

Estimated food consumption of minke whales *Balaenoptera acutorostrata* in Northeast Atlantic waters in 1992-1995

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ABSTRACT

Data on energy requirements, diet composition, and stock size were combined to estimate the consumption of various prey species by minke whales (*Balaenoptera acutorostrata*) in Northeast Atlantic waters. In the period 1992-1995, the stock of 85,000 minke whales appeared to have consumed more than 1.8 million tonnes of prey per year in coastal waters off northern Norway, in the Barents Sea and around Spitsbergen during an assumed 6 month stay between mid-April and mid-October. Uncertainties in stock estimates suggest a 95% confidence range of 1.4 – 2.1 million tonnes. The point estimate was composed of 602,000 tonnes of krill *Thysanoessa* spp., 633,000 tonnes of herring *Clupea harengus*, 142,000 tonnes of capelin *Mallotus villosus*, 256,000 tonnes of cod *Gadus morhua*, 128,000 tonnes of haddock *Melanogrammus aeglefinus* and 54,500 tonnes of other fish species, including saithe *Pollachius virens* and sandeel *Ammodytes* sp. Consumption of various prey items by minke whales may represent an important mortality factor for some of the species. For example, the estimated annual consumption of herring corresponds to about 70% of the herring fisheries in the Northeast Atlantic in 1995. Minke whale diets are subject to year-to-year variations due to changes in the resource base in different feeding areas. Thus, the regional distribution of consumption of different prey items is highly dynamic.

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Introduction

Attempts to develop multispecies models for the management of marine resources have led to increased interest in the quantitative analysis of the feeding ecology of top predators. An important top predator in the North Atlantic is the boreo-arctic minke whale *Balaenoptera acutorostrata*. The Northeast Atlantic stock, assumed to be one of four minke whale stocks in the North Atlantic, is confined to the waters of Spitsbergen, the Barents Sea, Norwegian coastal waters, the North Sea and other waters off the United Kingdom and Ireland (Anonymous 1977). Part of the Northeast Atlantic stock of minke whales migrates northwards to feeding areas in the Norwegian and Barents Seas in

spring, and southwards to breeding areas of unknown location in the autumn (Jonsgård 1966). These animals are reported to feed on various species of zooplankton and fish, particularly herring *Clupea harengus*, capelin *Mallotus villosus* and cod *Gadus morhua* (Jonsgård 1951, 1982). In order to obtain quantitative data for evaluation of the ecological significance of predation by minke whales, extensive studies of the energetics and diet of the whales were conducted in a research programme on marine mammals, initiated by Norwegian authorities in 1988.

A sampling programme was carried out in 1988-1990, in which 51 minke whales were taken. The

purpose was to study the energetics and the digestive physiology of the whales, and in particular, to estimate their energy requirements (see Folkow and Blix 1992, Nordøy *et al.* 1993, Olsen *et al.* 1994a, Olsen *et al.* 1994b, Blix and Folkow 1995, Nordøy 1995). Although pilot studies to examine diet were also carried out (Nordøy and Blix 1992), dietary composition was not studied in detail until 1992-1994, when the stomach contents of 223 minke whales were analysed, and prey availability was estimated simultaneously (Haug *et al.* 1995a, Haug *et al.* 1995b, Haug *et al.* 1996a, Haug *et al.* 1997a, Skaug *et al.* 1997) (Fig. 1). Collection of data for digestive, thermoregulatory, and energetic studies was also continued (see Mårtensson *et al.* 1994, Olsen *et al.* 1996, Kvasdheim *et al.* 1996). Following the termination of scientific whaling in 1994, sampling for feeding ecology studies has continued in connection with commercial whaling operations (Haug *et al.* 1996b, Haug *et al.* 1997b).

In the present paper, we have combined data on the energy requirements, the diet composition, and the stock size of Northeast Atlantic minke whales (sighting surveys in 1995, see Schweder *et al.* 1996), to estimate their consumption of various prey items. Such information is of importance for assessment of the ecological role of the minke whale, and for fisheries management in Norwegian and adjacent waters.

Fig. 1:
Stomach contents of
a minke whale.

Photo: Per Erik Mårtensson



MATERIAL AND METHODS

Modelling strategy

The chemically bound energy of food eaten by minke whales may be expended (converted to heat or work) through oxidative processes at a rate which is reflected in the oxygen consumption of the animal, or it can be deposited as muscles, blubber, visceral fat and, in pregnant females, a foetus. Additionally, some ingested energy is lost in the urine and faeces. The total daily energy expenditure of free-living minke whales has been estimated from indirect recordings of oxygen consumption rates in freely swimming animals (Blix and Folkow 1995), and consequently include energy costs for maintenance, locomotion, thermoregulation, excess postprandial heat production, maternal costs of gestation etc. The amount of energy deposited through tissue growth has been estimated for males and females of various age groups, from differences in the masses and energy densities of various tissues in whales sampled during spring and autumn (22 and 42 individuals, respectively; Nordøy *et al.* 1995). Energy costs of lactation were not included, since the majority of minke whale calves are weaned before arriving in Norwegian and adjacent waters (Jonsgård 1951). The expended and deposited energy, the metabolizable energy (ME), is obtained by intake of an even larger amount of energy, the gross energy intake (GEI), the difference between the two being made up of energy lost in urine (ca. 8%, Lavigne *et al.* 1982) and faeces (ca. 8%, Nordøy *et al.* 1993, Mårtensson *et al.* 1994). The GEI equals the energy requirements of the animals.

