

# Stomach contents of sperm whales *Physeter macrocephalus* stranded in the North Sea 1990–1996

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**ABSTRACT:** Stomach contents of 17 sperm whales *Physeter macrocephalus* stranded in Scotland and Denmark during 1990–96 were analysed. All were sub-adult or adult males and stranded between November and March. They had presumably entered the North Sea during their southward migration from feeding grounds in Arctic waters. Other studies indicate that the majority of the whales were apparently healthy. The diet of these whales was found to consist almost entirely of cephalopods, principally squid of the genus *Gonatus* (hereafter '*Gonatus*', but probably *G. fabricii*, an oceanic species characteristic of Arctic waters). The other prey species identified were also mostly oceanic cephalopods: the squids *Histioteuthis bonnellii*, *Teuthowenia megalops* and *Todarodes sagittatus* and the octopus *Haliphron atlanticus*. Although these results are consistent with other recent studies in the area based on single stranded whales, they differ from results of work on whales caught during commercial whaling operations in Icelandic waters (1960s to 1980s) in that little evidence of predation on fish was found in the present study. Remains of single individuals of the veined squid *Loligo forbesi*, the northern octopus *Eledone cirrhosa* and the saithe *Pollachius virens* provided the only possible evidence of feeding in the North Sea. We infer that sperm whales do not enter the North Sea to feed. The timing, and large and uniform sizes of the *Gonatus* species eaten (most had mantle lengths in the range 195 to 245 mm), as estimated from measurements of the lower beaks, and the seasonality of the strandings is consistent with the whales having fed on mature squid, possibly spawning concentrations—as has recently been reported for bottlenose whales. Assuming that the diet recorded in this study was representative of sperm whales during the feeding season, as much as 500 000 t of *Gonatus* could be removed by sperm whales in Norwegian waters each year and up to 3 times that figure from the eastern North Atlantic as a whole. Evidence from other studies indicates that *Gonatus* is an important food resource for a wide range of marine predators in Arctic waters.

**KEY WORDS:** Feeding ecology · Cetacea · Stranding · *Gonatus* · Cephalopoda

## INTRODUCTION

Sperm whales *Physeter macrocephalus* L. are the largest toothed whales (Odontoceti), reaching lengths up to 18.3 m (Rice 1989). They are found in deep waters of all oceans, from the equator to the edges of the polar pack ice. Sperm whales are able to dive longer and deeper than any other cetacean. Dives last-

ing 60 to 90 min are frequently reported in the literature (Rice 1989) and there is evidence of dives down to 2000 m or more (Heezen 1957, Norris & Harvey 1972, Clarke 1976, Rice 1978).

The social organisation of sperm whales is unique and complex. There is seasonal segregation of the sexes, with females and calves usually remaining in low latitudes all year round (Best 1979). In the northern hemisphere females and calves do not normally travel to latitudes above 40° to 45° N (Berzin 1971), although

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there are occasional records from the North Atlantic (Harmer 1917, Fraser 1974, Berrow & Rogan 1997, Smeenk 1997). 'Bachelor' and mature males undertake migrations to higher latitudes in spring/summer. In the northern hemisphere, they leave warm waters at the beginning of summer to reach feeding grounds on the perimeter of the polar zone, returning again in winter. During this southward migration, sperm whales are rarely seen on the continental shelf of the North Sea. More commonly they travel from the deep waters around Norway, Iceland and Greenland through the Rockall Trough (west of the British Isles) and the deep ocean basins west of the Iberian Peninsula (Smeenk & Addink 1993).

There are no accurate figures for the total number of sperm whales in the world. Prior to modern (20th century) whaling, the world population of sperm whales is estimated to have been around 3 million and to have been reduced to less than 2 million (Rice 1989). Figures for the North Atlantic specifically are similarly uncertain. Gambell (1976) estimated a total population size of around 22 000 sperm whales in the Atlantic. The 1982 Report of the International Whaling Commission (IWC) Sub-Committee on Sperm Whales gave tentative figures for the initial and current population of sperm whales in the North Atlantic (Gosho et al. 1984). Gunnlaugsson & Sigurjónsson (1990) and Sigurjónsson & Víkingsson (1992) gave more recent figures for the North Atlantic (9645 whales north of 50° N).

