DIET STUDIES BASED ON CONTENTS FROM TWO SEPARATE STOMACH COMPARTMENTS OF NORTHEAST ATLANTIC MINKE WHALES *BALAENOPTERA ACUTOROSTRATA*

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Minke whales (*Balaenoptera acutorostrata*) have a multichambered stomach system. Recent diet studies of northeast Atlantic minke whales have been based on reconstructed contents of the forestomach. In this study, however, a comparison of contents from two stomach compartments, the forestomach and the remaining stomach chambers, respectively, was carried out. The aim was to investigate whether these two stomach compartments differed with regard to total estimated content weight and diet composition, and what possible implications that might have for the analyses of minke whale diets. A total of 148 fore- and remaining stomachs, sampled in 1992 and 1993, were analysed. The estimated initial forestomach contents weighed significantly more than the initial contents estimated from the remaining stomachs. This was probably a result of several factors such as minke whales being caught at various states of satiation, the rapid digestion of some otoliths in the remaining stomachs and the influence of prey types on meal sizes leading to large variations in forestomach content weights. In spite of these differences between estimated fore- and remaining stomach content weights, there was negligible difference between the two compartments with regard to frequency of occurrence and percentage weight of prey. The results obtained seem to indicate that the contents from the forestomachs are sufficient to adequately describe minke whale diets.

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INTRODUCTION

Understanding the relationship between predator and prey populations is a key area of ecology. It is also of considerable importance in the management of fish stocks that are harvested by man. With the increased attention being paid to multispecies interactions, predator-prey relationships are essential in predictions of yield and of the ecological effects of exploiting particular species. Furthermore, monitoring of changes in predator populations can provide valuable information about changes in the distribution and abundance of prey when the latter are not amenable to direct study.

The minke whale *Balaenoptera acutorostrata* is probably one of the most important top-predators in the Northeast Atlantic. Based on data from 1995, SCHWEDER et al. (1996) estimated the abundance of minke whales in the Northeast Atlantic to 112 000 animals (CV = 0.104, sd = 11 639). Its feeding ecology has been studied quite thoroughly during the period May-September as part of a three-year (1992-1994) scientific whaling programme (HAUG et al. 1995, 1996, 1997; SKAUG et al. 1997).

These feeding studies revealed that minke whales appear to have a flexible feeding pattern and the ability to adapt to local prey abundance. The species composition of the observed diet was considerably varied in space. Capelin *Mallotus villosus* and krill *Thysanoessa* spp. dominated the diet in the northern areas around Spitsbergen and Bear Island, while further south, in coastal waters of North Norway and Russia, herring *Clupea harengus* predominated, accompanied by various gadoid fish species.

The minke whale stomach consists of four chambers (OLSEN et al. 1994). The 1992-1994 minke whale diet studies were based on analyses of contents sampled from the first chamber, the forestomach (HAUG et al. 1995,1996). However, the contents from the remaining three compartments (including also the duodenal ampulla) were also collected both in 1992 and 1993. This enabled us to address the question as to whether sampling from the forestomach only is sufficient to evaluate the diet of the animals. Also, it was assumed that a comparison of the two stomach compartments might show whether individual minke whales changed prey seldom or often. In this paper the following two questions are addressed:

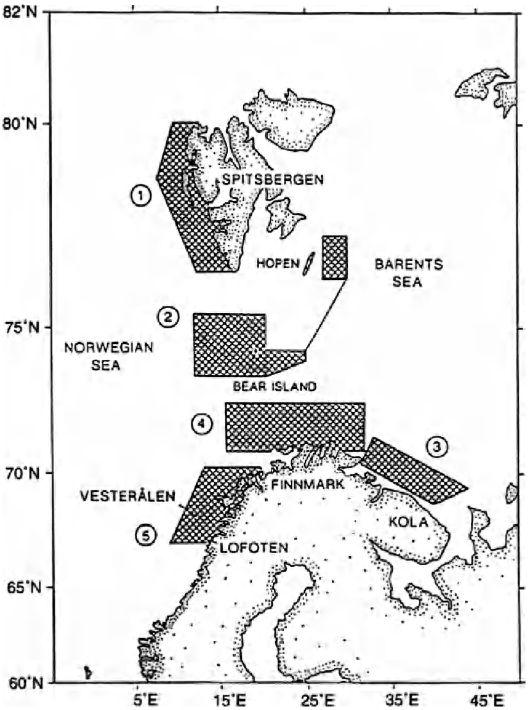

Fig. 1. Five sub-areas where minke whales were sampled during the Norwegian scientific catch in 1992-1993. Sub-areas 1 and 2 (Spitsbergen and Bear Island, respectively) were denominated 'North', and sub-areas 3,4 and 5 (Kola, Finnmark and Lofoten/ Vesterålen, respectively) were denominated 'South'.

