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DIET AND FOOD AVAILABILITY FOR NORTHEAST ATLANTIC MINKE WHALES *BALAENOPTERA ACUTOROSTRATA*

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ABSTRACT

Ecological studies of the Northeast Atlantic minke whale (*Balaenoptera acutorostra*) were carried out during spring (mainly April-May), summer (June-July) and autumn (August-September) in 1993 and 1994. Four small-type whaling vessels were chartered for operations in four selected subareas in Norwegian and adjacent waters. To ensure random sampling of whales, stringent sampling procedures, where the vessels searched for whales along predetermined transects within each subarea, were applied. Estimates of potential prey abundance were obtained from a review of results from synoptic surveys and from long-term survey series. Samples were obtained from 63 and 70 whales in 1993 and 1994, respectively. Results from forestomach analyses indicate a minke whale diet where fish play a very prominent role during most of the season. Diets varied between both periods and areas. Gadoid fish species dominated the spring diet. In summer and autumn the diet in the northmost areas (Spitsbergen and Bear Island) was primarily characterized by krill *Thysanoessa* spp., to a much lesser extent by capelin *Mallotus villosus*. This is consistent with an increase in krill and severe decrease in capelin availability in these areas in 1993 and 1994 compared with previous years. In the coastal areas of North Norway, herring *Clupea harengus* is the dominant planktivorous fish, and was also the most important food item for the whales both in summer and autumn. To some extent, however, the herring was accompanied by some gadoid species during summer. Whale consumption of 0-group fish was rather limited. Statistical analyses of potential prey preferences indicate a preference for herring and capelin. Given the opportunity to choose, it appears that minke whales will generally favour these two prey species before other actual species such as krill and gadoid fish species.

INTRODUCTION

In the management of fish stocks in the Barents Sea (and other areas), increased attention has been paid to multispecies interactions. This has given analyses of the feeding ecology of the most numerous top predators in the area particular actuality. Thus, studies of the feeding ecology of important predators are currently being carried out on cod *Gadus morhua* (Mehl 1989, Aijad 1990, Mehl & Sunnanå 1991), sea birds (Barrett & Furness 1990, Barrett *et al.* 1990, Erikstad 1990, Erikstad *et al.* 1990, Anon. 1994a) and harp seals *Phoca groenlandica* (Nilssen 1995). From 1992, also the minke whale *Balaenoptera acutorostrata* is included in this list of studied top predators (Haug *et al.* 1992, 1995a). In addition to biological input requested by multispecies modellers, information on minke whale ecology would help understand better which environmental processes reduce feeding opportunities for the species (and competitors such as fin *Balaenoptera physalus* and humpback *Megaptera novaeangliae* whales; see Christensen *et al.* 1992) and which may, in future, cause changes in density dependent parameters such as mortality, growth and fecundity (see Masaki 1979, Lockyer 1981, 1990).

The minke whale is probably the most common whale species in the Northeast Atlantic (abundance estimate based on data from 1989: 75.600, CV = 0.16, 95% CI 56.400-107.200; Schweder *et al.*, 1995). The species is boreo-arctic with migrations to feeding areas in the far north in spring and early summer, and southwards to breeding areas in the autumn (Jonsgård, 1966). The Northeast Atlantic stock is known to feed on various species of zooplankton and fish, particularly herring *Clupea harengus*, capelin *Mallotus villosus* and cod (Jonsgård, 1951, 1982; Christensen, 1972, 1974; Øritsland & Christensen, 1982). The collapse (and subsequent changes in migration patterns and times of spawning) of two important stocks of potential prey species, Norwegian spring spawning herring in the early 1970s and Barents Sea capelin in the mid 1980s (Røttingen 1990, Anon., 1994b, 1995a), is likely to have had an impact on the feeding habits and possibly also the migratory behaviour of minke whales. Reports from stomach inspections made during previous commercial catches are, therefore, difficult to put in present-day perspective because they relate to periods and areas with changing prey availability, or with prey abundance very different from today.

During a limited Norwegian scientific catch of Northeast Atlantic minke whale in 1988-1990, some pilot studies of the diet of the captured animals were conducted (Nordøy & Blix 1992). In order to evaluate the present ecological significance of the species, a more comprehensive scientific whaling program was initiated in Norway in 1992: This program would particularly address questions concerning feeding ecology, by using stomach analyses and concurrent estimates of prey availability, and seasonal variations in energetic status (Haug *et al.* 1992). To fulfill the scientific objectives of this program, a three year sampling of minke whales in different areas in Norwegian and adjacent waters at different times of the year (spring, summer and autumn) was necessary. The sampling design was based on statistical analyses aimed at keeping the catch at an absolute minimum while making it possible to obtain statistical estimates with acceptable precision. The rationale of the sampling design was to optimize performance with respect to future calculations of the relative consumption of the various prey items throughout the whole sampling area.

The extent of the program and the many activities which had to be coordinated made it necessary to test the methodology on a reduced scale during the summer of the first year of operations. Stomach contents from 92 minke whales were collected during July-August in 1992 (Haug *et al.* 1995a). The results from analyses of this material revealed a diet almost completely dominated by fish. There was, however, considerable heterogeneity in species composition between the areas. Capelin dominated the minke whale diets in the two northernmost study areas (Spitsbergen and Bear Island). Further south, in coastal areas of North Norway and Russia, herring was the most important food item, but was accompanied by significant amounts of sand eel *Ammodytes* sp., cod, haddock *Malanogrammus aeglefinus* and saithe *Pollachius virens*. Statistical comparisons of parts of the 1992 whale stomach material with results from concurrent estimates of prey availabilities indicate that minke whales may be quite flexible in their choice to feed, adapting well to local prey abundance situations (Skaug *et al.* 1995). However, there are some indications that the minke whales may be reluctant to feed upon plankton.

The scientific catch activities for 1993 and 1994 were similar to those in 1992, but were extended over three separate periods (spring, summer and autumn). This substructured design with respect to both sampling area and time of the year enables a further evaluation of the geographical and now also of the temporal variations in the minke whale diet. Furthermore, samples in the same areas from three consequtive years (1992-1994) enables evaluation of potential year-to-year variations. These evaluations are the purposes of this paper. Concurrent evaluation of prey abundance was performed both in 1993 and 1994, and, with reference to the results given in Skaug *et al.* (1995), a further elaboration of predator/prey relationships will be attempted.

MATERIAL AND METHODS

Sampling of whales

Minke whales are not uniformly distributed in the area of interest, but rather occur in aggregations which presumably depends on the availability of food. From a review of the spatial distribution of previous catches (Øien *et al.* 1987) and observations made during sightings surveys (Øien 1991), five separate sampling areas were defined and used in the 1992 investigations: West of Spitsbergen, Bear Island, coast of Kola, coast of Finnmark and Lofoten/Vesterålen (see Haug *et al.* 1992, 1995a). Unfortunately, Russian authorities refused any scientific whaling in the Russian economic zone in 1993 and 1994. This left one of the 1992 sampling areas (coast of Kola) unsurveyed and reduced the 1993 and 1994 field work to incorporate only four areas (Fig. 1).