Early studies of sperm whale diets made use of whales killed commercially and mainly consisted of analyses of single stomachs or observations of the food remains regurgitated by the whales after being harpooned (Beale 1839, Bennet 1840, Buchanan 1896, Millais 1906, Clarke 1956; see Berzin 1971 for a review). Studies carried out during the main period of commercial whaling in the 20th century, based on substantial sample sizes, provided extensive information on diets and feeding ecology throughout the world (see Kawakami 1980 and Rice 1989 for reviews).

Few of the early studies included any quantitative analysis of the food remains, but some areas (e.g. the Pacific) were studied in more detail than others. The results of these studies showed that, as a general rule, cephalopods are the most important food category, followed by fish (Kawakami 1980). Diet composition of sperm whales has been found to vary between regions, months, seasons and years, as well as between sexes and in relation to age or body length (Matthews 1938, Mizue 1951, Betesheva 1960, 1961, Tarasevich 1963, Berzin 1971, Clarke 1980, Kawakami 1980, Mikhalev et al. 1981, Rice 1989). Most studies have recorded squid as the most commonly eaten cephalopods, although octopods have also been found, typically in whales caught in coastal waters (Berzin 1971).

Sperm whales are recorded as taking a significant proportion of fish in their diet in North Atlantic and Arctic waters. Fish are recorded in sperm whale diets in some of the earliest studies from this area (Haldane 1905, Millais 1906, Murray & Hjort 1912). In larger-scale studies, Roe (1969) and Martin & Clarke (1986) found fish to be the most numerous prey of male sperm whales caught off Iceland. Fish were also found to be important in the diet of sperm whales captured along the Gulf of Alaska and in the east Bering Sea (Okutani & Nemoto 1964).

Following the IWC moratorium on all sperm whaling in 1985, most recent studies have been based mainly on analyses of stomach contents from single stranded whales (Clarke et al. 1980, Dong 1984, Pascoe et al. 1990, Viale et al. 1992, Ostrom et al. 1993, González et al. 1994, Lick et al. 1995, Clarke 1997, Clarke & Pascoe 1997). Additionally, faecal samples have been collected from live sperm whales (Papastavrou et al. 1989, Whitehead et al. 1989, Smith & Whitehead 1993, Whitehead 1996) and stable isotope ratios have been used to make inferences about feeding (Ostrom et al. 1993). There has been no large-scale study of sperm whale diets in Northern waters since Martin & Clarke (1986).

Remains of sperm whales have been found in archaeological sites in Orkney dating from as early as the 9th or 10th century (Turner 1871) and strandings of this species in Northern Europe have been recorded in the literature since the 16th century (Smeenk 1997). The distinctive head and teeth of sperm whales, together with their size, make them one of the best-reported whale species (Evans & Scanlan 1989). Most of the stranded whales for which sex has been determined have been adult or sub-adult males, but there have been a few cases of juveniles and one female stranding (Harmer 1917, Fraser 1974, Berrow & Rogan 1997). Some stranding events have apparently involved whole groups of males (e.g. 11 males stranded in Orkney in December 1994 and 16 in Denmark in March 1996). The number of sperm whales stranded annually on North Sea coasts appears to have risen dramatically in the last 10 to 15 yr. In 1988 and 1990, recorded strandings in the area reached double figures for the first time this century. In 1994, 27 sperm whales were stranded. A further 25 strandings were recorded in 1996 (see Smeenk 1997 for a review of historical trends).

Recent single and mass strandings of sperm whales in Scotland and Denmark between 1990 and 1996 provided a unique opportunity to study the diet in an area for which few recent data are available and to compare the results from stranded whales with results from whales studied during whaling activities off Iceland in the 1960s to 1980s.

In addition to describing and quantifying the diet, we address the question of whether sperm whales enter the North Sea to feed. We also estimate the amounts of different prey species eaten by sperm whales during the summer feeding season.

## METHODS

**Sample collection.** All the sperm whales stranded in the Northeast Atlantic analysed in this study were males. The stranding locations are indicated in Fig. 1 and full details of total length, age, blubber thickness, etc. are given in Table 1. It was not possible to examine the whole gut of any of the whales since it was necessary to work alongside the local authorities responsible for disposing of the carcasses, who permitted opening of the carcasses only immediately before burial. Information on the age of the whales, based on growth increments in the teeth, was provided by Dr C. Lockyer.

