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Theme Session on Trophic Dynamics of Top Predators: Foraging Strategies and Requirements , and Consumption Models

Foraging behaviour of minke whales *(Baiaenoptera acutorostrata)* in the southern Barents Sea

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ABSTRACT

Stomach content samples from 23 minke whales ***Balaenoptera acutorostrata,*** caught during the Norwegian commercial whaling in the period May-June 1999, were collected in two areas in the southern Barents Sea. Simultaneously, a comprehensive resource survey was conducted in order to identify and estimate the abundance of potential prey items for the whales in the same sub-areas. The small-scale resource surveys revealed significant variations in absolute and relative prey abundance both between areas and, temporally, within areas. This was, to some extent, also reflected in the whale diets, which was particularly dominated by herring ***Clupea harengus*** and capelin ***Mallotus villosus.*** Both these prey items were subjected to population specialization, i.e., they were taken frequently by many whales. Using the obtained data on diet and prey abundance to assess quantitatively possible prey selectivity of the minke whales in the area, it appears that capelin was preferred over all other prey items.

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INTRODUCTION

Detailed, process-oriented studies are important in understanding food webs such as those of the Barents and Norwegian Seas in the northeast Atlantic, where the top predators are critically dependent on a small number of prey nodes. Where critical prey nodes are sparse, the potential for strong non-linearity in feeding preferences is great. Thus, no simplifying assumption of constant suitability can be invoked. Quantification of prey suitability for the top predators is very important in the work with MULTSPEC, a multi species model now under development for the Barents Sea (Ulltang 1995, Bogstad et al. 1997).

The northeast Atlantic stock of minke whales ***Balaenoptera acutorostrata*** is one of the top predators implemented in MULTSPEC. In order to evaluate the present ecological significance of this stock, a scientific whaling programme, addressing particularly questions concerning feeding ecology by using stomach analyses and, in some cases, concurrent estimates of prey availability, was conducted in 1992-1994 (Haug ***et al.*** 1995a, b, 1996, 1997, Lindstrøm ***et al.*** 1997, Skaug ***et al.*** 1997). The programme was a large-scale study, originally intended to address two issues: i) Describe the diet of minke whales in the northeast Atlantic; ii) Evaluate prey selectivity of minke whales. In retrospect it is evident that answers to the first question were most efficiently obtained with the applied methods. The programme was not equally helpful in elucidating the prey-preference function in minke whales, a question more efficiently addressed using small and medium scale studies of the dynamics of minke whale foraging in relation to the densities of various prey types in certain selected areas.

To address the latter questions more adequately, an approach with application of medium and small-scale survey design was attempted during the Norwegian commercial whaling operations in 1998 and 1999. These investigations intended to provide and analyse new field data necessary for proper evaluation of how minke whales might be expected to respond to variations in abundance, distribution, patch characteristics and relative composition of prey species. In addition to help elucidate the underlying processes of whale prey preferences, so relevant in the construction of multispecies models in a boreal system such as the Barents Sea, results from such studies will also provide a better understanding of possible minke whale responses to predicted future ecosystem changes.

Commercial whaling occurs opportunistically. Sampling from commercial catches will, therefore, yield stomach samples from areas with much minke whale foraging activities. Such areas were of special interest for this project, which was carried out in May-June in 1998 and 1999 in close co-operation with the commercial whaling fleet. It was necessary to choose a relatively restricted area (maximum 1000 nautical mile^2) where several commercial whale vessels were hunting and where whale diet data could be secured from a selected number of vessels. A region in the southern Barents Sea (coastal areas of Finnmark, Norway), where whale diets usually comprise a mixture of several prey species (Haug *et al.* 1996), was chosen as the most convenient study area.

Simultaneously with the whaling operations, research vessels ("Jan Mayen" in 1998, "Johan Ruud" in 1999) equipped with acoustical instrumentation conducted resource surveys in the study area. Assessment of resources included tracking temporal changes in spatial distribution, such as diurnal vertical and horizontal migrations. Stratification of the water column into several depth strata proved to be a useful sampling strategy.

Lindstrøm & Haug (2000) reported results from the 1998 fieldwork. The aim of this paper is to present the results from the 1999 fieldwork. The ecological situation in the study area had changed from 1998 to 1999 - the presented analyses aims to investigate how these changes may have affected the foraging strategies and prey selectivity of the minke whales by comparing the 1998 and 1999 results.

MATERIAL AND METHODS

Sampling of minke whales

A total of 23 minke whales were caught during the Norwegian commercial whaling in two areas in the southern Barents Sea in May-June 1999 (Fig. 1). The whales were distributed with 14 and 9 individuals in areas 1 (7-9 June) and 2 (2-7 June), respectively. The minke whales were killed according to whaling procedures described by Haug *et al.* (1996), and immediately taken onboard the vessel for dissection and biological sampling. All whales were sampled opportunistically by whalers in areas with expected high densities of whales (see Christensen & Oien 1990).

Analyses and reconstruction of stomach contents

Short after a whale was onboard the whale vessel, the complete digestive tract was removed as soon as possible (30-60 minutes *post mortem).* The minke whale stomach consists of four chambers (see Olsen *et* al. 1994). Previous studies indicate that stomach contents from the first stomach compartment, the forestomach, are sufficient to describe the minke whale diets (Lindstrøm *et al.* 1997). Therefore, only contents from the forestomach were used in this investigation. This resulted in 23 minke whale forestomach samples. The contents were treated and analysed according to Haug *et al.* (1995a, 1996).

