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On the Variation in Size and Individual Composition of Minke Whale (*Balaenoptera acutorostrata*)

by

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Abstract

Forestomach contents from 223 northeast Atlantic minke whales (*Balaenoptera acutorostrata*), caught in scientific whaling operations in Norwegian and adjacent waters in 1992-1994, were analysed with reference to the feeding behaviour of the species. More than half of the examined forestomachs had single-prey contents, thus indicating an ability of the whales to pursue single-species aggregations of prey. This was particularly evident for krill (*Thysanoessa* spp.), herring (*Clupea harengus*) and capelin (*Mallotus villosus*), while a more frequent occurrence of gadoid species in mixed-prey forestomachs may indicate that these are either harder to find in single-species aggregations or that they may occasionally be eaten while pursuing the same prey as the minke whales. Within a given area, it appears that small and large whales exploit the same resources, the larger whales taking larger food quanta per meal than the small ones. Substantial variations in observed weights of forestomach contents suggest that minke whales usually feed during long and well defined feeding bouts separated by non-feeding periods. Krill is, however, usually found in stomachs with little contents suggesting that it may be consumed during shorter and more frequent feeding bouts. That krill is more dispersed than any of other prey items may have contributed to this. The available data may present an indication that the feeding activity of minke whales is relatively low during night.

Introduction

The minke whale (*Balaenoptera acutorostrata*) is a boreo-arctic baleen whale which, in the North Atlantic, migrates regularly to feeding areas in the far north in spring and early summer, and southwards to breeding areas in the autumn (Jonsgård, 1966). Based on data from 1989, an abundance estimate of 75,600 (CV = 0.16, 95% CI 56,400-107,200) is given for the northeast Atlantic stock (Schweder *et al.*, MS 1995). The northeast Atlantic minke whale is, therefore, an important top predator. Its predatory role has been studied quite thoroughly during the period May-September in 1992-1994 in a scientific whaling programme where questions concerning the feeding ecology of the species were addressed (Haug *et al.*, MS 1992).

In contrast to their stenophageous krill-eating counterparts in the Antarctic (Kawamura, 1980; Bushuev, 1986; Ichii and Kato, 1991), the northeast Atlantic minke whales are rather euryphageous, feeding on a number of prey items including both fish and crustaceans (Jonsgård, 1951; 1982; Nordøy and Blix, 1992; Haug *et al.*, 1995a; b; in subm.). The 1992-1994 minke whale ecology studies have produced detailed information about the prey composition in stomachs of 223 minke whales (of known sex and size) caught in 5 geographical subareas in Norwegian waters (Fig. 1). This has raised the possibility to analyse several important aspects of the feeding behaviour of the species, and this paper addresses the following four questions:

i) Will an individual whale choose one particular prey species or a mixture of several prey species?

ii) Will large and small whales choose different types of prey?

iii) Will the prey type influence the amount of prey each whale consumes?

iv) Do the whales show particular diurnal rhythms in feeding behaviour?

Material and methods

Sampling of whales

Whales taken in the scientific whaling operations were sampled randomly, using a sampling procedure where whales were searched for along predetermined transects, randomly laid out in each area (Haug *et al.*, MS 1992). The transects were designed in saw-tooth patterns, mainly according to the principles used during the previous shipboard sightings surveys NASS-89 (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, depending on 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 50mm and 60mm harpoon guns fitted with grenade harpoons, equipped with 22g penthrite grenades (Øen 1995). Dead whales were immediately brought aboard the vessel for dissection and biological sampling. Of the 223 animals (121 females and 102 males) from which stomach content data were obtained, 92, 63 and 68 were taken in 1992 (July-August), 1993 (May-September) and 1994 (May-September), respectively. The whales ranged in total body length (measured from the tip of the upper jaw to the notch between the tail flukes) from 442 to 883 cm (Fig. 2).

Analyses of minke whale stomach contents

The complete digestive tract was cut out of the whale as soon as possible (1-3 hours *post mortem*). Minke whale stomachs consist of a series of four chambers Olsen *et al.* (1994a). Experience from pilot studies performed during scientific whaling in 1988-1990 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 was used in the present analyses. The onboard and laboratory treatment of the forestomach contents were as described in detail by Haug et al. (1995a).

Otoliths were collected and identified to the lowest possible taxon, preferably to species (Breiby, 1985; Härkönen, 1986). The total numbers of each fish species were determined by adding the number of fresh specimens, the number of intact sculls and half the number of free otoliths. Random subsamples of otoliths were measured, and otolith length - fish length/weight correlations were used to estimate the original fish weight. Erosion of otoliths, which is a problem in studies of seal stomachs (Pierce and Boyle, 1991), is not considered a problem in these studies as the analyses were restricted to the contents of the forestomach where digestive glands are completely absent and no gastric acids are produced (Olsen *et al.*, 1994a).