Chartered whaling vessels, fitted for the whaling operations with crew and equipment as outlined by Christensen & Øien (1990) and in agreement with new regulations enforced by the Directorate of Fisheries, were used to catch the whales. The primary weapons used to kill minke whales in the Norwegian small-type whaling are 50 mm and 60 mm harpoon guns fitted with grenade harpoons, equipped with 22 g penthrite grenades (Øen 1992). An important goal of the scientific whaling is to obtain samples representative for each area; all whales present in the area should have the same probability of being caught. This calls for a procedure of random sampling that ensures geographical scattering within each area and avoids preference for any particular size, sex, behavior or other attribute (see Haug *et al.* 1992). To obtain this randomization, a stringent searching procedure along predetermined transects, randomly laid out in each area, was used. In addition, when a whale was observed during search, an all-out attempt was made to catch that whale, regardless of catchability. The transects were designed in saw-tooth patterns, mainly according to the principles used during the previous shipboard sightings surveys NASS-89 (Øien 1991). Experience gained in previous years were used to perform slight modifications in both the 1993 and 1994 transects. In order to make the searching operations as efficient as possible, a certain amount of freedom was given to modify transect lines during the course of operation, depending on factors such as ice-cover, weather conditions, and observations of minke whale abundance.

Minke whales are known to occur in Norwegian waters from March/April to October (Jonsgård 1951), and the scientific whaling had to be restricted to this period.

The 1993 operations were confined to three periods: Spring (April 15-May 15), summer (June 15-July 12) and autumn (August 25-September 20). The collected material include samples from 63 whales (28 males and 35 females, ranging in size between 442 and 880 cm). Difficult weather conditions and low whale abundance (no whales observed at Spitsbergen, very few observed in the other areas, Haug *et al.* 1994a) severely hampered the 1993 spring operations when only 4 whales were caught. During summer 1993 the whale abundance situation appeared similar to the observations made in 1992 (Haug 1993, Haug *et al.* 1994a), and 32 whales were caught. Changes in relative distribution of the whales appeared to have occurred between summer and autumn, particularly in the northmost areas where the animals seemed to have left both the Spitsbergen and Bear Island subareas in favour of areas further east in the Barents Sea (Haug *et al.* 1994a). To secure samples from whales in the northern areas also during autumn, the Bear Island subarea was extended in a northeastward direction during the course of operations. A total of 27 whales were sampled in the autumn period.

Based on the experience gained in 1993, some changes were made in the survey design in 1994 (Haug *et al.* 1994b). Due to the low number of whales observed in the beginning of the 1993 spring period, the start of the 1994 operations were postponed two weeks. This resulted in the following three sampling periods in 1994: Spring (April 30 - June 6), summer (2-28 July) and autumn (August 27-September 22). The Spitsbergen area was only surveyed during the summer period, and in the autumn period the Bear Island area was extended northeastwards (Fig. 1). The collected material contains samples from 70 whales (25 males and 45 females, ranging in size between 485 and 900 cm). The weather conditions during spring were better in 1994 than in 1993. Despite the postponed operational start, however, it appeared that the abundance of whales was still lower in spring, when 18 animals were obtained, than in summer and autumn, when, respectively, 38 and 14 animals were obtained (Haug *et al.* 1994b). While the summer conditions in 1994 were comparable with those in 1993, long periods with difficult weather conditions resulted in the rather low number of whales caught in autumn 1994.

Analyses of minke whale stomachs

Killed minke whales were immediately taken onboard the vessel for dissection and biological sampling. The complete digestive tract was removed as soon as possible. Minke whale stomachs consist of a series of four chambers (Olsen *et.al.* 1994). Experience from pilot studies performed during the scientific whaling in 1988-1990 suggested that sampling from the first chamber (the fore-stomach) would give sufficient data to evaluate the diet of the animals (Nordøy & Blix 1992). Therefore, only contents from this stomach chamber was used in the present analyses. The fore-stomach contents were separated from the rest of the stomach contents and transfered to a tub where the volume was measured. The content was then transfered to a perforated tub where the liquid-free phase could be measured before it was emptied into a sieve system consisting of three sieves (20 mm, 5 mm and 1 mm) and washed out. Fresh specimens of fish were separated from the rest of the material and identified. The specimens were counted, total lengths were measured and the weights of large fish were recorded. Representative subsamples of fresh material was collected also for small fishes (from the 20-mm sieve) and crustaceans (from the 5-mm and 1-mm sieves) and kept frozen for later laboratory treatment. The remaining material was washed repeatedly with seawater in order to separate fish otoliths from the rest of the material. Subsamples including all intact skulls and free otoliths were also collected from the 5 mm and 1 mm sieves and kept frozen for later analyses in the laboratory.

In the laboratory, the total weight of the subsamples was recorded after thawing. The numbers of individuals of each fish species (small fishes) were recorded and total lengths and weights of fresh fishes were recorded (in the subsamples collected from the 20 mm sieve).

For crustaceans, random subsamples of 200 individuals (collected from the 5 mm and/or the 1 mm sieves) were weighed and analyzed with respect to species composition. Total weight and the number of individuals were recorded for each species in the subsample, and this was used to obtain crude estimates of the numerical contribution of each prey species. Mean weights of fresh crustaceans (as obtained from random samples collected from pelagic trawl catches carried out by one of the whaling vessels in the Bear Island area during the scientific whaling in 1992, see Haug *et al.* 1995a) were used to obtain crude estimates of the original biomass of the crustaceans eaten by the minke whales.

Subsamples consisting of digested fish material were placed in a tray, washed and strained through three sieves (2 mm, 1 mm and 0.25 mm) in order to separate otoliths and intact skulls from the rest of the material (Treacy & Crawford 1981, Murie & Lavigne 1985). The otoliths were identified to species or to the lowest possible taxon (Breiby 1985, Härkönen 1986). In samples consisting of a very large number of small otoliths, the total number was estimated by weighing all the otoliths (dry) and a subsample (about 10%) in which the number of otoliths were counted. Larger otoliths (from cod, haddock and saithe) were separated into left and right otoliths and divided into geometric classes (with 0.49 mm steps) in order to achieve a more accurate number. The total number of each fish species in the fore-stomach contents was determined by adding the number of fresh specimens, the number of intact skulls and half the number of free otoliths. Fish otoliths, particularly small and tiny ones from species such as herring and capelin, are known to be unresistant to exposure to gastric acids (Murie & Lavigne 1985, Jobling & Breiby 1986, Jobling 1987, Pierce & Boyle 1991). The problems with erosion of otoliths, which is particularly conspicuous in studies of seal stomachs (Pierce & Boyle 1991), is probably not a problem in these minke whale diet studies as the analyses were restricted to the forestomach contents where no gastric acids are produced. Digestive glands are completely absent in minke whale forestomachs where the degradation of food items occurs mainly as bacterial fermentation, and the pH appears to remain at a relative constant level of approximately 6.5 (Olsen *et al.* 1994).

In analyses of the numbers of the smallest prey item in question, the krill *Thysanoessa* spp., a conversion factor was applied: The number of krill is given as average "capelin biomass units", i.e., the actual number of krill specimens observed was divided by 100 since the weight of 100 average krill is similar to the weight of one average capelin.

Random subsamples of otoliths from each species (200 otoliths) were measured and otolith length - fish weight correlations were used to reconstruct the original fish weight. For capelin and herring, correlation equations were obtained from unpublished data kindly provided by the Institute of Marine Research, Bergen, Norway. For sand eels *Ammodytes* spp. and 0-group gadoids the correlation equations were calculated on the basis of material obtained in resource survey trawlings performed in conjunction with the scientific whaling in 1992 (see Haug *et al.* 1995a). All other correlation equations were taken from Härkönen (1986).

Feeding indices, commonly used in stomach analyses of top predators (Hyslop 1980, Pierce & Boyle 1991), were used to estimate the dietary contribution of different prey items. Since no feeding index gives a complete or fully realistic picture of dietary composition, the data were recorded as: (1) Percentages of empty stomachs and stomachs containing one or more specimens of each food item; (2) relative frequencies of occurrence of each prey item as a numerical fraction of all prey specimens found in the fore-stomachs; (3) relative contribution of each prey species to the total diet, expressed in terms of calculated fresh mass.