In the laboratory, intact fish specimens were identified using gross morphological characteristics (Pethon 1985). In order to reduce some of the main sources of uncertainty in reconstruction of stomach contents, such as differential passage and degradation rates of different fish types and sizes (Bigg & Fawcett 1985, da Silva & Nelson 1985, Murie & Lavigne 1986, Markussen & Øritsland 1992) and accumulation of hard remains such as otoliths, only fresh or moderately digested fish prey were included in the present analysis.

The estimation of crustacean biomass at time of ingestion is a major problem when reconstructing the forestomach content of minke whales, not only because they lack hard parts that are resistant to the forestomach microbes (Nordøy *et al.* 1993, Olsen *et al.* 1994) but also due to passage and degradation rates that most likely differ from those of other prey type. To obtain estimates of crustacean abundance's comparable with those of fish, only the in situ biomass of crustaceans was used in the reconstruction's involving this prey item.

In order to make the diet and prey abundance data comparable with each other, the prey organisms were grouped into the following seven prey categories: Krill *Megunyctephanes norvegica* and *Thysanoessu sp.,* herring, capelin, gadoids and juvenile gadoids. The two latter groups are mixture of cod *Gadus morhua,* haddock *Melanogrammus aeglefinus* and saithe *Pollachius virens.*

A variety of approaches have been used to quantify the importance of different prey items in the diet of predators, and there is no consensus as to which method is most appropriate. The following three indices were used to describe the minke whale diets in this study:

1. The frequency of occurrence of each prey item, (*Fj*):

$$Fj = \left(\frac{fj}{ft}\right) x100$$

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

2. The individual biomass index, BI_j:

$$BI_j = \frac{1}{n}\sum_{j=1}^{n}(b_{ij}/b_i)\times 100$$

where b_{ij} is the biomass of prey category i in whale no. j, b_i is the total biomass of all prey categories in whale no. j, and n is the total number of examined whales containing food (see Lindstrøm et al. 1997).

3. The specific abundance, P_j:

$$P_j = \left(\frac{\sum b_{ij}}{\sum b_{tj}}\right)\times 100$$

where b_{ij} has been defined above and b_{tj} is the total biomass of all prey categories in whales containing prey itemj (Amundsen 1995, Amundsen et *al.* 1996).

In order to illustrate the relative prey importance and possible feeding strategy of the whales a method presented by Amundsen et *al.* (1996) was used, This implies that the prey specific abundance (P_j) was plotted against the frequency of occurrence (F_j) of each prey item (see explanatory diagram in Fig. 2). In the diagram the vertical axis represents the feeding strategy of the predator in terms of degree of specialization. The predator has specialized on prey items located in the upper part of the graph, whereas prey located in the lower part of the graph have been eaten more occasionally (generalization). Prey items located in the upper left part of the graph indicate individual specialization, i.e., few predators has exploited the actual prey item in large amounts, whereas prey in the upper right part of the graph indicate population specialization, meaning that these prey items are frequently taken by many predators. If all prey items are distributed in the upper left part of the graph there is a high between-phenotype component (BPC; different predators specialize on different prey types), whereas if prey items are distributed in the lower right part of the graph there is a high within-phenotype component (WPC; most individuals exploit many prey types simultaneously). The distribution pattern of prey points along this upper left-lower right diagonal is, therefore, indicative of the contribution of between- and within-phenotype components to the niche width. In both cases the population will be generalistic, displaying a broad niche width.

Estimation of prey abundance

The resource survey conducted in parallel with the whaling operations was carried out using the research vessel "Johan Ruud" in the period 2-10 June 1999. Standard acoustic survey methods were applied when estimating the abundance of potential prey (Foote 1991), including a 38 KHz Simrad EK-500 splitbeam echosounding system (Bodholt et *al.* 1989) and a BE1 post processing system (Foote *et al.* 1991).

In order to detect concentrations of zooplankton such as krill, the minimum threshold was set to -88 dB SV. The echo integration was carried out along predetermined transect in areas where whales were being or had been caught. The allocation of acoustic values was carried out on the basis of the acoustic character of each species and the trawl samples. Both pelagic and demersal trawling was performed in response to potential changes in the echo sounder registrations. For pelagic trawling, a 10 fathom trawl (Finnsnes, Norway) fitted with a Scanmar depth recorder was used. Demersal trawling was carried out using a 1200 mesh shrimp trawl with rubber bobbins. Both trawls were fitted with an 8 mm net inside the codend thereby making it possible to sample fish juveniles and larger zooplankton. Pelagic and demersal trawling was standardized to 30 and 20 min duration, respectively, and the towing speed was approximately 3 knots.

As soon as the trawl catch was aboard, it was sorted by species using standard identification keys (Enkell 1980, Pethon 1985). In order to estimate the species-composition in the trawls, the different fish species were counted and weighed separately. Zooplankton was only weighed. In case of large trawl catches, sub samples were taken, and these were treated as described above. For each fish species, the length and weight of 100 specimens, when available, was registered. Samples of zooplankton and smaller fish species such as herring, capelin and O-group gadoids, were frozen for later analysis.

The standard echo integration, described in detail by MacLennan & Simmonds (1992), was used to estimate the abundance of potential prey species in each area. The recorded SA per square nautical mile (nm^2) and 10 m depth channel was averaged over 1 nautical mile, and distributed on the following 10 groups: krill, herring, capelin, juvenile gadoids, cod, haddock and other fish. When illustrating the distribution of prey types in each area, cod, haddock and saithe were pooled and named as gadoids. In order to cover the most potential forage depth of minke whales, the water column was divided in the following two depths strata: O-50 m and 50-100 m. The total depth in the areas varied from 380 m in area 1 to 450 m in area 2.

