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Do Minke Whales (*Balaenoptera acutorostrata*) Exhibit Particular Prey Preferences?

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Abstract

By comparing data from analyses of forestomach contents from 44 Northeast Atlantic minke whales (*Balaenoptera acutorostrata)*, caught in scientific whaling operations in coastal areas of North Norway and Russia in July–August 1992, with results from concurrent measurements of prey abundance, performed using trawls and acoustic devices, the following question was addressed: in an idealized situation where all actual prey species are available in equal amounts, do minke whales have a positive or negative preference for any particular species? Three different statistical methods (one qualitative, two quantitative), all relying on assumptions about whale behaviour and prey distribution, were applied to the data. Limitations of the experimental design and the implications for the assumptions of the analyses certainly calls for some caution when interpreting the results. Nevertheless, the presented analyses seems to support a view that minke whales are quite flexible in their choice of food, adapting well to local prey abundance situations with few, if any, strong preferences. Under idealized conditions, however, the whales may be more reluctant to feed upon plankton, mainly krill (*Thysanoessa* sp.), than upon other prey items such as herring (*Clupea harengus*) and capelin (*Mallotus villosus)*. The absence of plankton patches in concentrations suitable for minke whale feeding in the surveyed areas may have contributed to this possible negative preference, even though the resource surveys showed that krill contributed significantly to the total available prey biomass.

Key words: feeding behaviour, minke whales, Northeast Atlantic, prey preference

Introduction

Recent attempts to analyse multispecies interactions and ecosystem functions in Norwegian waters have actualized ecological studies of several top-predators. The minke whale (*Balaenoptera acutorostrata*) is probably the most numerous whale species in the Northeast Atlantic. Its predatory role has therefore been studied quite thoroughly during the period 1992–94, in a scientific whaling program where particular questions concerning the feeding ecology of the species have been adressed (Haug *et al.*, MS 1992; 1995a; 1995b; 1996a).

The minke whale is a boreo-arctic species which, in the North Atlantic, migrates regularly to feeding areas in the far north in spring and early summer, and then returns southwards to breeding areas in the autumn (Jonsgård, 1966). In contrast to the rather stenophagous krill-eating minke whales in the Antarctic (Kawamura, 1980; Bushuev, 1986; Ichii and Kato, 1991), the Northeast Atlantic minke whales are euryphagous, feeding on a variety of prey items including both fish and crustaceans (Jonsgård, 1951; 1982; Nordøy and Blix, 1992; Haug *et al.*, 1995a, 1995b, 1996a).

The 1992–94 minke whale ecology studies have revealed considerable differences in whale diets between geographical subareas in Norwegian waters (Haug *et al.*, 1995a; 1995b; 1996a). Capelin (*Mallotus villosus*) and krill (*Thysanoessa* sp.) dominated in the northmost areas. Further south, in coastal waters of North Norway and Russia, herring (*Clupea harengus*) was the major prey species, accompanied by considerable amounts (numerically as well as in terms of biomass) of sand eels (*Ammodytes* sp.) and gadoid fish species such as cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*) and saithe (*Pollachius virens*).

The minke whale appears to have a flexible feeding pattern and to adapt to local prey availability situations. If, however, all prey species are equally available, do minke whales prefer any particular species? Since parts of the recent ecological studies of minke whale diets were accompanied by concurrent measurements of prey abundance, this paper attempts to answer this question with the application of statistical methods.

Materials and Methods

Sampling of whales

An important goal of the scientific permit catches was to obtain samples representative of each area, with all whales present in an area having 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, behaviour or other attribute (Haug *et al.*, MS 1992). To obtain this randomization, a sampling procedure of searching for whales along predetermined transect lines, laid out randomly in each area, was used. In addition, when a whale was observed during the search, an all-out attempt was made to catch that particular whale. The transects were designed in saw-tooth patterns, mainly according to the principles used during the previous shipboard North Atlantic Sightings Surveys (NASS-89, see e.g. Øien, 1991). 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, taking into account factors such as ice-cover, weather conditions and observations of minke whale abundances.

Chartered whaling vessels, fitted for whaling operations with crew and equipment as outlined by Christensen and Øien (1990) and in agreement with new regulations enforced by the Directorate of Fisheries in Norway, 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, 1995). Dead whales were immediately taken aboard the vessel for dissection and biological sampling. Stomach content data used in our analyses were obtained from 44 of a total of 56 animals caught in three subareas on the coast of Norway (Lofoten/ Vesterålen and Finnmark) and Russia (Kola) in July and August 1992 (Fig. 1).

Analyses of minke whale stomachs

The complete digestive tract was taken out of the whale as soon as possible (1–3 hours *post mortem*). A minke whale stomach consists of a series of four chambers (Olsen *et al.*, 1994), and pilot studies performed during the scientific whaling in 1988–90 suggested that sampling from the first chamber (the forestomach) would give sufficient data to evaluate the diet of the animals (Nordøy and Blix, 1992). Therefore, only contents from this stomach chamber were used in the present analyses. The onboard and laboratory treatment of the forestomach contents were as described in detail by Haug *et al.* (1995a).

From the contents, fish otoliths were collected and identified to the lowest possible taxon (Breiby, 1985; Härkönen, 1986). The total number of each fish species was determined by adding the number of fresh specimens, the number of intact sculls and half the number of free otoliths. Random subsamples (200 or as many as possible) of otoliths were measured, and otolith length – fish length/weight correlations were used to estimate 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 and 0-group gadoids the correlation equations were calculated on the basis of material obtained in the present resource survey trawlings. All other correlations were taken from Härkönen (1986). Erosion of otoliths, which is a problem in studies of seal stomachs (Pierce and Boyle, 1991), was not considered a problem in these minke whale diet studies, as the analyses were restricted to the contents in the forestomach where digestive glands are completely absent and no gastric acids are produced (Olsen *et al.*,1994).