Prey abundance

During the period (early spring to late autumn) when minke whales are distributed in areas of the northern Norwegian Sea and the Barents Sea, large dynamic changes occur in the composition and distribution of fish. Main contributory factors are the feeding migrations of many fish species (including in particular the large stocks of adult and immature herring) and the very important occurrence of the 0-group fish which, through larval drift from spawning areas along the Norwegian coast, arrive in the Barents Sea in July (Dragesund *et al.* 1973, Bergstad *et al.* 1987, Røttingen 1990, Anon. 1994b, 1995a).

Potential minke whale prey species include fish and zooplankton (see Haug *et al.* 1995a). Of several methods used to estimate absolute abundance of fish stocks, acoustic surveys are probably the commonest (McLennan & Simmonds 1992). To conduct an acoustic survey aimed at absolute abundance estimation, prior knowledge of behaviour and acoustic properties of the species in question are essential. This includes:

1) Knowledge of the character of the target fish, i.e., species and length distribution.

2) Knowledge of acoustic properties (i.e. target strength) in order to express the acoustic quatities in terms of fish density.

3) Knowledge of the extent and variability in distribution in order to design an optimal sampling coverage.

In addition to the variations in abundance and species composition, all estimation of prey biomass per area in the summer season by using traditional accoustic survey techniques is difficult also for two other reasons: 1) Fish feed near the surface and thus out of range of the echo sounder; and 2) the accoustic properties of fish (i.e. target strength) in summer are generally poorly known. Due to these methodological problems, the abundance of prey organisms cannot always be given on the basis of research vessels survey carried out synoptically with the sampling of whales. Thus, both interpolations from surveys carried out at other times of the year and data from established time series had to be included in the assessment of the prey organisms in the Barents Sea in the minke whale feeding period.

The prey abundance estimations were based on data drawn from regular Norwegian resource surveys designed for the mapping of relevant resources (e.g. commercially interesting gadoid fish species, herring, capelin, prawns and zooplankton), not all of them necessarily of interest as potential whale prey. These surveys form part of a time series, and are carried out at the time of the year which is thought to give the most reliable estimates of abundance of each actual species. At other times of the year the survey conditions can be less favourable, e.g. the concentrations of a fish stock may be mixed with other species or with plankton or the fish may be feeding near the surface or very close to the shore and, therefore, out of the sampling range of the echo sounder.

Absolute abundances of the actual species were given for the whole Barents Sea (including the sampling areas Spitsbergen, Bear Island and Finnmark) and Lofoten/Vesterålen. Based on existing knowledge about passive drift, migrations and distribution of the various resources, the seasonal dynamic changes in the Barents Sea were taken into consideration by allocating different percentages of the stocks to northern (north of 74°N, including the areas Spitsbergen and Bear Island) and southern (south of 74°N, including Finnmark) areas throughout the period of interest. Thus, all capelin was defined as distributed in the northern area, all herring in the southern area. Furthermore, haddock was assumed to be represented with only 5%, 10% and 10% of the total Barents Sea stock in the north during, summer and autumn, respectively. The corresponding numbers for cod in the northern areas of the Barents Sea was set to 20%, 30% and 40%, respectively.

Data collected during the resource mappings include hydrogaphy (temperature and salinity, recorded from surface to bottom using a CTDO-sonde), acoustic measurements performed with scientific echo sounders connected to BEI postprocessing systems (Badholt *et al.* 1989, Foote 1991, Foote *et al.* 1991), and supplementary trawl (benthic and pelagic) hauls to sample the observed scatters.

Comparison of stomach contents with prey availability - statistical methods

The whale's choice of prey is influenced by the following two factors:

i) The amount in which the different species are available in the area where the whale is searching for food.

ii) The food preference of the whale.

The ecological studies of minke whale diets in 1992 (Haug *et al.* 1995a) showed the importance of i). The importance of ii) was studied by Skaug *et al.* (1995) using various statistical approaches to the 1992 diet and food availability data. In the present analyses, problem ii) is approached using the available 1993 and 1994 data in addition to the data from 1992 given by Haug *et al.* (1995a).

Testing for prey preference is done pairwise. For simplicity, the two species compared are denoted A_1 and A_2. Consideration of all pairs of species may yield a picture of the total preference pattern of the whale. To simplify the analyses, the observed prey was grouped in 7 categories: 0-group fish, bottom fish (other than cod and haddock), capelin, pelagic (including sand eel and saithe), plankton (including krill and other crustaceans), herring and cod+haddock.

Pooling of areas in the presentation of resource data necessitated similar pooling in the statistical analyses of food preferences. Thus, a whale located in one of the following sea areas is considered: Northern Barents Sea (including Spitsbergen and Bear Island), Southern Barents Sea (including Kola and Finnmark) and Lofoten/Vesterålen. The absolute amounts (reconstucted biomass) of A_1 and A_2 contained in the whale stomach are denoted X_1 and X_2, respectively. Define

$$Q = \frac{X_1}{X_1 + X_2}$$

as the fraction of prey A_1 relative to A_2 contained in the whale stomach. It is assumed that $X_1 + X_2 > 0$.

The total amounts (reconstructed biomass) of A_1 and A_2 available in the actual sea area are denoted Y_1 and Y_2, and the relative amount of A_1 is defined as

$$s = \frac{Y_1}{Y_1 + Y_2}.$$

Testing for preferences

The hypothesis is:

H: The whale has no preferences (between A_1 and A_2),

which will be tested versus the alternative that A_1 is being preferred. To test if A_2 is being preferred the role of A_1 and A_2 is changed.

If the whale has no prey preferences, i.e., the whale does not distinguish between A_1 and A_2, the contents of the whale stomach should reflect the prey abundance situation in the sea. If, on the other hand, the whale prefers A_1 more than A_2 it can be expected that Q is larger than s. Thus, a natural test statistic is:

I = fraction of whales with $Q > s$,

with large values of I leading to rejection of H. Whales which neither have A_1 nor A_2 in the stomach are disregarded.

For the calculation of the p-value the success probability $\Pr(Q > s)$ is needed. It is not obvious how to model the distribution of Q. The question is whether to use a discrete distribution where Q only takes on the values $Q = 0$ or $Q = 1$, or whether intermediate values also should be allowed for. Both approaches are tried here.

First it is assumed that the whale stomach only contains one single prey species at the time, so $Q = 0$ or $Q = 1$. Then it is reasonable to assume that when H is true

(1) $\Pr(Q > s) = s,$

which is interpreted as the long run frequency of stomachs containing A_1. The p-value is found using the normal approximation (Bickel & Doksum 1977) to the distribution of I.

The opposite viewpoint is that the whale stomach always contains both A_1 and A_2, so that Q follows a continuous distribution. For instance, when H is true X_1 and X_2 can be assumed to be independent and exponentially distributed (Bickel & Doksum 1977) with expectations proportional to s and 1-s (the same factor of proportionality) so that

(2) $\Pr(Q > s) = \frac{1}{2}.$

The p-value is found by using that I has a binomial distribution (Bickel & Doksum 1977) with success probability 0.5.

The true distribution of Q is neither purely discrete or purely continuous, but something between these two extremes. The stomach data show that some whale stomachs contain nearly exclusively one prey species, while other contain two or more species in comparable amounts (Haug *et al.* 1995b). Rather than making very explisite assumptions about the distribution of Q, two p-value are calculated: one using (1) and another using (2).

Sources of error

The p-values could be erroneous for several reasons:

i) There are uncertainties in the prey abundance estimates.
ii) The prey abundance will vary during the period of scientific whaling.
iii) There may be systematic non-homogeneity in the distribution of prey within the areas considered.