In order to analyse the spatial abundance of prey, the abundance (tons per nm^2) of krill, herring, capelin and gadoids (cod, haddock and saithe) were interpolated by fitting a polynomial cubic function, and visualised by contour plots. Additionally, as a measure of prey patchiness, the coefficient of variation (C.V.) was used.

Analyses of foraging selectivity

There have been many attempts to quantify selective predation (e.g. Ivlev 1961, Manly 1972, Chesson 1978). There is, however, no general agreement in the literature about which of these indices gives the best measure of preference, but Krebs (1989) considered Chesson's a (Chesson 1978) to be the best index of preference for most situations. This index has proved useful in numerous prey selectivity studies (e.g. Lawson et al. 1998). The minke whale foraging selectivity was, therefore, analysed using Chesson's index for constant prey populations:

$$\alpha i = \frac{ri}{ni} * \frac{1}{\sum_{j=1}^{m} rj / nj}$$

where αi is Chesson's a ranging from zero to one, *ri* and rj is the proportion of prey type *i* or j in the whale diet (*i* and $j=1,2,3,\ldots,m$), *ni* and *nj* is the proportion of prey type *i* or j in the environment. *m* is the total number of prey types, Interpretation of the results: selective predation does not occur if $\alpha i = 1/m$, while when $\alpha i > 1/m$ more species *i* occurs in the diet than expected by random feeding, i.e. species *i* is preferred by the whales. Conversely, if $\alpha i < 1/m$ less occurs in the diet than expected, i.e., prey species *i* is avoided by the whales. In order to test the null hypothesis (I-IO), that northeast Atlantic minke whales are not prey selective, Chesson's a, calculated for each prey type, was tested for significant deviance from random feeding *(l/m)*. This was accomplished by constructing approximate 95 % CI for Chesson's a of each prey, and comparing these with the value of random feeding. The confidence intervals were constructed based on 5000 bootstrap replications of the Chesson's index of each prey (Efron & Tibshirani 1993). Such bootstrap techniques have been proved useful in previous analyses of predator diets (e.g. Jiang & Jorgensen 1996, Lawson & Stenson 1997, Lindstrøm et *al.* 1998b).

The prey selectivity results were based on four assumptions: (i) the analysed minke whales represent a random sample from all the animals in that particular area; (ii) the prey abundance estimates were reliable and constant throughout the period of sampling; (iii) the reconstruction of forestomach contents were reliable; (iv) the minke whales had fed in the same area as they were caught. The first assumption is difficult to investigate, but since there is no scientific evidence indicating that size and/or sex are important contributors to minke whales diet composition nor catchability, assumption (i) was considered to be satisfied. The use of only undigested prey items increased the probability that (iii) and (iv) were satisfied. The validity of (ii) is difficult to confirm and will be discussed later.

RESULTS

Whale diets and foraging strategy

A total of 10 and 8 whales had stomach content indicating that they had fed recently in areas 1 and 2, respectively. In area 1, the whale diets were dominated by capelin (70%) and herring (30%), while in area 2 herring (52%), followed by capelin (36%) and krill (12%), comprised the whale diets (Fig. 3).

Capelin and herring appeared to have been subjected to population specialization, i.e., they were taken frequently by many predators, in areas 1 and 2, respectively (Fig. 3). The intensive feeding on these prey species resulted in narrow diet widths in both areas. Krill, to some extent also capelin, appeared to have been subjected to some degree of individual specialization (few whales took large bouts) in area 2 (Fig. 3). The foraging strategy results must be interpreted cautiously, particularly with regard to prey species that were eaten by few whales (e.g., krill and gadoids) due to the low sample size.

Prey abundance

The resource survey in area 1 (1900 nm^2), conducted in the period 8-10 June, revealed that approximately 80% of the prey biomass was distributed in the upper 50 m (Fig. 4). Krill, mainly *Thysanoessa* sp., dominated the prey biomass in the upper 100 m (89%) followed by herring (6.5%) and capelin (3.4%). Gadoids occurred only below 50 m. The spatial distribution of prey varied considerably between species and depths. Krill appeared to be the most evenly distributed prey in the upper 100 m (C.V. =1.8-2.8) while capelin (C.V.=5.5-11.2), herring (C.V.=8.3-8.6) and gadoids (C.V.=6.0-10.8) occurred more patchily (Fig. 4). The spatial correlation (Spearman's rank correlation coefficient, r_s) beween the prey species (per nm^2) was low in the upper 100 m (r_s=-0.06-0.44).

Area 2 (approximately 700 nm^2) was surveyed three times in the period 2-8 June (Fig. 1). The three surveys revealed that 63-73% of the prey biomass was distributed in the upper 50 m, depending on the survey (Fig. 5a). Herring comprised 50-82% of the prey biomass in the upper 50 m. The relative importance of krill in the upper 100 m increased with time from 17% during the first survey (2^1) to 35.7% during the third (23). The importance of gadoids varied from 17.3% during the second survey to 27% during the first survey. Capelin occurred only in small, patches and comprised less than 1% of the total prey biomass in the upper 100 m independent of survey. The comparison of the three surveys revealed considerable spatial and temporal variations in prey biomass in the upper 100 m (Fig. 5a,b). Interestingly, herring appeared to be relatively stationary, while the distribution of krill and capelin changed quite much between the surveys. The spatial distribution of gadoids and krill in the upper 100 m showed the highest inter-species correlation, ranging from r_s=0.58-0.78 during survey 2^1 to r_s=0.7-0.78 during survey 2^2 (Fig.5a, b)

Foraging selectivity

In order to have significant significant positive or negative selective predation, the chesson errorbar (95% CI) must not overlap the horizontal dotted line that indicates neutral selectivity ($1/m$). In area 1, the whales had selected capelin positively in all depths as indicated by the consistent non-overlap between errorbars and the line of neutral selectivity (Fig. 6). Krill and gadoids appeared to have been completely avoided, while herring had been exploited as expected by random feeding. In area 2, the whales had preyed apparently randomly on krill, herring and capelin, while gadoids had been more or less completely avoided by the whales (Fig. 4).