For crustaceans, subsamples were weighed and analysed with respect to species composition. Total weight and the number of individuals were recorded for each species in the subsample, and this was used

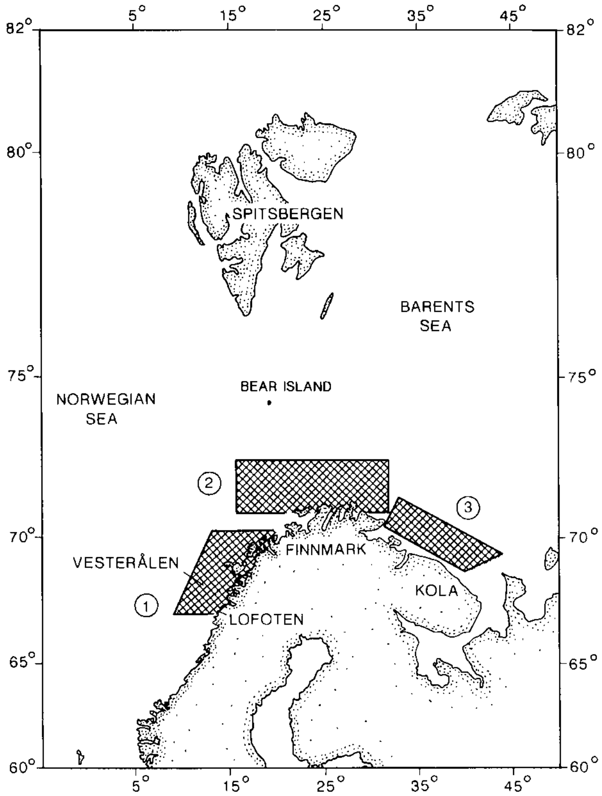

Fig. 1. Map showing the sampling areas in Lofoten/Vesterålen (1), Finnmark (2) and Kola (3).

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 whaling vessel operating in the waters around Bear Island during the scientific whaling period, see Haug *et al.*, 1995a) were used to obtain crude estimates of the original biomass of the crustaceans eaten by the minke whales.

Several feeding indices are commonly used in stomach analyses of top predators (Hyslop, 1980; Pierce and Boyle, 1991). In this presentation, only the relative contribution of each prey species to the total diet expressed in terms of calculated fresh weight, was used. The stomach contents from the 3 areas in question were originally divided into 14 species/taxa (Haug *et al.*, 1995a). Based on their dietary importance and in order to simplify the statistical exercises, these species/taxa were combined into 7 new categories: plankton (almost exclusively krill and a few other crustaceans), 0-group (fish, mainly herring and to a minor extent some gadoids), herring, capelin, cod+haddock, pelagic (sand eels and saithe) and bottom (various demersal fish species). This selection of prey grouping is assumed not to constrain the effectiveness of the current experimental design.

Estimation of prey abundance

The marine resources in the three sampling subareas were surveyed using the research vessel *Johan Ruud* during the period 11–20 July 1992. The R/V *Johan Ruud* carried out an acoustic survey using standard methods (Foote, MS 1991), where a Simrad EK 500 scientific echo sounder (Bodholt *et al.*, 1989) and a BEI post-processing system (Foote *et al.*, 1991) were used. A minimum acoustic threshold of -88 dB SV was applied to measure acoustically the abundance of larger zooplankton. The partitioning of the acoustic data and allocation of these to species were carried out on the basis of the acoustic character of each species and the results of trawl surveys. Both pelagic and demersal trawls were used to sample the observed scatters.

The standard echo integration method, described in detail by MacLennan and Simmonds (1992), was used to estimate the relative abundance of the most common prey species in the sampling areas. The acoustic parameter measured by the echo integrator is the area backscattering coefficient S_A:

$$S_A = 4\pi (1852)^2 \int_{z_1}^{z_2} S_v d_z$$

which is the integral of the volume backscattering coefficient, S_v, within the depth layer z_1 to z_2, normalized to square nautical miles, with unit m^2/nm^2. When the echo sounder and integrator are calibrated, as here, using standard targets (see Foote *et al.*, 1987), S_A is an absolute, acoustic linear unit, proportional to fish (and plankton) area density. The proportionality factor $\bar{\sigma}$ (mean echo ability) is:

$$\bar{\sigma} = 4\pi \times 10^{0.1 \times \overline{TS}}$$

where $\overline{TS}$ is the mean target strength of the scattering organisms. The target strength (and therefore σ) varies between species, and will also vary with body length in fish species according to the relation:

$$TS = A + B \log L$$

where L is fish length (in cm) and A and B are species-specific constants. All A and B values (except those for capelin) were taken from MacLennan and Simmonds (1992). The capelin values used (A = -74, B = 19.1) were developed at the Institute of Marine Research, Bergen, Norway (Nakken and Dommasnes, 1977).

Consequently, the length composition of each of the fish scatterers were used to convert from S_A to fish density in number per unit volume. To calculate biomass, the mean weights of each fish species were used. For plankton organisms the target strength is normally considered directly related to biomass, and density may be calculated directly from the S_A-values when the TS/biomass relation is known. The calculated biomass per square nautical mile and 50 m depth channel was averaged over 5 square nautical miles, and distributed on the following groups of targets: 0-group fish, plankton, cod + haddock, herring, capelin, other pelagic fish, and other demersal fish.

Bad weather hampered the resource surveys and resulted in a less than perfect coverage in some of the areas. The results should, however, give reliable information on the typical distribution and density of species.