Point ii) is particularly important for Lofoten/Vesterålen, where the prey abundance estimates are based on a single resource survey carried out during a very short period (summer 1992 and autumn in 1993). Random variations in the distribution of prey resources will not cause severe trouble. Point iii) addresses particularly possible systematic differences between different parts of the sea area, for instance between Spitsbergen and Bear Island. Certainly, this problem could have been overcome by dividing the surveyed sea areas into more homogeneous sub-areas, but this is impossible due to the lack of fine scale estimates of prey abundance.

Since whales are considered in different areas at different times, some of the effects of i)-iii) may hopefully cancel out. It is, however, difficult to quantify the sizes of the potential errors in the p-values.

RESULTS

Whale stomach contents

The 1993 data

During the summer period a minimum of 10 different prey species were identified in the stomachs of the minke whales (Table 2). The corresponding numbers during spring and autumn were 9 and 7, respectively. Only fish was found in the spring. During the summer and autumn, crustaceans (mainly krill) were conspicuous in the northmost areas (Spitsbergen and Bear Island/Hopen), but were accompanied by fish. Further south (the Finnmark and Lofoten/Vesterålen areas) fish (herring in particular) also dominated the summer and autumn diets.

Analyses of the relative frequencies of occurrence (by numbers) of prey items (Fig. 2) revealed a pure fish diet for the whales taken in the spring period (particularly capelin in the Bear Island area, gadoids in the Norwegian coastal areas). In the summer period, krill occurred most frequently in the Spitsbergen and Bear Island area, herring in the Finnmark area, while in Lofoten/Vesterålen a more varied diet was observed, containing particularly krill, herring, sand eels and gadoids. Krill was the most numerous prey species in the two northmost areas also in the autumn period, however, now also accompanied by appreciable numbers of fish (0-group herring and cod in Spitsbergen, capelin in Bear Island / Hopen). 0-group gadoids (almost exclusively cod) was the most numerous prey species in the Finnmark autumn material, while the autumn samples taken in Lofoten/Vesterålen was comprised almost exclusively of herring.

Based on calculated fresh biomass (Fig. 3), gadoid fish (cod in Bear Island and Finnmark, haddock and saithe in Lofoten/Vesterålen) contributed most to the diet of the minke whales taken during the spring period. During the summer, krill was particularly conspicuous (92%) in the Spitsbergen area. In all other areas, fish contributed most to the summer diet biomass: cod and haddock with 63% in Bear Island, herring with nearly 100% in Finnmark, and haddock, herring and saithe with 90% in Lofoten/Vesterålen. In the autumn, krill contributed most to the whale diet in Spitsbergen (88%) and in Bear Island/Hopen (80%), while herring dominated the diet biomass in the two coastal areas (74% in Finnmark, 96% in Lofoten/Vesterålen).

The 1994 data

In 1994, a minimum of 12 different prey species was identified in the stomachs of the minke whales in the atumn period (Table 4). The corresponding values during spring and summer were 8 and 10, respectively. Spitsbergen was only surveyed during summer when krill dominated in the stomachs. This prey item was conspicuous also in the Bear Island area during spring and summer, while fish (capelin and cod in particular) and the amphipod *Parathemisto libellula* occurred most frequently in this area during autumn. Diets of whales taken in the two southern areas (Finnmark and Lofoten/Vesterålen) were generally characterized by fish diets (herring in particular, but also some gadoids) in all seasons.

The relative frequency of occurrence of prey items (Fig. 2) emphasizes the dominance of krill in the Spitsbergen area during summer and a very prominent role in the Bear Island area during spring and autumn. In all other seasons/areas surveyed in 1994, various fish species were the most frequent occurring prey items in the whale stomachs: capelin occurred most frequently during autumn in the Bear Island area, herring were most frequent in Finnmark during spring and summer and in Lofoten/Vesterålen during autumn, 0-group herring were most frequent in Finnmark during autumn, and gadoids and sand eels were most frequent in Lofoten/Vesterålen during spring and summer, respectively.

Reconstructions of fresh biomass (Fig. 3) restricts the importance of krill only to the summer period when it dominated both in the Spitsbergen (99%) and in the Bear Island (69%) area. The spring period was mainly characterized by fish, in particular cod (95%, 42% and 37% in the Bear Island, Finnmark and Lofoten/Vesterålen areas, respectively), herring (54% in Finnmark) and haddock (46% in Lofoten/Veserålen). The summer period was characterized by a conspicuous dominance of herring both in Finnmark (79%) and Lofoten/Vesterålen (52%), but in the latter area also sand eels and cod occurred in considerable amounts (26% and 16%, respectively). Cod dominated the autumn menu both in the Bear Island area (57%, however accompanied with 40% capelin) and in Finnmark (69%), while in Lofoten/Vesterålen the herring now exhibited an almost virtual monopoly (nearly 100%) on the whale diet.

Prey abundance

The given prey estimates (Table 3) are taken from long time series summarized in ICES Working Group reports (Anon. 1995a, b) and from synoptic surveys.

North of 74°N in the Barents Sea (including the areas Spitsbergen and Bear Island) capelin is the most important planktivorous fish species (Dragesund *et al.* 1973, Røttingen 1990). From Table 3 it is evident that the availability of capelin decreased throughout the period from spring to autumn, and there is also a marked decrease in capelin availability during the period 1992-1994. The biomass of other fish species is known to be rather small in the northern Barents Sea in spring and early summer. The availability of fish increases, however, in and after July, mainly as a result of an icreasing amount of 0-group fish (herring and cod in particular, see Anon. 1994b, 1995a, c) which drift northwards with the warm North Atlantic Current, but also due to feeding migrations of gadoid species from spawning areas further south (see Bergstad *et al.* 1987).

The most important planktivorous fish in the southern Barents Sea (south of 74°N, including the Finnmark area) is young and adolescent Norwegian spring spawning herring (Table 3). In spring, immature herring start feeding migrations into the Finnmark area from nursery areas further to the east (see Røttingen 1990, Anon. 1994b, 1995c). As seen from Table 3, there will also be considerable amounts of cod and haddock available in the area, presumably feeding on the herring, both during summer and autumn. From the end of July the fish biomass in the southern Barents Sea are usually further augmented by influx of 0-group fish species which are transported into the area by currents from south-west. These 0-group fish concentrations are usually dominated by cod and herring (Anon. 1994b, 1995c). As seen from Table 3, the abundance estimate of 0-group herring was lower in 1994 than in 1993, whereas the opposite was the case for young immature (1+) herring.

Resource data from the Lofoten/Vesterålen area are only available from the autumn period in

1993. However, it is generally known that in spring, stocks of adult gadoid fish (cod, haddock and saithe) migrate northwards through this area on their way from spawning grounds to summer feeding areas (Bergstad *et al.* 1987). There are also concentrations of immature herring in the area, usually distributed close to the coast, while adult herring migrate at 200-400 meters depth to the west of the continental slope during spring (Røttingen 1990, 1992). In summer, some fish species (saithe, cod, immature herring) feed in the Lofoten/Vesterålen area, while the amount of fish biomass increases substantially in autumn due to the arrival of adult herring which migrate towards their wintering area in the inner Vestfjord (Røttingen 1992, Anon. 1994c). The latter is clearly reflected in Table 3.

The overall zooplankton production in 1993 in the areas of interest to the minke whale surveys was probably above average and considerably larger than in 1992 (Anon. 1994c). A further slight increase in zooplankton production was observed in 1994 (Arne Hassel, Institute of Marine Research, Bergen, Norway, pers. comm.). The yearly production of krill in the Barents Sea has been estimated to 50-70 million tonnes (Drobysheva & Panasenko 1984). The main species of krill in this area are *Thysanoessa inermis*, *T. raschii*, *T. longicaudata* and *Meganyctiphanes norwegica*. However, the exact standing stock biomass (in tonnes) of krill in the particular areas and times of minke whale sampling cannot be given.