DISCUSSION

The observed diet composition of minke whales in the southern Barents Sea, comprised mainly of krill, capelin, herring and gadoids (exclusively haddock), may provide the impression of a specialist forager. In fact, approximately three out of four whales had fed on one single prey type only, particularly herring or capelin. The remaining whales had fed on two prey types. The main prey species appeared to have been subjected to a population specialization, yielding consistently narrow diet widths in both areas. Thus, the dietary importance of capelin and herring, and the fact that the bulk of minke whale diets were comprised of relatively few species, confirms previous feeding ecological studies of minke whales both in the northeast Atlantic and in the western north Pacific (Kasamatsu & Tanaka 1992,Haug et *al.* 1995a,b, 1996, Lindstrom et *al.* 1998a, Tamura et *al.* 1998, Lindstrom & Haug 2000). Moreover, the conducted resource surveys revealed significant variations in absolute and relative prey abundance both between the two areas and, temporally, within areas. This was, to some extent, also reflected in the whale diets. Previous investigations have also shown large scale geographical and temporal variations in minke whale diets in the northeast Atlantic (Haug *et al.* 1995a,b, 1996;Lindstrøm & Haug 2000).

In area 1, the whales appeared to have selected capelin while krill and gadoids seemed to have been avoided. The lack of interest for gadoids may be due to their low availability, particularly in the uppermost layers, but the avoidance for krill is more difficult to understand given that this prey item was about 25 times more abundant than capelin in the upper 100 m. A plausible explanation to the observed prey selectivity results may be that minke whales require a higher foraging threshold for krill compared with capelin partly due to lower energy density (see Piatt & Methven 1992). The reason for this possible explanation can not be ascertained from the present data, but the general lower energy density of krill (Mårtensson *et al.* 1996) could be a contributory factor. In area 2, the whales appeared to have fed less selectively in comparison with area 1. All but one prey type, the gadoids, appeared to have been preyed upon randomly in this area.

The present results partly confirms the study of Lindstrom and Haug (2000) in the same period and region in 1998 where it was demonstrated that capelin had been positively selected by the whales while gadoids and herring had been either avoided or fed on randomly. Despite that herring was G. 30 times more abundant in area 2 in 1999 as compared with 1998, the selectivity analysis yielded approximately the same chesson values. However, it should be kept in mind that the synopticity between whale and resource sampling was low in 1998, implying that the abundance of herring in the area in 1998 may have been higher when the whales were actually caught. This is further emphazised from the observations made in 1999 that the availability of prey species in small-scaled areas may vary considerably on rather short time scales. In the 1999 small-scale study, a better synopticity between whale and resource sampling than in 1998 was both aimed and achieved.

The fact that whales appear to find capelin easier to use than krill, herring and gadoids may have several contributory explanations such as mobility, schooling behaviour and possible anti-predator responses. Minke whales usually pursue concentrated prey resources, or they may themselves concentrate the prey by active pursuit and herding (Hoelzel et *al.* 1989). Species specific responses by prey to such predator behaviour is probably important for the prey selection of the latter. Some degree of adaptive diet choice, which may be inferred for minke whales from the observed foraging strategy and selectivity, may have important ecological consequences because it can provide stability in predator-prey systems when other stabilizing mechanisms are absent due to density-dependent mortality which causes preferred prey to decline in abundance (Hassel & May 1974, Murdoch & Oaten 1975).

A potential uncertainty that may have altered the prey selectivity results in this study concerns the estimation of krill biomass. The entire resource survey was probably susceptible to methodological biases due to the mixture of zooplankton and fish and as a result of different fishing efficiencies of the trawl to fish and zooplankton. Although, there was a high degree of subjectivity involved in the estimation of krill biomass, other surveys conducted in the Barents Sea in August-September 1999 yielded similar krill abundance's as observed in this study (ICES 2000).