1. Do the estimated forestomach contents in general weigh more than the contents in the other three chambers? If so, do all prey groups contribute similarly to the difference?
2. Does the prey composition in the forestomachs (FS) differ significantly from that in the remaining stomachs (RS)?

MATERIAL AND METHODS

Sampling of minke whales

The total sampling area was divided into five separate sampling areas in 1992: West of Spitsbergen, Bear Island, coast of Kola, coast of Finnmark and Lofoten/Vesterålen (Fig. 1). In 1993, Russian authorities did not permit scientific whaling operations in the Russian economic zone (coast of Kola), thus reducing the 1993 field work to only the remaining four sampling areas.

Whales taken in the scientific whaling were sampled randomly using a sampling procedure where the whales were searched for along predetermined transects randomly laid out in each area (Haug et al. 1995, 1996). The minke whales were killed according to the whaling procedures described by Øen (1995).

Analyses and reconstruction of minke whale stomach contents

As soon as the whale was onboard the vessel, the complete digestive tract was carefully excised from the body cavity (1-3 hours *post mortem*) and divided in two compartments, the forestomach and the remaining stomachs. The latter included contents from the fundic chamber, the pyloric chamber and the duodenal ampulla (see Olsen et al. 1994). A total of 91 and 57 fore- and remaining stomachs were examined in 1992 and 1993, respectively. The onboard and laboratory treatments of all samples were as described by Haug et al. (1995).

Intact specimens of fish were identified according to gross morphological characteristics (Pethon 1985), while sagittal otoliths and crustaceans were identified to lowest possible taxon (Enkell 1980; Breiby 1985; Härkönen 1986). Within each of the two stomach compartments, the total number of each fish species was calculated by adding the number of fresh specimens, intact skulls and half the total number of fish otoliths. For large gadoids, such as cod, haddock and saithe, free otoliths were separated into right and left otoliths and divided into geometric classes (with 0.2 mm intervals) whereas otoliths present in a skull, were paired and measured. From otolith length-fish length/ weight regressions and random sub-samples of 200 undigested otoliths (or as many as possible) from each fish species, the initial prey weights at the time of ingestion were estimated.

When estimating the biomass of crustaceans found in the fore- and remaining stomachs at the time of ingestion, mean individual weights of digested crustaceans were recorded for each stomach compartment. These weights were based on the weighing of a known number of individuals (usually 250-300) in a sub-sample, taken from each stomach compartment. Using known mean weights of fresh crustaceans, the original biomass of the crustaceans eaten by the minke whales was crudely estimated.

Presentation of the minke whale diet

Due to the observed heterogeneity in the diet between the five original sampling areas, these areas were pooled into a northern (Spitsbergen and Bear Island) and a southern area (Kola, Finnmark and Lofoten/Vesterålen). These two areas will subsequently be denominated 'North' and 'South', respectively.

In order to simplify the statistical exercises when comparing the two stomach compartments, food items were grouped into the following taxa: zooplankton [krill, copepods (*Calanus* sp.) and amphipods (*Parathemisto* sp.)], herring, capelin, cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), pelagic fish [sandeel (*Ammodytes* sp.) and saithe (*Pollachius virens*)] and various fish. Food items that contributed less than five percent of the total estimated weight in a stomach compartment were omitted from the analyses.

