielding favourable conditions by increasing primary and secondary production and by physically aggregating zooplankton (Mann and Lazier 1996). In our study, we found no persistent correlations between physical habitat variables and prey abundance, except for a negative association between 0-group fish and depth in all 3 years. The lack of persistent correlations suggests that the simple habitat variables included in our analyses, depth, SST and sdSST, were not sufficient to capture the link between oceanographic processes and prey within the study area. In contrast to our results, previous studies have demonstrated that both zooplankton and 0-group fish abundance are highly related to ocean temperature. In Atlantic and mixed waters, krill (Euphausiids) and *Calanus finmarchichus* dominate the zooplankton community, while in colder waters amphipods and *C. hyperboreus* and *C. glacialis* dominate (Tande 1989 and references therein, Dalpadado and Skjoldal 1991, Dalpadado *et al.* 1998). Similarly, 0-group herring are restricted to warmer water masses, while 0-group cod inhabit colder water masses than the herring (Haug *et al.* 1995). Hence, the lack of correlations between SST and zooplankton and 0-group fish in our study likely demonstrate that, while the species specific abundances are related to temperature, the total, pooled abundances of these prey groups are independent of temperature. Nevertheless, zooplankton and 0-group fish distributions were positively correlated, likely due to similar influence by oceanographic processes in this area. Generally, advection and retention of zooplankton and 0-group fish within the study area is related to currents interacting with bottom topography and to water column stratification (Helle and Pennington 1999, Edvardsen *et al.* 2003). The lack of correlations between habitat and prey variables may demonstrate that these processes are not adequately covered by the habitat variables used in the present study. Furthermore, the study area constitutes a narrow section mainly enclosing the shelf break and oceanographic processes associated with the steep topography. A wider area, including larger areas of the deep Norwegian and the shallow Barents seas may be required to identify clear relationships between depth, SST, fronts and prey distributions. Both herring and capelin are found south of or along the polar front, and herring are generally confined to warmer waters than capelin (Huse and Toresen 1996, Nilssen and Hopkins 1992). During the 3 years, abundance of both capelin and herring increased in the northern part of the study area (Røttingen 2001, Fig. 5 and 6), possibly as a result of the increased temperatures due to an increased inflow of Atlantic water. There was a general lack of correlation between pelagic fish and zooplankton (Table 3). Pelagic fish prefer the larger sized zooplankton such as krill and amphipods (Huse and Toresen 1996, Dalpadado *et al.* 2000). Hence, pooling zooplankton abundance across all size groups may have concealed any zooplankton pelagic fish relationships.

Cetacean habitat and prey selection

Minke whales

Although cosmopolitan, minke whales are regarded as a shelf species (Horwood 1990). Nevertheless, in this study minke whales were observed on and off the shelf throughout the study area, except the in the deepest south western areas (Fig. 8). That is consistent with observations from earlier sighting surveys in this area (Øien 1990, Øien 1991, Schweder *et al.* 1997). Depth was therefore not a significant explanatory variable in the model of minke whale habitat and prey selection. Minke whales were, however, associated with colder water masses, possibly due to the absence of minke whales in the southern areas with highest SST. Minke whales are not generally confined to colder water masses in the Barents Sea area, as they are also numerous in warm Atlantic waters in the southern Barents Sea (Schweder *et al.* 1997).

Minke whales were associated with herring in all years, and with capelin in 2000 and 2001. In 2000 and 2001, when little capelin and herring were present in the study area, minke whales were generally observed where capelin or herring were present, although they were also observed on cruise line segments where pelagic fish were absent (Figs 5, 6, and 8). In 2002, when pelagic fish abundance increased, minke whales were observed only on segments where pelagic fish were present (Figs 5, 6, and 8). Studies based on stomach analyses of minke whales harvested in the Barents and Norwegian Seas have demonstrated that minke whale diet varies both regionally and temporally, depending on prey availability. Minke whales selectively foraged on capelin and herring but switched to krill when the availability of capelin and herring decreased (Haug *et al.* 1995, Lindstrøm (MS) 2001, Haug *et al.* 2002, Lindstrøm *et al.* 2002), although they may also feed on gadoid and 0-group fish (Haug *et al.* 1995, Lindstrøm *et al.* 2002). In the Norwegian Sea, minke whales may feed predominantly on adult herring (Olsen and Holst 2001). In our study, minke whales were associated with capelin in 2000 and 2001, when both capelin and herring were scarce. In 2002, when herring was abundant and more abundant than capelin, minke whales were associated only with herring. Hence, selection of herring versus capelin may be conditional on the relative densities of the 2 species. As gulp feeders, the profitability of minke whale foraging is strongly related to prey densities (Piatt and Methven 1992). However, these results should be interpreted with care. Due to the low abundances of herring and capelin in 2000 and 2001 these results are based on only a few observations of overlap.

