Feeding strategy and prey selectivity in common minke whales (*Balaenoptera acutorostrata*) foraging in the southern Barents Sea during early summer

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ABSTRACT

Stomach content samples from 33 minke whales (*Balaenoptera acutorostrata*), caught during Norwegian commercial whaling between May-June 1998, were collected in four sub-areas in the southern Barents Sea. Simultaneously, a comprehensive resource survey was conducted in order to identify and estimate the abundance of potential prey items for the whales in the four sub-areas. Krill (*Thysanoessa* sp. and *Meganyctphanes norvegica*) dominated the diet in all but one sub-area although pelagic fish such as capelin and herring also contributed significantly. The minke whales displayed monophagus feeding in all sub-areas investigated, including the medium-scale area resulting from pooling of all sub-areas. The small-scale resource surveys revealed significant variations in absolute and relative prey abundance between sub-areas, while the temporal (1-7 days) variations in relative prey biomass within sub-areas appeared to be less significant for all prey items, except herring (*Clupea harengus*) and perhaps capelin (*Mallotus villosus*). Krill was by far the most important prey item available in all areas, followed by either herring, cod (*Gadus morhua*) or saithe (*Pollachius virens*), depending on sub-area and survey. Although minke whale prey preference appeared to vary greatly in space, some new features of minke whale foraging behaviour were evident. Minke whales showed a strong preference for capelin, whereas gadoids (cod, haddock (*Melanogrammus aeglefinus*) and saithe) appeared to be avoided by the whales. Krill appeared to have been either avoided, fed upon randomly or were the preferred prey depending on sub-area and analyses level.

KEYWORDS: BARENTS SEA; FEEDING STRATEGY; MINKE WHALE; PREY ABUNDANCE; PREY SELECTIVITY

INTRODUCTION

The common minke whale (*Balaenoptera acutorostrata*) is a boreo-arctic species which migrates northward to feeding areas in spring and early summer, and southwards to breeding areas in the autumn (Jonsgård, 1966). It is the most numerous baleen whale species in the Northeast Atlantic (see Schweder *et al.*, 1997), where it exploits a variety of species and sizes of prey such as krill (*Thysanoessa* sp.), herring (*Clupea harengus*), capelin (*Mallotus villosus*) and various gadoids (Jonsgård, 1951; 1982; Christensen, 1972; 1974; Haug *et al.*, 1995a; b; 1996; 1997; In press; Lindstrøm *et al.*, 1997; In press; Skaug *et al.*, 1997). Recent feeding studies suggest that minke whales have a flexible feeding pattern and adapt to local prey abundance (e.g. Haug *et al.*, 1996).

The Barents Sea ecosystem has undergone substantial changes over the last three decades. The most conspicuous are the disappearance and subsequent reappearance of immature Norwegian spring spawning herring and the Barents Sea capelin (Røttingen, 1990; Hamre, 1994; Gjøsæter, 1995; 1998; Dragesund *et al.*, 1997; Gjøsæter *et al.*, 1998). These changes are likely to have had an impact on the feeding habits and possibly the migratory behaviour of minke whales. In addition, major changes in the numbers of common minke whales in the Barents Sea at least between the 1930s and early 1980s (Schweder and Volden, 1994), suggest that it is likely that the predation on these prey species as well as the intra-specific competition for prey has diminished.

Several theoretical studies (e.g. Abrams, 1984; Fryxell and Lundberg, 1994) suggest that the dietary choice of a predator may have important implications for predator-prey dynamics, directly through predation as well as indirectly

through competition. Thus, to understand how minke whales may respond to ecosystem changes, knowledge of how their foraging strategy and diet choice vary in various food availabilities, both in time and space, is essential.

To assess the potential resource selection by a predator, that predator's diet must be compared with the availability of prey resources in its environment. Prior to this study, information about prey preference in the Northeast Atlantic in relation to spatial scales was sparse. The results of one large-scale study suggested that minke whales had no particular prey preferences (Skaug *et al.*, 1997). However, a combination of the size of the area studied and poor temporal overlap between the sampling of whales and potential prey reduced the reliability of this study. The choice of study area and its boundaries may have a significant impact on the prey selection results, particularly when the spatial and temporal abundance of prey varies greatly (Manly *et al.*, 1993). The aim of this study was therefore to study the feeding strategy and prey selectivity of minke whales by using medium- and small-scale survey designs.

Whale samples were obtained from commercial catches, which occurred opportunistically in high-density areas of minke whales. Based on the spatial and temporal distribution of the whale samples, feeding strategy and prey selectivity studies of minke whales were carried out in four small-scale sub-areas and one medium-scale pooled area. Additionally, an even finer 'micro-scale' analysis of individual minke whale prey selectivity was conducted in one of the sub-areas. To assess the resource availability in these selected sub-areas, a standard acoustic survey was performed using a research vessel.

Although there have been many attempts to quantify selective predation (e.g. Ivlev, 1961; Manly, 1972; Chesson, 1978), there is no general agreement in the literature about

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which index gives the best measure of preference. In this study, Chesson's selectivity index was applied to examine the prey preference of minke whales, mainly because it eliminates any differences that might arise due to abundance differences in the diet or the environment (Krebs, 1989). The index was calculated for each prey type and then tests carried out to examine for deviations from random feeding. This was done by calculating approximate 95% confidence intervals for the expected index value for each prey species.

MATERIAL AND METHODS

Whale sampling

A coastal region in the southern Barents Sea (see Fig. 1), where whale diets have been found to comprise a mixture of several prey species (Haug *et al.*, 1996), was chosen as the study area. The 33 minke whales included in this study were collected during commercial whaling operations from May-June 1998 (Fig. 1), with 12, 1, 13 and 7 individuals sampled from sub-areas 1, 2, 3 and 4, respectively. The whales were killed according to whaling procedures described by Haug *et al.* (1996), and immediately taken onboard the vessel for dissection and biological sampling.

Once onboard, the complete digestive tract was removed as soon as possible (30-60 minutes *post mortem*). The minke whale stomach consists of four chambers (see Olsen *et al.*, 1994). However, since previous studies have indicated that stomach contents from the first stomach compartment (the forestomach) are sufficient to describe the diets (Lindstrøm *et al.*, 1997), only contents from the forestomach were used in this study. The forestomach contents were separated from the rest of the stomach contents and transferred to a tube where the volume was measured. The contents were then transferred to a system consisting of three sieves (20mm, 5mm and 1mm) in order to filter off liquid from the rest of the material. Undigested specimens of fish were separated from the rest of the material, identified, counted and total lengths were measured (see Haug *et al.*, 1995a; 1996).

In the laboratory, intact fish specimens were identified using gross morphological characteristics (Pethon, 1985) and divided into four digestion states as defined by Lindstrøm *et al.* (1998a). In order to reduce some of the main sources of uncertainty in reconstruction of stomach contents, such as: (1) differential passage and degradation rates of different fish types and sizes (Bigg and Fawcett, 1985; da Silva and Neilson, 1985; Murie and Lavigne, 1986; Markussen and Øritsland, 1992); and (2) accumulation of hard remains such as otoliths, only undigested or moderately digested fish prey were included in the present analysis. In addition to undigested specimens, however, otoliths from herring and capelin were used to estimate the original fish length by using regression equations between fish otolith length and fish length (mm). These regression equations (Herring: $FL = 13.82 + 56.40 \times$ otolith length, $n = 224$, $r^2 = 0.93$, $p < 0.001$; Capelin: $FL = 31.80 + 49.60 \times$ otolith length, $n = 845$, $r^2 = 0.77$, $p < 0.001$) were based on material obtained from the present resource survey trawling.