Statistical methods

Three different statistical methods for making inferences about the feeding preferences of the whales are presented. All three methods rely on strong, sometimes different, assumptions about the behaviour of the whales and the distribution of the prey resources. The considerations leading to these assumptions are subjective, and it is not claimed that the assumptions are satisfied exactly. That the models may be based on different, and sometimes contradictory, assumptions should not confuse the analysis, but rather shed light upon the problem from different angles.

Notations

Consider k different prey species or prey groups $A_1, ..., A_k$ as potential feed for minke whales, and let $d_1, ..., d_k$ be the corresponding prey densities close to a randomly chosen whale. As proposed in Haug *et al*. (MS 1992) the preference for the different groups can be measured by the feeding probabilities:

$$\Pr(A_i \text{ is chosen} \mid d_1, ..., d_k),\ i = 1, ..., k \qquad (1)$$

If data from n whale stomachs is available, accompanied by concurrent measurements of $d_1, ..., d_k$, these probabilities can be estimated by regression methods. However, when prey densities are not known locally, but only on an aggregated level, other measures of preference must be considered.

We will compare the preferences for only two prey species or prey groups at the time. However, by considering all such pairs of species/groups it is assumed that we can get a relatively consistent picture of the total preference pattern of the whale. For simplicity denote the two prey groups by A_1 and A_2, and let y_1 and y_2 be the total amount of A_1 and A_2 in the sea area of sampling. The relative amount of A_1 is defined as

$$s = \frac{y_1}{y_1 + y_2} \qquad (2)$$

Assumptions

The statistical methods were based on the following assumptions:

i) s is known exactly,

ii) s is constant throughout the period of sampling,

iii) The contents of the different whale stomachs might be considered as statistically independent, given s.

The semi-randomized sampling scheme for catching of whales ensures that iii) is satisfied. The validity of i) and ii) must be discussed for each particular data set. The sensitivity of the results with respect to a failure of i) and ii) is investigated below in the section "Robustified method".

Method 1

This is a qualitative method, aimed to compare prey fractions in minke whale stomachs to prey fractions in the ocean. Formally we want to test the hypothesis

H: There is no prey preference

versus the two alternatives: A_1 is preferred more than A_2, and *vice versa*. A simple binomial test for the hypothesis H is constructed. The idea is that if the whale systematically seeks A_1, the relative amount of A_1 in the stomach is likely to be larger than s. For an arbitrary whale let X_1 and X_2 be the absolute amount of A_1 and A_2, respectively, contained in the whale's stomach, and define

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

as the fraction of A_1 relative to A_2. The binomial test is then obtained from the frequency of whales with $Q > s$ among those with either A_1 or A_2 (or both) in the stomach. To calculate the *p*-value, the success probability

$$q = \Pr(Q > s)$$

is needed. To calculate q we assume that Q follows a beta distribution (Bickel and Doksum, 1977) with parameters $\alpha_1 = cs$ and $\alpha_2 = c(1-s)$ when H is true. The parameter $c>0$ characterizes the degree of dispersion in Q. The beta distribution is often used for compositional data (Aitchison, 1986). An arbitrary beta distributed random variable Z, with parameters α_1 and α_2, has expectation and variance:

$$E(Z) = \frac{\alpha_1}{\alpha_1 + \alpha_2} \text{ and } Var(Z) = \frac{\alpha_1 \alpha_2}{(\alpha_1 + \alpha_2)^2 (\alpha_1 + \alpha_2 + 1)},$$

respectively.

Thus $E(Q) = s$ and $Var(Q)=s(1-s)/(1+c)$ under H.

The unknown parameter c, which is assumed to be common for all pairs of species (A_1, A_2), must be estimated from data. The estimate is found by minimizing, with respect to c, the sum of

$$\left\{ V\hat{a}r\,(Q) - \frac{s\,(1-s)}{1+c} \right\}^2$$

over all pairs of species and all areas, where $V\hat{a}r\,(Q)$ is the empirical variance of Q.

Method 2

This quantitative method aims to compare prey fractions in the ocean with dominant prey in the whale stomachs. The preferences for two species A_1 and A_2 are compared. The preference for A_1 is represented by a preference parameter $\gamma \in [0,1]$. The values $\gamma > 0.5$, $\gamma = 0.5$ and $\gamma < 0.5$ correspond to a positive preference for A_1, no preference for either A_1 or A_2, and negative preference for A_1, respectively. In addition to *assumptions* i–iii) above we need the following assumption:

iv) The contents of the whale stomach consist entirely of one prey type.

Some stomachs, however, have mixed content (Haug *et al.*, 1996b), and they are classified according to which prey species dominates. When comparing A_1 to A_2, stomachs with other dominating content are disregarded.

Further, we assume that the process in which the whale chooses its prey consists of the following two steps:

1) *Large-scale choice*: The whale seeks out areas in which there is a high density of preferred prey.

2) *Small-scale choice*: Faced with a choice among available prey items while feeding, the whale preys on the most abundant item in the neighbourhood, irrespective of which other species might be present.

Thus, *Method 2* assumes that the minke whale is short-range oportunistic in feeding, but with prey preferences directing its whereabouts.