Predator-prey relationships

In the predator-prey analyses, minke whale stomach data from the 1992 summer investigations (see Haug *et al.* 1995a) was used in addition to the 1993 and 1994 stomach data. Furthermore, data from resource surveys, specially designed to support the minke whale investigations with prey abundance data, in Lofoten/Vesterålen and Finnmark in 1992 (Haug *et al.* 1995a, Skaug *et al.* 1995) were applied to supplement the data given in Table 3. Only periods and areas with sufficient data from both minke whale stomachs and resource surveys were included in the analyses. Furthermore, when comparing the preferences for two prey species A_1 and A_2, not all the available observations could be used. First, stomachs which contained neither A_1 nor A_2 had to be excluded. Second, it was decided that only whales from areas/periods where both A_1 and A_2 constituted more than 5% of the total prey resources should be used in the comparisons.

Application of these principles yields Table 4, showing the number of whales which can be compared for each pair of prey species. Since the table is symmetrical in A_1 and A_2, only the lower half of the table is given. Note the two zeros; for the corresponding species no comparisons can be made.

Tables 5 and 6 show the p-values from the prey-preference tests when (1) and (2) are being used. For instance, in the first row of the two tables are given the p-values corresponding to tests of preference for 0-group fish in favour of each of the other species.

The significance level is taken to be 0.05, and significant p-values are given with bold face types. Tables 5 and 6 yield the same patterns: Plankton and cod+haddock seem to be disliked in comparison with most other species. For the significant p-values which do not involve plankton or cod+haddock, substantial differences between Table 5 and Table 6 occur. For instance, for 0-group fish versus bottom fish, Table 6 gives a significant p-value of 0.0003, while the corresponding p-value in Table 5 (0.1941) is clearly non-significant. However, herring versus pelagic fish which is significant in Table 6 and close to significance in Table 5, thus indicating that the minke whales may prefer herring rather than pelagic fish.

Because of possibly failing assumptions the p-values might be erroneous and should be interpreted carefully. This applies especially to the p-values which are based on observations from one area/period only. The significant p-values which are based on observations from more than one area/period are (with numbers of areas/periods in parentheses): 0-group fish versus plankton (2), 0-group fish versus cod+haddock (3), capelin versus cod+haddock (10), pelagic fish versus plankton (2), herring versus pelagic fish (2) and herring versus cod+haddock (7).

DISCUSSION

Norteast Atlantic minke whales are piscivorous

Fish were the most conspicuous constituents of the diet of minke whales examined in Norwegian and adjacent waters during surveys made both in spring, summer and autumn in 1993 and 1994. The present investigation, therefore, confirms the euryphagous nature of North Atlantic minke whales suggested from previous summer observations made in Norwegian waters during both commercial (Jonsgård 1951, 1982) and reserach whaling (Nordøy & Blix 1992, Haug *et al.* 1995a). Similar piscivorous feeding behaviour is documented for minke whales from other North Atlantic areas such as off Canada (Sergeant 1963) and western Greenland (Larsen & Kapel 1981), and also from Japanese waters

(Kasamatsu & Tanaka 1992). These observations are in contrast to the rather stenophagous krill-eating minke whales in the Antarctic where, however, the availability of relevant fish prey is probably small (Kawamura 1980, Bushuev 1986, Ichii & Kato 1991).

From the presented 1993 and 1994 data, and taking into consideration also the results from comparable investigations made in 1992 (Haug *et al.* 1995a), it is evident that considerable heterogeneity in diet occurs among the geographical areas investigated, between the investigation periods, and from year to year.

Gadoid species characterize the spring diet

The results may point towards a dominant role of gadoid fish (cod and haddock, to some extent also saithe) in the spring diet of minke whales in the investigated areas. This seems consistent with previous observations made in Lofoten in the 1940s (Jonsgård 1951, 1982). The rather few whale observations made during the spring period in the northmost areas seems consistent with observations of a typical winter situation prevailing in these waters during the whole spring period (Rey 1993).

Capelin and krill in the north

In contrast to the summer 1992 investigations, when capelin dominated the whale diet in the northernmost parts of the investigated area (Spitsbergen and Bear Island, see Haug *et al.* 1995a), the dietary contribution of krill was much more conspicuous in the north in summer and autumn in 1993 and in summer in 1994. The recent prominent role of krill in the Spitsbergen area is consistent with previous summer observations made in 1950 (Jonsgård 1951, 1982) and in 1989 (Nordøy & Blix 1992). Stomach inspections in 1950 in the Bear Island area also revealed pelagic crustaceans to be the main food item, although often mixed with capelin (Jonsgård 1951). Interestingly, in 1989 the Barents Sea capelin stock still remained at a low abundance level, following a severe collapse in 1985/1986. However, very good recruitment in 1988 and 1989, accompanied with favourable climatic and food conditions that accelerated capelin growth, resulted in full recolonization of the species in the Barents Sea ecosystem by 1991 (Fossum 1992), and in 1992 it had recovered completely to its precollapse levels (Anon. 1994d). However, from 1992 to 1993 the capelin stock again decreased dramatically simultaneously with a marked increase in zooplankton production, in particular in these northern areas (Anon. 1994b). The situation with very low capelin abundance was even more pronounced in 1994 (Anon. 1995a, c) when also a further increase in available zooplankton amounts had occurred (Arne Hassel, Institute of Marine Research, Bergen, Norway, pers. comm.). These ecosystem changes may have contributed to the observed changes in minke whale diets in the northernmost areas between 1989 and 1994.

The 1994 autumn samples from the Bear Island area included mainly cod, to some extent also capelin. This seems consistent both with the observed changes in minke whale distribution in the northmost areas during late summer and autumn, yielding more overlap with capelin (Røttingen 1990), and also with the northwards migration of gadoids at this time of the year (Bergstad *et al.* 1987).

Herring and gadoids in the south

The capelin stock is mainly confined to the central and northern parts of the Barents Sea (Dragesund *et al.* 1973, Røttingen 1990), while the dominant planktivorous fish along the Norwegian coast and in the southern Barents Sea is the Norwegian spring spawning herring. In contrast to the now very decreased capelin stock, the stock of Norwegian spring spawning herring has been increasing in recent years (Anon. 1994b, 1995a). The difference in prey abundance situation in the southern coastal areas as compared with the north was also reflected in different whale diets. Thus, herring was an important prey component on minke whale diets in the coastal areas of North Norway both in 1993 and 1994. Similar observations were made during summer in 1992 (Haug *et al.* 1995a), and summer and early autumn predation of minke whales upon herring was observed in Lofoten and Vesterålen both in the 1940s (Jonsgård 1951, 1982) and in 1988 (Lydersen *et al.* 1991, Nordøy & Blix 1992).

The pronounced importance of 0-group herring in the whale diet, as observed during summer in 1992 (Haug *et al.* 1995a), was not found to the same extent in the Finnmark and the Lofoten/Vesterålen subareas in any parts of the 1993 or 1994 surveys. It is worth noticing that the 1992 year class of herring was very strong, while those from the two following years were considerably weaker (Anon. 1994b, 1995a, c). The 1993 and 1994 autumn diets of minke whales from the Lofoten/Vesterålen area was completely dominated by adult herring, while during summer the diet was more mixed with a particularly large representation of haddock and, to some extent, also saithe. The vast autumn appearance of adult Norwegian spring spawning herring in Lofoten/Vesterålen is a relatively recent phenomenon, related to the rebuilding of this stock (Røttingen 1990, 1992). Prior to the collapse of this stock in the late 1960s, the adults wintered in the open sea northeast of Iceland. In Finnmark in 1993, where herring dominated the whale diet in both summer and autumn, the whales were also observed to have eaten considerable quantities of 0-group gadoid fish in the autumn. A similar minke whale predation upon 0-group fish was observed in Finnmark in August 1988 (Nordøy & Blix

1992). The 1994 summer situation in Finnmark resembled that of 1993, while the 1994 autumn samples were very limited and yielded a dominance of gadoids.