Samples of the stomach contents from the sperm whales stranded in Denmark were collected under the auspices of the Danish Stranding Network run by the Fisheries and Maritime Museum of Esbjerg, the Zoological Museum, University of Copenhagen and the Danish Ministry of Environment and Energy.

No material could be obtained from other strandings during this period. No stomach contents were found in 4 sperm whales stranded in Belgium during 1994 (Thierry Jauniaux pers. comm.). A sperm whale stranded on 31 March 1997 in the Firth of Forth (Scotland) was fully dissected by staff at the Royal Scottish Museum but its stomach was reported to be empty (J. Herman pers. comm.).

**Diet analysis.** Cephalopod beaks were identified using published guides (Clarke 1980, 1986, Pérez-Gándaras 1986) and a reference collection of oceanic cephalopod beaks. Standard measurements were taken on the lower beaks—rostral length (LRL) for decapods and hood length (LHL) for octopods (Clarke 1980, 1986), using either callipers or a binocular microscope

Fig. 1. Northeast Atlantic and North Sea showing the locations of strandings in the present study, the distribution of *Gonatus lacricii* including known spawning areas. Latitude and longitude are shown in degrees and the 200 m depth contour is indicated by the dashed line. The shaded areas show (Area 1) the distribution of *Gonatus* as reported by Kristensen (1983) and (Area 2) the extension to the distribution proposed by Børke (1995). Areas A–D mark the spawning areas proposed by Wiborg (1979): (A) west of Svalbard, (B) between Iceland and Jan Mayen, (C) off Vesterålen and (D) off Møre. Sites of recent strandings (1–9, after Smeenk 1997) are also marked: (1) Sanday, Orkney Islands, (2) Nairn, (3) Cruden Bay, (4) Firth of Forth, (5) Koksijde and Nieuwpoort, (6) Rømø Island, (7) Fanø, (8) Nymindegab and (9) Skagen