An assessment of the amount of food required to supply the GEI depends on information on the proportions in which different prey items are taken. Minke whales in the Northeast Atlantic are often observed in aggregations along the coast of northern Norway, in the Barents Sea and along the coast of Spitsbergen (Øien *et al.* 1987). The diet has been shown to vary between geographical areas, and with different seasons of the year (Haug *et al.* 1995a, Haug *et al.* 1995b, Haug *et al.* 1996a). There are also substantial seasonal variations in the energy densities of many of the prey items (Mårtensson *et al.* 1996). This necessitated a substructuring of the food requirement calculations, and also required that some

assumptions be made.

Modelling assumptions

1. Northeast Atlantic minke whales were assumed to feed within various subareas during a period lasting for 180 days from April 15 to October 15. The feeding period was divided into three seasons: spring (Apr 15 - Jun 15), summer (Jun 16 - Aug 15) and autumn (Aug 16 - Oct 15).
2. The distributional area was divided into three geographical subareas, as described by the Scientific Committee of the International Whaling Commission (Fig. 2; Anonymous 1993):
 ES = Spitsbergen and Bear Island
 EB = Barents Sea and coastal areas of Finnmark and Kola
 EC = Vesterålen and Lofoten
3. The Northeast Atlantic minke whale stock size and distribution within subareas was extrapolated from the results of the NILS-95 sightings survey (Schweder *et al.* 1997). All stock estimates are given with uncertainty levels indicated, but only the point estimates were used in the present consumption calculations. The point estimate for the entire

Northeast Atlantic stock was 112,125 animals. However, since diet data from the North Sea (EN, see Anonymous 1993) do not exist, these animals were excluded from the analyses, which were confined to the subareas ES, EB and EC (Table 1).

4. Of the 225 minke whales caught randomly during the Norwegian scientific whaling programme in 1992-1994, 45.8% were males and 54.2% were females (Nordøy *et al.* 1995, Haug *et al.* 1997a). In the present analyses, we have assumed that the same sex ratios applies to the entire stock.
5. The stock was divided into two classes: animals which were physically mature (all whales with body length ≥ 8 m, see

Table 1. Minke whale abundance estimates (N) with standard deviations (SD) and coefficients of variation (CV) for the three subareas ES (Spitsbergen and Bear Island), EB (Barents Sea and coastal areas of Finnmark and Kola) and EC (Vesterålen and Lofoten). Estimates were based on the results of the NILS-95 sighting survey (Schweder *et al.* 1997).

SUBAREA	ABUNDANCE (N)	s	cv
ES	25,969	2,908	0.112
EB	56,330	7,651	0.136
EC	2,462	562	0.228

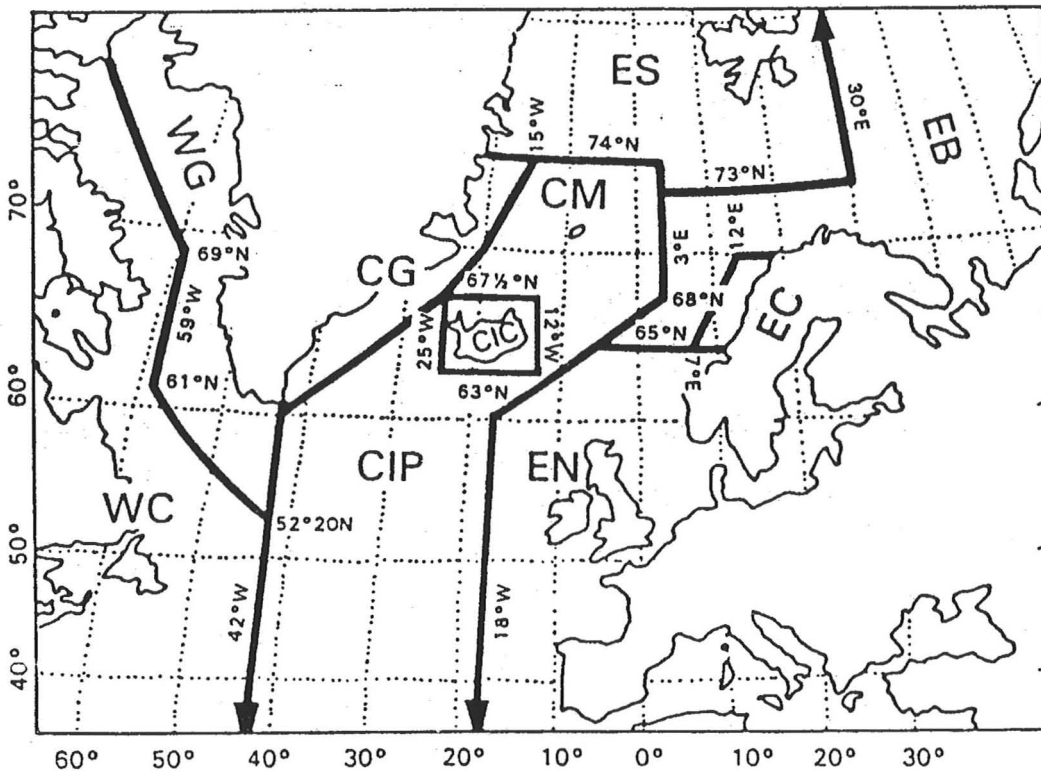


Fig. 2. Geographical subareas used in management of minke whales in the North Atlantic. The subareas included in the present study are ES (Spitsbergen and Bear Island), EB (Barents Sea and coastal areas of Finnmark and Kola) and EC (Vesterålen and Lofoten). From Anonymous (1993).