For crustaceans, the total weight and the number of individuals were recorded for each species in subsamples, and this was used to obtain crude estimates of the numerical contribution of each prey species. Known mean weights of fresh crustaceans were used to obtain crude estimates of the original biomass of the crustaceans eaten by each whale.

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 (in kg), was used. The stomach contents were originally divided into 12 species/taxa (Haug *et al.*, 1995a; b; in subm.). Based on their dietary importance and in order to simplify the statistical exercises, we have chosen to combine these species/taxa into 7 new categories, 0-group fish, capelin, cod+haddock, herring, pelagic, plankton and other species (see Table 1), when approaching **questions i** and **ii**.

Statistical methods

When addressing **question i**, any food item which contributed to more than 1% of the total biomass in the forestomach was classified as a valid prey for a given whale.

When approaching **questions ii** and **iii,** the following simplifying assumption had to be made:

(1) The whale forestomach contains only one type of prey.

This assumption is not perfectly consistent with data, and in practice we have to classify each forestomach according to which prey species is dominating. In the analysis of **questions iii,** the effect of relaxing Assumption (1) is studied. We denote the different prey species by $A_1,....,A_k$. Following Haug *et al.* (MS 1992) we let T $\in$ {1,....,k} indicate the type of prey that the forestomach contains, for instance T=2 means that the whale has eaten A_2.

According to Christensen (1981), female and male northeast Atlantic minke whales mature at approximate body lengths of 715 and 675 cm, respectively. This information constitute the rationale behind the selection of 700 cm as the limit above and below which the whales were classified as large and small, respectively. When **question ii** is addressed, our aim is to test the hypothesis:

> H: Large (> 7m) and small (< 7m) whales have the same feeding preference pattern.

We introduce M which indicates whether the whale is large (M=1) or it is small (M=2). The hypothesis H can then be formulated as T and M being statistically independent.

Based on observations of T and M from n whales the hypothesis can be tested. The statistical problem is known as testing for independence in a two-way contingency table (Dobson 1983). Define X_{ij} as the number of whales for which T=i and M=j. The Pearson statistic is defined as

$$\chi^2 = \sum_{i=1}^{k}\sum_{j=1}^{2}\frac{\{X_{ij}-\hat{X}_{ij}\}^2}{\hat{X}_{ij}},$$

where $\hat{X}_{ij}$ is the expected value of X_{ij} given that H is true. When H is true χ^2 has an approximate chi-square distribution with k-1 degrees of freedom. Thus the p-value for the test is calculated as

$$\text{p-value} = \Pr\{\chi^2 > \chi^2_{obs}\},$$

where χ^2_{obs} is the test statistic calculated from the observations.

When we address **question** iii, we let V_t be the weight of the contents of a whale forestomach at time t. As t varies, V_t follows a cyclical pattern, where it decreases as digestion proceeds, and increases rapidly when the whale is having a meal. In addition to this variation it is reasonable to believe that V_t also depends on factors such as the size of the whale and the type of prey.

We sampleds each whale at a random time point in its feeding cycle, and we denote the value of V_t which is observed by V. Let l be the length of the whale. In the following discussion we are conditioning on the values of l and T. A plausible model is

$$V = \mu(T,l)\cdot Z,$$

where $\mu(T,l)$ is a function and Z is a positive random variable with expectation E(Z)=1. Thus $E(V) = \mu(T,l)$, and the variance of V is proportional to $\mu^2(T,l)$.

The random variable Z represents the fact that the whale is caught at a random time point in its feeding cycle. A possible choice of μ is

$$\log\{\mu(T,l)\} = \beta \cdot \log(l) + \alpha_T, \quad T = 1,\dots,k, \tag{2}$$

where β and $\alpha_1,\dots,\alpha_k$ are regression parameters with $\alpha_1,\dots,\alpha_k$ belonging to the species $A_1,\dots,A_k$. We remark that in this model $E(V)$ is proportional to l^β. From mathematical considerations we expect $\beta = 3$, since the weight of the whale is approximately proportional to the cube of its length (Horwood, 1990). On a log scale the model for V becomes:

$$\log(V) = \beta \cdot \log(l) + \alpha_T + \log(Z) \ , \tag{3}$$

which can be fitted by standard linear regression methods (Dobson, 1983).