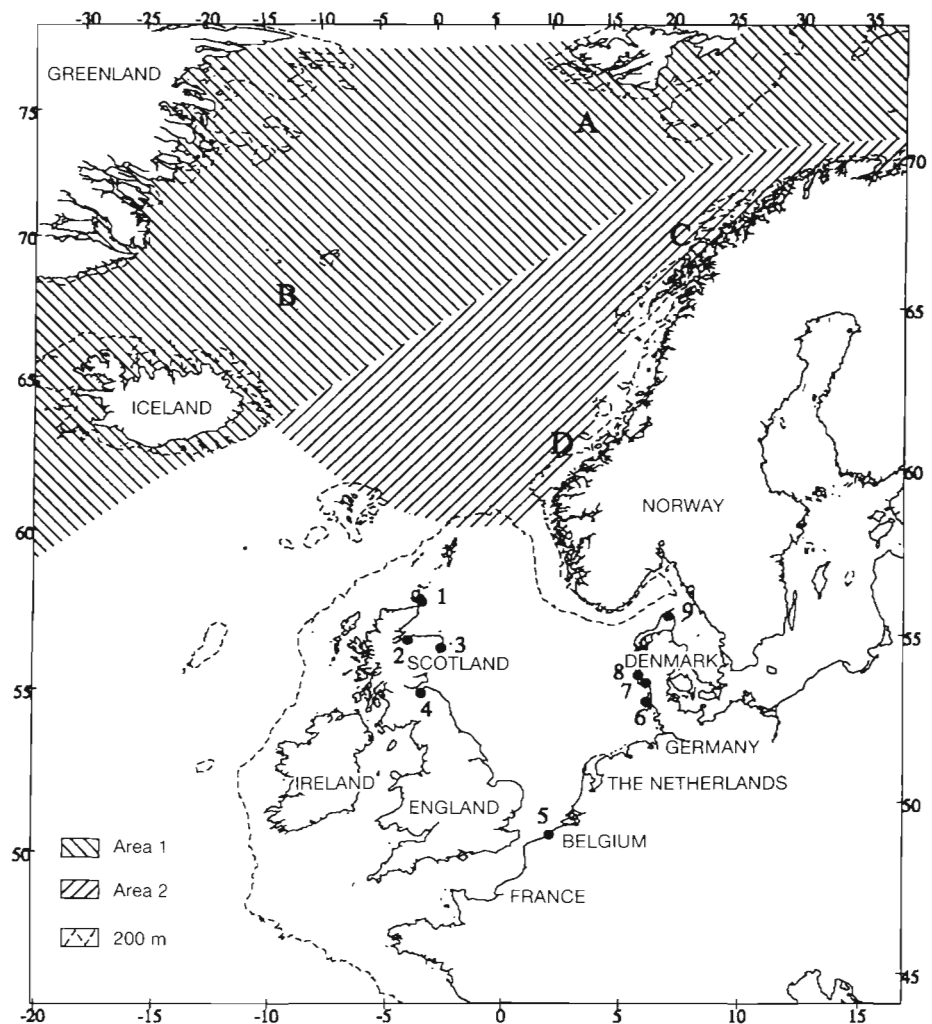


Table 1 *Physeter macrocephalus*. Stranding events in the Northeast Atlantic 1990 to 1996 from which stomach contents were analysed and stranding events during the same period in which stomachs were reported to be empty. Dates given as d/mo/yr

Country	Date	Place	No. of whales	Samples collected	Length (m)	Age (yr)	Blubber thickness (mm)
Scotland	07/12/94 <sup>a</sup>	Orkney Islands	11	4	12–13.4	20–25	95–135
	23/03/95	Nairn	1	1	13.7	20–25	
	28/01/96 <sup>a</sup>	Cruden Bay	6	5	12.1–13.75	20–25	120–140
	31/03/97	Firth of Forth	1	0 <sup>b</sup>	15.20	42	
Denmark	17/11/90	Nymindegab	1	1	11.85		
	01/12/91	Fanø	1	1	11.73		
	25/01/96	Skagen	1	1	13.10		
	27/03/96 <sup>a</sup>	Rømø Island	16	4	11.75–13.2	20–34	
Belgium	18/11/94 <sup>a</sup>	Koksijde	3	0 <sup>b</sup>	14.4–15.4	22–28	150–160
	18/11/94	Nieuwpoort	1	0 <sup>b</sup>	18.2	>29	150

<sup>a</sup>Mass stranding (i.e. involving more than 2 whales)  
<sup>b</sup>No food remains were found in stomachs

fitted with an eyepiece graticule. All the undamaged lower beaks found were measured, except in 2 cases when random sub-samples of *Gonatus* sp. beaks were measured (1000 beaks measured from 2351 and 981 beaks measured from 4549 respectively). In both cases the running mean of the measurements was plotted against the number of beaks measured and it was found to have stabilised at approximately 200 beaks (Fig. 2) so the sample measured is thought to be adequate. Mantle length (ML) and body weight of cephalopod prey were estimated from lower beak measurements, using regressions from Clarke (1986). For *Haliphron atlanticus* we had insufficient reference material to construct a regression relating LHL and body weight, and the size was therefore estimated based on comparison with the size of beaks of reference specimens. In *Todarodes sagittatus*, maturity can be

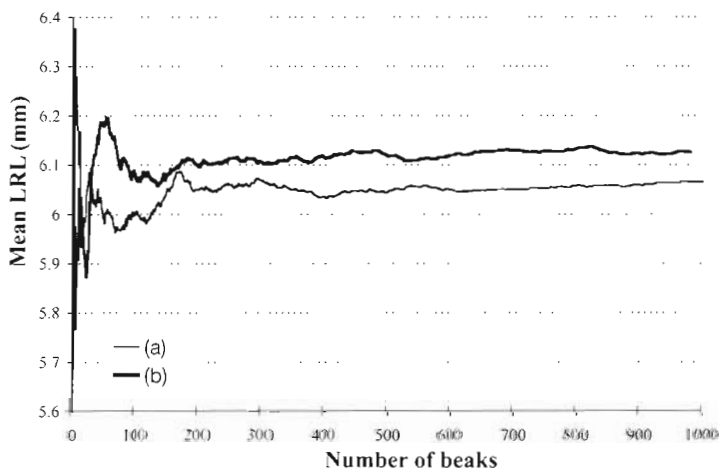


Fig. 2. Running mean of lower rostral length (LRL) of *Gonatus* sp. plotted against number of beaks measured for (a) Whale 3 from the Orkney mass stranding and (b) Whale 305 from the Cruden Bay mass stranding

inferred from the lower beaks: those with pigmented wings correspond to maturing or mature squid (Hernández-García & Piatkowski 1998). A single fish bone found in one stomach was identified by comparison with reference material and the original fish size was estimated using a regression derived from 15 specimens of that species in the reference collection.

