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

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ABSTRACT

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

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

INTRODUCTION

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

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

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

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

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

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

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

Table 1

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

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

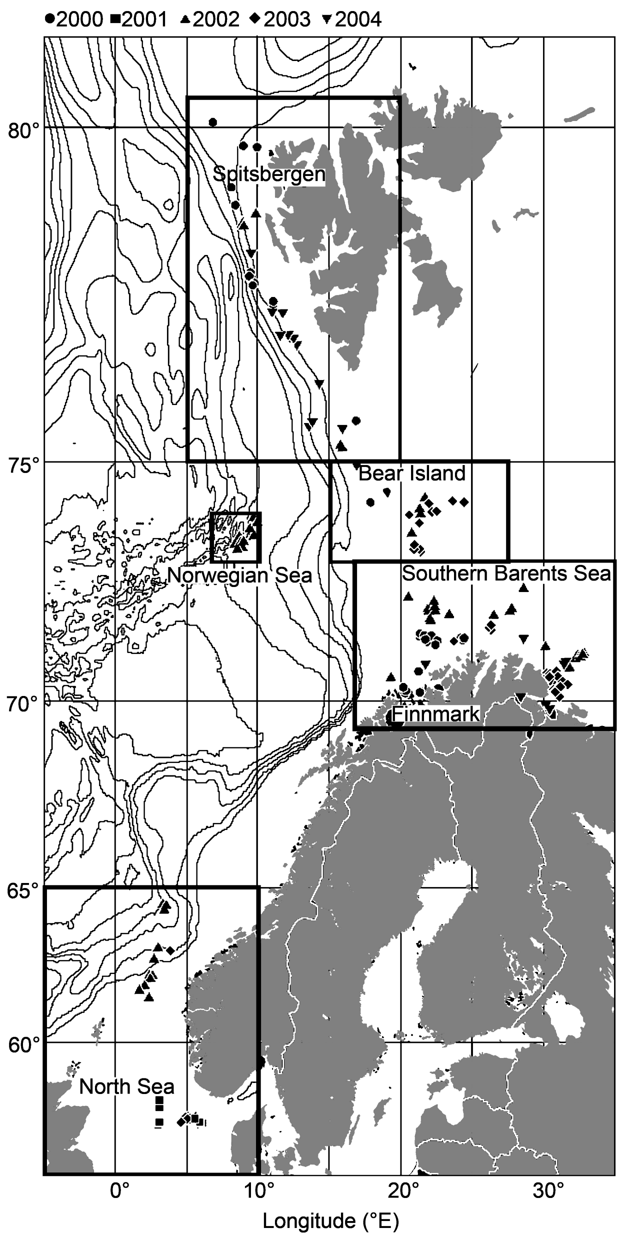

Fig. 1. Catch positions of the minke whales sampled in Spitsbergen (SB), Bear Island (BI), Southern Barents Sea (SBS), Norwegian Sea (NOS) and North Sea (NS) during May-June, 2000-04.

MATERIALS AND METHODS

Whale sampling

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

Treatment of stomach contents

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

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

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

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

Table 2

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

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

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

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

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

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

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

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

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

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

Statistical framework

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

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

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

RESULTS

Diet composition

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

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

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

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

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

Table 3

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

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

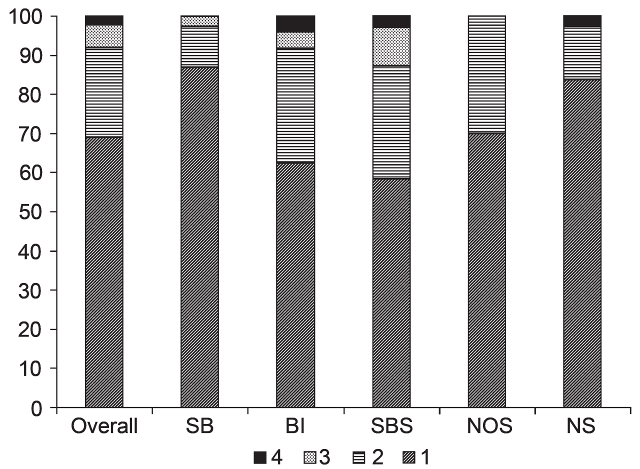

Fig. 2. The number of prey species in individual minke whale stomachs (% of all stomachs in each area) for the five sampling areas, with sampling years 2000-04 pooled.