The hypotheses we want to test are that of no effect of whale size:

$$H_{size} : \beta = 0 \ ,$$

and that of no effect of prey type:

$$H_{type} : \alpha_1 = \dots = \alpha_k \, .$$

To test H_{size} we fit the submodel

$$\log\{\mu(T,l)\} = \alpha_T \ , \tag{4}$$

and compare the residual sum of squares (RSS) to the RSS of the full model (2). The RRS is a measure of how well the model fits the data. Similarly, to test H_{type} we fit

$$\log\{\mu(T,l)\} = \beta \cdot \log(l) + \alpha, \tag{5}$$

where α is the common value of the α_T 's.

To remove the assumption (1) we define $d = (d_1,\dots,d_k)$, where d_i is the relative amount of A_i in the stomach. A reasonable model is

$$\log\{\mu(T,l)\} = \beta \cdot \log(l) + \sum_{i=1}^{k} \alpha_i \cdot d_i \, . \tag{6}$$

Note that if the assumption (1) is satisfied, i.e. that only one d_i is non zero, then this model reduces to the model (2).

To investigate whether the volume of the forestomach contents of the whales varies systematically during a 24 hrs period (**question iv**), the first step will be to plot the stomach volume against time of capture for all the whales in the material. In addition, a nonparametric trend curve for the forestomach volume data is plotted, using the local regression routine "loess" in S-plus (Chambers and Hastie, 1993). Error bounds (95% cofidence limits) are added to facilitate evaluation of possible significant deviations of the trend curve from the mean volume of all the stomachs.

Results

All computations which follow were carried out using the statistical software S (Becker *et al.*, 1988).

Question i

Using 1% of the total biomass in a given stomach as the lower limit for which an observed prey item should be considered valid, it appears that approximately 56% of the whales had only one prey category in their forestomach (Fig. 3). In the remaining 44%, species from either 2, 3, 4 or 5 prey categories were found simultaneously in the individual stomachs.

Of the single-prey forestomachs, 39%, 35% and 18% contained krill, herring (also 0-group) or capelin, respectively. The remaining 8% included either sand-eels or gadoids (saithe, cod or haddock).

Question ii

Table 2 shows the values of X_{ij} for $i \in \{1,\ldots,6\}$ and $j \in \{1,2\}$ and the corresponding expected values $\hat{X}_{ij}$. From these two tables we find $\chi^2 = 4.16$ which gives a p-value $= 0.53$. Thus the hypothesis H is not rejected. In these calculations the S-plus function loglin() was used.

Also, H was tested within the five sampling areas Spitsbergen, Bear Island, Finnmark, Kola, Lofoten-Vesterålen (Fig. 1). The hypothesis was not rejected in any of these areas.

Question iii

As seen from Fig. 4, a linear relation between the log-transformations of observed minke whale forestomach content weights and the corresponding whale lengths seems plausible, although the variation around the best fitted straight line is large. The figure serves as a motivation for including the term $\log(l)$ in (2).

From Fig. 5, a box plot of observed forestomach contents weights (V) for the different prey categories, it is seen that V tends to be large for cod+haddock and for herring, and small for plankton.

Table 3 shows the estimates of the parameters in the linear model (3) together with their standard deviations. The estimated value $\hat{\beta} = 3.5$ is relatively close to the value $\beta = 3$ which is what we expect from mathematical considerations. We further see that the prey categories cod+haddock and herring have the largest estimated α values and that plankton has the smallest α value. These findings are in correspondence with Fig. 5.

To test the hypothesis H_{size} we compare RSS for the model (4) to RSS of the full model (2). The p-value for this test is found to be $1.5 \cdot 10^{-6}$, so the hypothesis, that there is no effect of whale length on meal size, is very clearly rejected. Similarly we test H_{type} by comparing RSS for the model (5) to RSS of the full model (2). This yields a p-value of $8.8 \cdot 10^{-5}$ which also clearly rejects the hypothesis that there is no effect of prey type on meal size. Here, p-values and parameter estimates were calculated using the S function lm().

It should be pointed out that the residuals from the fit of the model (3) do not appear to be normally distributed. This fact has no effect on the estimation of parameters, since the model is not based on a normal assumption. However, the calculated p-values are only exact when $\log(Z)$ in (3) has a normal distribution, but for both H_{size} and H_{type} the rejection is so clear that the deviation from normality should have no effect on the conclusion.