The estimation of crustacean biomass at time of ingestion is another major problem when reconstructing the forestomach content of minke whales, not only because they lack hard parts that are resistant to the forestomach microbes (Nordoy *et al.*, 1993; Olsen *et al.*, 1994) but also due to
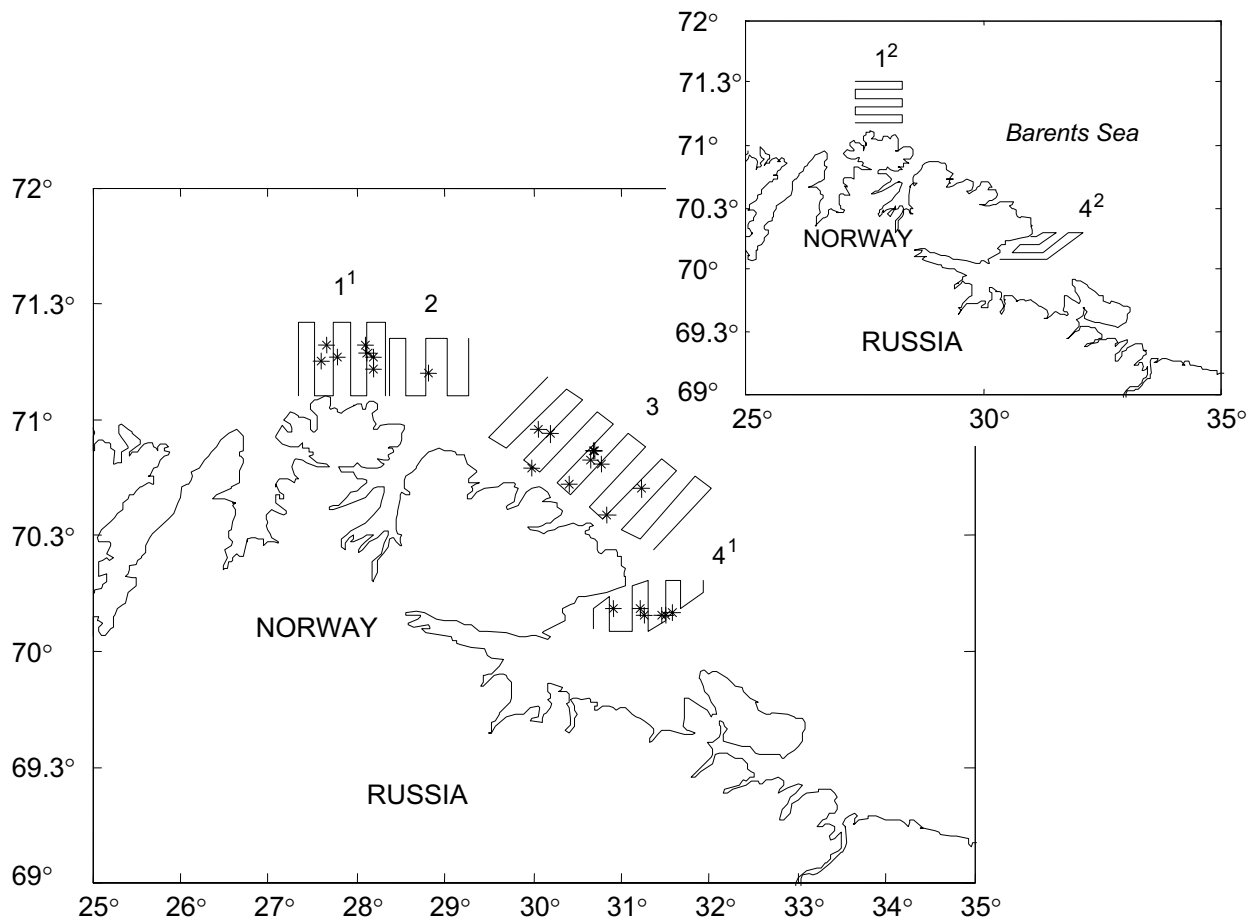

Fig. 1. Catch positions for 33 minke whales (asterisk) sampled in four sub-areas along the coast of Finnmark in North Norway during Norwegian commercial whaling in May-June 1998. The track lines for the four resource surveys in sub-areas 1, 2, 3 and 4 are also shown. 1^1 and 4^1 show the first coverage of sub-areas 1 and 4, respectively, and 1^2 and 4^2 show the second.

passage and degradation rates that most likely differ from those of other prey types. Due to difficulties in assessing the reconstructed weights, only the *in situ* biomass of crustaceans was used.

In order to illustrate the relative prey importance and possible feeding strategy of the whales, specific abundance, *Pi* was used:

$$P_i = \left(\frac{\sum_{j=1}^{n} b_{ij}}{\sum b_{ti}} \right) .100$$

where b_{ij} is the biomass of prey category i in whale number j, and b_{ti} is the total biomass of all prey categories in all whales containing prey item i (see Amundsen, 1995; Amundsen *et al.*, 1996). The prey specific abundance (P_i) was plotted against the frequency of occurrence (F_i) of each prey item:

$$F_i \left(\frac{f_i}{f_t} \right).100$$

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

In the explanatory diagram (Fig. 2), the vertical axis represents the feeding strategy of the predator in terms of degree of specialisation. The predator has specialised on prey items located in the upper part of the graph, whereas prey located in the lower part of the graph have been eaten more occasionally (generalisation). Prey items located in the upper left part of the graph indicate individual specialisation, i.e. few predators have exploited the actual prey item in large amounts, whereas prey items in the upper right part of the graph indicate population specialisation, meaning that these prey items are frequently taken by many predators. If all prey items are distributed in the upper left part of the graph there is a high between-phenotype component (BPC: different predators specialise on different prey types), whereas if prey items are distributed in the lower right part of the graph there is a high within-phenotype component (WPC: most individuals exploit many prey types simultaneously). The distribution pattern of prey points along this upper left-lower

right diagonal is, therefore, indicative of the contribution of between- and within-phenotype components to the diet width. In both cases the population will be generalistic, displaying a broad diet width.
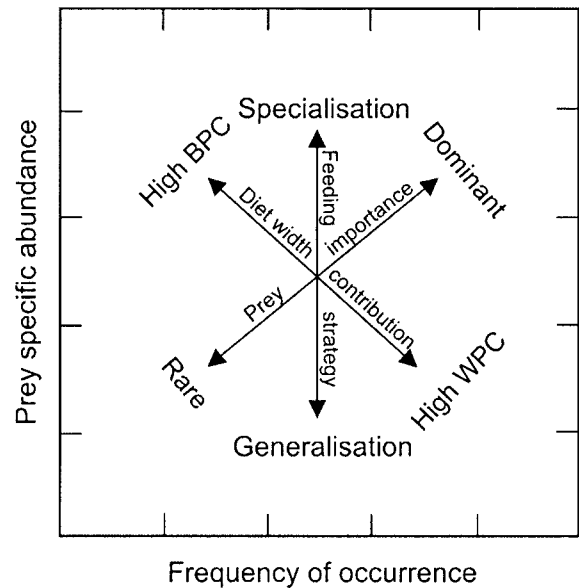

Fig. 2. Explanatory diagram for interpretation of feeding strategy, diet width contribution and prey importance using the method of Amundsen *et al.* (1996).