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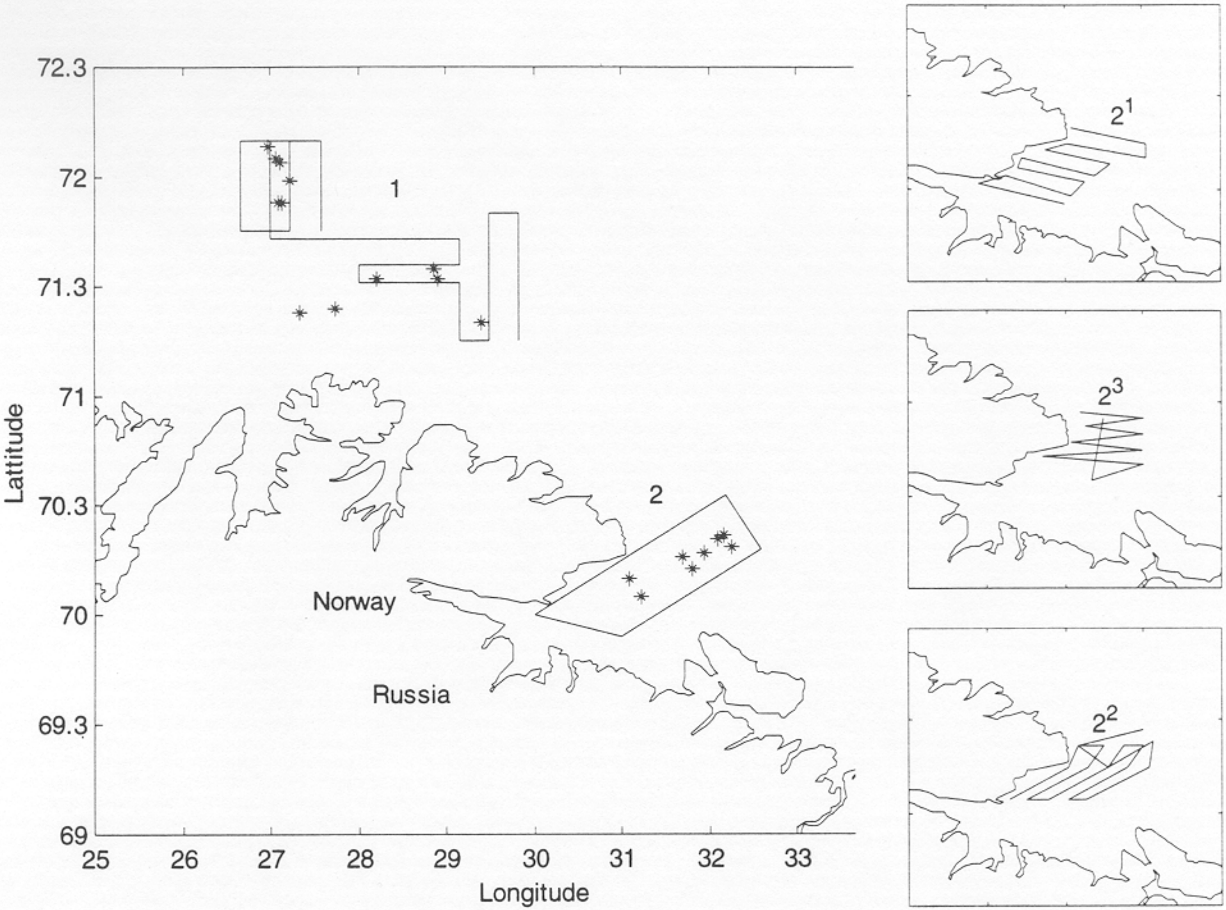

Figure 1. Catch positions for the 23 minke whales (asterisk) sampled in two areas in the southern Barents Sea during the Norwegian traditional whaling in May-June 1999. The track lines for the resource mapping survey are also shown. 2^1, 2^2 and 2^3 is the first, second and third coverage of area 2, respectively.

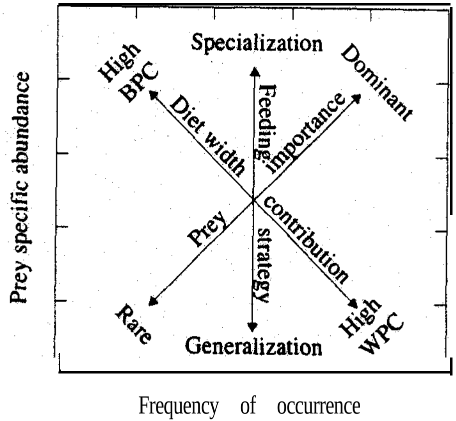

Figure 2. Explanatory diagram for interpretation of feeding strategy, diet width contribution and prey importance from the Amundsen et al. (1996) method. See text for further explanation.

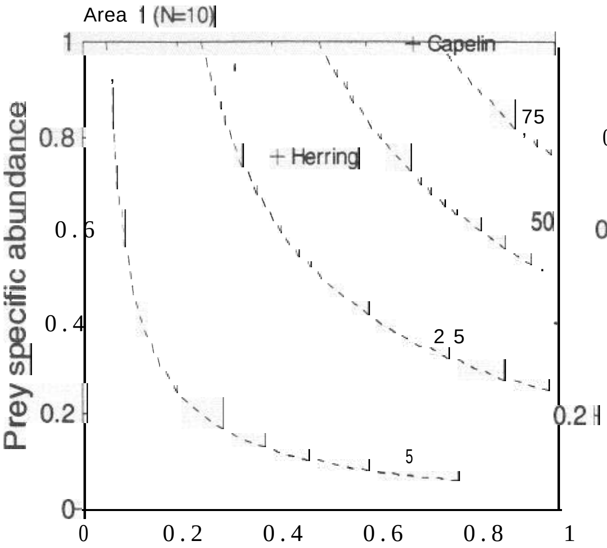

Figure 3. Feeding strategy plots for minke whales in two areas in the southern Barents Sea in May-June 1999. The isolines represents various values of relative prey biomass. N=number of whales included in the analysis.