Finally, the parameters of the model (6) are estimated. Recall that this model is a generalization of the model fitted above in the sense that model (6) does not rely on assumption (1), i.e., that the whale stomach contains only one type of prey. The parameters in (6) have the same interpretation as the parameters in (2). Table 3 shows the estimated parameters for the model (6). It is seen that except for the category cod+haddock, which has a higher value of α in model (6) than in model (3), there are very small differences between the two models. This implies that the assumption that whale stomachs contains only one type of prey is not critical for the analysis.

Question iv

Evidently, the observed total contents volumes in the forestomachs varies substantially (Fig. 6). However, when comparing the trend curve with the mean volume of all the 223 forestomachs (33.2 l), there seems to be some evidence of diurnal variation. Mean forestomach volumes tend to decrease during night, whereafter an increase seems to prevail between 0800 hrs and 1600 hrs. However, this observed trend only explains a little part of the total variation in the data material since only the observed minimum around 0800 hrs in the morning deviates significantly from the 33.2 l mean volume.

Discussion

The first question addressed was whether each individual whale chose only one particular prey species or if the forestomach content could be a mixture of several prey types. Apparantly, both alternatives occurred in our study. The prominent role of krill, herring and capelin in the single-prey forestomachs emphasizes the importance of these species in the diets of northeast Atlantic minke whales (see also Haug *et al.*, 1995a; b; in subm.). Presumably, the minke whales are able to seek and feed on single-species aggregations of all these species even though it is acknowledged that there is a slight possibility that they may be somewhat reluctant to feed upon krill when alternative prey is available (Skaug *et al.*, MS 1995). The occurrence of gadoid species in a few single-prey forstomachs shows that these species may also be target species for feeding minke whales. Their more frequent occurrence in mixed-prey stomachs may, however, indicate that they are, at least occasionally, eaten while pursuing the same prey as the minke whales. Relatively dense schools of gadoids (cod, haddock and saithe) may occur in February-May in their spawning areas along the Norwegian coast south of Finnmark (Bergstad *et al.*, 1987). Probably with the exception of young (< 45 cm in total length) saithe, none of these gadoid species are known to occur in single-species aggregations outside the spawning season (Olav Rune Godø, Institute of Marine Research, Bergen, Norway, pers. comm.). Except in the area Lofoten/Vesterålen in May it is thus rather unlikely that minke whales taken in the scientific whaling operations could have had any oportunity to pursue spawning aggregations of gadoids. The unavailability of dense single-gadoidspecies aggregations may thus also have contributed to the low occurrence of cod, haddock and saithe in single-prey forestomachs.

The size composition of the whales taken randomly in the 1992-1994 scientific catch operations resembles that observed in the commercial catches around 1980, i.e., with relatively small number of whales smaller than 6 m in total body length (Øien, 1988). When comparing large (>7 m) and small (< 7 m) whales, there is no statistical evidence of size-dependent differences in feeding patterns. This is true both when the different sampling areas are treated separately and when the whole material is pooled. Whales of all ages, therefore, appear to exploit the same resources within a given area.

The observed size of a whale meal seems to be related to both the size of the whale and the prey type eaten. There is a considerable variation in the observed meal sizes, with an apparent increase occurring approximately proportional to the cube of the length of the whale. The latter could also be expected from simple mathematical considerations since bigger whales have bigger stomach volumes. The variations in observed forestomach content weights may indicate that minke whale feeding behaviour tends towards large, well defined meals rather than more continuous feeding of smaller quanta which may have resulted in more even and generally low weights of forestomach contents.

The latter may, however, apply to whales feeding on plankton (which was almost exclusively krill). In general, minke whale meals consisting of plankton tended to be small while those consisting of cod+haddock and herring were larger than meals consisting of any other species. There is no evidence of large differences in the digestibility of the various prey items found in minke whale stomachs (Nordøy *et al.*, 1993; Mårtensson *et al.*, 1994; Olsen *et al.*, 1994a; b), nor are there any arguments for a quicker passage of krill through (and evacuation from) the minke whales' gastrointestinal tract than of other food items (Erling S. Nordøy, Dept. of Arctic Biology, University of Tromsø, pers. comm.). The structure of the exosceleton (including both wax esters and chitin) of the krill might, however, result in a delayed passage of this prey item, and it has been proposed that the multi-chambered stomach of minke whales is an adaption to increase passage time of such complex structures (Olsen *et al*, 1994a). Thus, the reasons for the generally small contents in krill-forestomachs must probably be sought elsewhere. It is known that under favourable feeding conditions, krill-eating Antarctic minke whales usually have one single daily peak feeding period (Boshuev, 1986; Ichii and Kato, 1991). This result in large daily variations in the amounts of forestomach contents, while in areas with less stable and more dispersed krill concentrations the differences in daily feeding activity is much smaller. The present observations appear to be similar to the latter, and could indicate that the concentrations of krill in patches pursued by the northeast Atlantic minke whales may have been low and insufficient for the whales to satiate themselves by feeding only once-a-day.