Estimation of prey abundance

Parallel with the whaling operations, a standard acoustical survey was conducted aboard the research vessel *Jan Mayen* along predetermined transects in the sub-areas where whales were being or had been caught. Two of the sub-areas (1 and 4) were surveyed twice, while sub-areas 2 and 3 were surveyed once (Table 1). The time lag between the first and second survey in sub-areas 1 (1^1 and 1^2) and 4 (4^1 and 4^2) was 7 and 1 days, respectively.

Continuous acoustic recordings of fish and euphausiids were made by a calibrated echo integration unit consisting of a 38kHz Simrad EK-500 splitbeam echosounding system (Bodholt *et al.*, 1989), connected to a BEI post processing system (Foote *et al.*, 1991). A minimum acoustic threshold

Table 1

Acoustic resource survey conducted during the feeding ecology study of minke whales in the southern Barents Sea in June 1998. Date, size, degree of coverage (DOC) and bottom depth of each survey area. The results are given in average abundance (by weight, ton) of potential prey items per n.mile^2 for two depth strata: 0-100m and 100-bottom. The coefficient of variation (CV) is given in parentheses.

Sub-area	Date	Size (n.mile^2)	DOC	Bottom depth (m)	Depth (m)	Krill	Herring	Capelin	Cod	Haddock	Saithe	Other gadoids
1^1	4-5	380	7.2	32-415	0-100	17.15 (0.9)	1.28 (4.2)	4.23 (1.6)	2.05 (2.8)	0.48 (2.5)	5.85 (3.1)	0.36 (3.8)
					100-bottom	14.82 (1.2)	0.02 (10.9)	2.97 (1.7)	19.95 (1.5)	2.85 (1.6)	9.30 (2.1)	2.08 (1.8)
1^2	11-12	380	6.9	59-413	0-100	23.02 (0.9)	0	2.12 (2.3)	0.52 (3.3)	0.24 (3.0)	11.90 (5.1)	0
					100-bottom	12.41 (1.0)	0	0.58 (2.2)	8.04 (0.8)	0.54 (1.5)	1.48 (4.7)	0.84 (1.1)
2	1-2	285	5.6	82-415	0-100	24.95 (1.0)	0	6.01 (1.7)	0.07 (6.4)	0.05 (7.7)	0.19 (9.5)	0
					100-bottom	32.88 (0.9)	0	6.26 (0.8)	4.67 (1.4)	2.30 (1.7)	2.34 (6.2)	0.12 (4.2)
3	2-3	928	9.1	92-365	0-100	22.65 (0.9)	15.29 (4.7)	3.14 (1.3)	2.23 (3.1)	2.45 (7.9)	4.54 (4.9)	0.15 (6.6)
	5-6				100-bottom	26.34 (0.9)	0.29 (2.5)	8.03 (0.7)	13.95 (1.2)	1.98 (3.9)	3.07 (3.9)	1.20 (2.4)
4^1	6-7	250	6.4	74-340	0-100	17.78 (1.1)	8.43 (3.4)	2.93 (1.8)	11.26 (3.6)	8.48 (1.5)	0	0
					100-bottom	18.92 (1.3)	1.59 (1.5)	2.47 (1.2)	46.11 (2.1)	6.34 (1.4)	0	0.32 (2.5)
4^2	8-9	270	6.7	73-330	0-100	21.93 (0.9)	0.18 (2.3)	2.73 (1.4)	12.21 (2.3)	7.61 (1.9)	0.25 (4.2)	0.02 (7.1)
					100-bottom	13.79 (0.9)	0.06 (3.7)	2.81 (1.5)	34.15 (1.3)	12.25 (1.1)	0.64 (2.6)	0.36 (1.7)
Pooled area					0-100	21.11 (1.0)	7.43 (6.3)	3.64 (1.7)	4.57 (4.3)	3.30 (4.4)	3.00 (5.4)	0.13 (6.6)
(1^1+ 2+ 3+4^1+ 4^2)					100-bottom	22.11 (1.1)	0.33 (3.3)	5.30 (1.1)	21.18 (2.1)	4.27 (2.1)	3.44 (3.6)	1.00 (2.6)

of -88dB Sv was applied to detect euphausiids. The allocation of acoustic values (Sa, area backscattering coefficient) was carried out on the basis of the acoustic character of species and trawl samples. Both pelagic and demersal trawling was performed in response to potential changes in the echo sounder registrations. For pelagic trawling, a 14 fathom trawl (Harstad, Norway) fitted with a Scanmar depth recorder was used, while a *Super Campelin* 1,800 mesh shrimp trawl was used for demersal trawling. Both trawls were fitted with an 8mm net inside the codend thereby making it possible to sample fish juveniles and euphausiids. Pelagic and demersal trawling were standardised to 30 and 20 minutes duration respectively, and the trawling speed was approximately 3 knots.

As a result of different fishing efficiencies of the trawls with respect to fish and euphausiids, and due to the low frequency of the echosounder for detection of euphausiids, the trawl catches were used only to confirm euphausiid presence or absence. Therefore, the partitioning of acoustic values between fish and euphausiids was made subjectively by reducing the volume backscattering coefficient (Sv) to a fixed level until euphausiids were assumed to be removed (e.g. Lindstrøm *et al.*, 1998b). However, since the echo intensity decreases with the range to the target due to beam spreading and absorption (see McLennan and Simmonds, 1992), euphausiids distributed in deeper water layers were assumed to be removed at lower Sv-values than those distributed near the surface. The remaining Sa-values were then partitioned among the different fish species according to standard procedures (see McLennan and Simmonds, 1992). The recorded Sa-values, averaged over one n.mile^2, were converted to numbers (ρ) according to the relation:

$$\rho = \frac{Sa}{4\pi.10^{0.1\overline{TS}}}$$

where $\overline{TS}$ is the mean target strength of scattering organisms, which varies between species and body length. In order to cover the most potential foraging depth of minke whales, the water column was divided into the following two depth strata: 0-100m and 100-bottom.

As a measure of the sampling intensity, Aglen (1989) defined the 'degree of coverage' as $d = D/\sqrt{A}$ where D is the total length (in n.miles) of the cruise track and A is the size (in n.miles^2) of the surveyed area. Aglen (1989) suggested that a d-value of 6 or more was sufficient. In this study the degree of coverage varied from 5.6 in sub-area 2, to 9.1 in sub-area 3 (Table 1).