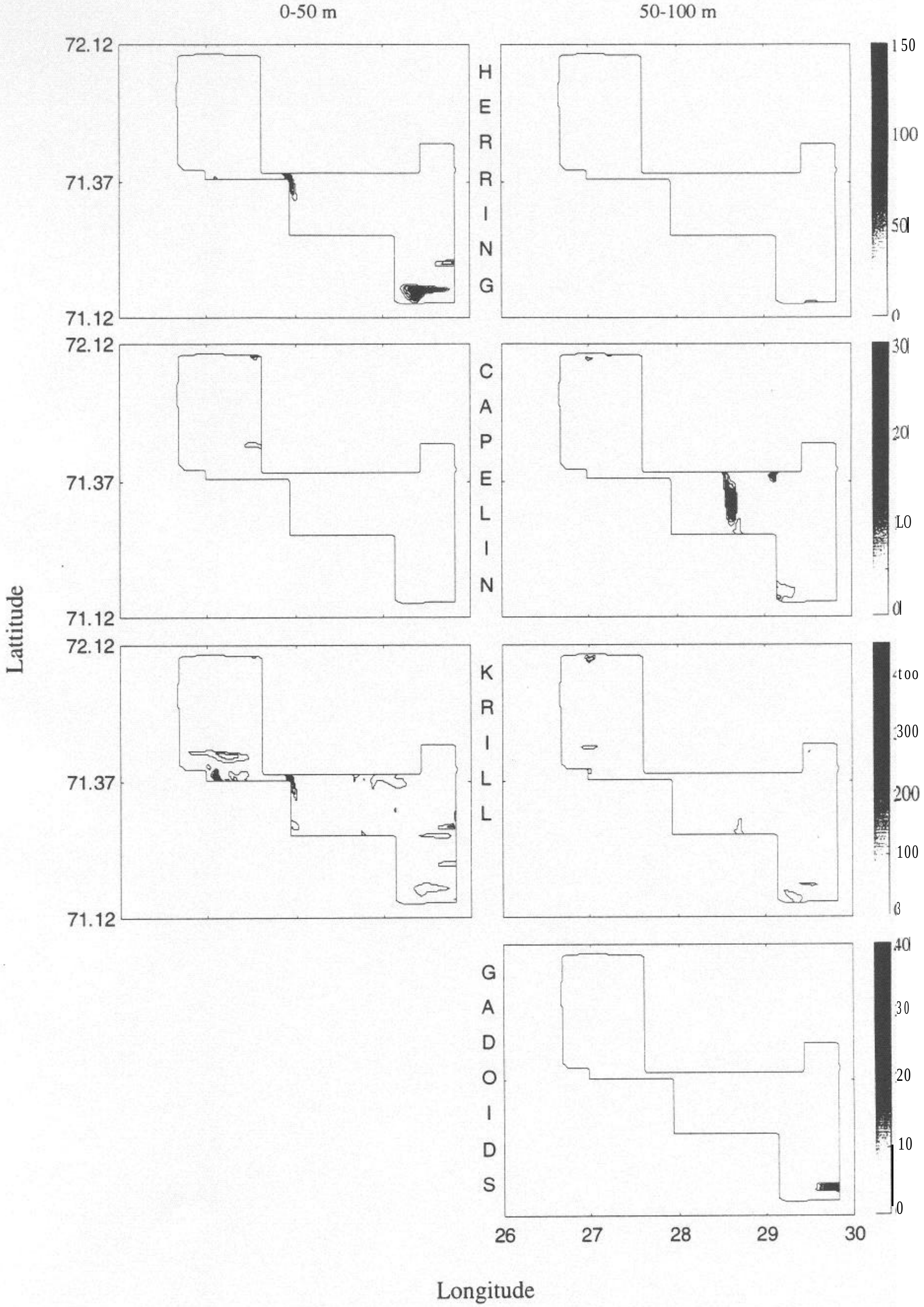

Figure 4. Spatial abundance (in tons) of minke whale prey in two depth layers (0-50 m and 50-100 m) in area 1. The prey abundance data (tons/nm^2) were interpolated by fitting a polynomial cubic function. The gadoid group consists of cod, haddock and saithe.