Although the observed forestomach volumes appear to vary substantially during a 24 hrs period, the available data may present a weak indication that the feeding activity of the minke whales is relatively low during night. Interestingly, recent results from tracking of minke whales, tagged with VHF-radio transmitters off the coast of North Norway, yielded significantly lower frequencies of surfacing rates during night than during day (Folkow and Blix, 1993). These observations may support a view that the minke whales rest during night, whereas their feeding activities are allocated to daytime hours.

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Table 1. Definition of the prey categories used in the statistical analyses connected to questions ii and iii. (see text for further explanations).

Prey category	Original species/taxa included
0-group fish	0-group herring *Clupea harengus* 0-group gadoids
Pelagic	Sand eels *Ammodytes* sp. Saithe *Pollachius virens*
Capelin	Capelin *Mallotus villosus*
Cod + haddock	Cod *Gadus morhua* Haddock *Melanogrammus aeglefinus*
Herring	Herring *Clupea harengus*
Plankton	Krill *Thysanoessa* spp. Various crustaceans
Others	Various other fish species

Table 2. Testing potential heterogeneity in feeding habits among small (< 7 m) and large (> 7 m) minke whales: Observed and expected (in parentheses) values of X_{ij} to be used in the calculations in the applied Pearson statistics (see text for further explanations).

	PREY CATEGORIES					
	0-group	capelin	cod+haddock	herring	pelagic	plankton
SMALL WHALES	13 (12)	19 (18)	22 (24)	43 (39)	8 (8)	38 (43)
LARGE WHALES	5 (6)	9 (10)	15 (13)	17 (21)	4 (4)	29 (24)

Table 3. Testing the effect of whale length and prey type on meal size: Estimation of the parameters α and β in model (3) and in model (6), the values for the latter being given in parentheses. S.D. = standard deviation. See text for further explanations.

	β	Estimates of α for					
		0-group	capelin	cod+haddock	herring	pelagic	plankton
Estimate	3.50 (3.46)	- 4.32 (- 4.43)	- 4.67 (- 4.54)	- 3.33 (- 2.85)	- 3.97 (- 3.94)	- 4.35 (- 4.47)	- 4.77 (- 4.72)
S.D.	0.71 (0.71)	1.42 (1.44)	1.43 (1.44)	1.40 (1.42)	1.43 (1.45)	1.44 (1.45)	1.40 (1.41)