In order to estimate the variation in prey abundance, and hence prey availability, within and between sub-areas one needs to know the correlation length (i.e. the minimum distance between two uncorrelated observations) of resource samples in each sub-area. Harbitz and Lindstrøm (2001) analysed the spatial prey abundance in the four defined sub-areas by applying directional variograms and cross-variograms (e.g. Cressie, 1993). Their study revealed a correlation length of *ca* 10-15 n.miles, dependent on species. Because a relatively large proportion of the variation was not autocorrelated or autocorrelated at a finer scale than 1 n.mile, each 10 n.mile^2 was treated as an independent resource sample, independent of species. This yielded a total of 14, 14, 10, 27, 10 and 11 independent 10 n.mile^2 prey abundance samples in the resource surveys in sub-areas 1-4 (1^1, 1^2, 2, 3, 4^1 and 4^2, respectively) where sub-areas 1 and 4 were surveyed twice. In order to construct 95% confidence intervals, the resource samples in each individual sub-area

were bootstrapped 5,000 times. The confidence intervals were corrected for possible acceleration and bias (see Efron and Tibshirani, 1993).

The coefficient of variation (CV) was used as a measure of patchiness.

Analyses of foraging selectivity

To assess the biomass proportion of the various prey items in the whale diets, the individual mass index BI_i (see Lindstrøm *et al.*, 1997) was applied:

$$BI_i = \frac{1}{n}\sum_{j=1}^{n}\left(\frac{b_{ij}}{b_{tj}}\right).100$$

where b_{ij} is the biomass of prey category i in whale number j; b_{tj} is the total biomass of all prey categories in whale number j; and n is the total number of examined whales containing food.

Minke whale foraging selectivity was analysed using Chesson's index for constant prey populations:

$$\alpha_i = \frac{r_i}{n_i}.\frac{1}{\sum_{j=1}^{m}\frac{r_j}{n_j}}$$

where α_i is Chesson's α ranging from zero to one; r_i and r_j is the proportion of prey type i or j in the whale diet (i and $j = 1,2,3,....,m$); n_i and n_j is the proportion of prey type i or j in the environment; and m is the total number of prey types. In interpretating these results; selective predation does not occur if $\alpha_i = 1/m$, while when $\alpha_i > 1/m$ more species i occurs in the diet than expected by random feeding, i.e. species i is preferred by the whales. Conversely, if $\alpha_i < 1/m$ less species i occurs in the diet than expected, i.e. prey species i is avoided by the whales.

The prey selectivity analysis was performed on two vertical (0-100m, 0-bottom) and three horizontal spatial scales depending upon the temporal overlap between whale and resource samples. The horizontal scales were defined as: (1) a 'micro-scale' (*ca* 28 n.miles^2); (2) a 'small-scale' defined as the individual sub-areas 1, 3 and 4 (250-928 n.miles^2); and (3) a 'medium-scale' defined as the pooled individual sub-areas 1-4 (1^1, 2, 3, 4^1 and 4^2; *ca* 2,300 n.miles^2). In sub-area 1, the whales were caught 1 and 7 days prior to the resource surveys 1 and 2 (1^1 and 1^2), respectively, while the whales in sub-area 4 were caught 7 and 8 days prior to the resource surveys 1 and 2 (4^1 and 4^2), respectively. Therefore, the whale diets in sub-area 1 were compared with the prey availability for survey 1 (1^1), while the whale diets in sub-area 4 were compared with the prey availability for surveys 1 and 2 (4^1 and 4^2) pooled. The prey selectivity analysis in sub-area 1 was performed on two vertical scales (0-100m, 0-bottom) at population level, i.e. the whale diets were pooled and compared with prey availability for the entire sub-area. Additionally, the high temporal overlap between whale samples and survey 1 allowed analysis of minke whale prey selectivity on a finer scale ('micro-scale') at an individual level, i.e. each individual whale was compared with the prey availability in a 3 n.mile radius from the sample site (*ca* 28 n.miles^2). The prey selectivity analysis in sub-areas 3 and 4, and in the medium-scale area, was performed on a lower vertical resolution (0-bottom) at the population level due to the low temporal overlap between whale and resource samples (2-12 days).

In order to test the null hypothesis (H$_0$), that minke whales in the area are not prey selective, Chesson's α, calculated for each prey type, was tested for significant deviation from random feeding (1/m). This was accomplished by constructing approximate 95% CI for Chesson's α of each prey, and comparing these with the value of random feeding. At the population level, the confidence intervals were estimated from 5,000 bootstrap replicates of both the diet and resource data (see Efron and Tibshirani, 1993). At the individual level, Chesson's α was calculated for each individual whale and then bootstrapped 5,000 times, whereafter the confidence intervals could be estimated. Similar bootstrap techniques have proved useful in other analyses of predator diets (e.g. Jiang and Jørgensen, 1996; Lawson and Stenson, 1997; Lindstrøm *et al.*, 1998b).

In addition to the prey selectivity analysis, minke whale preferences regarding prey size were studied by comparing the length distribution of the most important fish prey consumed by the minke whales (herring and capelin) with specimens sampled from the trawl hauls.

RESULTS

Whale diets

Fig. 3 shows that the diet of minke whales in sub-area 1 was dominated by capelin, followed by krill. The latter was a mixture of *Meganyctephanes norvegica* and *Thysanoessa* sp. Capelin and krill constituted 61.4% and 27.5% of the prey biomass, respectively. One whale had consumed gadoids, haddock only. The single whale caught in sub-area 2 (not shown in Fig. 3) had fed exclusively on krill. In sub-area 3, where only capelin and krill had been consumed, the latter was found in all but one whale and constituted a major part of the prey biomass (90%). Capelin was only found in approximately 15% (2 whales) of the stomachs, but in considerable amounts when present. Krill was by far the most important prey type in sub-area 4, both in terms of frequency of occurrence (*ca* 75%) and relative prey biomass (*ca* 55%). Herring and capelin were consumed by 45% and 55% of the whales in sub-area 4, respectively, but with considerably lower prey specific abundances (i.e. low relative consumption per whale) than krill. When all four sub-areas (1, 2, 3 and 4) were pooled, krill dominated the diet followed by capelin, herring and haddock. Again, a very high prey specific abundance (few whales took large bouts) of haddock was reflected.

Prey abundance

The four defined sub-areas varied in size from *ca* 250-928 n.miles^2 (Fig. 1, Table 1). Sub-area 2 is only mentioned briefly since no prey selection analysis was conducted for this sub-area.