The total number of individuals of each cephalopod species present in a stomach was estimated as the number of lower or upper beaks (whichever was higher). The total weight represented by the beaks of each species in each stomach was estimated as  $(\text{sum of weights represented by beaks measured})/(\text{proportion of individuals measured})$ .

Overall diet composition was calculated by summing the weights of all prey from each set of samples and expressing the weight of each species as a proportion of that total. Thus, each whale contributes to the overall diet in proportion to the total prey weight in its stomach.

#### Estimation of population food consumption.

Data on diet were used to derive crude estimates of total cephalopod consumption by the population. Length estimates were obtained for 48 sperm whales stranded in the area over the period of this study (including the 42 whales in Table 1; additional data from Kompanje & Reumer 1995, Lick et al. 1995, E. Rogan pers. comm.). These data were assumed to be representative of the North Atlantic 'population'. For each whale, body weight ( $W$ , kg) was estimated from length ( $L$ , m) using Lockyer's (1991) regression equation:  $W = 0.0218L^{2.74}$ . Although derived from a small sample of whales (44) from the North Pacific and Antarctic, this remains the best available regression.

Sergeant (1969) and Lockyer (1981) estimated the amount of food consumed by sperm whales to be 3 to 3.5% of their body weight per day. We used the median value of 3.25% of average body weight. Alternative calculations were based on Sigurjónsson & Víkingsson's (1992) equation for daily energy requirements ( $E$ , kcal d<sup>-1</sup>):  $E = 206.25 W^{0.783}$ . Energy densities are not available for all the prey species (see Croxall & Prince 1982, Clarke et al. 1985) but *Gonatus* spp. are recorded as having an energy density of 3.78 kJ g<sup>-1</sup> (or 0.903 kcal g<sup>-1</sup>) by Clarke et al. (1985), and this value was used to convert estimated food requirements from energy to weight. We calculated  $E$  for each of the 48 stranded whales for which weight had been estimated and took the average. This information on daily food consumption was also used to estimate the number of days of feeding represented by the beaks recovered from each stomach.

Estimates of sperm whale abundance in the eastern North Atlantic were taken from Christiansen et al. (1992) for Norwegian waters (5231) and Sigurjónsson & Víkingsson (1992) for Icelandic waters (9645); both cases were based on results from sightings surveys in June-July 1989. We assume that these figures remain applicable for the period of our study.

Annual consumption of cephalopod prey ( $C_i$ , t) was then estimated as

$$C_i = N \times P_i \times F \times T$$

where  $i$  identifies the prey category,  $N$  is the sperm whale population size,  $P_i$  is the proportion by weight of prey category  $i$  in the diet, for which we used pooled data from all the studied whales,  $F$  is the average weight of food eaten daily per sperm whale (we used 2 different estimates as described above) and  $T$  is the number of days whales spend in the feeding grounds. Initially we set  $T$  at 120 d, which corresponds to the summer feeding period assumed by Sigurjónsson & Víkingsson (1992).

Since values of most of these parameters are provisional, we also explore the consequences of (1) a smaller population size, and (2) a shorter feeding period. We discuss the rationale for these modifications further below.