Consider the area in step 2), and let

$$R = \frac{\text{amount of } A_1}{\text{amount of } A_1 + A_2}$$

and assume that the local amounts of A_1 and A_2 are statistically independent and exponentially distributed (Bickel and Doksum, 1977) with expectations proportional to $\gamma \cdot s$ and $(1-\gamma)(1-s)$, respectively. The factor of proportionality is assumed to be the same for both A_1 and A_2, and thus cancels out in R. Prey abundance has skewed and long-tailed distribution, so the exponential distribution might not be too unrealistic. With this choice, it can be shown that:

$$(A_1 \text{is chosen}) = \left\{ 1 + \frac{(1-\gamma)(1-s)}{\gamma \cdot s} \right\}^{-1} \qquad (3)$$

Let

$$Z = \frac{\text{number of whales which have chosen } A_1}{n}$$

be the fraction of whales with A_1 in the stomach amongst the n whales that have chosen either A_1 or A_2. The moment estimator of γ is found by equating Z and the probability (3), and then solving for γ. This yields the estimator:

$$\hat{\gamma} = \frac{(1-s)\,Z}{(1-s)\,Z + s\,(1-Z)} \qquad (4)$$

The hypothesis $H: \gamma = 0.5$ can be tested using $\hat{\gamma}$ as a test statistic, with values of $\hat{\gamma}$ larger than 0.5 indicating preference for A_1. The *p*-value can be calculated using the fact that $n \cdot Z$ has a binomial distribution with parameters n and s.

Method 3

This method is quantitative, and aims to compare prey fractions in minke whale stomachs with prey fractions in the ocean, and allows each stomach to contain different types of prey. The preference for a single species *A* is compared to the preference for what might be called the remaining species. The remaining species consists of all species except for *A*. Again $\gamma \in [0, 1]$ is the preference parameter, but now γ must be interpreted relative to the available prey composition. Still $\gamma > 0.5$, $\gamma = 0.5$ and $\gamma < 0.5$ have the interpretation as positive preference for *A*, neutrality to a choice between *A* and the remaining species, and negative preference for *A*, respectively.

It is assumed that the contents of the whale stomach were the remains of the latest two meals before capture, and that each meal consisted of one type of prey only (possibly different for the two meals), and let $X \in \{0,1,2\}$ be the number of meals which consisted of *A*. In practice *X* is determined according to the following rule:

$$\begin{aligned} X = 0 &\text{ if the stomach contains less than 10\% of } A, \\ X = 1 &\text{ if the stomach contains between 10\% and 90\% of } A, \\ X = 2 &\text{ if the stomach contains more than 90\% of } A. \end{aligned} \tag{5}$$

As in *Method 2* let *s* and *R* be respectively the global and local relative amount of *A*, but now relative is with respect to the total prey resources, not to a single prey species. Still the choice of prey is thought of as being divided into a large- and a small-scale choice. In the small-scale choice it is assumed that the whale chooses *A* with probability *R*. Then the distribution of *X* conditional on *R* is binomial with $n = 2$,

$$\Pr\{X = x \mid R = r\} = \frac{2}{x!\,(2-x)!}\, r^x (1-r)^{2-x}, \quad x = 0, 1, 2$$

It is assumed further that *R* has a beta distribution with parameters:

$$a_1(\gamma) = \frac{\varepsilon(\gamma)\, s}{\varepsilon(\gamma)\, s + (1-s)} \text{ and } \alpha_2(\gamma) = 1 - \alpha_1(\gamma)$$

where $\varepsilon(\gamma) = \gamma/(1-\gamma)$. Some motivation for this choice of parameters is needed. Most importantly

$$E(R) = \alpha_1(\gamma) = \begin{cases} 0, & \gamma = 0 \\ s, & \gamma = 0.5 \\ 1, & \gamma = 1 \end{cases}$$

which is necessary for the model to make sense. The more general parameterization $c \cdot \alpha_1$ and $c \cdot \alpha_2$, where $c > 0$ is a constant and α_1 and α_2 are given as above, also has this property, i.e. *c* only influences the variance of *R*, not its expectation. Since *R* is unobserved, *c* cannot be estimated from data, and $c = 1$ has been subjectively chosen. It can be argued that c should be a small number since the resulting beta distribution then puts most of its mass on the extreme values ($R = 0$ and $R = 1$), which is what is expected in real life. Further, since $\alpha_1 + \alpha_2 = 1$, it follows that $Var(R) \to \alpha_1 \alpha_2 = 1$ as $c \to 0$, so the model does not depend critically on *c* when *c* becomes small.

The beta-binomial likelihood of a whale with *x* of its two last meals being of type *A*, is

$$L(\gamma \mid x) \propto \frac{\Gamma\{\alpha_1(\gamma) + x\}\, \Gamma\{\alpha_2(\gamma) + 2 - x\}}{\Gamma\{\alpha_1(\gamma)\}\, \Gamma\{\alpha_2(\gamma)\}}$$

where Γ is the gamma function (Bickel and Doksum, 1977). Let $x_1, ..., x_n$ be data from *n* whales. The maximum likelihood estimate $\hat{\gamma}$ of γ is found by maximizing

$$\sum_{i=1}^{n} \log L(\gamma \mid x_i)$$

with respect to γ. The maximization has to be done numerically.

The *p*-value for test of $\gamma = 0.5$ is

$$p - \text{value} = Pr\{|\hat{\gamma} - 0.5| > |\hat{\gamma}_{obs} - 0.5|\}$$

which can be found by Monte Carlo methods.

Robustified method

The statistical methods presented so far are based on *assumptions* i) and ii). In practice only a crude estimate of *s* is available, and the true value of *s* will vary over time. If this fact is not taken into account the calculated *p*-values can be erroneous. To illustrate how to improve the analysis, *Method 1* is used as an example.

In an attempt to make the model more robust we regard the quantities *s*, y_1 and y_2 appearing in Equation (2) as random, and to emphasize this they are denoted by capital letters *S*, Y_1 and Y_2. With this viewpoint the *p*-value in *Method 1* can be considered as a conditional *p*-value, given the value of *S*. Expectation with respect to *S* is then obtained by Monte Carlo simulation.

The above approach is a reasonable way to make the model robust against failure of *assumption* i), but is not as well suited for failure of *assumption* ii). However, modelling a realistic development of S over time based on the available data is very difficult, and this approach is not tried here.