Sub-area 1 was surveyed twice, and results from the first acoustic survey (1^1) revealed that krill, mainly *Meganyctphanes norvegica*, comprised more than 50% of the total prey biomass in the upper 100m and was
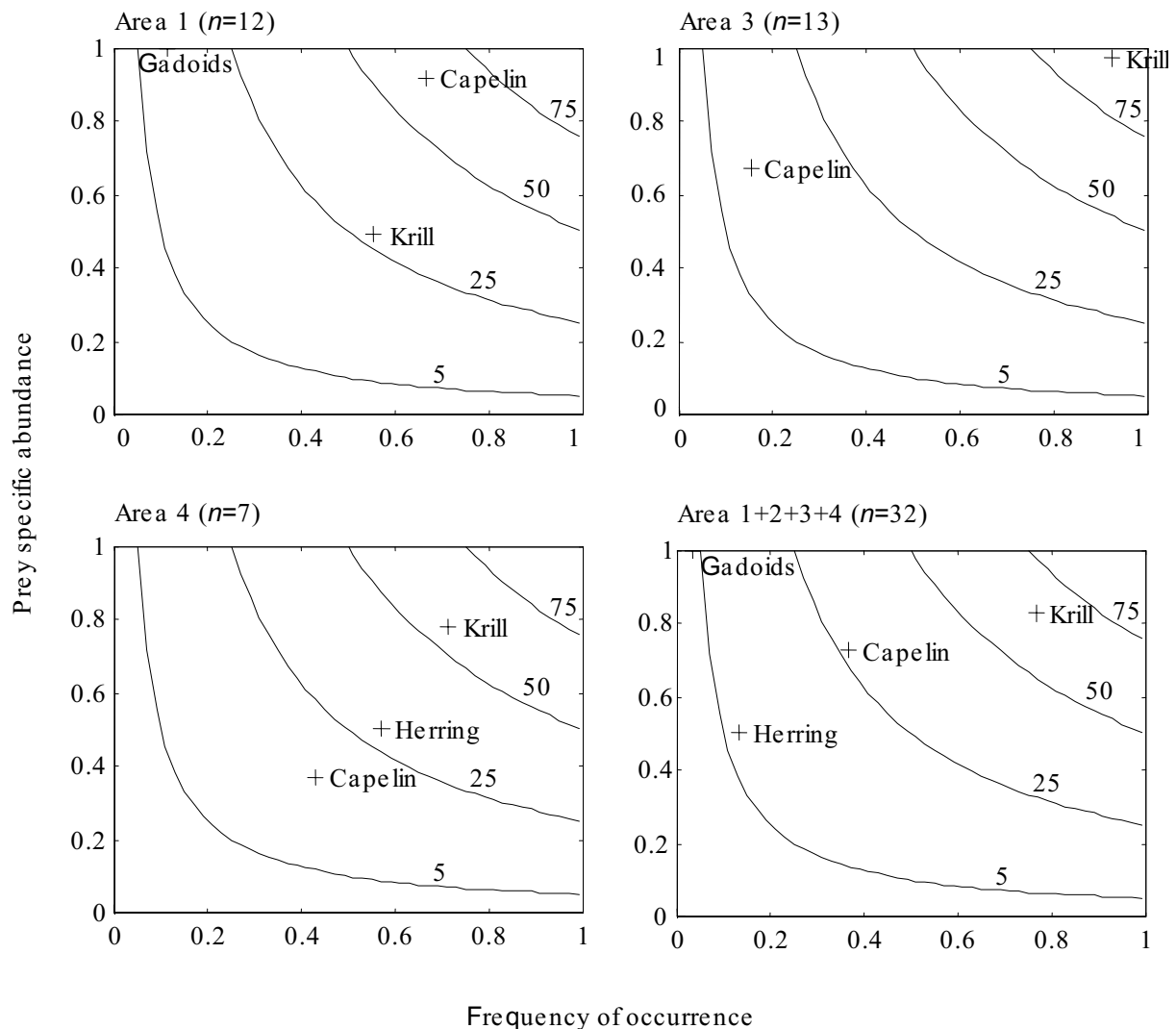

Fig. 3. Feeding strategy plot for minke whales in sub-areas 1, 3 and 4 and in all sub-areas pooled in the southern Barents Sea in May-June 1998. The isolines represent various values of relative prey biomass. n = number of whales included in the analysis.

significantly more abundant ($p < 0.05$) than all other prey types within this depth range (Table 1, Fig. 4). Gadoids (cod, haddock and saithe) and capelin constituted *ca* 27% and 13% respectively of the prey biomass above 100m. Below 100m, however, gadoids were by far the most abundant prey group (62%), followed by krill (29%) and capelin (*ca* 6%). The spatial distribution of prey items varied greatly between prey groups. Krill appeared to be most evenly distributed (CV = 0.9-1.0), followed by capelin (CV = 1.6-1.7), gadoids (CV = 1.5-3.1) and herring (CV = 4.2-10.9). The major concentration of gadoids was distributed along the shelf break in the southern part of the sub-area in all depth layers.

The second survey (1^2) in sub-area 1 was conducted 5 n.miles more to the north, and outside the continental shelf, due to commercial fishing activity in the south. Krill, mainly *Meganyctphanes norvegica*, dominated the prey biomass above (*ca* 61%) and below (*ca* 52%) 100m (Table 1, Fig. 4). Three changes had occurred between the two surveys in this sub-area: herring had disappeared and the relative abundance of capelin and gadoids had decreased significantly ($p < 0.05$) and non-significantly ($p > 0.05$), respectively (Fig. 4).

In sub-area 2, krill completely dominated the prey biomass above (*ca* 80%) and below (*ca* 68%) 100m, followed by capelin (*ca* 19% and *ca* 13%, respectively) (Table 1, Fig. 4).

Krill, particularly *Meganyctphanes norvegica*, was the most abundant prey species in sub-area 3, both above and below 100m (*ca* 45% and 48%, respectively) (Table 1, Fig. 4), followed by herring (30.3%) in the upper 100m and gadoids (35%) below 100m. Krill and capelin were rather evenly distributed in the upper 100m (CV of 0.9 and 1.3, respectively), while gadoids were mainly distributed along the shelf break in the southern part of the survey area (CV = 3.1-7.9). Herring was very patchily distributed in the upper 100m in the northeastern part of the sub-area (CV = 4.7).