Several feeding indices are commonly used in stomach analyses of top predators (Hyslop 1980; Pierce & Boyle 1991). No feeding index, however, gives a complete or fully realistic picture of dietary composition. The estimated masses of individual minke whale forestomach contents vary considerably (0-250 kg, see Haug et al. 1997) in response to the various states of satiation the whales were caught at. By using traditional numerical and mass fractions of individual prey categories to describe the minke whale diet, forestomachs containing large amounts of food are given exaggerated importance compared to those containing little food. This problem may be avoided, however, by using an alternative mass index, calculated by summarising the percentage of each prey species from each individual whale and dividing this by the total summarised percentages of all prey specimens from all whales. This Weight Index gives each forestomach the same importance irrespective of the very variable content mass, and is defined as:

$$\mathrm{WI}_i = \frac{\sum_{t=1}^{n} \mathrm{W}_{ti}}{\sum_{i=1}^{7}\sum_{t=1}^{n} \mathrm{W}_{ti}}$$

WIi = the relative contribution by weight (%) of species **i** in fore- or remaining stomachs
wti = relative contribution of biomass (%) by species **i** to the contents in stomach **t**
n = number of fore- and remaining stomachs included in the investigation

In addition to the Weight Index, the frequency of occurrence index was used when analysing possible differences between the two stomach compartments.

Analysing and comparing weights of the fore- and remaining stomach contents

In order to analyse possible total content weight differences between the two stomach compartments, the mean estimated weight (± 95% C.I.) of fore- and remaining stomach contents was plotted for each area. Furthermore, in order to investigate which prey categories might have contributed most to these differences, the mean absolute difference (± 95% C.I.) in biomass between the two stomach compartments was calculated and plotted for each prey group:

$$\mathrm{W}_i = \frac{\sum_{j=1}^{n} \left| \mathrm{W}_{\mathrm{FS}ij} - \mathrm{W}_{\mathrm{RS}ij} \right|}{n} \pm 95\%\ \mathrm{C.I.}$$

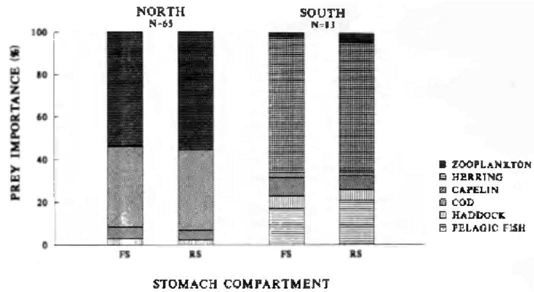

Fig. 2. Food composition, measured by the Weight Index (see text), in minke whale forestomachs (FS) and remaining stomachs (RS) in two areas in the Northeast Atlantic. N = number of fore- and remaining stomachs examined.

Wi = mean weight difference of prey group **i** between fore- and remaining stomachs
$\mathbf{W}_{\mathbf{FS}ij}$ = weight of prey group **i** in forestomach **j**
$\mathbf{W}_{\mathbf{RS}ij}$ = weight of prey group **i** in remaining stomach **j**
n = number of whales

Statistical testing

A Chi-square test was used to test for differences in frequency of occurrence of different prey categories between the two stomach compartments. All pairwise comparisons of stomach compartments was conducted by a Wilcoxon signed test. A Mann-Whitney U-test was used to test for differences among prey groups regarding the absolute difference in weight between the two compartments. P-values less than 0.05 was considered statistically significant. The statistical tests were carried out using SYSTAT (Wilkinson 1990).

Table 1. Testing potential differences among fore- and remaining stomachs; a) in the percentage Weight Index, applying a Wilcoxon signed test; b) in the frequency of occurrence of prey groups applying a Pearson chi-square test. P-values less than 0.05 were considered statistically significant.

FEEDING INDICES	STATISTICAL TEST		PREY GROUPS					
			Zoo-plankton	Herring	Capelin	Cod	Haddock	Pelagic fish
a)								
Weight Index	Wilcoxon	P:	0.12	0.11	0.71	0.03	0.52	0.28
b)								
Freq. occurrence	Pearson	χ^2:	0.14	3.47	0.13	0.20	0.39	2.75
		P:	0.71	0.06	0.72	0.66	0.54	0.10