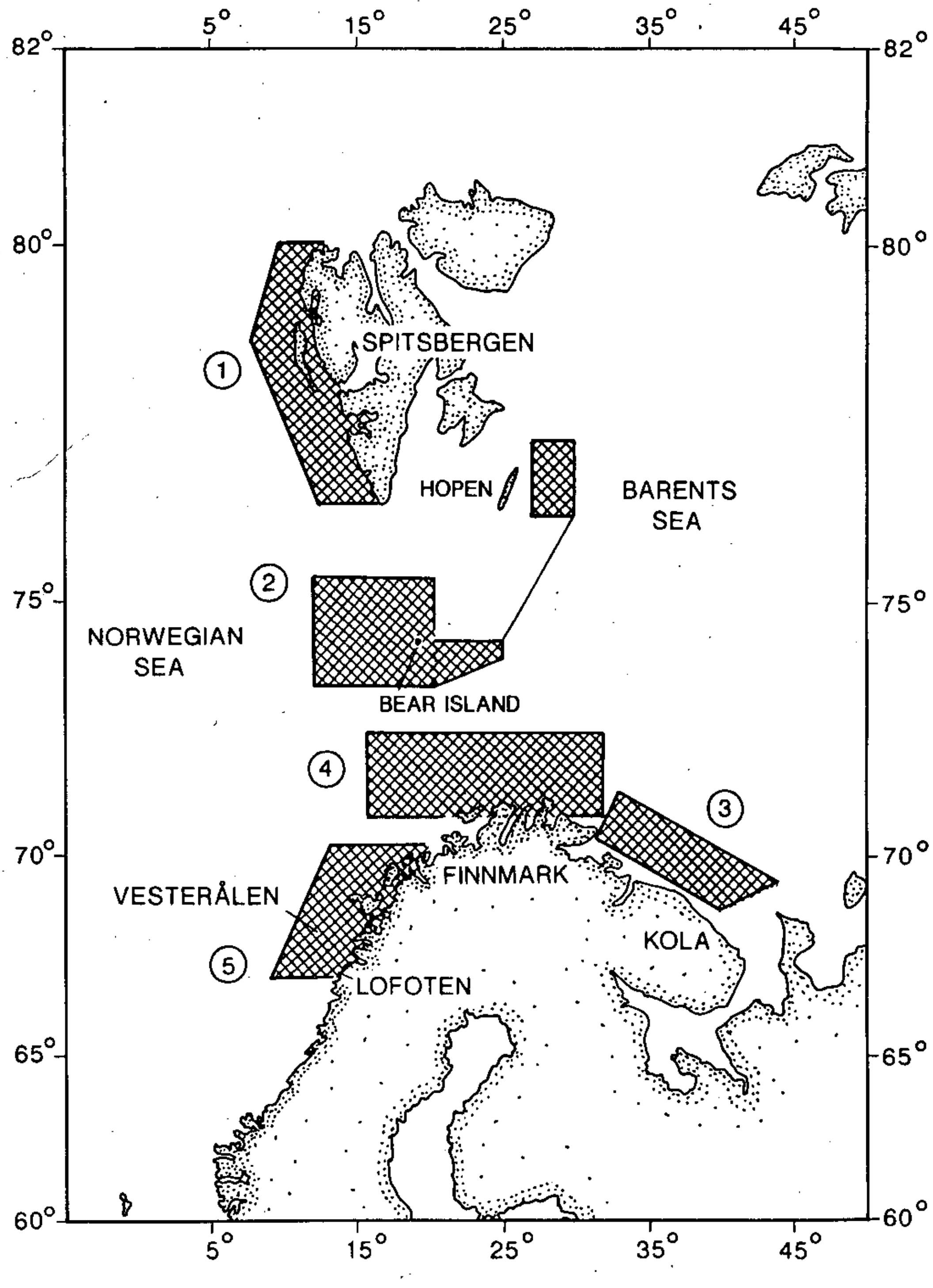

Fig. 1. Selected operational sub-areas where minke whales were sampled during the Norwegian scientific catch in 1992-1994. 1=Spitsbergen, 2=Bear Island, 3=Kola, 4=Finnmark, 5=Lofoten-Vesterålen.

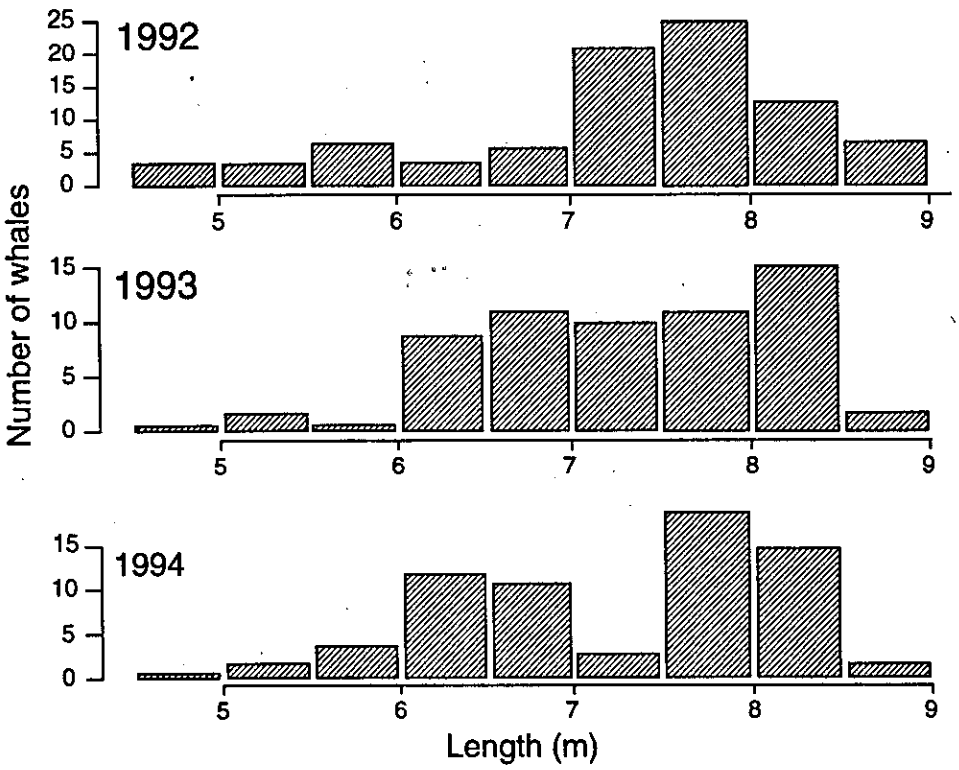

Fig. 2. Size composition (in 0.5 m length groups) of minke whales sampled during the Norwegian scientific catch in 1992-1994.