During the first survey in sub-area 4 (4^1) gadoids (*ca* 40%), particularly cod, were the most abundant prey in the upper 100m followed by krill (*ca* 36%) and herring (*ca* 17%). Below 100m, gadoids (*ca* 69%) and krill (*ca* 25%) comprised the major part of the prey biomass (Table 1, Fig. 4). Krill (CV = 1.1-1.3) appeared to be relatively homogeneously distributed compared with gadoids (CV = 1.2-3.6) and herring (CV = 1.5-3.4).
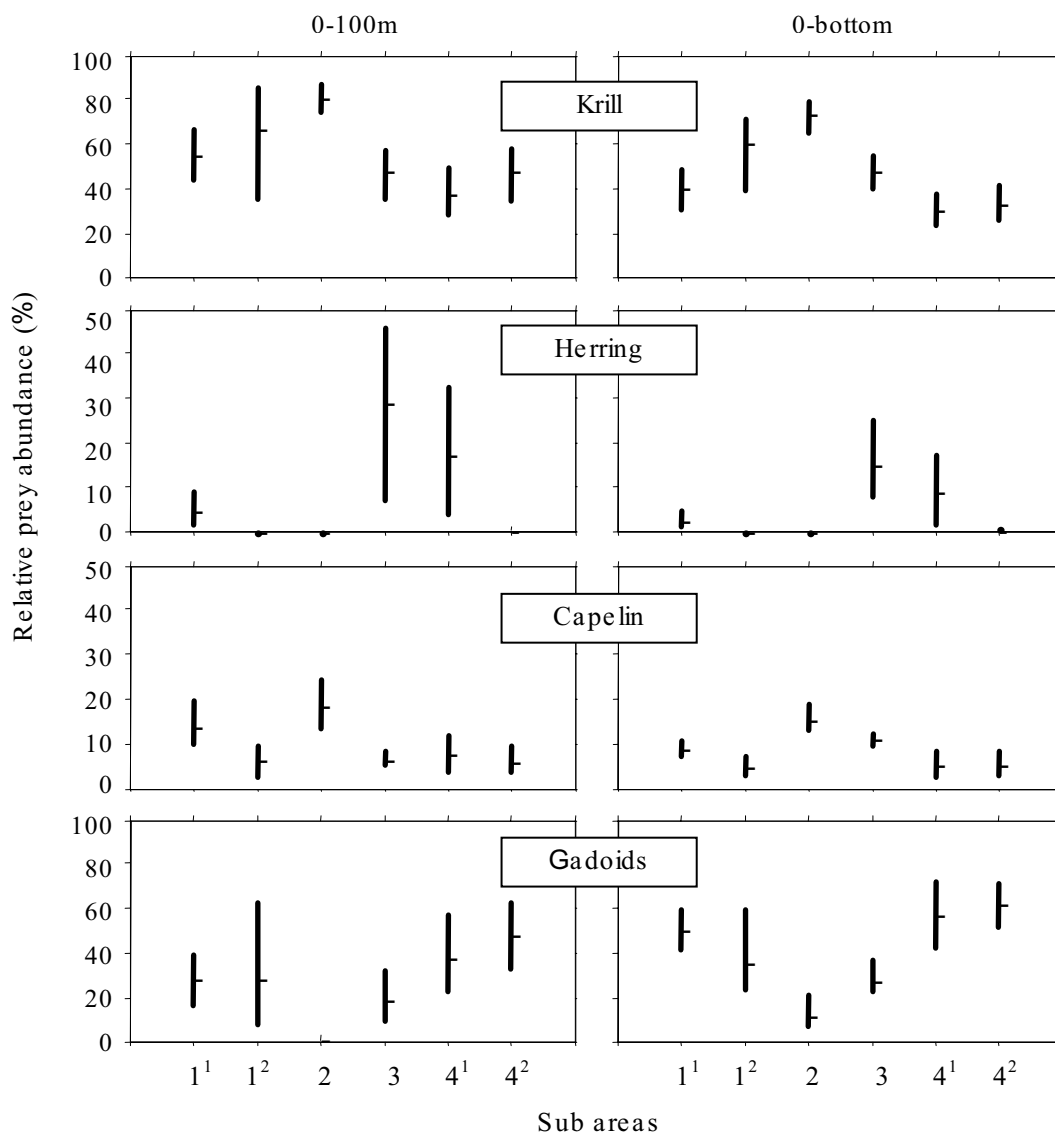

Fig. 4. Relative biomass (%) of prey species in four sub-areas and two depth scales in the southern Barents Sea in May-June 1998. The errorbars (95% CI) were determined from 5,000 bootstrappings of the resource data. The confidence intervals have been corrected for possible acceleration and bias

During the second survey in sub-area 4 (4^2), krill was the predominant prey in the upper 100m (49%), followed gadoids (45%) (Table 1, Fig. 4). Below this depth, gadoids (particularly cod) were by far the most abundant prey type (73%), followed by krill (22%). Herring was almost absent during this survey. Two changes had occurred between the two surveys, i.e. within 24 hours, in sub-area 4: herring had more or less disappeared from the sub-area and krill appeared to be distributed more shallowly during the second survey. Furthermore, saithe were present only during the second survey. Despite these observed changes, prey availability did not change significantly between the two surveys, except for the herring (Fig. 4). Similar to survey 1 (4^1), krill (CV = 0.9) were more homogeneously distributed than capelin (CV = 1.4-1.5), gadoids (CV = 1.1-4.2) and herring (CV = 2.3-3.7).

Foraging selectivity

In order to have significant selective predation or avoidance, the errorbar (95% CI) associated with the Chesson's selectivity index must not overlap the horizontal dotted line that indicates neutral selectivity ($1/m$, see Fig. 5). Herring were excluded from the prey selectivity analysis due to the significant temporal variation in herring abundance. The small-scale analysis of selective predation at the population level (PL) showed rather variable results among the three sub-areas examined (Fig. 5). In sub-area 1, where whale diets were compared with the results from acoustic survey 1^1, the whales had positively selected capelin in both depths. This is indicated by the consistent non-overlap between errorbars and the line of neutral selectivity, while krill and gadoids appeared to have been avoided. The 'micro-scale' analysis, measured at an individual level (IL) in sub-area 1, showed a similar selectivity pattern to the small-scale analysis, i.e. capelin was positively selected by the whales while it appeared that the whales had fed on krill randomly (upper left panel, Fig. 5). In sub-area 3, where the temporal overlap between whale and resource samples ranged from 2-12 days, the whales had fed exclusively on krill and capelin. The results from the foraging selectivity analysis indicated that krill had been positively selected by the whales, while gadoids had been completely ignored (Fig. 5). Capelin had been exploited randomly. In sub-area 4, where the whales were sampled approximately 7 days prior to the resource survey, the minke whales had preyed apparently randomly on all prey species except for gadoids (which had been completely avoided by the whales, Fig. 5).

The medium-scale analysis, with the four sub-areas 1-4 pooled, showed that minke whales had positively selected capelin, as indicated by consistently non-overlapping errorbars with neutral selectivity lines (Fig. 5), while krill appeared to have been exploited randomly and gadoids had been significantly avoided.
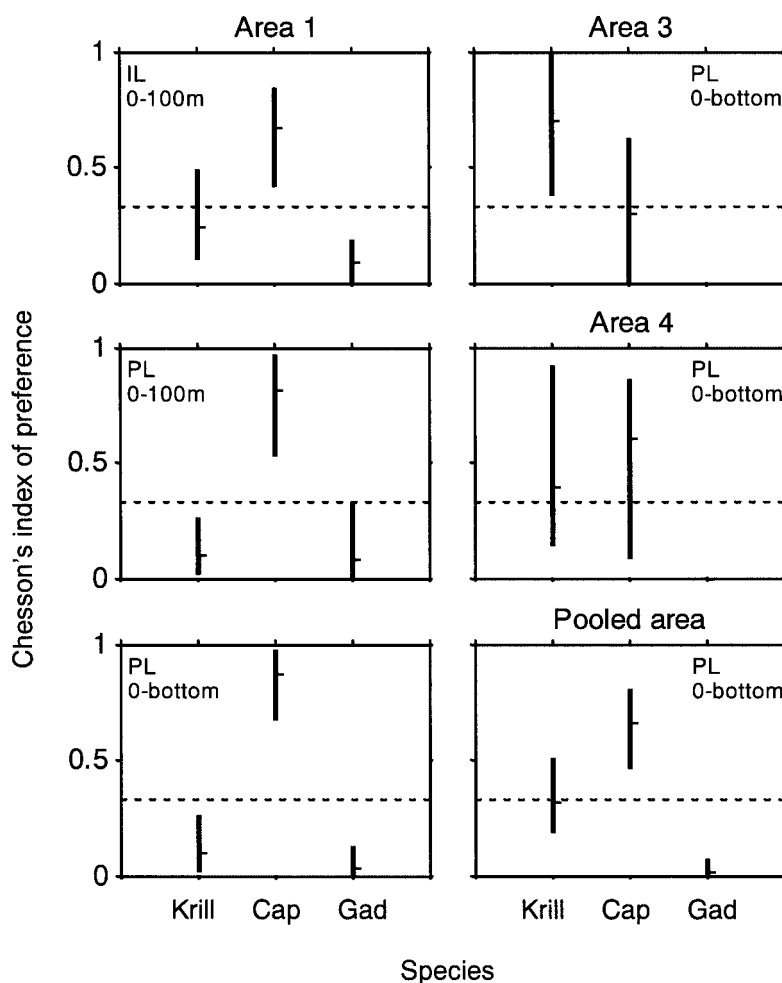