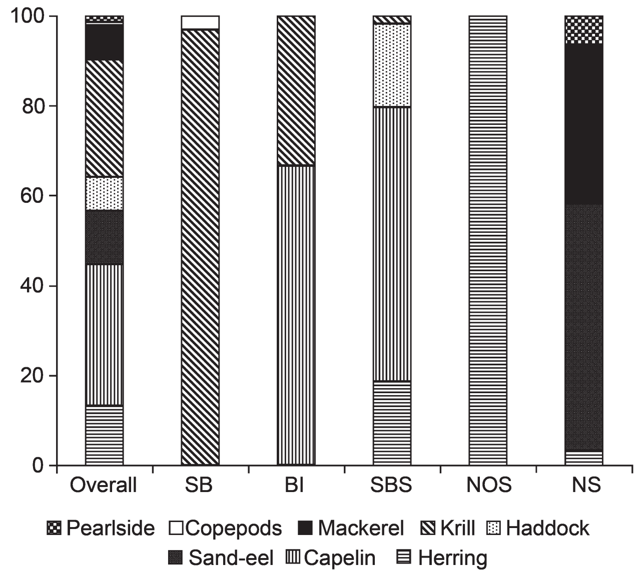

Fig. 3. Prey items in single prey stomachs (% of all stomachs in each area) of minke whales for the five sampling areas (Spitsbergen (SB), Bear Island (BI), Southern Barents Sea (SBS), Norwegian Sea (NOS) and North Sea (NS)) with sampling years 2000-04 pooled.

Area-to-area variation

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

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

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

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

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

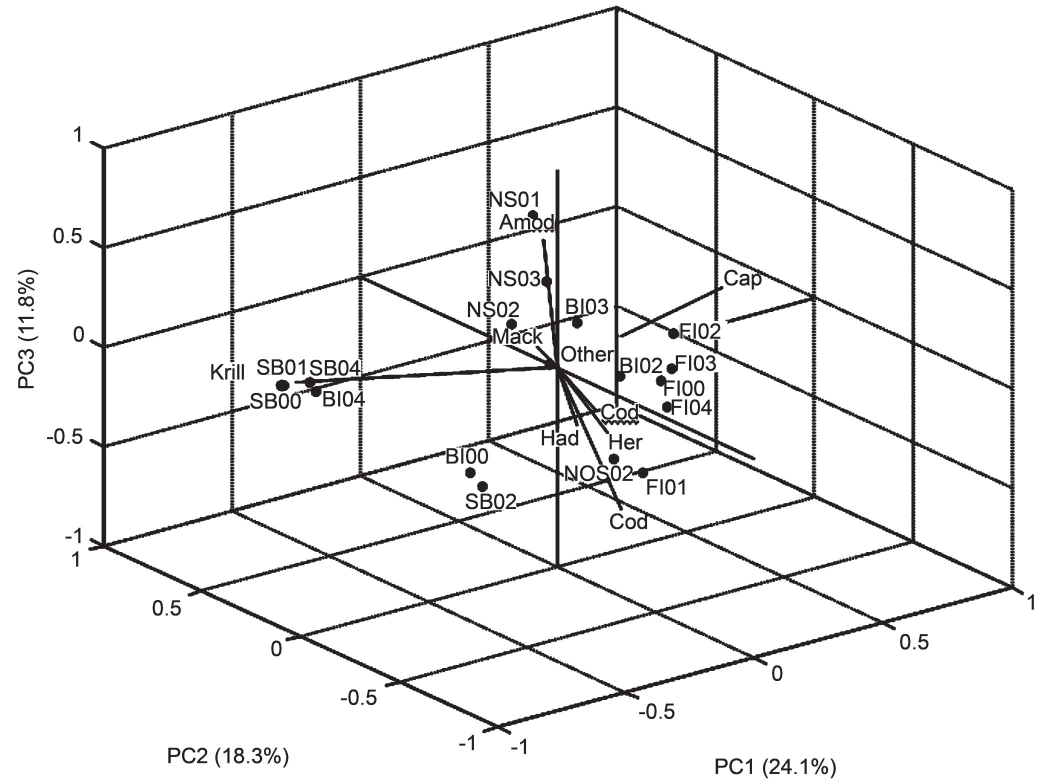

Fig. 4. PCA ordination plot of axes 1, 2 and 3 with prey species (arrows) and sampling sites for minke whales from the areas North Sea (NS), Norwegian Sea (NOS), Bear Island (BI), Spitsbergen (SB) and Southern Barents Sea (SBS) in the different sampling years. The first three axes 1-3 accounts for 24.1,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