## RESULTS

In all of the Scottish samples, food remains consisted almost entirely of cephalopod beaks (Table 2). A total of 6177 upper and 3846 lower beaks were recovered from the mass stranding on 7 December 1994; 1478 upper and 1171 lower beaks from the single stranding on 23 March 1995 and 6838 upper and 6501 lower beaks from the mass stranding on 28 January 1996. No

Table 2. *Physeter macrocephalus*. Prey species found in stomachs of sperm whales stranded in Scotland and Denmark 1990 to 1996, showing numbers of beaks (upper beaks, lower beaks) in each stomach and overall importance (% weight) in the sample of stomachs. Dates given as d/mo/yr. Single Danish strandings include data from 3 separate events: Nymindégab 17/11/90; Fanø, 1/12/91; Skagen, 25/1/96

Prey category	Orkney, 7/12/94		Nairn, 23/3/95		Cruden Bay, 28/1/96		Single Danish strandings		Rømø Island, 27/3/96	
	No. of beaks	% wt	No. of beaks	% wt	No. of beaks	% wt	No. of beaks	% wt	No. of beaks	% wt
<i>Loligo forbesi</i>	-	-	-	-	0, 1	0.02	-	-	-	-
<i>Gonatus</i> sp.	6168, 3826	99.02	1439, 1106	95.15	6721, 6355	93.37	949, 764	99.80	1163, 613	96.28
<i>Histioteuthis bonnellii</i>	1, 5	0.13	0, 2	0.31	0, 84	2.63	0, 1	0.20	0, 2	0.21
<i>Histioteuthis</i> sp.	1, 0	-	-	-	-	-	-	-	-	-
<i>Teuthowenia megalops</i>	0, 13	0.09	0, 60	3.06	0, 37	0.36	-	-	0, 5	0.13
<i>Todarodes sagittatus</i>	-	-	-	-	12, 7	1.04	-	-	-	-
<i>Eledone cirrhosa</i>	-	-	-	-	1, 0	0.04	-	-	-	-
<i>Haliphron atlanticus</i>	1, 2	0.77	1, 3	1.48	4, 9	2.55	-	-	-	-
Unidentified Octopod	-	-	-	-	9, 3	-	-	-	-	-
Unidentified Cephalopod	6, 0	-	38, 0	-	91, 5	-	-	-	7, 0	-
<i>Pollachius virens</i>	-	-	-	-	-	-	-	-	1	3.38
Other fish remains	-	-	2 lenses, skate egg	-	2 lenses, eggs skate egg	-	-	-	1	-

cephalopod flesh was found. Fish remains consisted of 1 skate egg capsule and 2 eye lenses in the single stranding in March 1995 and 1 skate egg capsule, 2 fish lenses and some fish eggs in the mass stranding of January 1996.

Four cephalopod species were identified from the mass stranding in December 1994 and the single stranding in April 1995 (Table 2): *Gonatus* sp. (probably *G. fabricii* based on its geographic distribution, Kristensen 1983, Bjørke 1995), *Teuthowenia megalops*, *Histioteuthis bonnellii* and the octopus *Haliphron atlanticus*. For the mass stranding in January 1996, the main prey was again *Gonatus* sp. (hereafter '*Gonatus*'), and *H. bonnellii*, *T. megalops*, *Todarodes sagittatus* and the octopus *H. atlanticus* were also found. One whale had a lower beak of the squid *Loligo forbesi* and an upper beak of the octopus *Eledone cirrhosa* in its stomach. Another whale had a piece of net of approximately 100 × 30 cm in the stomach. The *T. sagittatus* lower beaks ranged in size from 8.33 to 10.50 mm LRL and had pigmented wings and were probably therefore from maturing or mature whales.

The estimated ML of *Gonatus* from the mass stranding in December 1994 ranged from 155 to 295 mm

(4.67 to 8.00 mm LRL), with most of the squid being between 195 and 245 mm ML (5.50 and 6.72 mm LRL, Fig. 3a). The *Teuthowenia megalops* ranged in size from 185 to 255 mm ML (4.33 to 5.98 mm LRL, Fig. 3b). From the single stranding in March 1995, estimated ML for *Gonatus* varied between 175 and 295 mm (5.00 to 8.00 mm LRL), with 2 clear modes of 225 and 245 mm respectively (6.33 and 6.67 mm LRL) and those of *T. megalops* ranged from 145 to 275 mm ML (3.24 to 6.47 mm LRL), with a single mode at 225 mm ML (5.23 mm LRL). Finally, from the mass stranding of January 1996, ML for *Gonatus* ranged from 145 to 295 mm (4.33 to 8.00 mm LRL), with most of the squid grouped between 225 and 245 mm (6.33 and 6.67 mm LRL), and ML for *T. megalops* ranged from 165 to 315 mm (3.67 to 7.50 mm LRL).