Both krill and 0-group fish are alternate prey for minke whales (Haug *et al.* 1995). Yet no positive associations between minke whales and plankton or 0-group fish were observed in 2000 and 2001 when pelagic fish abundance was low. In both 2000 and 2001, minke whales were generally observed in areas where there was no zooplankton present (Figs 3 and 8). There were incidents of overlap between minke whales and 0-group fish, although associations were less consistent than between pelagic fish and minke whales. Hence, neither zooplankton nor 0-group fish seemed important as alternative prey for minke whales in this region.

Fin whales

With the exception of 2 observations in 2000, all fin whale observations were recorded in the northern part of the study area (Fig. 9). This is in accordance with sighting surveys conducted in the area in 1999 when in fact no fin whales were recorded around Bear Island, which in the 1995 survey was the main area of abundance. The northerly distributions are also in contrast to earlier reports on fin whale distributions, where fin whales were observed west of the shelf break from the Norwegian coast to west of Svalbard (Øien 1990, Christensen *et al.* 1992). With their northerly distribution, fin whales were associated with colder and deeper water masses, although they were also observed in shallower areas south and west of Svalbard (Fig. 9). At the study area scale fin whales were associated with steep temperature gradients only in 2000, but at the core area scale fin whales were associated with steep temperature gradients all years.

Fin whales are generally more common in deeper waters than are minke whales (Øien 1990, Skov *et al.* 1995, Gregr and Trites 2001, Weir *et al.* 2001, Simard *et al.* 2002), but may also use inshore shallow feeding grounds (Christensen *et al.* 1992, Gregr and Trites 2001). Fin whales have also been related to areas with complex bottom relief and slopes, which are features involved in aggregating prey (Woodley and Gaskin 1996, Simard *et al.* 2002). In our study, few fin whales were observed in the deepest waters distant from the shelf break, suggesting an affinity to topographic features related to the shelf break rather than the deep waters of the Norwegian Sea.

At the study area scale fin whales were positively associated with capelin in all years, and with 0-group fish and herring in 2001 (Table 5). Prey associations changed slightly when repeating the analysis for the core area, as there was a positive association also between fin whales and 0-group fish in 2002 (Table 6). These results suggest that fin whales prefer capelin to herring when both species are available. However, due to the similar distributions of herring and capelin within the fin whale core area (Figs 5 and 6), the roles of capelin and herring may be confounded in the analyses. Fin whales were also associated with 0-group fish in 2001 and 2002, the years with highest 0-group abundance within the core area. Fin whales are known to have a broad diet consisting of copepods, krill and pelagic fish (*e.g.* Woodley and Gaskin 1996, Flinn *et al.* 2002, Simard *et al.* 2002). To our knowledge, fin whales have not previously been associated with 0-group fish. Nevertheless, given the breadth of the fin whale diet, we might expect fin whales to use the various resources available. No association between fin whales and zooplankton was observed. Due to the high degree of similarity between 0-group fish and zooplankton distribution within the core area (Figs 3 and 4) it is dif-