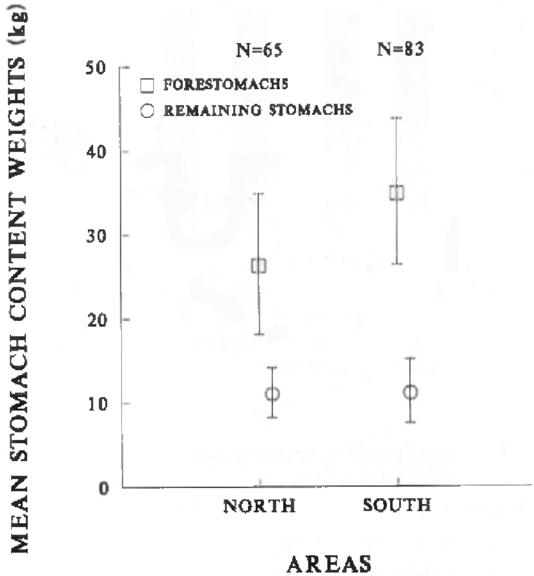

Fig. 3. Mean estimated weights (with 95 % C.I.) of minke whale fore- and remaining stomach content plotted for the two areas. N = number of fore- and remaining stomachs examined.

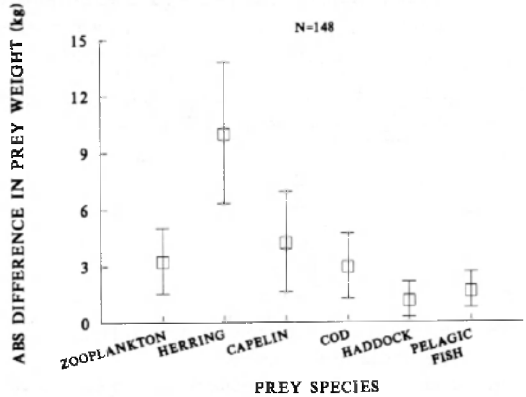

Fig. 4. The mean of absolute differences (mean and 95 % C.I.) in estimated weights of six prey groups between fore- and remaining stomach content. N = number of fore- and remaining stomachs examined.

RESULTS

Samples from fore- and remaining stomachs were obtained from 65 and 83 minke whales in the areas 'North' and 'South', respectively.

Food was found in 98.7 % and 95.3 % of the fore- and remaining stomachs, respectively. The degree of degradation of the contents varied substantially between the two stomach compartments, and approximately 50 % and 95 % of the fore- and remaining stomach contents, respectively, were partly or completely digested.

Considering the relative importance of different prey categories using the Weight Index (Fig. 2), zooplankton (almost exclusively krill) and capelin dominated the minke whale diet in the two northernmost regions (Spitsbergen and Bear Island) whereas further south (Kola, Finnmark and Lofoten/Vesterålen), herring predominated followed by pelagic fish.

The prey composition in the two stomach compartments were very similar (Fig. 2). This is also supported by the statistical analyses using a Wilcoxon signed test, which however, revealed slightly significant differences in the amount of cod between the forestomachs (FS) and the remaining stomachs (RS) (Table 1). There was no difference in the frequencies of occurrence of any prey between the two stomach compartments (Table 1).

The estimated weights of the fore- and remaining stomach contents ranged from being empty to 250 kg and 100 kg, respectively. It appears from testing with Mann-Whitney U-tests that forestomachs in general contain significantly more food than the remaining stomachs (Fig. 3). This difference was larger in area 'South' (35.1 kg vs. 11.3 kg) compared with area 'North' (26.5 kg vs. 12 kg). The two areas were, however, statistically identical with regard to estimated forestomach content weights (Fig. 3).

Fig. 4 illustrates the mean of absolute differences (mean and 95 % C.I.) in weights of seven prey groups between fore- and remaining stomach content. The absolute difference varied significantly (Mann-Whitney U-test) between prey groups, and herring, capelin and zooplankton (almost exclusively krill), in that order were the three prey categories where the difference was largest.

DISCUSSION

Methodological problems

Since the forestomach contents were to be analysed separately from the contents of the remaining stomach, mixing of contents between the two stomach compartments had to be avoided as far as possible. Mixing of contents may, however, have occurred through the relatively large orifice between the forestomach and the fundic chamber (Olsen et al. 1994). This was to difficult to avoid since the digestive tract has to be excised from the cavity before ligation of the stomach compartments. Such mixing seemed to include mainly the small prey items (particularly zooplankton) and otoliths which were trapped within skulls, flesh and bones. The extent to which mixing may have affected the diet result is difficult to assess.