- Christensen 1981) and the rest, which were classified as immatures. Based on the size distribution of 223 animals caught during the 1992-1994 scientific whaling programme (see Haug *et al.* 1997a), 24% of the whales were assumed to be mature and 76% immature.
6. According to Christensen (1981), ca. 95% of all sexually mature females of the Northeast Atlantic stock of minke whales are pregnant annually. In our calculations, we have assumed that all physically mature females were pregnant. Based on the length distribution of immatures (Haug *et al.* 1997a) and unpublished data on body length vs pregnancy rates for 50 females (Erling S. Nordøy, unpublished data), we calculated that 25% of the physically immature females were also pregnant.
 7. Based on a length - mass relationship for minke whales caught in July/August (Folkow and Blix 1992), physically mature whales (assigned a body length of ≥ 8 m, under assumption 5) were predicted to have a body mass which averaged 5,900 kg (95 % CI, 4,800 to 7,000 kg) during the modelling period. The average body length of immatures of 7 m (Nordøy *et al.* 1995) was used in a similar way to predict an average body mass of 3,800 kg (95 % CI, 3,000 to 4,400 kg) for this group. Further, we assumed that the daily energy expenditure of matures was 80 kJ/kg (Blix and Folkow 1995), regardless of sex and season, i.e., 470,000 kJ/day for adults. The value was determined based on recordings of respiratory rates (Blix and Folkow 1995) and lung volumes (Folkow and Blix 1992) of minke whales, and on published respiratory data (tidal volume as a fraction of lung volume, and the fraction of oxygen in the lung that was taken up by blood) for other cetacean species (e.g., Wahrenbrock *et al.* 1974). The coefficient of variance (*cv*) of the value was estimated to be 0.25. Immatures were assumed to maintain elevated basal metabolic rates (BMR) due to growth. Growing mammals in general appear to maintain resting metabolic rates that are approximately twice as high as the BMR predicted according to Kleiber (1975) (e.g., Lavigne *et al.* 1986). The one existing study of metabolic rates in young, growing baleen whales (grey whales *Eshrichtius robustus*, see Wahrenbrock *et al.* 1974) indicates that this may be true also for these mammals. Therefore, we have assumed that immature minke whales maintain a field metabolic rate which corresponds to that of adults (i.e., 80 kJ/kg), plus a value corresponding to the BMR according to Kleiber (1975), to account for the fact that they were growing. In doing this, the resulting estimate of average daily energy expenditure of immatures was found to be 445,000 kJ/day (estimated *cv*=0.25).
 8. The average increase in muscle mass due to growth / replacement of muscle and deposition of fat in muscle, was assumed to be 350 kg (95% CI, 155 to 550 kg) for matures and 247 kg (95% CI, 100 to 400 kg) for immatures over a period of 112 days (based on data by Nordøy *et al.* 1995). The resulting growth rate was extrapolated to apply for a period of 180 days. Energy densities of muscle samples were lower in spring (5.4 kJ/g) than in summer and autumn (6.0 and 7.0 kJ/g, respectively; Nordøy *et al.* 1995), and we assumed that less energy was deposited as fat, and more as re-growth of skeletal muscle, in spring than in summer/autumn. Given the lower energy density of muscle fibers than of fat, the proportional increase in muscle mass would be expected to be higher in spring than during the rest of the feeding season, and 40% of the increase in muscle mass was therefore assumed to take place in spring, while the corresponding values for summer and autumn were both assumed to be 30%.
 9. Blubber deposition was assumed to amount to 208 kg (95% CI, 140 to 275 kg) in matures and 136 kg (95% CI, 80 to 195 kg) in immatures over a period of 112 days (based on data by Nordøy *et al.* 1995). The resulting rate of deposition was extrapolated to apply for a period of 180 days, and the deposition of blubber was assumed to take place with 20% occurring during spring, 30% during summer, and 50% during autumn. This was based on the assumption that more energy is deposited as muscle growth, and less as blubber, in spring than in autumn, and also that most prey species were more energy-rich in autumn than in

spring. The energy densities of deposited blubber were set at 27.5 ± 2.5 kJ/g during spring, and 30.6 ± 3.0 kJ/g during summer and autumn (Nordøy *et al.* 1995).

10. Visceral fat deposits were insignificant in animals caught in spring, but were substantial in animals caught in autumn. The visceral fat deposition was assumed to amount to 94 kg (95% CI, 75 to 112 kg) in matures and 63 kg (95% CI, 47 to 79 kg) in immatures, over a period of 112 days (based on data by Nordøy *et al.* 1995). The resulting rate of deposition was extrapolated to apply for a period of 180 days, and deposition of visceral fat was assumed to take place with 40% occurring during summer and 60% during autumn. The energy density of deposited visceral fat was assumed to be similar to that of blubber, i.e., 30.6 ± 3.0 kJ/g during both summer and autumn (Nordøy *et al.* 1995).
11. Foetal growth was assumed to result in a foetal body mass of 45 kg (95% CI, 38 to 53 kg) in mid-October (Nordøy *et al.* 1995), and the exponential growth was assumed to take place with 10% occurring in spring, 30% in summer and 60% in autumn. The energy density of the foetus was assumed to be constant (3.80 ± 0.14 kJ/g) during growth (Nordøy *et al.* 1995).
12. The sum of the energy expenditure and the energy deposited in muscle, blubber, visceral fat and foetus corresponds to the metabolizable energy (ME). ME was assumed to represent 92% of the digestible energy (DE), the remaining 8% being lost in the urine (Lavigne *et al.* 1982). DE, in turn, represents 92% of the gross energy intake (GEI), if assuming 8% of GEI was lost in the faeces (Nordøy *et al.* 1993, Mårtensson *et al.* 1994).
13. Data on seasonal changes in energy densities of prey were taken from Mårtensson *et al.* (1996). The energy densities of saithe *Pollachius virens* and haddock *Melanogrammus aeglefinus*, for which energy density data do not exist, were assumed to be similar to those of cod.
14. Finally, we assumed that all seasonally varying parameters (energy density of prey, blubber deposition, muscle growth, visceral fat deposition, foetal growth) changed in the same manner, regardless of latitude.