The important question is how to model the distributions of Y_1 and Y_2, and thereby the distribution of S. We have chosen to do this by letting Y_1 and Y_2 be independent and gamma distributed (Bickel and Doksum, 1977) with parameters determined by the requirements:

$$E(Y_1) = \hat{y}_1 \text{ and } E(Y_2) = \hat{y}_2$$

and that

$$cv(Y_1) = cv(Y_2) = 0.4$$

Here $\hat{y}_1$ and $\hat{y}_2$ are the prey abundance estimates based on the resource survey, and $cv(Y_i)$ is the coefficient of variation of Y_i, defined as $cv(Y_i) = SD(Y_i) / E(Y_i)$, where $SD(Y_i)$ is the standard deviation of Y_i. The requirement $cv = 0.4$ results from considerations about the design of the resource survey. It is in general very difficult to quantify the uncertainty of the prey abundance estimates $\hat{y}_1$ and $\hat{y}_2$, but 0.4 was chosen as a presumably realistic upper bound on $cv(Y_i)$.

Results

Applicability of material

Prey abundance estimates are given in Table 1. As commented by Haug *et al*. (1995a) the abundance of several species may have been underestimated. Thus, only the species which occurred in "considerable amounts" were compared in the analyses. As a selection criterion $s \geq 0.1$ was used. One exception from this rule was that capelin in Finnmark was included, even though it had $s = 0.08$, due to the general interest to include capelin in the analysis, and since the limit $s = 0.1$ was chosen arbitrarily. These considerations yielded three sets of comparable species for the three areas in question (Table 2).

Tables 3–5 show the stomach contents for each whale taken in the three areas in 1992. One question is whether assumption ii) can be believed to hold for these data sets. A striking feature of the Finnmark area (Table 3) was that 0-group fish were almost absent in the first part of the whaling period when the resource survey was conducted (14–18 July), but then dominated the last part of the period. This indicated that the resource situation may have changed during the period of whaling. However, it was decided to use all the 19 observations from Finnmark, since an omission of observations would have to be done in a very *ad hoc* manner. For the Kola area, prey abundance estimates were only available west of 38°E. Thus, only whales 1–5 and 16–17 in Table 4 could be used in the analysis. In Lofoten-Vesterålen there are strong reasons to believe that the resource situation changed drastically from the first part of the whaling period, when the resource survey was performed (11–14 July), to the second part of the period. While herring was absent in the resource data, it dominated the stomach contents in the last part of the whaling period. However, since herring was not among the species to compare in Lofoten-Vesterålen, all the 18 observations were used in the analyses.

Statistical analyses

Method 1

The hypothesis is that the whale is neutral to a choice between A_1 and A_2. The alternative hypothesis is that the whale prefers A_1. The estimate of the dispersion parameter $\hat{c}$ is = 0.53. Table 6 gives the p-values obtained from comparisons of each pair of species within each of the three areas. For instance, the first row in Table 6 contains the p-values when A_1 is pelagic fish and A_2 herring, 0-group fish, capelin and plankton, respectively. All p-values with $A_2 = \{\text{plankton}\}$ are significant at the 0.05 level. Thus, there was some evidence that the whales may reject plankton in preference for other prey items. Further two p-values are significant in Finnmark: First $A_1 = \{\text{0-group fish}\}$ *versus* $A_2 = \{\text{pelagic fish}\}$, and second $A_1 = \{\text{herring}\}$ *versus* $A_2 = \{\text{pelagic fish}\}$.

Method 2

Table 7 shows the number of whales in which each prey item was dominant. Combined with Table 1, the A_1 preference parameter γ can be estimated when locality was taken as the sampling areas displayed in Fig. 1. The estimates (4) of γ for all pairs of species are given in Table 8. Note that all comparisons of 0-group fish with other prey items in Finnmark yielded $\hat{\gamma}$-values greater than 0.5. While this suggested that the whale prefers 0-group fish more than the other species, only two significant p-values were found: $A_1 = \{\text{0-group fish}\}$

TABLE 1. Estimates of prey abundance (in tons per sq. naut. mile) obtained in resource surveys in Lofoten-Vesterålen 11–14 July 1992, Finnmark 14–18 July 1992 and Kola 18–20 July 1992. The prey groups Bottom and Pelagic include, respectively, demersal and pelagic fish species other than those already listed.

	Prey Abundance						
Area	Plankton	Herring	Capelin	0-group	Cod + haddock	Bottom	Pelagic
Finnmark	21.4	16	5.5	10	0.5	2	12
Kola	18.8	26	1	0.6	0.4	1	9
Lofoten-Vesterålen	19.4	0	0	53	9	9	30

TABLE 2. Selected taxa (i.e., with relative abundance, $s \geq 0.1$, see text for further explanation) which can be compared in the three areas.

Finnmark	Kola	Lofoten-Vesterålen
Plankton	Plankton	Plankton
0-group		0-group
Pelagic	Pelagic	Pelagic
Herring	Herring	
Capelin		

versus A_2 = {pelagic fish}, and A_1 ={0-group fish} *versus* A_2 = {plankton}. Note that no clear negative preference for plankton was found using this model.

Method 3

Table 9 shows the number of meals which consisted of each prey type calculated according to the rule given in (5). Using this table and Table 1, the parameter γ can be estimated for the different species and areas (Table 10). Small values of $\hat{\gamma}$ were found in all three areas for plankton, but only the *p*-values for Kola and Lofoten-Vesterålen were significant. There were some indications of preference for 0-group fish in Finnmark ($\hat{\gamma}$ = 0.82), though the *p*-value was not significant. In the Monte Carlo evaluation of the *p*-values 200 simulations were used.