Krill was very scarce in the diets of minke whales sampled in coastal areas of North Norway in 1993 and 1994. Similar observations were made in these areas, and also in areas off the Kola coast, in 1992 (Haug *et al.* 1995a). This is different from some earlier observations: During summer in 1972-1973, krill was found to be the main minke whale prey on the Kola coast (Christensen 1972, 1974). However, in these years the herring stock had recently collapsed and the abundance of this species was very low (Røttingen 1990). Inspection of a few minke whale stomachs from the Finnmark coast in 1988 and 1990 revealed that they had been preying upon krill and on 0-group herring, cod and haddock (Nordøy & Blix 1992).

Prey preferences

The whales' preferences for different species were tested by pairwise comparison of species. Conclusions are qualitative, and no attempt to quantify the preferences has been made. Two sets of different assumptions for the test method have been used (either that the whale stomachs contained only one single prey species at the time, or that they contained a mixture of two prey species), and the data has been analysed under both. The results from the two methods do not fully agree, which could be expected from the different nature of the assumptions. The main conclusion from the analyses is that there may be some evidence that plankton and cod+haddock are less preferred prey species in comparison to several other species. A possible negative preference for plankton was also revealed in more detailed prey-preference analyses based on parts of the 1992 material (Skaug *et al.* 1995). Also, a preference of herring in favour of other pelagic fish seems evident. However, all results must be interpreted carefully since the assumptions on which the test methods rely may not always be fulfilled.

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Table 1. Ecological studies of minke whales 1993: Frequencies of empty stomachs and identified species of prey in stomachs of whales caught in spring, summer and autumn in four subareas in the Northeast Atlantic. N = number of stomachs examined.

	PERCENTAGE OCCURRENCE			
PREY ITEM	WEST OF SPITSBERGEN	BEAR ISLAND	COAST OF FINNMARK	LOFOTEN/ VESTERÅLEN
		SPRING		
		N = 1	N=1	N=2
Empty stomachs		0	0	0
Pisces				
Clupeidae				
Clupea harengus		100	100	100
Osmeridae				
Mallotus villosus		100		50
Myctophidae				
Benthosema glaciale		100	100	
Gadidae				
Gadus morhua		100	100	50
Melanogrammus aeglefinus		100	100	100
Pollachius virens				100
Unid. gadoid remains		100	100	
Ammodytidae				
Ammodytes sp				100
Scorpenidae				
Sebastes sp		100		
Cottidae				
Unid. cottid remains		100		
Unidentified remains		100	100	50
		SUMMER		
	N=14	N=7	N=5	N=6
Empty stomachs	0	0	20	0
Crustacea				
Amphipoda				
Parathemisto sp.	7.1			
Euphausiacea				
Thysanoessa sp.	85.7	71.4		50
Pisces				
Clupeidae				
Clupea harengus		42.9	80	50
Osmeridae				
Mallotus villosus	14.3	42.9		50
Myctophidae				
Benthosema glaciale				33.3
Gadidae				
Gadus morhua	7.1	28.6		
Melanogrammus aeglefinus		28.6		33.3
Pollachius virens				16.1
Unid. gadoid remains		28.6	20	50
Ammodytidae				
Ammodytes sp.	7.1	14.3		66.7
Scorpenidae				
Sebastes sp.		14.3	20	
Unidentified remains		28.6	40	66.7
		AUTUMN		
	N=3	N=5	N=7	N=12
Empty stomachs	0	0	0	0
Crustacea				
Euphausiacea				
Thysanoessa sp.	66.7	100		
Pisces				
Clupeidae				
Clupea harengus	33.3		100	100
Osmeridae				
Mallotus villosus		100	14.3	
Gadidae				
Gadus morhua	100		42.9	25
Melanogrammus aeglefinus	33.3		28.6	16.7
Pollachius virens				8.3
Unid. gadoid remains			14.3	8.3
Argentinidae				
Argentina silus				8.3
Unidentified remains	33.3			16.7

Table 2. Ecological studies of minke whales 1994: Frequencies of empty stomachs and identified species of prey in stomachs of whales caught in spring, summer and autumn in four subareas in the Northeast Atlantic. N = number of stomachs examined.

PREY ITEM	WEST OF SPITSBERGEN	BEAR ISLAND	COAST OF FINNMARK	LOFOTEN/ VESTERÅLEN
		PERCENTAGE OCCURRENCE		
		SPRING		
		N = 5	N=7	N=6
Empty stomachs		0	0	0
Crustacea				
Calanoida				
Calanus sp.		20	0	0
Euphausiacea				
Thysanoessa sp.		80	28.6	0
Pisces				
Clupeidae				
Clupea harengus		40	100	83.3
Osmeridae				
Mallotus villosus		20	28.6	33.3
Gadidae				
Gadus morhua		20	14.3	66.7
Melanogrammus aeglefinus		40	28.6	66.7
Pollachius virens		0	14.3	50
Unid. gadoid remains		0	28.6	0
Scorpenidae				
Sebastes sp		20	0	0
Unidentified remains		20	42.9	83.3
		SUMMER		
	N=12	N=10	N=9	N=6
Empty stomachs	0	0	0	0
Crustacea				
Calanoida				
Calanus sp.	0	10	0	0
Amphipoda				
Parathemisto sp.	50	10	0	0
Euphausiacea				
Thysanoessa sp.	100	100	11.1	0
Pisces				
Clupeidae				
Clupea harengus	16.7	10	100	83.3
Osmeridae				
Mallotus villosus	8.3	30	0	0
Gadidae				
Gadus morhua	0	20	11.1	16.7
Melanogrammus aeglefinus	0	0	33.3	66.7
Pollachius virens	0	0	0	83.3
Unid. gadoid remains	25	40	33.3	50
Ammodytidae				
Ammodytes sp.	0	0	0	66.7
Cottidae				
Unid. cottid remains	0	10	0	0
Unidentified remains	0	20	22.2	50
		AUTUMN		
		N=6	N=3	N=5
Empty stomachs		0	0	0
Crustacea				
Amphipoda				
Parathemisto sp.		66.7	0	0
Euphausiacea				
Thysanoessa sp.		16.7	0	0
Pisces				
Clupeidae				
Clupea harengus		16.7	66.7	100
Osmeridae				
Mallotus villosus		83.3	66.7	0
Gadidae				
Boreogadus saida		33.3	0	0
Gadus morhua		66.7	33.3	0
Melanogrammus aeglefinus		16.7	66.7	0
Pollachius virens		0	0	0
Unid. gadoid remains		33.3	66.7	0
Zorcidae				
Lycodes sp.		16.7	0	0
Ammodytidae				
Ammodytes sp.		0	66.7	60
Scorpenidae				
Sebastes sp.		0	33.3	0
Cottidae				
Unid. cottid remains		16.7	0	0
Unidentified remains		66.7	66.7	60

Table 3. Estimated abundance (in 1000 tonnes) of different fish stocks in relevant areas of minke whale sampling in 1993 and 1994. The abundances are given by the two areas Barents Sea and Lofoten/Vesterålen. In the statistical analyses, however, the resources of the Barents Sea are assumed to be distributed in a northern Barents Sea area (NBS, north of 74°N, including the sampling areas Spitsbergen and Bear Island) and a southern Barents Sea area (SBS, south of this latitiude, including Finnmark and Kola) according to the following key: During all periods of minke whale sampling, all capelin were assumed to be distributed in NBS and all herring in SBS. Gadoids are also assumed to be distributed mainly in SBS, however, with 20%, 30% and 40% of the cod, and 5%, 10% and 10% of the haddock being distributed in NBS in spring, summer and autumn, respectively. Herring 1+ means one-year-old and older herring.