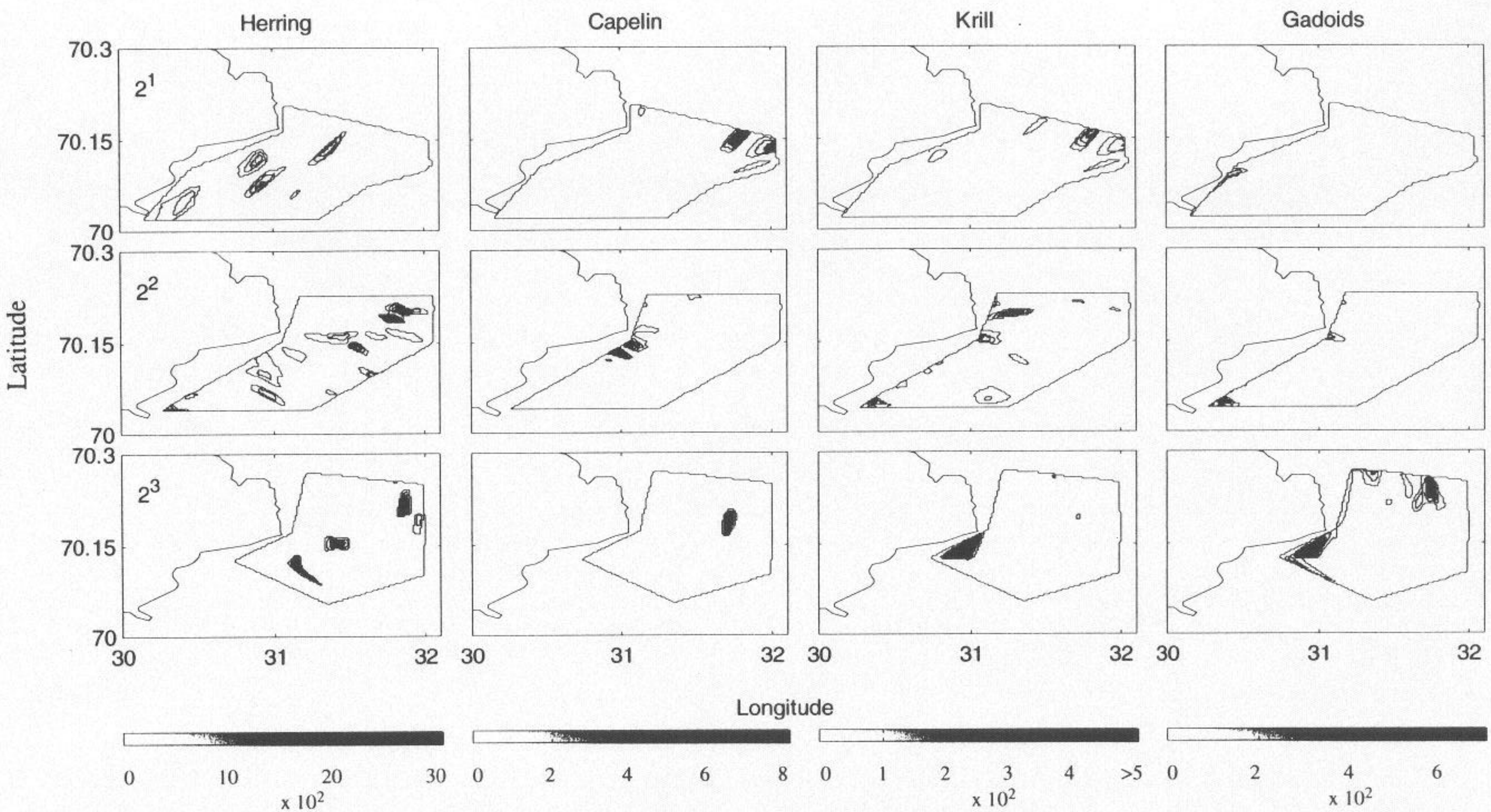

Figure 5a. Spatial abundance (in tons) of minke whale prey in the upper 50 m during three surveys (2^1, 2^2 and 2^3) in area 2. The prey abundance data (tons/nm^2) were interpolated by fitting a polynomial cubic function. The gadoid group consists of cod, haddock and saithe.