Determination of relative diet composition

Diet composition, classified according to sub-area and season, was estimated from data collected during sampling in 1992-1994 and 1995 (Haug *et al.* 1995a, Haug *et al.* 1995b, Haug *et al.* 1996a, Haug *et al.* 1996b). The 1992 diet data from area ES were excluded from the analyses due to the collapse in the capelin stock between 1992 and 1993 (see Hamre 1994, Gjøsaeter 1995). All diet composition data were based on reconstructed prey biomass in minke whale forestomachs (see Haug *et al.* 1995a, Haug *et al.* 1996a), and the prey organisms were grouped into the following 8 taxa: krill (*Thysanoessa* spp.), herring, capelin, cod, haddock, saithe, sandeel (*Ammodytes* sp.) and others. The diet composition was presented as percentage mass of each prey group using the individual mass index:

$$(Eq. 1) \quad WI_i = \frac{1}{n} \sum_{j=1}^n (b_{ij}/b_j) \cdot 100$$

where b_{ij} is the estimated biomass of prey group i in whale number j , b_j is the total mass of all prey groups in whale number j , and n is the total number of examined whales. Recorded masses of individual minke whale forestomach contents vary considerably (0-250 kg), presumably in relation to the feeding and digestive phases in which the whales were caught (see Haug *et al.* 1997a). By using this individual mass index, each forestomach is given the same importance irrespective of the prey mass contained.

Modelling procedure

The modelling procedure largely followed that outlined by Nordøy *et al.* (1995): Estimates of ME were made for four classes of animals (physically mature males, physically mature (pregnant) females, growing pregnant females, immatures) and for each of the three seasons (spring, summer and autumn) (Table 2). These ME values were then multiplied by the numbers of animals of each class within each of the three defined subareas. The ME values for all classes were summed for each season and area and the sums were converted to GEI values as described. The GEI values were inserted into Eq. 2, together with the calculated fractional proportions of the different prey items (i) in the diet (F_i , see Table 4) and the energy densities of the prey

items (E_i , see Table 5), and the equation was solved for the total consumed biomass (X), for each subarea and season:

$$\text{(Eq. 2)} \quad \text{GEI} = \Sigma(F_i \cdot E_i \cdot X).$$

RESULTS

Energy expenditure (for maintenance, locomotion, thermoregulation etc.) constituted the bulk (76-93%) of the energy requirement of whales in all groups (Table 2). During spring > 90% of ME was expended for these purposes in all groups. The proportion of energy deposited in foetus by pregnant females was very small (0.05-0.3%). The major proportions of energy storage occurred as blubber deposition, particularly in autumn when 56-58% of stored energy was deposited as blubber. In general, energy requirements were higher in autumn than in spring and summer.

Estimates of energy requirements (Table 3) and food consumption (Table 6) varied considerably between subareas, along with differences in minke whale abundance in different subareas. Thus, food consumption was greatest in subarea EB, due to the large number of whales present.

Assuming a point estimate of 84,761 minke whales in the subareas ES, EB and EC, their total food consumption in the period between 15 April and 15 October was estimated to amount to more than 1.8 million tonnes, of which 602,000 tonnes was krill, 633,000 tonnes herring, 142,000 tonnes capelin, 255,000 tonnes cod, 128,000 tonnes haddock and 54,500 tonnes other fish species, including saithe and sandeel (Table 6, Fig. 3).

The prey composition varied considerably both between periods and geographical subareas. The consumed biomass was larger in spring than in both summer and autumn. In the northernmost subarea (ES), the diet consisted mostly of krill, particularly during spring and summer when this food item made up 85% to 88% of the biomass consumed by the whales (Table 4). Capelin and cod were also important prey items in ES, at least during the autumn. Diet composition appeared to be more variable in subareas EB and EC than in subarea ES. Herring appeared to be

particularly important in subareas EB and EC, but while immature fish were taken in subarea EB, the whales in subarea EC consumed mature herring (Tables 3 and 5). In summer and autumn, herring constituted 58% to 96% of the consumed biomass in these two subareas (Table 6). In subarea EB, krill and capelin were taken in large amounts during spring, and sandeel during summer. Cod and haddock were consumed in considerable quantities in all periods.

DISCUSSION

Minke whales of the Northeast Atlantic represent one of the most euryphagous stocks of baleen whales (Haug *et al.* 1995a, Haug *et al.* 1996a), but the bulk of their diet is comprised of relatively few species. Krill and herring, the two most prominent prey items in the diet, were consumed in approximately equal amounts. Together, these two prey species accounted for 68% of the total biomass eaten. Gadoids (cod, haddock and saithe) represented 21%, and capelin 8% of the consumed biomass. Recent studies of minke whales have revealed dietary heterogeneity between years, presumably as a result of changes in prey resources in the feeding areas of the whales (Haug *et al.* 1995b, Haug *et al.* 1996a, Haug *et al.* 1997b). Thus, the temporal distribution of consumption of different prey items is dynamic, and the results presented here represent an annual average for the period 1992-1995. It is important to emphasise that the presented calculations, yielding a total annual consumption of approximately 1.8 million tonnes of biomass for the period in question, were based on single point estimates for several parameters where variation certainly occurred, including the estimate of minke whale abundance. By including the quantified 95% confidence limits of the abundance estimates (see Schweder *et al.* 1997) into the present consumption calculations, the estimated annual consumption by the stock would fall within a range of approximately 1.4 to 2.1 million tonnes of biomass.