Robustified method 1

The robustification was introduced to take account for the uncertainty in the prey abundance estimates. Robustified *p*-values were calculated for *Method 1* using 200 Monte Carlo simulations and are given in Table 11. All *p*-values for which A_2 = {plankton} were significant. No other of the *p*-values which showed significance in *Model 1* (Table 6) were now significant. Thus, using robustified methods the only thing that could be claimed is that the whales dislike plankton.

Discussion

During the 1992–94 minke whale ecology studies, substantial heterogeneity in whale diets was observed between geographical areas in Norwegian waters, capelin/krill being the dominant prey items in the northernmost Arctic areas while herring was the most abundant prey found in the whale stomachs in the southernmost coastal areas (Haug *et al.*, 1995a; 1995b; 1996a). These differences seem to be consistent with the differences in prey availability in these areas: While the capelin stock is mainly confined to the central and northern parts of the Barents Sea (Dragesund *et al.*, 1973), the dominant planktivorous fish along the Norwegian coast and in the southern Barents Sea is the Norwegian spring spawning herring (Røttingen, 1990; Anon., MS 1994). From 1992 to 1993, a shift from capelin to krill as the dominant prey item for the minke whales was concurrent with an increase in krill and a severe decrease in capelin availability in the northern areas (Haug *et al.*, 1995b).

The presented results from 1992 reveal that both the total biomass and the species composition of available prey was very different in the three subareas investigated along the coast of North Norway (Lofoten/Vesterålen and Finnmark) and Russia (Kola). It is evident that the largest potential prey biomass was recorded in the Lofoten/Vesterålen area. 0-group fish (mainly herring) contributed particularly to this large biomass, and occurred along a gradient of decreasing abundance from west to east (Lofoten/Vesterålen, via Finnmark to Kola). A similar west-to-east abundance variation in 0-group herring was found in the minke whale stomachs from these areas (Haug *et al.*, 1995a).

TABLE 3. Date, position and stomach contents (kg) distributed between the different prey groups in 19 minke whales taken off the coast of Finnmark in 1992. See also Table 1.

Whale No.	Date	Position N	Position E	0-group	Capelin	Cod+ Haddock	Pelagic	Herring	Plankton	Bottom
1	12.07	77.21	24.00	0.00	12.11	0.00	0.00	0.03	0.00	0.00
2	15.07	71.53	16.41	0.00	0.00	0.00	0.00	0.11	0.00	0.00
3	18.07	71.11	27.54	1.08	0.00	1.45	1.26	0.00	0.00	0.00
4	19.07	71.27	29.54	0.00	10.34	7.75	12.06	219.84	0.00	0.00
5	20.07	71.28	27.45	0.00	0.02	0.00	0.03	0.45	0.00	0.00
6	21.07	71.28	28.26	0.00	0.01	0.00	0.02	119.16	0.00	0.00
7	22.07	71.45	31.19	0.00	0.77	0.00	0.00	0.38	0.00	0.00
8	25.07	71.25	27.42	0.05	0.00	0.00	0.00	0.04	0.00	0.00
9	26.07	71.25	27.51	23.79	0.23	43.16	0.01	34.20	0.00	0.21
10	27.07	71.24	25.14	18.02	0.88	51.46	0.01	3.82	0.00	0.04
11	27.07	71.25	24.56	18.34	0.00	0.00	0.01	0.52	0.00	0.00
12	28.07	71.16	25.02	6.88	0.00	0.00	0.01	0.00	0.00	0.00
13	03.08	71.18	25.10	38.56	0.01	1.41	0.00	0.07	0.00	0.00
14	03.08	71.20	25.22	12.82	0.00	0.00	0.00	0.01	0.00	0.00
15	08.08	71.25	27.28	0.00	0.00	0.00	0.00	3.09	0.00	0.00
16	13.08	70.49	21.34	27.70	0.00	0.00	1.48	0.00	0.00	0.00
17	13.08	71.06	21.53	50.26	0.00	0.00	0.00	0.00	3.29	0.00
18	13.08	71.10	21.18	0.88	0.00	0.00	0.00	0.00	3.28	0.00
19	13.08	70.52	21.19	0.00	0.00	0.00	0.02	0.42	2.93	0.01

TABLE 4. Date, position and stomach contents (kg) distributed between the different prey groups in 19 minke whales taken off the coast of Kola in 1992. See also Table 1.

Whale No.	Date	Position N	Position E	0-group	Capelin	Cod + Haddock	Pelagic	Herring	Plankton	Bottom
1	10.07	70.59	32.53	0	0.00	0.00	0.00	0.42	0.00	0.00
2	15.07	70.32	32.33	0	0.04	0.02	0.11	123.20	0.00	0.00
3	15.07	70.41	32.45	0	0.00	0.00	0.02	6.52	0.00	0.00
4	16.07	70.52	32.44	0	1.98	0.00	1.36	87.08	0.00	0.00
5	26.07	69.41	38.20	0	0.00	4.93	3.14	0.02	0.00	0.01
6	27.07	69.08	39.12	0	0.00	0.00	43.85	0.01	0.00	0.00
7	29.07	69.24	41.16	0	0.00	3.98	43.89	0.01	0.00	0.01
8	30.07	69.28	41.37	0	0.00	0.00	3.01	0.01	5.12	0.00
9	30.07	69.44	41.17	0	0.00	90.72	4.01	0.04	0.00	0.04
10	30.07	69.35	41.08	0	0.00	10.07	7.87	0.01	0.00	0.02
11	30.07	69.34	41.07	0	0.02	36.06	8.11	0.94	12.08	0.09
12	01.08	69.25	41.19	0	0.00	0.00	21.98	0.00	0.00	0.00
13	02.08	69.26	40.46	0	0.00	16.67	5.43	0.18	0.00	0.02
14	02.08	69.25	40.46	0	0.00	18.56	28.38	0.46	0.00	0.04
15	03.08	69.20	39.18	0	0.00	23.10	9.06	0.05	0.00	0.02
16	04.08	69.48	34.48	0	0.01	88.80	0.03	2.54	0.00	0.03
17	04.08	69.48	34.49	0	0.00	4.45	0.00	1.60	0.00	0.00
18	02.08	69.19	40.33	0	0.00	0.00	23.44	0.02	0.00	0.00
19	01.08	69.30	41.19	0	0.00	1.65	1.07	0.00	0.00	0.03