In the minke whale forestomach, there are no gastric glands, and digestion of food mainly occurs as bacterial fermentation. In the remaining stomachs, i.e., fundic chamber, pyloric chamber and duodenal ampulla, the digestion of food occurs by acids and enzymes (Mathiesen et al. 1990; Olsen et al. 1994). Thus, otoliths and various calcareous remains are usually digested in the remaining stomachs. Nordøy et al. (1993) suggested that approximately 90 % of the dry matter of the most common prey species (krill, herring, cod and haddock) disappears in the forestomachs. This high degree of disappearance of dry matter in the forestomachs may explain the observed difference in digestive status between the forestomach contents and the contents in remaining stomachs. Often only calcareous remains such as bones, teeth, otoliths and otic capsules of fish, and some flesh of crustaceans were found in the remaining stomachs.

Fish otoliths were essential in the estimation of initial weights of fish at time of ingestion, particularly in the remaining stomachs where approximately 95 % of the contents were partly or completely digested. Although only undigested otoliths were used when estimating the fish weight at time of ingestion, the digestion of otoliths may have biased the estimation of the total remaining stomach content weights to some extent. Also the biomass estimates of crustaceans were very crude since they lack resistant hard parts that can be used to estimate the initial number and biomass at time of ingestion.

Dietary comparison of the two stomach compartments

One of the questions addressed initially was whether there were weight differences of the contents between the stomach compartments. *A priori* the difference in weight of food between forestomach and remaining stomachs would be expected to be a function of loss of material by digestion, the initial size and composition of the different meals, and the number of meals from which the food in the remaining stomachs comes. Obviously, there are considerable differences between estimated fore- and remaining stomach content weights, the total reconstructed weight of prey in the forestomachs usually being greater than that for the remaining stomachs. This may imply that the remaining stomachs contain remains of only one previous meal. Due to the bacterial fermentation instead of regular digestion in the forestomach (Olsen et al. 1994), a significant loss of hard parts in this compartment is hardly to be expected. If no difference (or the reverse) between the stomach compartments had been detected, the implication would presumably have been that remains of more than one meal were present in the remaining stomachs. The fact that the whales were caught at various state of satiation i.e. some whales were caught at the start or in the middle of a feeding event whereas others were caught between two feeding events, certainly contributed to the observed weight differences.

The large variations in weights between the two stomach compartments (Fig. 4) for particular prey groups could result either from variation in meal composition and/or digestion rates. For all prey types, weight in the remaining stomachs was considerably lower, implying consistent meal composition and digestion of otoliths in the remaining stomachs. This may particularly be true for the fragile herring and capelin otoliths. The combination of minke whales being caught at different state of satiation, the digestion of otoliths in the remaining stomachs, and the suggestion by Haug et al. (1997) that minke whales feeding upon herring, cod and haddock tend towards large, well defined meals which generally result in more varied and larger weights of forestomach contents, may explain why herring was by far the most important contributor to the differences between observed fore- and remaining stomach content weights.

The other question addressed was whether there was difference in prey composition in the two stomach compartments. Despite the differences between the fore- and remaining stomachs with regard to recalculated content weights, the frequency of occurrence and percentage weight of prey were only negligibly different between the stomach compartments. Only the amount of cod appeared to vary slightly. Even if individual whales varied their diet between meals, population diet compositions from analyses of forestomach and remaining stomachs would probably still be similar on average. Consequently, systematic differences are only likely to be seen if digestion results in significant differences (between prey species) in the rate of loss of hard parts. Given the marked change in herring weights between forestomach and remaining stomachs it may seem surprising that the proportion of herring in the two compartments did not also appear to be more different. Nevertheless, it seems that the contents of the forestomachs only are sufficient to describe the minke whale diet adequately.

The 1992-1994 minke whale feeding studies were based on the forestomach contents, which can only give information about the last feeding event of each animal. Since the contents in the remaining stomachs may correspond to a meal taken some time before the contents found in the forestomach, a comparison with forestomach contents might give some insight into the extent to which minke whales tends to change prey. The observed homogeneity between the two investigated stomach compartments may indicate that minke whales do not usually change prey as often as from one feeding bout to another. However, since we know little about digestion rates and passage times of different prey types in minke whales, these results should be interpreted cautiously.

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