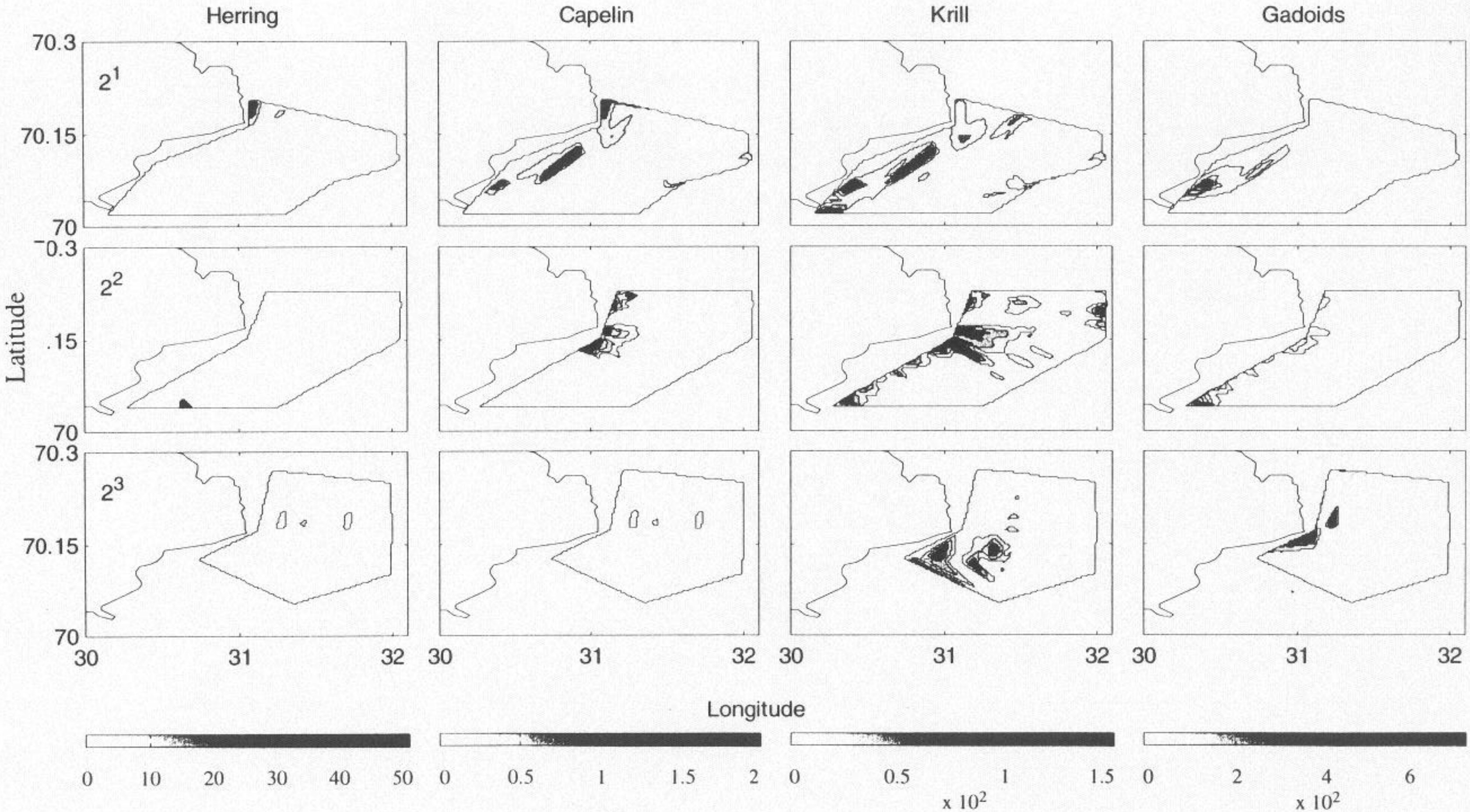

Figure 5b. Spatial abundance (in tons) of minke whale prey in 50-100 m depth during three surveys (2^1, 2^2 and 2^3) in area 2. The prey abundance data (tons/nm^2) were interpolated by fitting a polynomial cubic function. The gadoid group consists of cod, haddock and saithe.

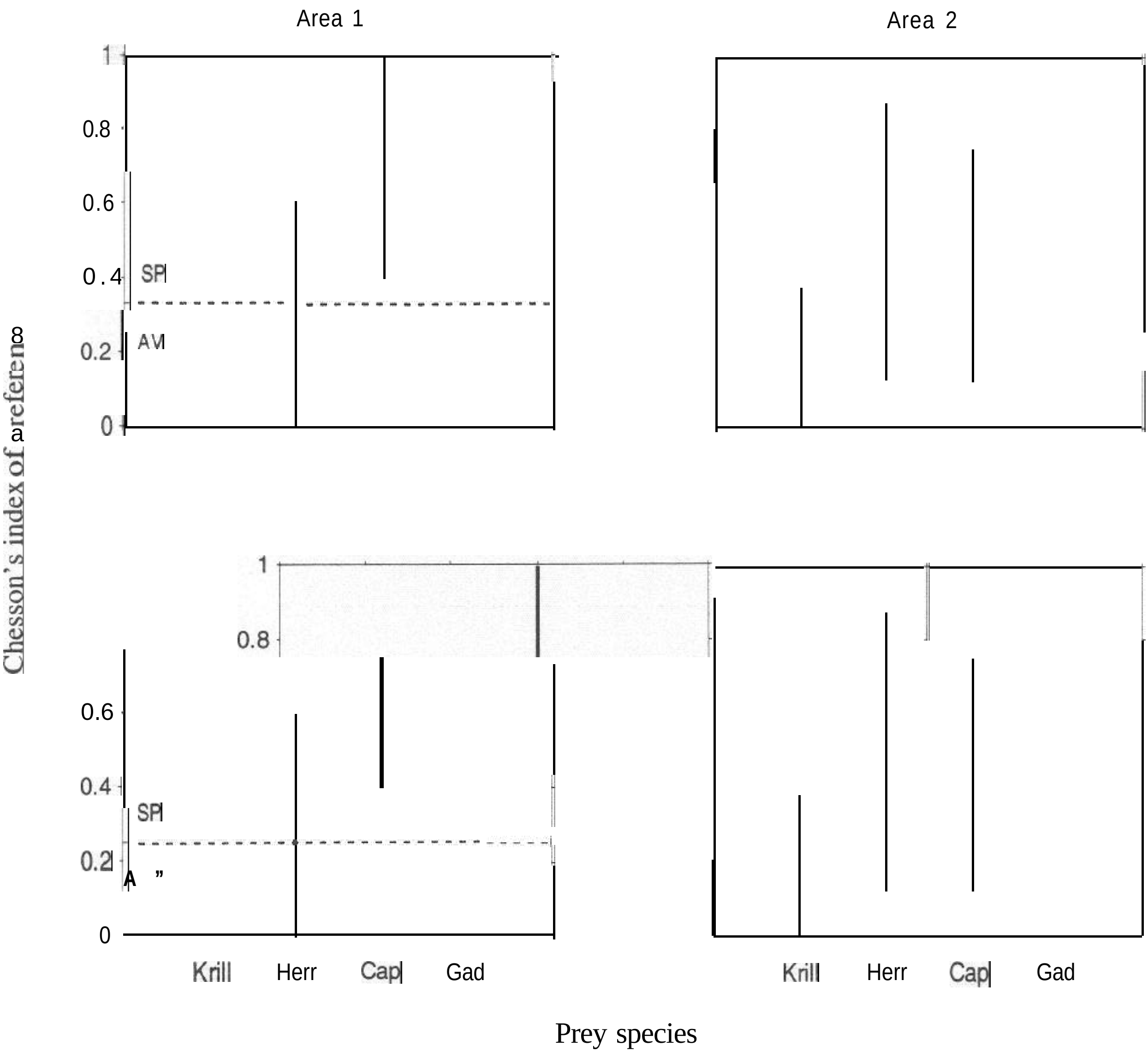

Figure 6. Minke whale feeding selectivity calculated for 4 prey species in two areas in the southern Barents Sea in May-June 1999. Chesson's measure of preference (α_i) with errorbars (95% CI) determined from 5000 bootstrappings of the data are shown for two depth scales, from top to bottom: 0-50 m and 0-100 m. The dotted line indicate the estimate of neutral selectivity $(1/m)$. Selective predation (SP) occur if the error bar is above this line, while avoidance (AV) occur if the error bar is below, and does not overlap, the dotted horizontal line. Random feeding is assumed if the errorbar overlap the line of neutral selectivity.