		PREY					
AREA	PERIOD	COD	HADDOCK	SAITHE	CAPELIN	HERRING (1+)	HERRING (0-group)
Barents Sea 1992							
	Summer	2500	280		3500	850	
Barents Sea 1993							
	Spring	1650	200		2000	800	0
	Summer	2500	300		1000	1500	0
	Autumn	2400	300		800	1500	800
Lofoten/Vesterålen 1993							
	Autumn	90	45	250		2900	
Barents Sea 1994							
	Spring	1500	200		450	1500	0
	Summer	2300	280		300	1500	0
	Autumn	2200	270		200	2850	250

Table 4. The number of whales used to test the prey-preference hypothesis for each pair of prey categories (A_1 and A_2).

A_1 / A_2	0-group	bottom fish	capelin	pelagic	plankton	herring	cod+haddock
0-group	x						
bottom fish	15	x					
capelin	16	0	x				
pelagic	32	14	14	x			
plankton	27	5	11	25	x		
herring	28	0	14	30	16	x	
cod+haddock	20	7	51	13	4	48	x

Table 5. The p-values for the prey-preference tests for each pair of prey categories (A_1 and A_2) using assumption (1) (see text for further explanation). Significant p-values (< 0.05) are given with bold face types.

A_1 / A_2	0-group	bottom fish	capelin	pelagic	plankton	herring	cod+haddock
0-group	x	0.1941	0.3617	0.2000	**0.0000**	0.2006	**0.0056**
bottom fish	0.8059	x	-	0.9215	**0.0112**	-	0.6473
capelin	0.6383	-	x	**0.0191**	**0.0000**	0.8336	**0.0176**
pelagic	0.8000	0.0785	0.9809	x	**0.0003**	0.9446	**0.0241**
plankton	1.0000	0.9888	1.0000	0.9997	x	0.9991	0.9795
herring	0.7994	-	0.1664	0.0554	**0.0009**	x	**0.0001**
cod+haddock	0.9944	0.3527	0.9824	0.9759	**0.0205**	0.9999	x

Table 5. The p-values for the prey-preference tests for each pair of prey categories (A_1 and A_2) using assumption (2) (see text for further explanation). Significant p-values (< 0.05) are given with bold face types.

A_1 / A_2	0-group	bottom fish	capelin	pelagic	plankton	herring	cod+haddock
0-group	x	**0.0003**	0.0717	0.0814	**0.0000**	0.7709	**0.0001**
bottom fish	0.9997	x	-	0.9995	**0.0156**	-	0.6367
capelin	0.9283	-	x	0.3036	0.0730	0.9963	**0.0001**
pelagic	0.9186	**0.0005**	0.6964	x	**0.0000**	0.9999	**0.0001**
plankton	1.0000	0.9844	0.9270	1.0000	x	0.9936	0.9688
herring	0.2291	-	**0.0037**	**0.0001**	**0.0064**	x	**0.0106**
cod+haddock	0.9999	0.3633	0.9999	0.9999	**0.0312**	0.9894	x

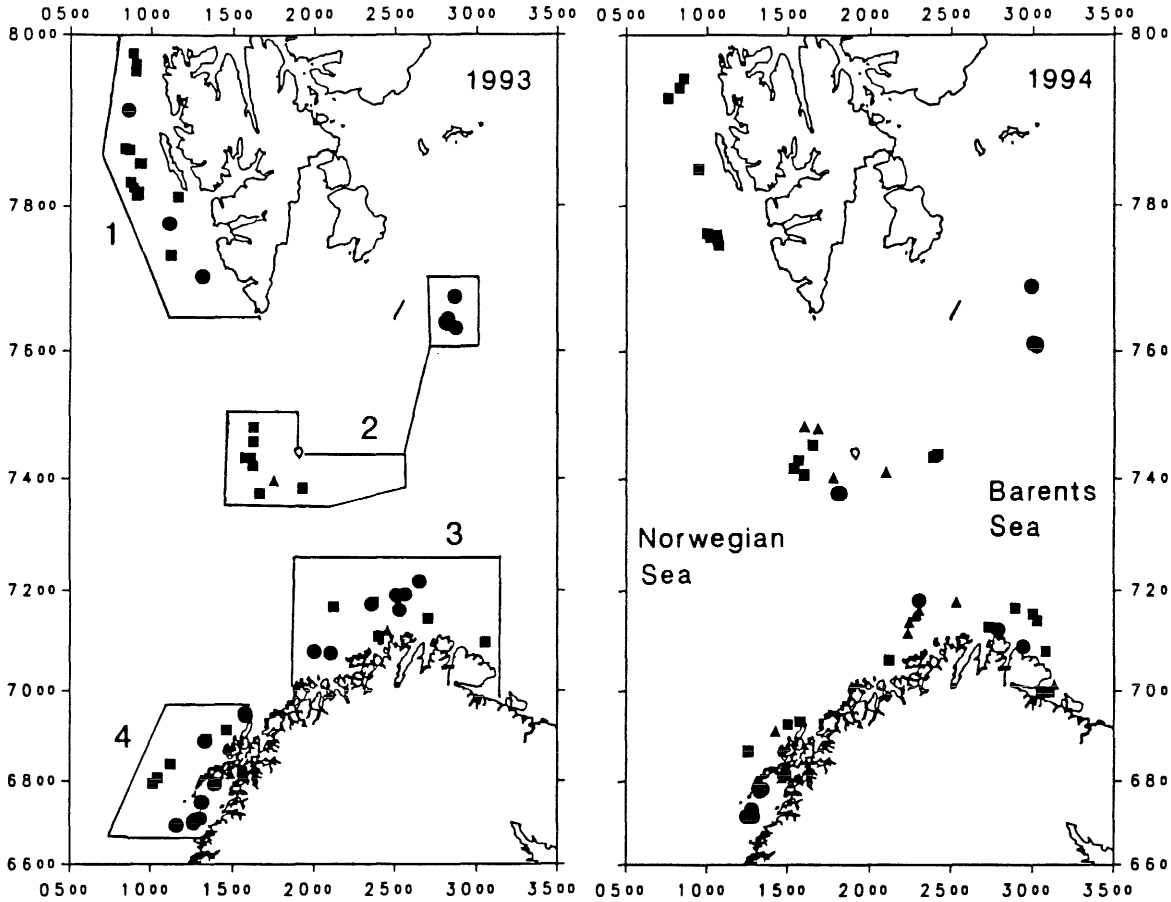

Fig. 1. Catch positions for minke whales shot during the Norwegian scientific catch operations in four areas (1 = Spitsbergen, 2 = Bear Island, 3 = Finnmark, 4 = Lofoten/Vesterålen) in spring (triangles), summer (squares) and autumn (circles) in 1993 and 1994.