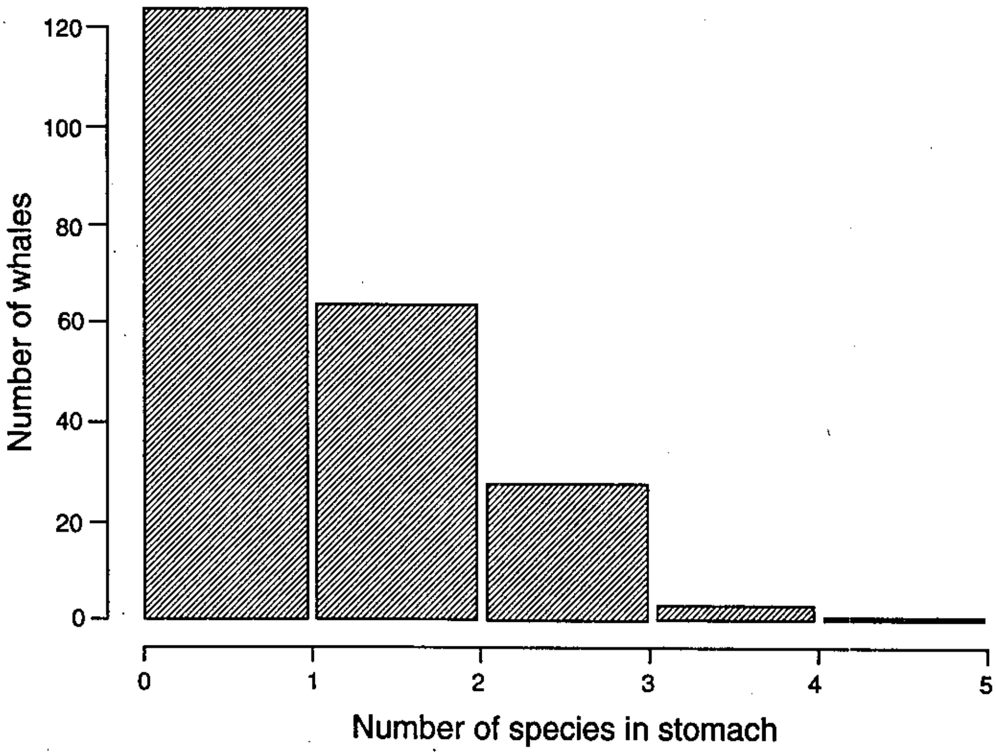

Fig. 3. Distribution of the number of different prey species found in each forestomach of minke whales sampled during the Norwegian scientific catch in 1992-1994. To be registered as present in a forestomach, a species had to constitute more than 1% of the total weight of the forestomach contents.

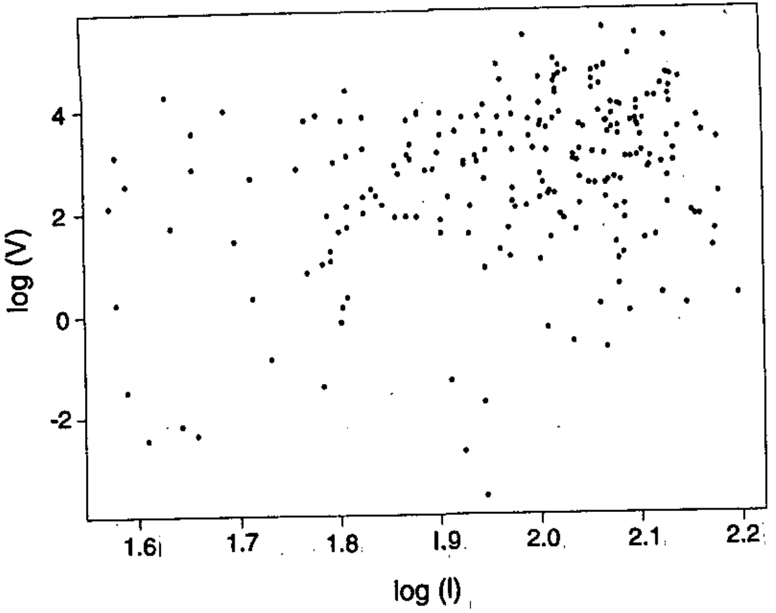

Fig. 4. Log-transformations of observed minke whale forestomach content weights (log(V)) plotted against log transformations of whale lengths (log(l)). Data from whales sampled during the Norwegian scientific catch in 1992-1994.