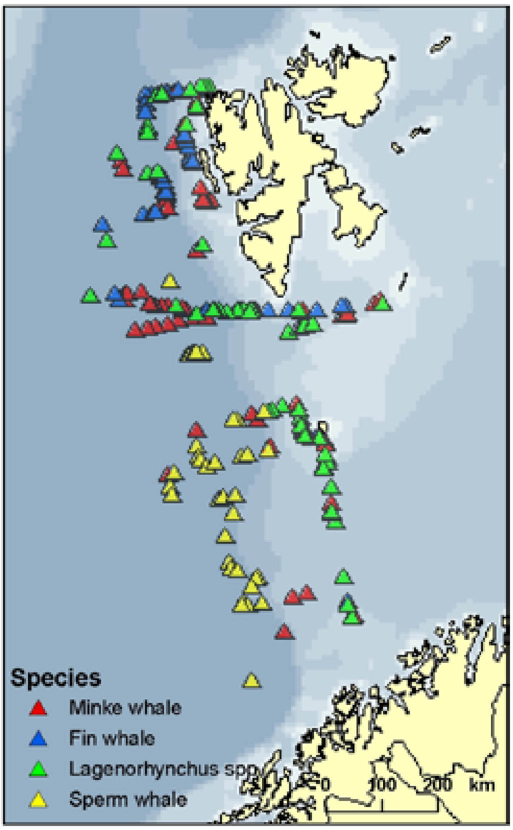


Fig. 7. Distribution of minke, fin and sperm whales, and Lagenorhynchus dolphins, observed in 2000, 2001 and 2002.

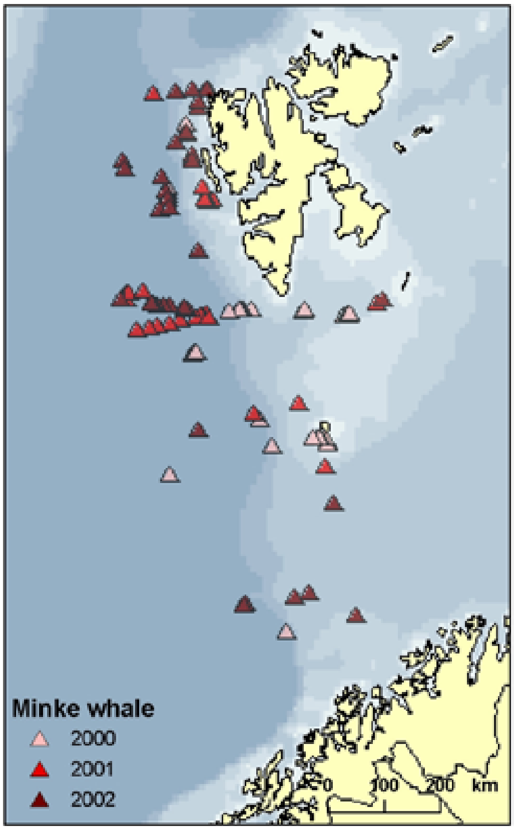


Fig. 8. Distribution of minke whales in 2000, 2001 and 2002.

ficult to assess whether this lack of association is due to fin whales not preying on zooplankton or due to confounded variables in the model.

The generalist behaviour of fin whales suggests that they utilize a range of prey items, and could therefore also be expected to use the deeper areas further south. Fin whales have previously been observed throughout the study area (Øien 1990, Christensen *et al.* 1992, suggesting that there has indeed been a northward shift in fin whale distribution prior to 2000. This distributional shift may be related to the increasing inflow of warm Atlantic water masses, which began in the late 1990's (Loeng and Sundby 2001). Fin whales are large mammals with a high foraging cost due to their lunge feeding strategy (Acevedo-Gutierrez *et al.* 2002). Fin whales may therefore depend on dense prey aggregations above a certain threshold for efficient foraging, and this threshold may be higher than that for minke whales (Piatt *et al.* 1989, Acevedo-Gutierrez *et al.* 2002). In the northern areas the complex bottom topography may interact with the front between northward warm water current and southward cold water currents creating denser prey aggregations. Our data does not, however, reveal higher prey densities per 5 nm segment within the fin whale core area than within the study area (Figs 2-6). Nevertheless, despite the annual variation in prey abundance, both plankton and 0-group fish have been available within the fin whale core area each year. Thus, oceanographic and topographic features within the fin whale core area may act to increase the predictability of food supply within the core area.

Lagenorhynchus spp.

In contrast to the other species included in this study, both the distribution and abundance of *Lagenorhynchus* dolphins varied among years. From 2000 to 2002, there was a northward shift in the *Lagenorhynchus* dolphin distributions (Fig. 10). The numbers of individuals observed were 262, 168 and 422 in 2000, 2001 and 2002 respectively, and hence dolphin abundance did not correlate with the northwards distribution shift. However there was a general increase in group sizes during the 3 years (median group sizes 7, 10 and 11).