The finding that herring was the species consumed in largest amounts is supported by the results of previous studies suggesting that herring may be the most preferred prey item for Northeast Atlantic minke whales (Haug *et al.* 1996a, Skaug *et al.* 1997). Simulations run using

Table 2. Estimates of metabolizable energy requirements (ME, the sum of expended and deposited energy, given in kJ) of one individual from each of four groups of Northeast Atlantic minke whales during spring, summer and autumn. See text for explanations of how whale groups and seasons were defined, and of assumptions on which the calculations were based.

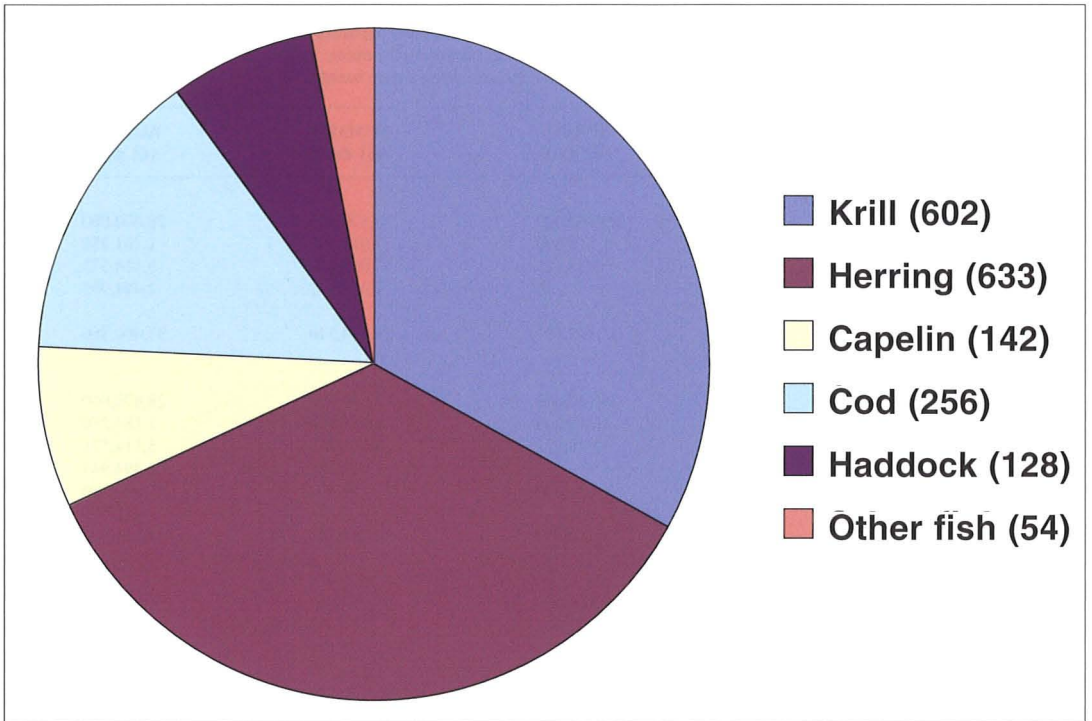
	SPRING (62 days)	SUMMER (61 days)	AUTUMN (61 days)
PHYSICALLY MATURE MALES			
Energy expenditure	29,140,000	28,670,000	28,670,000
Muscle growth/replacement	1,215,000	1,012,500	1,181,250
Blubber deposition	1,838,571	3,068,743	5,114,571
Visceral fat deposition	0	1,663,297	2,494,945
Sum ME	32,193,571	34,414,540	37,460,766
PHYSICALLY MATURE FEMALES			
Energy expenditure	29,140,000	28,670,000	28,670,000
Muscle growth/replacement	1,215,000	1,012,500	1,181,250
Blubber deposition	1,838,571	3,068,743	5,114,571
Visceral fat deposition	0	1,663,297	2,494,945
Foetal growth	17,000	50,000	100,000
Sum ME	32,210,571	34,464,540	37,560,766
PREGNANT GROWING FEMALES			
Energy expenditure	27,663,000	27,217,000	27,217,000
Muscle growth/replacement	857,443	714,536	833,625
Blubber deposition	1,202,143	2,006,486	3,344,143
Visceral fat deposition	0	1,114,763	1,672,144
Foetal growth	17,000	50,000	100,000
Sum ME	29,739,586	31,102,785	33,166,912
IMMATURES			
Energy expenditure	27,663,000	27,217,000	27,217,000
Muscle growth/replacement	857,443	714,536	833,625
Blubber deposition	1,202,143	2,006,486	3,344,143
Visceral fat deposition	0	1,114,763	1,672,144
Sum ME	29,722,586	31,052,785	33,066,912

Table 3. Estimates of the energy expenditure (ME) of four different groups of Northeast Atlantic minke whales during spring, summer and autumn in the three subareas ES (Spitsbergen and Bear Island), EB (Barents Sea and coastal areas of Finnmark and Kola) and EC (Vesterålen and Lofoten). Numbers of whales allocated to each subarea are based on estimates from the 1995 sighting survey. Total gross energy intake (GEI) was calculated from ME data for the whale population in each subarea and season. N = number of whales. All energy values are given in 10¹⁰ kJ.