Fig. 5. Minke whale feeding selectivity (Chesson's index) calculated for three prey species, at individual (IL) and population level (PL), in three sub-areas and the pooled area (1-4) in the southern Barents Sea in May-June 1998. Chesson's measure of preference (α_i) with errorbars (95% CI), determined from 5,000 bootstrappings of the diet and resource data, are shown for two depth scales: 0-100m and 0-bottom. The dotted line indicates the estimate of neutral selectivity ($1/m$). Selective predation occurs if the error bar is above this line, while avoidance occurs if the error bar is below, and does not overlap the dotted horizontal line. Random feeding is assumed if the errorbar overlaps the line of neutral selectivity.

Minke whales appeared to have foraged on significantly larger herring in sub-area 3 compared with sub-area 4, although the trawl hauls indicated an opposite situation with respect to abundance of size groups (Fig. 6, $\chi^2_{16,0.05} = 55.1$, $p < 0.05$). In sub-area 3 the whales had eaten a significantly larger proportion of large herring than found in the hauls ($\chi^2_{16,0.05} = 88.4$, $p < 0.05$), while the opposite was observed in sub-area 4 ($\chi^2_{16,0.05} = 48.6$, $p < 0.05$). In fact the length distribution of the herring eaten by the whales in sub-area 4 correlated significantly better with the length distribution of herring in sub-area 3. The capelin found in the whale stomachs in sub-area 1 were significantly larger than the specimens sampled from the trawl hauls (Fig. 6, $\chi^2_{13,0.05} = 49.4$, $p < 0.05$). In sub-area 3, however, the opposite was observed, i.e. the trawl specimens were significantly larger than the individuals eaten by the whales ($\chi^2_{13,0.05} = 47.4$, $p < 0.05$). In sub-area 4, minke whales appeared to have exploited the most numerous length groups of capelin ($\chi^2_{16,0.05} = 14.8$, $p > 0.05$). When comparing the length distribution of herring and capelin in the pooled area there was no significant difference in length of either fish species eaten by the whales and those observed in the hauls (Fig. 6).

DISCUSSION

The prey selectivity results in this study were based on four assumptions: (1) the analysed minke whales represent a random sample of the animals in a particular sub-area; (2) the estimated relative prey abundance was reliable and constant throughout the period of sampling; (3) the reconstruction of forestomach contents was reliable; (4) the minke whales had fed in the areas in which they were caught.

The first assumption is difficult to investigate since no-one has examined the catchability of minke whales with respect to sex and length. However, Haug *et al.* (1997; In press) showed that length is not an important contributor to diet composition. The diet composition may, however, be biased by sex because males and females appear to prefer different prey: males appear to prefer herring more than females, whilst females prefer capelin and saithe (Haug *et al.*, In press). Since the majority of minke whales (87.5%) in this study were females, the whale diets may therefore be biased towards capelin. The temporal variation in gender composition in the area is likely to be responsible for the preponderance of females in the samples (Jonsgård, 1951; Øien, 1988).

The use of only undigested prey items increases the likelihood that (3) and (4) are satisfied. The validity of (2) was only partly satisfied due to the temporal variations in absolute and relative prey abundance within small-scale areas with respect to herring, and perhaps capelin, and due to the subjectivity involved in the estimation of euphausiid biomass.

The temporal changes (1-7 days) in relative prey abundance within a small-scale area were particularly critical with respect to herring, which is in a migratory phase during this time of the year (see Røttingen, 1990), and perhaps capelin. It should be emphasised that the second survey in sub-area 1 was conducted more to the north than the first and did not cover the continental shelf as the first survey did. This may explain some of the observed
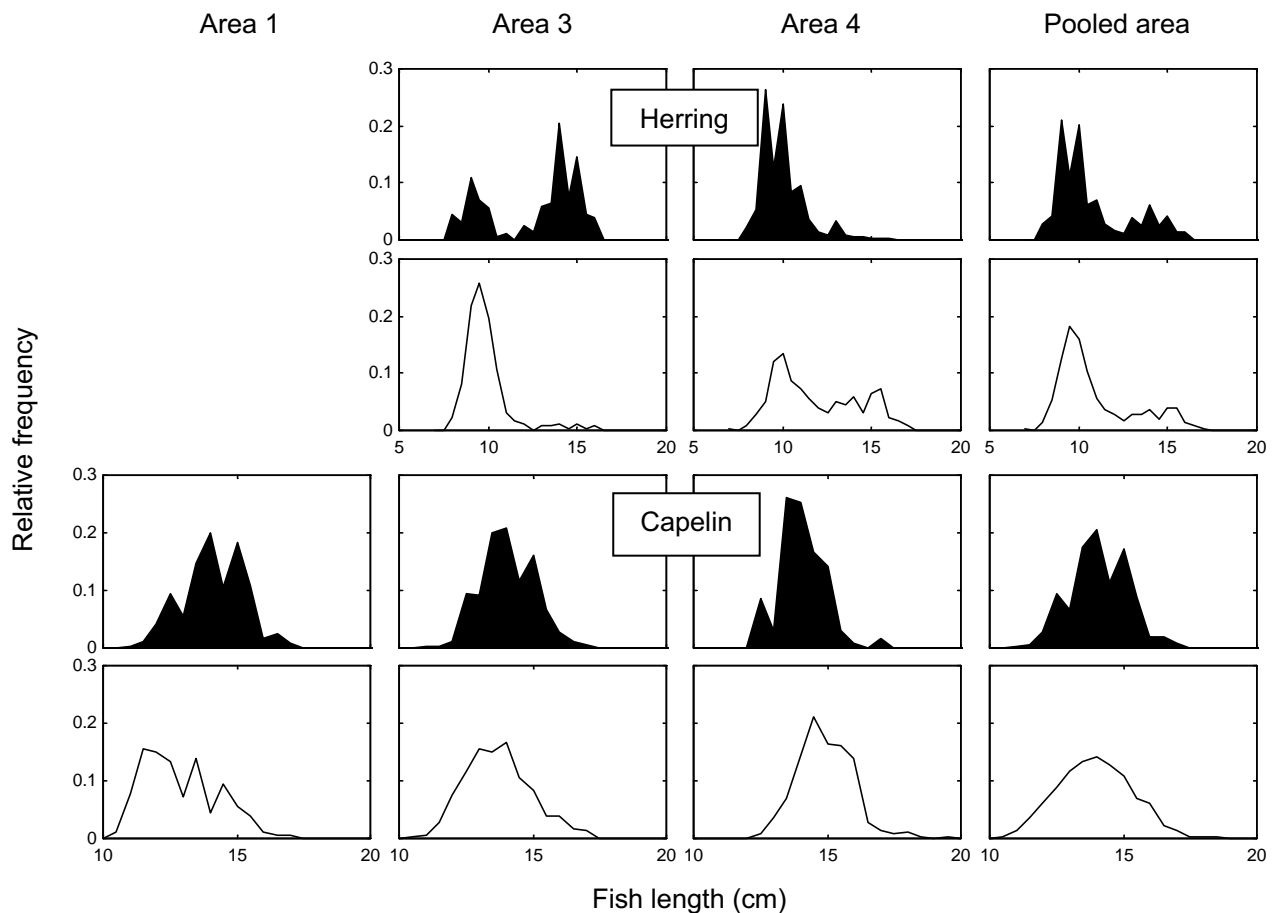