The selected model demonstrated that *Lagenorhynchus* dolphins were associated with sdSST and thus fronts in 2000 and 2001, but not in 2002. The lack of correlation with sdSST in 2002 may be due to poor coverage of the frontal zone south of Svalbard in 2002, or a consequence of the northward distribution shift away from the frontal zone (Fig. 10). Despite the use of the shelf area in 2000, depth was not included in the selected model. In 2000, depth and sdSST were correlated (Table 3) and thus possibly confounded.

Lagenorhynchus dolphins were also positively associated with capelin. *Lagenorhynchus* dolphins occupy a high trophic level, with a diet predominantly consisting of gadoid and pelagic fish (Hai *et al.* 1996, Kinze *et al.* 1997, Das *et al.* 2003). White-beaked dolphins have previously been reported to forage in the frontal zone south of Svalbard, but the prey targeted by the dolphins has not been observed (Mehlum *et al.* 1998). Murres (*Uria* spp.) foraging in the same frontal zone predominantly fed on polar cod and capelin, but also on krill, amphipods and *Gonatus* (Mehlum *et al.* 1998). Aggregations of capelin in this area were also seen during the 3 years of this study (Fig. 6). It is therefore reasonable to believe that *Lagenorhynchus* dolphins were preying on capelin, although polar cod, not sampled in this study, may also have been targeted. *Lagenorhynchus* dolphins also overlapped considerably with herring, indicating that herring may be a relevant prey species. Nevertheless, the lack of significant associations between the dolphins and herring suggest that there is no active selection for herring. Interestingly, the northward shift in *Lagenorhynchus* dolphin distributions coincide both with increasing temperatures and increasing capelin abundance in the north, further supporting capelin as an important prey species. Tracking capelin distributions may thus be the underlying process causing the northward distribution shift. Furthermore, the highest numbers of *Lagenorhynchus* dolphins were observed in 2002 when capelin was most abundant.

Sperm whales

Sperm whales were confined to the deeper south western part of the study area (Fig. 11), in good agreement with previous records of sperm whales within this area (Christensen *et al.* 1992). The selected model for the study area scale also demonstrated that sperm whales were significantly associated with depth, both at the study area and core area scales. Sperm whales were furthermore associated with SST, demonstrating an affinity to the warmer Atlantic water masses. The distribution of sperm whales is generally related to deeper water masses, slopes and underwater canyons (Waring *et al.* 2001, Gregr and Trites 2001, Hamazaki 2002). Although all sperm whale observations were recorded off the shelf, several sperm whales were observed in association with the slope (Fig. 11), suggesting that also in this area the continental slope is the preferred habitat for the sperm whales. However, deeper areas in the Norwegian Sea were poorly sampled in this study. Recent sighting surveys have shown that sperm whales use large parts of the Norwegian Sea proper with a focal point in the eastern part off northern Norway (Bleik Canyon). Their abundance is also apparently increasing and they have been recorded even in the far north off Spitsbergen.

At the study area scale, sperm whales were positively associated with 0-group fish and herring in 2000, but not in 2001 or 2002. At the core area scale, sperm whales were positively associated with 0-group fish in all years. Sperm whales prey on squid and fish (Santos *et al.* 1999, Bjørke 2001, Flinn *et al.* 2002, Santos *et al.* 2002). It is not likely that 0-group fish are important prey items for sperm whales, but fish may be attracted to 0-group fish aggregations that in turn attract sperm whales. In Icelandic waters, sperm whales commonly feed on redfish, cod and blue whiting as well as *Gonatus* squid, species which typically occur in warmer Atlantic water masses rather than Arctic or mixed water masses (Martin and Clarke 1986). In the Norwegian Sea, sperm whale foraging is associated with a particular deep scattering layer at 300-500 m depth, dominated by redfish and blue whiting (Sarvas 1999). Redfish and blue whiting also occur in deeper areas off the Barents Sea shelf (Aglen *et al.* 2002), and may thus be important prey within the study area.