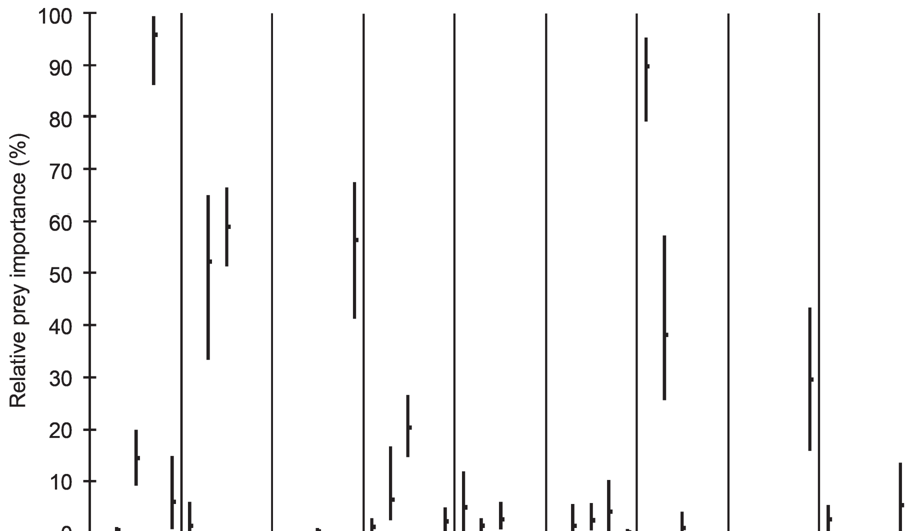

Fig. 5. Importance of different minke whale prey (WI) in the five different areas; Spitsbergen (1), Bear Island (2), Southern Barents Sea (3), Norwegian Sea (4) and North Sea (5). The means are given with a 95% confidence interval obtained by bootstrapping. All sampling years (2000-04) are pooled. The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