TABLE 5. Date, position and stomach contents (kg) distributed between the different prey groups in 18 minke whales taken in Lofoten-Vesterålen in 1992. See also Table 1.

Whale No.	Date	Position N	Position E	0-group	Capelin	Cod + Haddock	Pelagic	Herring	Plankton	Bottom
1	05.07	67.54	13.49	0.02	0.00	0.00	2.58	0.00	0	0.04
2	06.07	67.20	12.09	0.37	0.00	0.00	0.37	0.00	0	0.00
3	12.07	67.11	11.51	0.45	0.00	0.00	2.91	0.00	0	0.00
4	12.07	67.14	11.42	2.86	0.00	0.00	0.58	0.00	0	0.00
5	21.07	68.02	13.51	15.82	0.01	0.02	15.44	0.00	0	0.10
6	21.07	68.00	13.40	22.42	0.00	0.00	0.24	0.00	0	0.00
7	24.07	67.52	12.58	53.97	0.00	0.26	7.41	0.00	0	0.62
8	26.07	67.54	12.11	7.30	0.00	0.33	2.51	6.21	0	0.00
9	27.07	67.16	12.58	12.77	0.00	0.00	0.00	0.00	0	0.00
10	31.07	69.26	16.01	0.00	0.00	0.00	28.60	0.00	0	0.00
11	03.08	69.24	15.38	0.03	0.00	0.00	0.13	20.08	0	0.00
12	03.08	69.24	15.41	9.19	0.01	0.00	0.00	21.00	0	0.00
13	03.08	69.21	15.29	1.81	0.00	0.00	0.00	8.14	0	0.00
14	03.08	69.21	15.24	22.86	0.00	0.00	0.00	12.24	0	0.00
15	06.08	69.17	15.20	0.24	0.00	0.00	0.00	0.00	0	0.00
16	06.08	67.51	11.44	0.00	0.00	0.00	0.00	23.20	0	0.00
17	10.08	67.53	12.14	0.08	0.00	0.00	1.81	5.95	0	0.00
18	12.08	67.52	12.59	0.00	0.00	0.00	0.22	0.00	0	0.01

TABLE 6. Comparison of whale stomach contents and prey abundances using *Method 1*: *p*-values obtained from comparison of pairs (A_1/A_2) of prey alternatives.

A_1	A_2: Pelagic	Herring	0-group	Capelin	Plankton
Finnmark					
Pelagic		0.99	0.99	0.90	0.01
Herring	0.04		0.95	0.11	0.00
0-group	0.04	0.12		0.33	0.00
Capelin	0.23	0.97	0.84		0.00
Plankton	1.00	1.00	1.00	1.00	
Kola					
Pelagic		0.94			0.01
Herring	0.27				0.02
Plankton	1.00	1.00			
Lofoten/Vesterålen					
Pelagic			0.38		0.00
0-group	0.79				0.00
Plankton	1.00		1.00		

TABLE 7. Number of whales in which each prey item were dominant in the three areas of investigation. In cases where two groups of prey were co-dominant (applied only to one whale in the material), the following randomly chosen row of priority was used to allocate the whale to prey group: Plankton – Cod+Haddock – Pelagic – Capelin – Herring – 0-group.

Area	0-group	Cod + Haddock	Capelin	Pelagic	Plankton	Herring
Finnmark	7	3	2	0	2	5
Kola	0	3	0	0	0	4
Lofoten/Vesterålen	8	0	0	5	0	5

TABLE 8. Comparison of whale stomach contents and prey abundance using *Method 2*: $\hat{\gamma}$ – values obtained from comparison of pairs (A_1/A_2) of prey alternatives. *P*-values for the hypothesis *H*: γ = 0.5 are given in parentheses for each comparison.

	A_2				
A_1	Pelagic	Herring	0-group	Capelin	Plankton
Finnmark					
Pelagic		0.00 (1.00)	0.00 (1.00)	0.00 (1.00)	0.00 (1.00)
Herring	1.00 (0.06)		0.31 (0.95)	0.46 (0.74)	0.77 (0.13)
0-group	1.00 (0.00)	0.69 (0.13)		0.66 (0.33)	0.88 (0.01)
Capelin	1.00 (0.10)	0.54 (0.57)	0.34 (0.88)		0.80 (0.19)
Plankton	1.00 (0.41)	0.23 (0.97)	0.12 (1.00)	0.20 (0.97)	
Kola					
Pelagic		0.00 (1.00)			
Herring	1.00 (0.30)				1.00 (0.11)
Plankton		0.00 (1.00)			
Lofoten/Vesterålen					
Pelagic			0.52 (0.53)		1.00 (0.08)
0-group	0.48 (0.68)				1.00 (0.08)
Plankton	0.00 (1.00)		0.00 (1.00)		

TABLE 9. Number of whale meals eaten of each prey species, counted according to the classification rules given in (5) in the text.