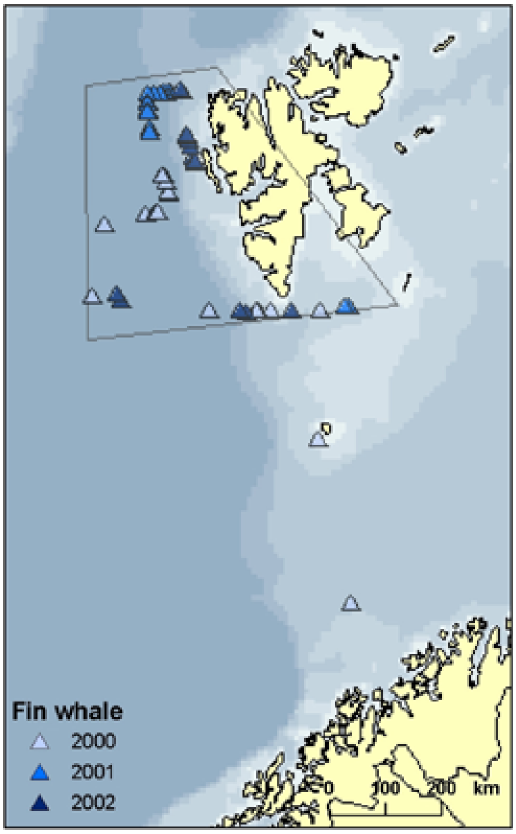


Fig. 9. Distribution of fin whales in 2000, 2001 and 2002. Polygon enclosing the defined fin whale core area is shown.

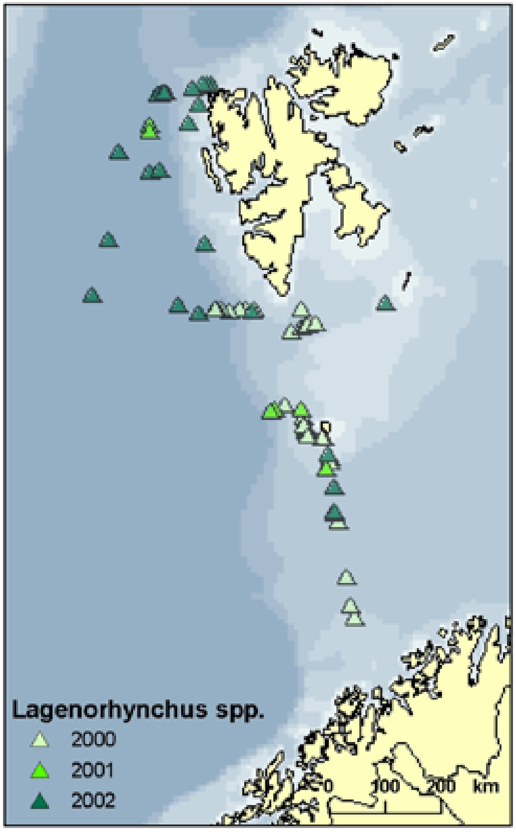


Fig. 10. Distribution of Lagenorhynchus dolphins in 2000, 2001 and 2002.

Sperm whale distribution and abundance did not vary between years. At lower latitudes the distribution of sperm whales is tightly associated with squid, and when squid abundance decreases, sperm whales may undertake long distance migrations to new areas with higher prey availability (Whitehead 1996, Jacquet and Whitehead 1996). However, at our latitudes sperm whales likely feed on a variety of prey species, enabling them to switch between prey species depending on availability. Sarvas (1999) demonstrated that when the deep scattering layer was absent, sperm whales foraged at greater depths, most likely on *Gonatus*. Nevertheless, in this study none of the prime prey items for sperm whales were sampled, thus the distributions of preferred prey are unknown.

Cetacean habitat and prey selection: Conclusions

The study area includes a relatively small section of the distribution of the included species. Hence, variation in abundance or distribution within the study area may be considered as relatively local changes, not necessarily indicating any large scale distributional changes. Nevertheless, how distributions change within the study area relative to changes in habitat or prey distributions likely gives an indication of the strategies used by the cetaceans. Minke whale distributions covered most of the study area and abundances varied little between years, despite the variation in abundance and distribution of prey. Hence, although strongly associated with pelagic fish, suggesting a rather specialised diet within this area during the study period, their wide and relatively invariable distributions suggest that minke whales are habitat generalists tracking their prey through a range of habitats. Fin whales, on the other hand, were restricted to the northern part of the study area in all 3 years, likely switching between prey species in response to environmental variability. Hence, fin whales appear as habitat specialists, possibly confined to areas with complex bottom topography and cold water masses. Only *Lagenorhynchus* dolphins changed in abundance and distribution during the 3 years, as they moved northwards coinciding with increased availability of capelin in the northern areas, suggesting that they have more specialised feeding patterns than minke and fin whales. For all species the selected models accounted for 15-34% of the deviance, leaving a substantial amount of variation in cetacean distributions unexplained. The best fit models were for fin whales (34%, study area scale) and sperm whales (31%, study area scale) which are the species with the most restricted geographic distributions, which therefore correlate well with the more static physical habitat variables such as depth and SST. In contrast, for minke whales, which occurred in most parts of the study area, the model explained only 15% of the deviance.