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

Year-to-year variation

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

Table 4

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

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

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

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

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

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

Sex-effect

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

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

Size composition of prey

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

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

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

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

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

Age composition of prey

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

DISCUSSION

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

Barents Sea

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

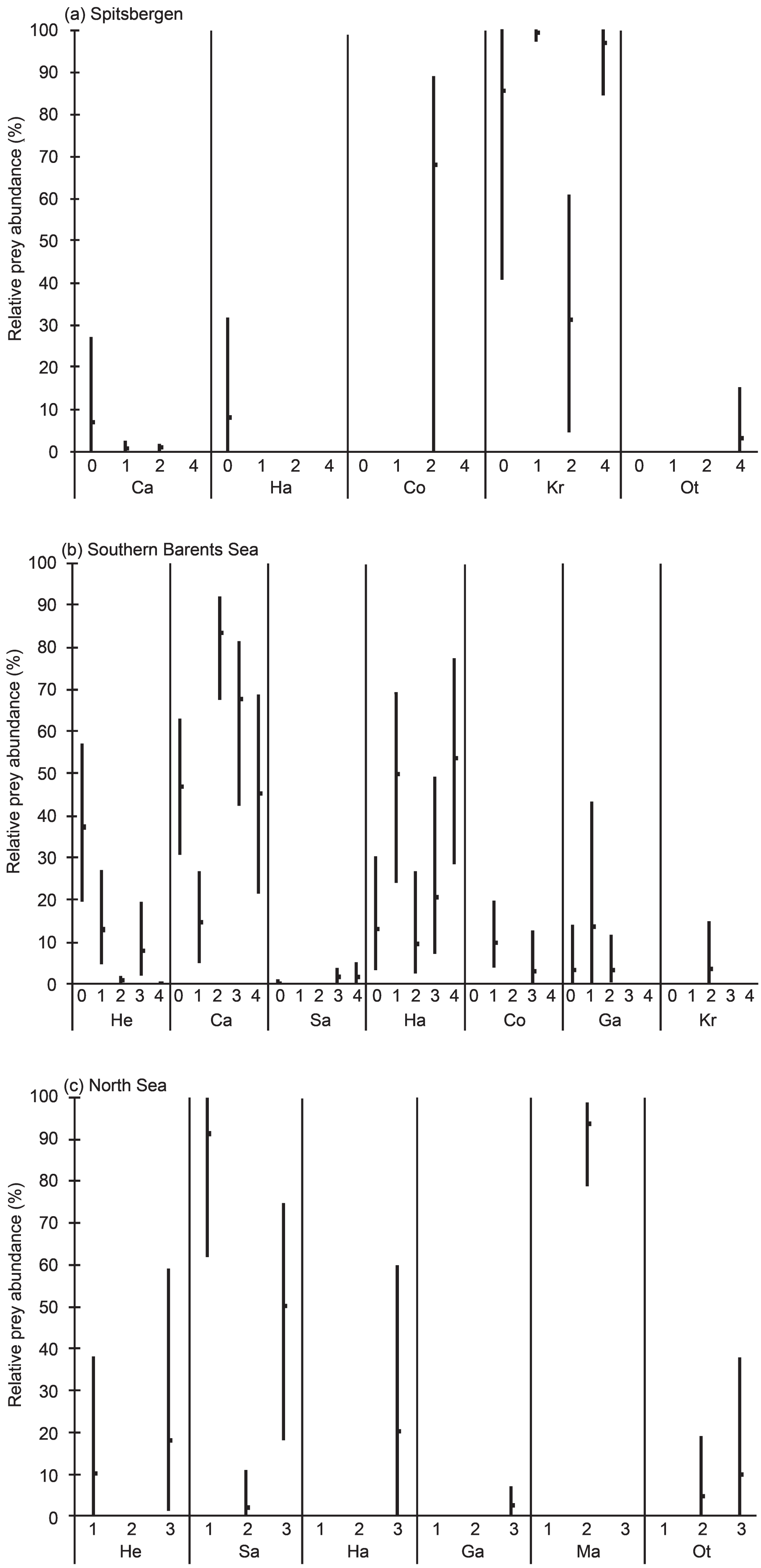

Fig. 6. Importance of different prey of minke whales in Spitsbergen (a), Southern Barents Sea (b) and North Sea (c) in 2000 (0), 2001 (1), 2002 (2), 2003 (3) and 2004 (4) (weighted biomass). The means are given with a 95% confidence interval obtained by bootstrapping. The different prey items are herring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

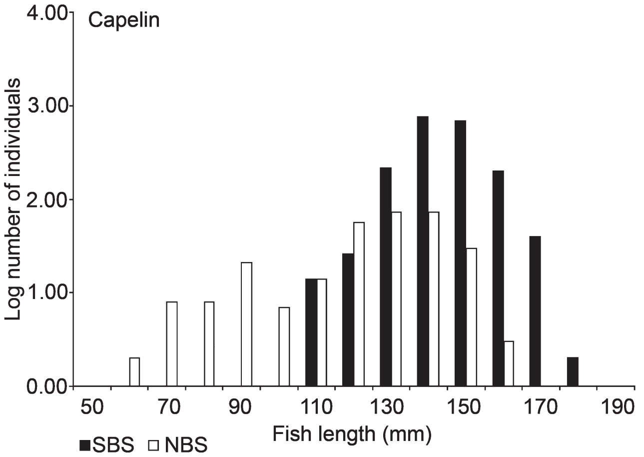

Fig. 7. Size distribution of capelin eaten by minke whales in the Southern Barents Sea (SBS) and Northern Barents Sea (NBS = Spitsbergen and Bear Island pooled) in 2000-04. Log transformed number of individuals of each size class (N).

Table 5

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

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

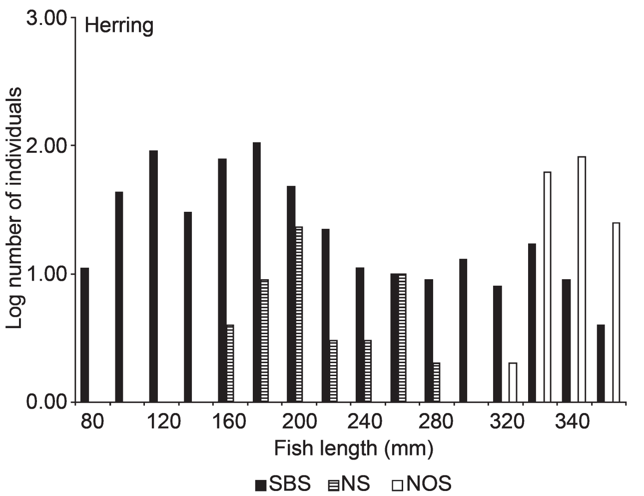

Fig. 8. Size distribution of herring eaten by minke whales in Southern Barents Sea (SBS), North Sea (NS) and Norwegian Sea (NOS) in 2000-2004. Log transformed number of individuals of each size class (N).