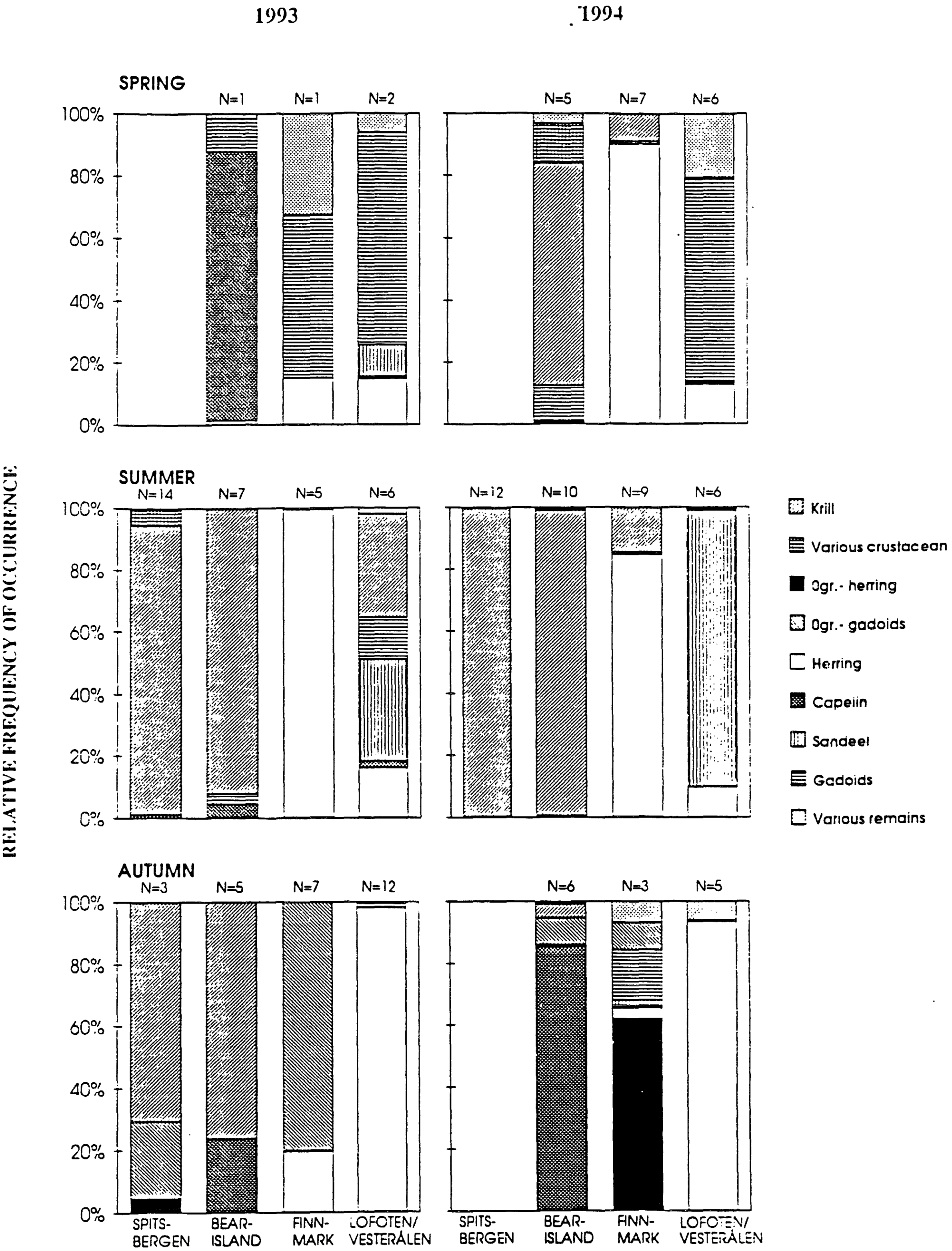

Fig. 2. Food composition, expressed as relative frequency of occurrence (by numbers) of prey organisms, in minke whales sampled in four areas in the Northeast Atlantic in spring, summer and autumn in 1993 and 1994. Herring and gadoids are presented as 0-group and one year and older fish. The actual numbers of krill were divided by 100 before presented in the figure. N = numbers of stomachs examined.

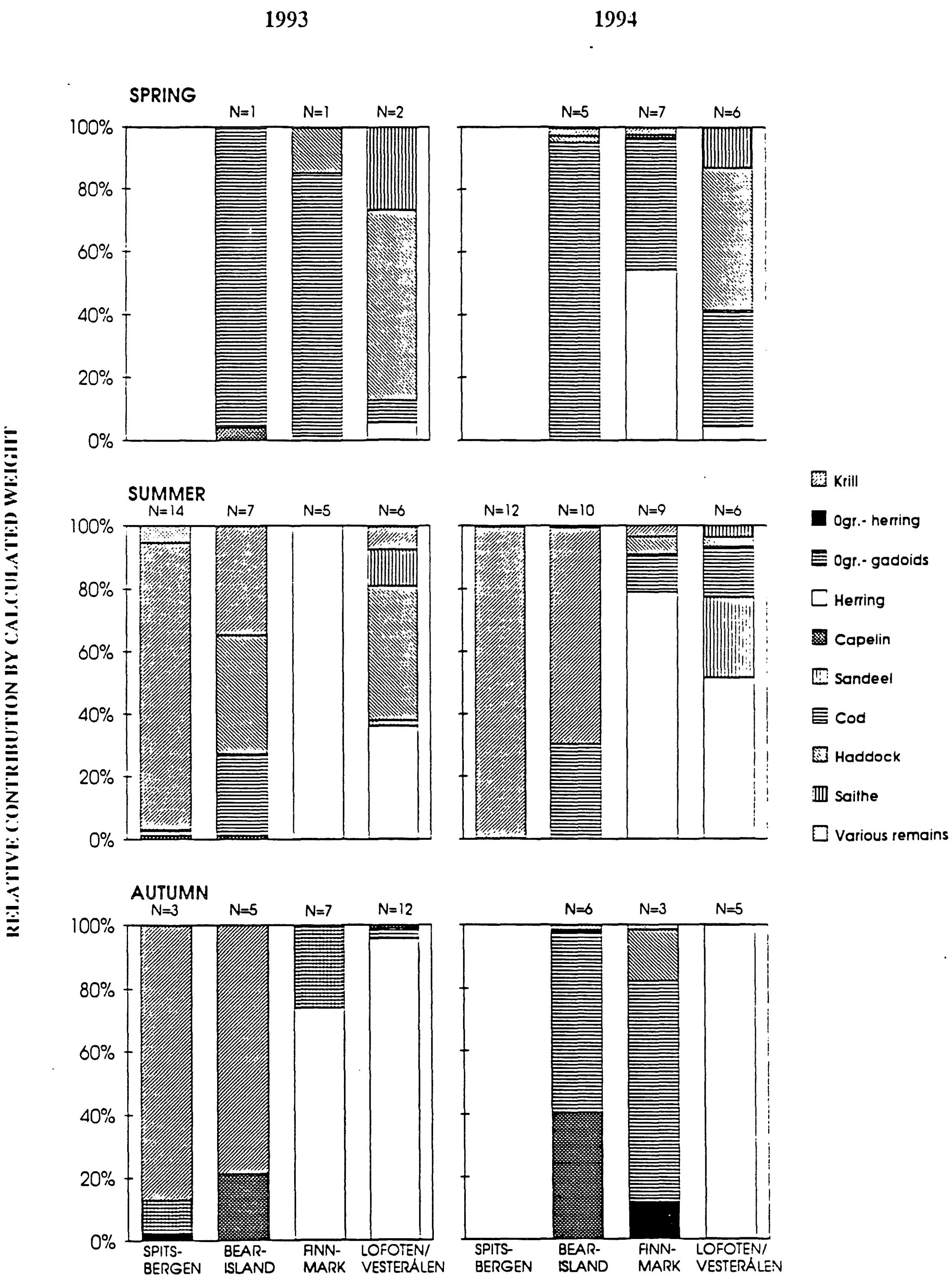

Fig. 3. Food composition, expressed as relative biomass (by calculated fresh mass) of prey organisms, in minke whales sampled in four areas in the Northeast Atlantic in spring, summer and autumn in 1993 and 1994. N = numbers of stomachs examined.