	N	SPRING	SUMMER	AUTUMN
Subarea ES				
Mature males	2,855	9.2	9.8	10.7
Mature females	3,378	10.9	11.7	12.7
Pregnant growing females	2,674	8.0	8.3	8.9
Immatures	17,062	50.7	53.1	56.3
Total number of whales	25,969			
Sum ME		78.8	82.9	88.6
Total GEI		93.2	98.0	104.8
Subarea EB				
Mature males	6,192	19.9	21.3	23.2
Mature females	7,328	23.6	25.3	27.5
Pregnant growing females	5,800	17.2	18.0	19.2
Immatures	37,010	110.0	114.9	122.4
Total number of whales	56,330			
Sum ME		170.7	179.5	192.3
Total GEI		201.0	212.0	227.0
Subarea EC				
Mature males	271	0.9	0.9	1.0
Mature females	321	1.0	1.1	1.2
Pregnant growing females	253	0.8	0.8	0.8
Immatures	1,617	4.8	5.1	5.4
Total number of whales	2,462			
Sum ME		7.5	7.9	8.4
Total GEI		8.8	9.3	10.0

Fig. 3.

Consumption of various prey items (in 1000 tonnes) by Northeast Atlantic minke whales in subareas ES, EB and EC in Norwegian and adjacent waters during a 180 days feeding period.



the Barents Sea multispecies model (MULT-SPEC) indicate that a minke whale consumption of herring of the magnitude reported in the present study is likely to affect the long term yield of the Norwegian spring-spawning herring stock (Bogstad *et al.* 1997). The spawning stock biomass of Norwegian spring-spawning herring was estimated to be approximately 3.9 million tonnes in 1995 (Anonymous 1996b), and the estimated annual consumption by minke whales (633,000 tonnes) corresponds to approximately 70% of the fishery for this stock in 1995 (902,226 tonnes, Anonymous 1996a).

Minke whale consumption of herring was almost exclusively confined to subareas EC and EB. Herring consumed in area EC were adult fish. Numbers of adult herring have increased in this area during late summer and autumn as a result of the gradual rebuilding of the stock after the collapse around 1970 (Røttingen 1990, Røttingen 1992). However, only 3% of the total consumption of herring took place in area EC, while 96% occurred in area EB, where immature fish were eaten. The southern Barents Sea has served as the main nursery area for immature herring (0-group and recruits up to 3-4 years old) since 1988 (Røttingen 1990, Hamre 1994, Gjøsaeter 1995). Improvements in herring

recruitment from 1988 onwards have increased the abundance of adolescent herring in minke whale feeding areas in the southern Barents Sea. The particularly strong 1991 and 1992 cohorts (Anonymous 1996a, 1996b) may explain the dominant role of immature herring in the minke whale diet in 1992-1995. However, during 1995 most of the herring of the 1991 and 1992 cohorts migrated westwards out of the Barents Sea, and since the 1993-1995 year classes of herring were rather weak (Anonymous 1996b), a reduction in the reliance on immature herring as prey might be expected. Results of dietary analyses carried out on minke whales sampled in 1996 support this (Haug *et al.* 1997b): herring was a less prominent component of the diet of Northeast Atlantic minke whales in 1996 than in the years 1992-1995.

Consumption of krill by minke whales was most pronounced in the northernmost area (ES). The prominent role of krill in the northern area seems to be consistent with the current status of the Barents Sea ecosystem: from 1992 onwards there has been a low abundance of capelin and an increase in zooplankton (Anonymous 1996b). In fact, a predator-prey interrelationship between planktivorous capelin and krill has been suggested for the area, where populations of the latter to

Table 4. Pooled data on the relative contribution of various prey species (in biomass) to the diet of Northeast Atlantic minke whales in subareas ES (Spitsbergen and Bear Island), EB (Barents Sea and coastal areas of Finnmark and Kola) and EC (Vesterålen and Lofoten) during spring, summer and autumn. The data are based on stomach content analyses of 223 whales taken in the period 1992-1995. N = number of whales studied.

SEASON	YEARS	N	KRILL	HERRING	CAPELIN	COD	HADDOCK	SAITHE	SANDEEL	OTHER
AREA ES										
Spring	93/94/95	22	87.8	0	0.3	8.8	3.0	0	0	0
Summer	93/94	43	85.7	0.1*	4.4	7.5	2.3	0	0	0
Autumn	93/94	14	41.3	2.8*	35.1	20.7	0	0	0	0
AREA EB										
Spring	93/94/95	27	25.2	35.1*	13.7	15.6	10.2	0	0	0.3
Summer	92/93/94	51	5.0	58.4*	3.7	10.5	7.0	0.2	15.0	0.2
Autumn	93/94	10	0	70.1*	0	19.4	10.3	0	0	0.2
AREA EC										
Spring	93/94	8	0	21.2**	0	21.9	46.5	10.3	0	0
Summer	92/93/94	31	3.5	60.4**	3.2	3.0	4.6	15.8	9.3	0.2
Autumn	93/94	17	0	96.6**	0	1.5	1.1	0	0.8	0
* Only immature fish										
** Only mature fish										

Table 5. Energy densities (in kJ/g) of prey species of Northeast Atlantic minke whales in spring, summer and autumn. Number of prey samples are given in parentheses. The values were derived from data presented by Mårtensson *et al.* (1996).