Area	Pelagic	Capelin	Herring	0-group	Plankton
Finnmark	1	3	13	17	2
Kola	1	0	9	0	0
Lofoten/Vesterålen	13	0	9	15	0

TABLE 10. Comparison of whale stomach contents and prey abundance using *Method 3*: $\hat{\gamma}$ values obtained by comparing each species to the remaining species. *P*-values for the hypothesis $\gamma = 0.5$ are given in parentheses for each comparison.

Area/Species	Pelagic	Capelin	Herring	0-group	Plankton
Finnmark	0.14 (0.26)	0.47 (0.965)	0.63 (0.575)	0.82 (0.11)	0.14 (0.17)
Kola	0.35 (0.36)		0.69 (0.865)		0.00 (0.00)
Lofoten/ Vesterålen	0.64 (0.65)			0.49 (0.98)	0.00 (0.00)

TABLE 11. Comparison of whale stomach contents and prey abundance using a robustified *Method 1*: *p*-values obtained from comparisons of pairs (A_1 / A_2) of prey alternatives.

	A_2				
A_1	Pelagic	Herring	0-group	Capelin	Plankton
Finnmark					
Pelagic		0.97	0.93	0.79	0.03
Herring	0.07		0.82	0.28	0.02
0-group	0.14	0.26		0.31	0.01
Capelin	0.29	0.87	0.79		0.01
Plankton	0.99	1.00	1.00	1.00	
Kola					
Pelagic		0.91			0.01
Herring	0.27				0.02
Plankton	1.00	1.00			
Lofoten/Vesterålen					
Pelagic			0.46		0.00
0-group	0.69				0.01
Plankton	1.00		1.00		

It seems that the 1992–94 minke whale ecology studies (Haug *et al*., MS 1992) have shown that the species is quite flexible in its choice of food, adapting well to local prey abundance situations. Results of statistical analyses here of parts of the 1992 material seem to support this. However, under conditions when all prey items are equally available, our detailed statistical analyses may indicate that the minke whale is somewhat reluctant to feed upon plankton. Such patterns were evident in all the areas studied. It is important to emphasize, however, that some methodological problems are involved in the analyses of plankton as a potential prey group. First, the acoustic plankton estimates should be regarded as considerably more uncertain than those for fish. Second, it is evident that while the biomass of plankton is large in all surveyed areas, the local densities may be quite low. Krill is an important constituent of the plankton and is also consumed by the minke whales (see Haug *et al.*, 1995a). However, krill meals were smaller than meals containing any other prey items, and may suggest that the krill patches pursued by the northeast Atlantic minke whales were scattered and in rather low densities (Haug *et al.*, 1996b). Baleen whales, minke whales included, are assumed to have a threshold foraging response to capelin density (Piatt and Methven, 1992), and the possibility that similar thresholds may exist also for planktonic prey items such as krill is obvious. Thus, when only the total biomass, and not the local density of plankton is considered, erroneous conclusions about negative preferences could well be drawn.

Despite observations of vast amounts of 0-group cod in the upper water layers, none were found in the stomachs from minke whales caught in the northernmost areas (Spitsbergen and Bear Island, see Fig. 1) of Norwegian and adjacent waters in 1992 (Haug *et al.*, 1995a). There were, however, some indications of a preference for 0-group fish (mainly herring to the west of 26°E , mainly cod to the east of this longitude) in Finnmark. This finding, however, was not significant when the uncertainty in the estimated prey abundance was taken into account in the robustified analysis.

The negative preference for plankton was found when comparing fractions in stomachs to overall prey fractions using both *Method 1* (all areas) and *Method 3* (Kola and Lofoten-Vesterålen), and it was also evident in the *robustified* analysis (all areas). However, when comparing the relative prey abundance to the fraction of whales with dominant prey contents (*Method 2*), no clear negative preference for plankton was found. One may thus ask if *Method 2* is as well suited for the problem as *Methods 1* and *3*, and the *assumption* iv) immediately springs to mind. The assumption that the whale stomach contains only one type of prey is not only a very rough simplification of the truth, in many cases it is clearly incorrect (see Haug *et al.*, 1996b).

There were some concerns also about the validity of *assumptions* i) and ii) (relative prey abundance was known exactly and was also constant throughout the period of sampling). Indeed, many whales in all areas were taken outside of the respective periods of prey resource sampling. Most probably, prey resources will have changed to some extent during the nearly 40 days period of whaling. Even though an attempt to account for this is performed by robustifying *Method 1*, it was evident that these identified limitations in the experimental design calls for some caution when interpreting the results.

The presented qualitative and quantitative analyses were based on parts of the data collected in 1992. An application of the full data set (collected during 1992–94) as it becomes available for analyses, may yield more conclusive results. However, it should be noted that the prey availability data from 1993 and 1994 are aggregated over even larger sea areas than the 1992 data (Haug *et al.*, 1996a) such that the test methods applied cannot be expected to be more powerful. An ideal design of a future experiment would be that each whale stomach be accompanied by information about the prey situation locally where and when the whale had its meal. Such synoptic small and medium scale studies of the dynamics of minke whale foraging in relation to densities of various prey types would certainly increase the power and validity of the test methods.

Several methods have been developed to measure food selectivity by comparing the composition of the diet with what is available in the environment, for instance in fish predators (see Wootton, 1990). The methods include both indices and statistical techniques, and they assume that the gut samples and habitat samples accurately reflect the relative abundance of prey consumed and present in the environment, respectively (Kohler and Ney, 1982). Given the identified uncertainties and limitations in the present experimental design, such assumptions would probably be violated, and an approach with development of a statistical methodology fitting the available data was, therefore, chosen. A more synoptic small and medium scale assessment of minke whale prey preferences would probably actualize the use also of existing theoretical models of prey selection, and results from such studies would also be more beneficial for development of predictive models of prey selection.

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