Sighting surveys and habitat selection modelling

Sighting surveys are primarily performed for assessing abundance and distribution of cetacean species, and when repeated over time for assessing temporal trends in cetacean abundance and distribution. Although they do not sample physical habitat or prey, as was done during the synoptic cruises in this study, sighting surveys may provide crucial input to studies of cetacean habitat selection when combined with useful habitat descriptors obtained from bathymetric maps, satellite images or output from numerical hydrodynamic models. Due to the temporal variation of the marine systems, examining habitat selection requires survey data and habitat information coinciding both in time and space. Satellite images provide information on SST, sea ice cover and primary productivity on a daily or weekly basis, and bathymetric maps provide information on depth and seabed topography. Incorporated in a GIS, a multitude of derived variables such as sea bed complexity, slope, fronts and upwelling plumes can be obtained. Although these habitat variables provide limited information on the ocean habitat, both pinniped and cetacean distributions may correlate with depth, SST, productivity, sea bed complexity, fronts, upwelling plumes and oceanographic circulation (this study, Jaquet and Whitehead 1996, Croll *et al.* 1998, Georges *et al.* 2000, Kasamatsu *et al.* 2000, Gregr and Trites 2001, Waring *et al.* 2001, Benson *et al.* 2002, Davis *et al.* 2002, Simard *et al.* 2002). Such studies increase our understanding of critical marine mammal habitat, and may allow identification on potential prey species, which are species occupying habitats selectively used by marine mammals.

As is clearly shown in our work, the resulting habitat and prey selection models depend on the resolution of the data obtained and the area included in the analyses. For instance, the use of pooled variables of zooplankton and 0-group fish distribution may have masked associations between cetaceans and prey species or size groups. Repeating the analyses on the core area scale for fin and sperm whales, yielded different habitat and prey associations than for the entire study area. Also the spatial resolution of the data acquired influence the resulting habitat and prey selection models, because different processes dominate at various scales, affecting the observed patterns in habitat and prey use (Rose and Legget 1990, Jaquet and Whitehead 1996, Fauchald and Erikstad 2002). In our study, temperature was sampled on a rather coarse scale (30 nm), enabling us to investigate cetacean distribution relative to the regional distribution of Atlantic and Arctic water masses. A finer resolution of the SST sampling might have allowed investigations of cetacean distribution relative to local bathymetrically related oceanographic features. Bathymetric maps and satellite images commonly used in habitat selection studies are freely available but have quite low resolution (*i.e.* 5-25 km or 2.5-13.5 nm), allowing for investigations of large scale and general patterns in habitat use only. Preferably, habitat and prey selection analyses should be repeated at several scales before firm conclusions on cetacean requirements are drawn.

Apart from increasing our understanding on cetacean ecology, habitat selection studies may also provide species habitat relationships valuable for proper assessment of population sizes and trends (Forney 2000). Environmental variability may cause shifts in cetacean distributions (Forney 2000, Kasamatsu *et al.* 2000, Benson *et*