PREY SPECIES	SEASON		
	SPRING	SUMMER	AUTUMN
Krill	2.97 (3)	5.8 (2)	5.53 (6)
Herring (mature)	6.36 (5)	12.7 (2)	11.9 (2)
Herring (immature)	4.6 (3)	7.9 (2)	6.48 (4)
Capelin	5.4 (4)	5.72 (4)	7.72 (5)
Cod	5.17 (3)	4.15 (2)	4.54 (5)
Haddock*	5.17	4.15	4.54
Saithe*	5.17	4.15	4.54
Sandeel**	6.0 (2)	6.0	6.0
Others***	6.0	6.0	6.0
* Energy density values for haddock and saithe are unavailable - they were set equal to those of cod.			
** Energy density values for sandeel are only available from spring. This value was assumed to apply also during the summer and autumn.			
*** Minke whale diets also included a small group of various prey items for which energy density data were not available - for simplicity these were set equal to the values for sandeel.			

a large extent are controlled by predation by the former (Dalpadado and Skjoldal 1996). Capelin appeared to be important as prey for the minke whales in the northernmost area in 1992, whereas, following the collapse of the Barents Sea capelin stock between 1992 and 1993 (Hamre 1994, Gjøsæter 1995), capelin was replaced by krill (Haug *et al.* 1996b, Haug *et al.* 1996a). These dramatic changes led us to exclude data for 1992 from the present analyses of food consumption by minke whales in area ES. There is some evidence that krill is a less preferred prey than herring and capelin (Haug *et al.* 1996a, Skaug *et al.* 1997), so it is to be expected that the importance of capelin will increase (from its

present consumption level of 142,000 tonnes) as the capelin stock recovers. In 1995, the Barents Sea capelin stock was at an all-time low level, with a total estimate of 195,000 tonnes (of which 120,000 tonnes were maturing) and with very poor year classes being produced in 1993, 1994 and 1995 (Anonymous 1996b). The Barents Sea capelin has been protected from fisheries since autumn 1993.

Analyses of the diet of Northeast Atlantic minke whales have revealed that cod and haddock may be less preferred prey than herring and capelin (Haug *et al.* 1996a, Skaug *et al.* 1997). Nevertheless, large amounts of commercially

Table 6. Estimated prey consumption (in tonnes) of Northeast Atlantic minke whales by prey species, geographical subarea (ES=Spitsbergen and Bear Island; EB=Barents Sea and coastal areas of Finnmark and Kola; EC=Vesterålen and Lofoten) and season.

SEASON	CONSUMPTION OF								
	KRILL	HERRING	CAPELIN	COD	HADDOCK	SAITHE	SANDEEL	OTHERS	TOTAL
AREA ES									
Spring	253,207	0	863	25,235	8,642	0	0	0	288,075
Summer	148,988	174*	7,650	13,034	3,998	0	0	0	173,848
Autumn	70,845	4,798*	60,217	35,526	0	0	0	0	171,387
AREA EB									
Spring	113,596	158,182*	61,771	70,314	45,993	0	0	1,353	451,209
Summer	15,675	183,096*	11,599	32,919	21,946	627	47,027	627	313,518
Autumn	0	269,574*	0	74,604	39,610	0	0	771	384,559
AREA EC									
Spring	0	3,452**	0	3,568	7,584	1,677	0	0	16,280
Summer	338	5,834**	308	290	443	1,525	899	20	9,658
Autumn	0	8,251**	0	127	93	0	68	0	8,540
TOTAL, ALL AREAS AND SEASONS									
	602,649	633,361	142,408	255,622	128,309	3,829	47,994	2,771	1,817,074
* Only immature fish ** Only mature fish									

important gadoids are eaten by the whales. Cod seems to serve as an important supplement to the more preferred species, both in subarea EB and ES. The estimated annual consumption of Northeast Arctic cod by minke whales in the period 1992-1995 (255,000 tonnes) was substantial when compared both with total fisheries (735,100 tonnes in 1995) and estimated total stock biomass (age 3 and older) which was 2 million tonnes in 1995 (Anonymous 1996c). The estimated consumption of haddock was approximately half that of cod (128,000 tonnes), the majority of the haddock being taken in subarea EB. The consumption of haddock was also large compared with the 1995 fisheries and total stock biomass (142,500 and 400,000 tonnes, respectively; Anonymous 1996c). The third gadoid species eaten by the whales, saithe, was mainly consumed in subarea EC, but the amounts taken were small. The estimated consumption rates of haddock and saithe are not as accurate as for the other species, since data on energy densities of these species were lacking. We do not think they

are far off the mark, however, since these gadoids are very likely to have energy densities close to those of cod, which were the values used in the present study.

Sandeel was consumed in some quantity during the summer, and in the summer of 1992, sandeel was found to be particularly important as food for minke whales in the southeastern parts of the Barents Sea (Haug *et al.* 1995a). Sampling could not be carried out in these areas in 1993 and 1994 (Haug *et al.* 1996a), possibly leading to some underestimation of the importance of sandeel as prey.

There were large seasonal differences in food consumption by minke whales. Spring was consistently the period of largest biomass intake, due to the low energy density in prey during this period of the year (i.e., the whales must eat larger quantities of biomass to obtain a given amount of energy). By autumn, the transfer of phytoplankton lipids upwards in the food chain (see

Falk-Petersen *et al.* 1990) had contributed to a substantial increase in the energy densities of species at higher trophic levels (Mårtensson *et al.* 1996). The apparent lower minke whale feeding rate in summer and fall as compared with spring was, therefore, compensated by the increased prey energy density. In fact, the greatest energy deposition in minke whales occurs late in the feeding season (in fall, see Næss *et al.* 1998), probably reflecting the time needed for the trophic system to transfer energy from primary producers to top predators. Similar patterns, with autumnal deposition of energy (lipids), have been observed for the harp seal *Phoca groenlandica*, another important top predator in the Barents Sea ecosystem (Nilssen *et al.* 1997).