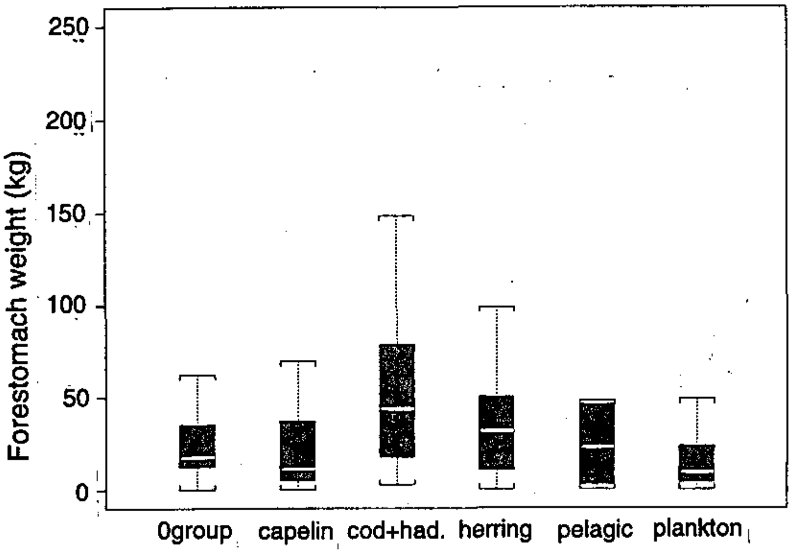

Fig. 5. Boxplot of minke whale forestomach weights (V) stratified by prey categories. The dark areas covers 50% of the observations, the white bar represent the median of the observation. Data from whales sampled during the Norwegian scientific catch in 1992-1994.

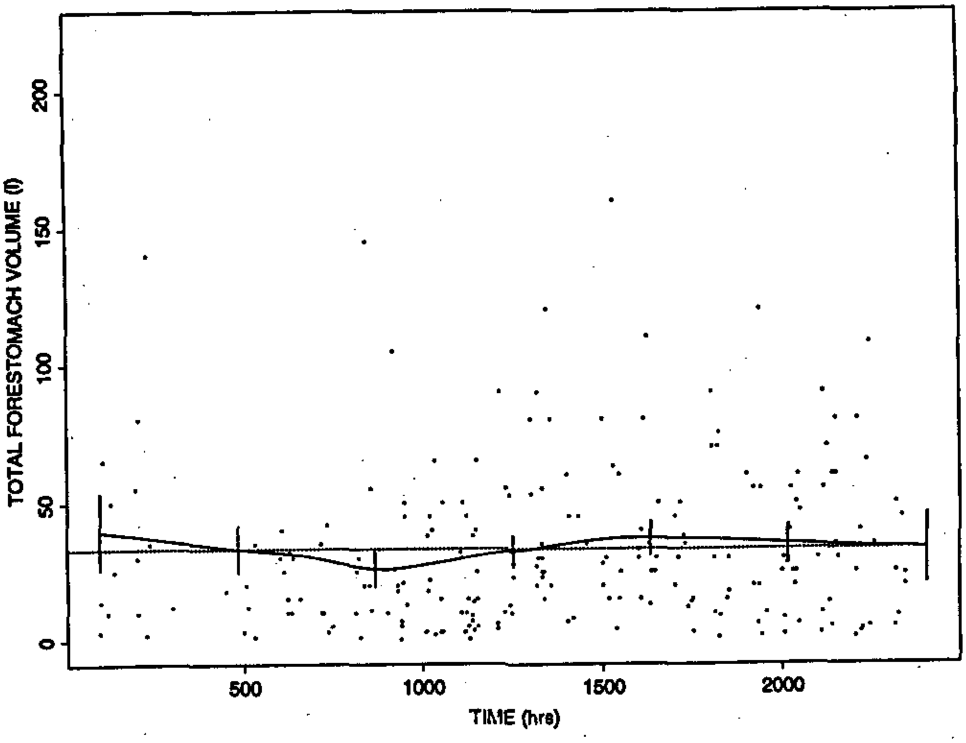

Fig. 6. Plot of observed forestomach volumes against time of capture (local time = GMT + 2 hrs) for the 223 minke whales sampled during the Norwegian scientific catch in 1992-1994. A nonparametric trend curve (solid line) with 95% confidence limits (vertical bars) as well as the mean value for all forestomach values (dotted line) is indicated.