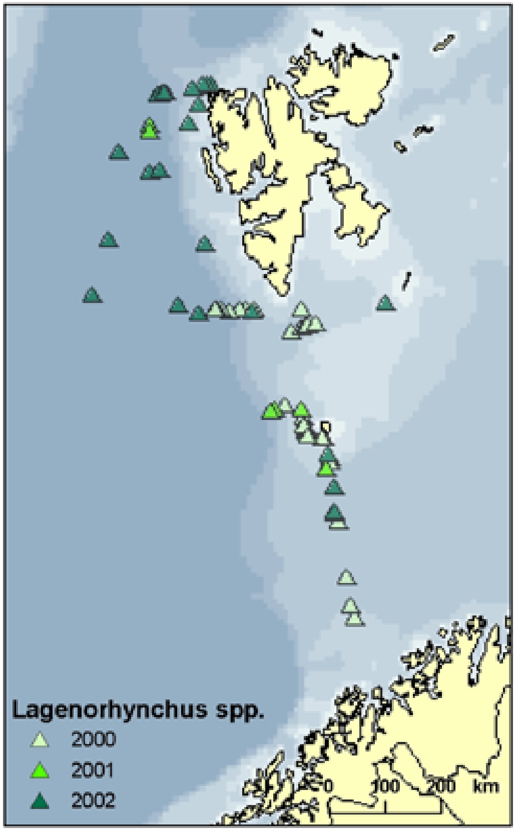


Fig. 10. *Distribution of Lagenorhynchus dolphins in 2000, 2001 and 2002.*

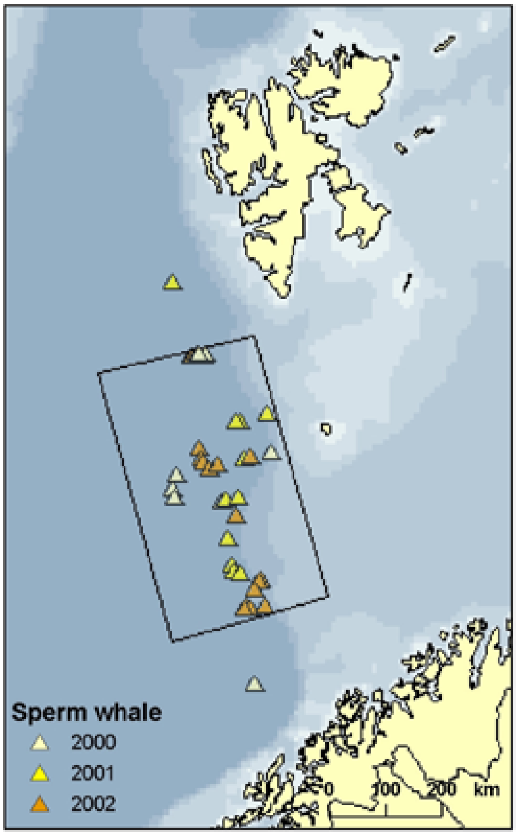


Fig. 11. *Distribution of sperm whales in 2000, 2001 and 2002. Polygon enclosing the defined sperm whale core area is shown.*

al. 2002). Such shifts may have occurred both in the fin whale and *Lagenorhynchus* dolphin distributions within the study area; fin whales likely shifted northwards prior to 2000, and *Lagenorhynchus* dolphins during 2000-2002. When such distribution shifts occur, variable proportions of cetacean populations are present within the often fixed areas covered by repeated sighting surveys. Thus distribution shifts add variability to abundance estimates, and introduce uncertainty when assessing whether the observed variation in abundance represents true changes in population size or distribution shifts. Having obtained predictive habitat selection models, *i.e.* models that have identified species habitat associations that are consistent across years, these associations can be used to correct for changes in estimated population sizes within areas due to environmental variability (Forney 2000). Also, if information on the real time distribution of relevant habitats is available, species habitat associations may aid decisions both on the spatial extent and stratification of sighting surveys (*e.g.* Pedersen *et al.* 2003), yielding increased precision of population abundance estimates (Forney 2000). Due to the limited amount of data available, the predictive ability of the selected models in the present study has not been evaluated, but such an evaluation will be performed when additional data have been collected. The selected models were able to account for a moderate proportion of the observed variation (percentage of deviance explained ranged from 15% for minke whales to 34% for fin whales) in the cetacean distributions. This, together with the lack of persistent correlations between habitat and prey variables, demonstrates a need for further exploration of habitat variables more relevant to the prey distribution and thus possibly more relevant for cetaceans. Additional data will also enable us to investigate nonlinear effects (*e.g.* preferred depth or temperature intervals) in both habitat prey and habitat cetacean relationships. Several cetacean habitat selection models, using both static bathymetric and dynamic oceanographic habitat variables, are able to predict cetacean distributions across years (Forney 2000, Gregr and Trites 2001, Hamazaki 2002). These studies demonstrate that habitat and prey selection models can be useful tools to increase our understanding of cetacean ecology and the underlying processes causing variation in cetacean abundance and distribution.

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