We have assumed that the results of the July-August 1995 sighting surveys in the Northeast Atlantic (see Schweder *et al.* 1997) described the distribution of the whales amongst the three sub-areas throughout the 180 days feeding period. Obviously, the distribution of the whales is expected to change from April to October (see Jonsgård 1951, Haug *et al.* 1996a), but the results of the surveys are the only quantitative information available. The assumption of a constant distribution through time obviously introduces some bias into the results. For example, during the autumnal migration the whales pass through the EC subarea and may feed on the adult herring in the area. As a result, the consumption of adult herring may have been underestimated.

The estimated food consumption rates in the present study are associated with uncertainties other than those mentioned above. For example, our assumptions concerning the duration of the feeding period in northern waters made it necessary to extrapolate from data (e.g., on energy deposition due to body and foetus growth and fat deposition, as well as on energy densities of prey species) that were collected within more narrow time frames, which introduces some uncertainties. Moreover, the estimate of energy expenditure used by us was made through indirect calculations of oxygen consumption rates, based on measurements of respiratory rates in freely swimming minke whales, on their lung capacities (determined in newly killed animals), and on literature data on respiratory variables for other

cetaceans (Blix and Folkow 1995), all factors obviously being associated with uncertainties. An assessment of the uncertainty associated with the energy expenditure estimate is particularly relevant, given its large influence on the energy requirements of these mammals, and, hence, on the estimated food consumption rates of the stock. The estimated uncertainty was found to be relatively low (CV of about 0.25), which reflects, in particular, the very small variations in respiratory rates observed in these mammals (Blix and Folkow 1995). When considering potential sources of errors, it should also be kept in mind that energetic studies of large and unmanageable baleen whales, particularly freely swimming ones, are inherently difficult, for very obvious reasons. We were reassured, however, by the fact that the estimate of energy expenditure rates of adult minke whales was found to correspond to approximately 2.2 times their estimated basal metabolic rate (Blix and Folkow 1995). This value is in accordance with the results from much more detailed studies of the energy expenditure of freely swimming adults/subadults of other marine mammal (pinniped) species, in which values corresponding to 2 - 3 times their basal metabolic rate have been reported (e.g., Lavigne *et al.* 1982, Markussen *et al.* 1990, Castellini *et al.* 1992, Lager *et al.* 1994). Moreover, estimated energy requirements for whales belonging to different age and reproductive groups differed by only about 10%, which suggest that our food consumption estimate is not particularly sensitive to potential errors with regard to the grouping of animals.

Erroneous assumptions concerning both diet composition and energy densities in prey species may have biased the results of the calculations, but sensitivity analyses were not performed to assess the possible influence of such errors. Shelton *et al.* (1997) attempted to quantify uncertainties associated with population size, residency, energy requirements and diet composition in Northwest Atlantic harp seal consumption estimates. They concluded that improved precision in consumption estimates would be obtained by improving knowledge on the diet composition, but this would not necessarily pertain to all prey groups. Uncertainty in population size was the smallest contributor to uncertainty concerning consumption rates (Shelton *et al.* 1997). To conclude the discussion of uncertain-

ties, we trust that our data represent the best available estimate of the food consumption of this stock, and that, in light of this, our many assumptions are justified.

Markussen *et al.* (1992) estimated the food consumption of the Northeast Atlantic minke whale stock to be 2.2 million tonnes of biomass. These authors used a simulation model in which they assumed that the consumption took place during a 5 month stay of a stock of 77,000 animals (point estimate) in Northeast Atlantic waters. The lack of quantified uncertainty in both the previous (2.2 million tonnes) and present (1.8 million tonnes) consumption estimate clearly calls for caution in any comparison. Nevertheless, it appears that considerable differences in assumptions may explain some of the discrepancy between estimates. Markussen *et al.* (1992) assumed that minke whales cover 90% of their estimated annual energy requirements during their summer stay in northern waters (by deposition of fat which is then mobilized and utilized as an energy source during the following winter). A similar strategy has been postulated for other northern hemisphere baleen whales (Lockyer 1987, Vikingsson 1995). Information on daily energy expenditure, the amount of energy deposited as fat, and growth of muscles and foetus seems to indicate that Northeast Atlantic minke whales would be unable to survive the winter on energy stores built up during the summer alone (see Nordøy *et al.* 1995). Our conclusions imply that these whales also feed on available sources in their wintering areas at lower latitudes and/or that parts of the stock remain on the feeding grounds at high latitudes for longer periods than the assumed 180 days, for some individuals perhaps even throughout the whole year. Data presented by Vikingsson (1995) show that the extent to which energy is deposited may differ considerably between reproductive classes in fin whales *Balaenoptera physalus*, and that these differences may relate to the latitudinal distribution of animals in various seasons. We were unable to detect similarly large reproductive class differences in energy deposition in Northeast Atlantic minke whales. Nevertheless, we believe that the food consumption rates predicted by Markussen *et al.* (1992) are overestimated, primarily due to assumptions concerning the seasonal migration/feeding strategies of minke whales.

In conclusion, results of the present study suggest that minke whales consume substantial amounts of food in Northeast Atlantic waters, and that their consumption of commercially exploited species such as herring and cod is large enough to be a concern for fisheries management. Refined estimates of the consumption of marine resources by minke whales in the Northeast Atlantic will require the collection of reliable data about the residency and diet of these mammals throughout the year.

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