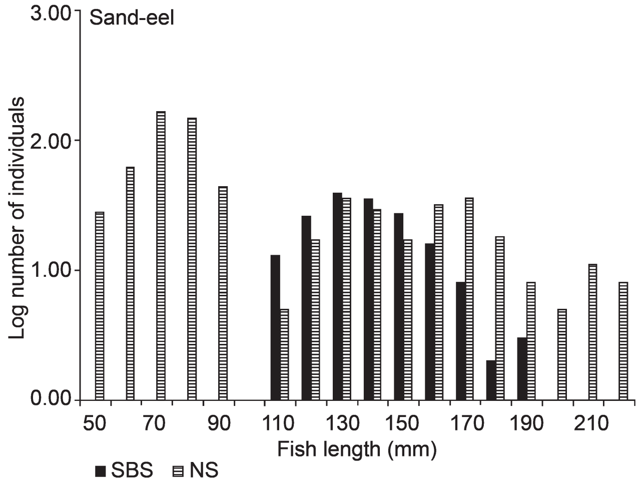

Fig. 9. Size distribution of sand eel eaten by minke whales in Southern Barents Sea (SBS) and North Sea (NS) in 2000-2004. Log transformed number of individuals of each size class (N).

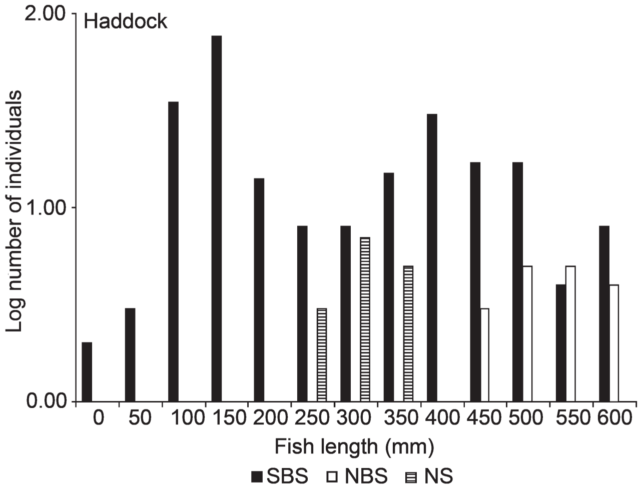

Fig. 10. Size distribution of haddock eaten by minke whales in the Southern Barents Sea (SBS), Northern Barents Sea (NBS = Spitsbergen and Bear Island pooled) and North Sea (NS) in 2000-04. Log transformed number of individuals of each size class (N).

Table 6

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

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

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

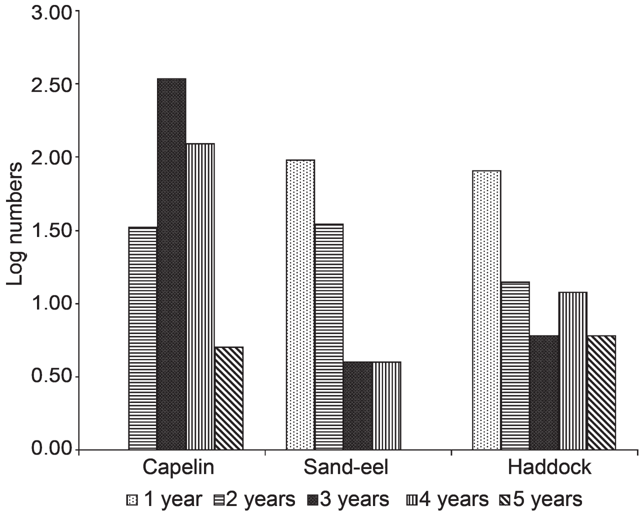

Fig. 11. Estimated age of prey by counting of otolith year rings of capelin (n=506), sand eel (n=139) and haddock (n=119) consumed by minke whales in the Southern Barents Sea in 2004.

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

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

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

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

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

Norwegian Sea

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

North Sea

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

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

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

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

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

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