Fig. 6. The length distribution of herring (upper) and capelin (lower) in minke whale diets (filled) and in the hauls (open) in three sub-areas (1, 3 and 4) and a pooled area (1+2+3) in the southern Barents Sea in May-June 1998.

differences in relative prey abundance that occurred between the two surveys in sub-area 1. The prey selectivity analysis in these sub-areas (3 and 4) was performed at the population level on a low vertical resolution (0-bottom), implying that small changes in relative prey abundance have little effect on the overall prey selectivity results because the distribution of selectivity estimates are based upon mean resource and diet samples. Certainly, the small sample size is a potential bias that may have contributed to too narrow confidence intervals (see Efron and Tibshirani, 1993). Therefore, interpretation of the foraging selectivity results from sub-areas 3 and 4 must be made cautiously.

Despite the high degree of subjectivity involved in the estimation of euphausiid biomass, other surveys conducted in the Barents Sea in August-September 1998 yielded similar krill abundance estimates as in this study (see ICES, 1999). Additionally, krill estimates here are well within range according to other krill studies in the southern Barents Sea (e.g. Dalpadado and Skjoldal, 1996). Nevertheless, if the euphausiid biomass has been underestimated (overestimated) in this study, then we have overestimated (underestimated) the Chesson values. This implies that the whales in sub-area 3 may not have significantly preferred krill.

In general, the spatial variation in prey abundance observed in the sea was reflected in the minke whale diets. Thus, this study substantiates previous feeding studies concluding that minke whales are able to adjust their foraging tactics to local prey abundance (e.g. Lindstrøm *et al.*, 1997; Skaug *et al.*, 1997; Haug *et al.*, In press). Observations of undigested food items give information about minke whale feeding behaviour immediately prior to capture. About two out of three whales had fed exclusively on one prey type, primarily krill, whereas the remaining whales had fed on two prey types. Thus, minke whales in this study seem to be specialist foragers. This is consistent with the expectations of optimal foraging theory (OFT), which predicts that feeding should be specialised when food resources are particularly abundant (e.g. Stephens and Krebs, 1986). This intensive feeding on krill and capelin yielded consistently narrow diet widths in all sub-areas, including the pooled area. The bulk of the minke whales' diet was comprised of relatively few species, a pattern observed in previous feeding ecological studies of minke whales both in the northeast Atlantic and in the western North Pacific (Kasamatsu and Tanaka, 1992; Haug *et al.*, 1995a; b; 1996; In press; Lindstrøm *et al.*, 1998a; Tamura *et al.*, 1998).

Overall, a strong preference for capelin and avoidance of gadoid fish were the most compelling results of this study. This study also indicates considerable spatial variation in feeding preference by minke whales with respect to capelin and krill. An example is the discrepancy in krill predation by the whales: krill were exploited intensively in sub-area 3 whereas in sub-areas 1 and 4 krill were either avoided or fed upon randomly by the whales; something which is difficult to explain given that the relative abundance of krill was similar in both sub-areas.

Although minke whales seek to exploit areas of high biomass, this biomass may be aggregated over a large range of spatial scales. At the smallest scale, pelagic shoaling prey such as capelin, krill and herring may form high-density patches of schools and swarms. The role of high-density patches has proved to be particularly important to North Atlantic right whales (*Eubalaena glacialis*) (Mayo and Marx, 1990; IWC, 2001). Thus, to a minke whale, the fundamental exploitable unit of prey is probably related to some function of patch size and density rather than to the number of individual prey in an area (e.g. Murphy *et al.*, 1988; Piatt and Methven, 1992). Identifying predator-prey relationships at spatial scales experienced by a minke whale within a single foraging bout may explain some of the spatial differences in their prey preferences, such as the discrepancy in krill and capelin predation by the whales in sub-areas 1, 3 and 4. This requires data on detailed structure and density of prey patches. The spatial resolution of the resource samples, as well as the temporal overlap between whales and resource samples in sub-areas 2-4, is far too coarse to examine such patch features. Some methodological problems are involved in the assessment of euphausiid availability, in that the estimation of euphausiid biomass is very difficult with use of single-frequency acoustics. The applied thresholding, i.e. assuming euphausiids are removed at a fixed level, is unable to detect and accurately estimate high-density aggregations of euphausiids.

The assertion that minke whales require some minimum threshold level of prey density for successful foraging (Piatt and Methven, 1992) may explain the low dietary importance of gadoid fish; these fish seldom occur in dense aggregations (Bergstad *et al.*, 1987). The formation of school swarms can be an anti-predator response (e.g. Hamilton, 1971). However, prey should do better by scattering when attacked by bulk-feeders such as minke whales, because minke whales usually pursue concentrated prey resources, or they may themselves concentrate the prey by active pursuit and herding (Hoelzel *et al.*, 1989). Species specific responses by prey to such predator behaviour is probably important for prey selection by predators.

There was a great discrepancy in minke whale selectivity between sub-areas concerning prey size. Part of this discrepancy is probably a result of using fish otoliths to estimate the original fish length since the actual site at which the fish was ingested by the whales is not known. This implies that fish sampled from a whale in sub-area 3 is likely to have been ingested elsewhere. Considering the results from the pooled area, where the whales had fed on the same sizes of capelin and herring as observed in the hauls, there is no reason to believe that minke whales are particularly selective concerning prey size which confirms previous studies (e.g. Haug *et al.*, 1997).

An important task of this study was to examine whether the spatial scale affected the selectivity estimates. The different results obtained, both between medium- and small-scale studies, and among small-scale studies, emphasises the usefulness in performing whale foraging behaviour studies on a range of scales (see also Russel *et al.*, 1992).

Although minke whale prey preference varies greatly in space, some new features of minke whale foraging behaviour were evident. Minke whales show a strong preference for capelin, whereas gadoids (cod, haddock and saithe) appear to be avoided by the whales. Part of the observed spatial variation in minke whale foraging selectivity may be a combination of spatial differences in prey patchiness and threshold foraging behaviour. The latter may have important ecological consequences because it can provide stability in predator-prey systems when other stabilising mechanisms are absent (Hassel and May, 1974; Murdoch and Oaten, 1975). The stabilising effects are due to density-dependent mortality as preferred prey decline in abundance. Future studies would demand higher temporal overlap between the whale and resource sampling as well as higher resolution of the resource data. It would also be more desirable to study the variation in habitat and prey selection of individual minke whales by use of time-depth recorders

and a research vessel to assess the resource availability at the smallest possible scale (e.g. Croll *et al.*, 2001; Guinet *et al.*, 2001).

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