Food remains from the Danish samples also consisted almost entirely of cephalopod beaks (Table 2), the highest numbers being 1069 upper and 601 lower beaks from one of the whales in the mass stranding on 27 March 1996. No cephalopod flesh was found. A single fish bone (the post-temporal bone of a gadoid fish, probably a saithe *Pollachius virens* weighing approximately 15 kg) and a fish eye lens, respectively, were

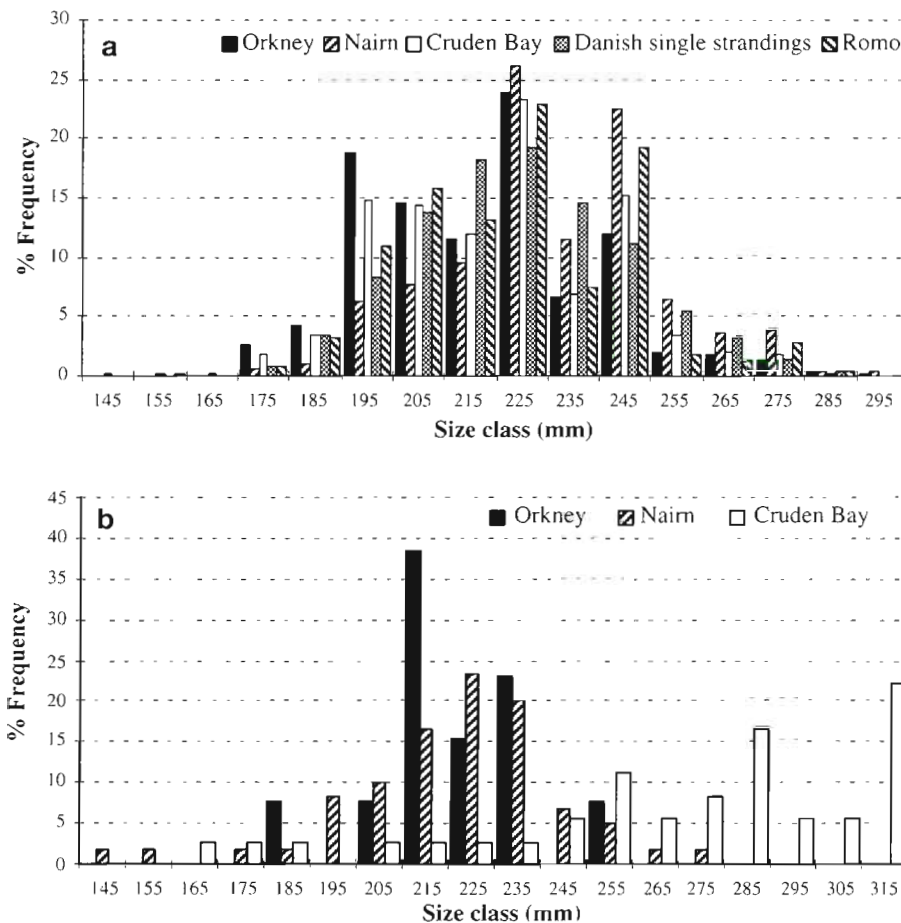


Fig. 3. Frequency distribution of estimated size (mantle length) of (a) *Gonatus* sp. and (b) *Teuthowenia megalops* in stomachs of sperm whales from the Orkney mass stranding, the sperm whale stranded in Nairn (Inverness), the Cruden Bay mass stranding, the single strandings in Denmark and the mass stranding in Rømo (Denmark). Sample sizes for *Gonatus* sp. were  $n_{\text{Orkney}} = 6273$  beaks,  $n_{\text{Nairn}} = 1439$ ,  $n_{\text{Cruden Bay}} = 6744$ ,  $n_{\text{Danish single strandings}} = 949$ , and  $n_{\text{Rømo}} = 1162$ . Sample sizes for *T. megalops* were  $n_{\text{Orkney}} = 13$  beaks,  $n_{\text{Nairn}} = 60$ , and  $n_{\text{Cruden Bay}} = 37$

found in 2 whales from the mass stranding in March 1996.

Only *Gonatus* and *Histioteuthis bonnellii* were identified from the single strandings in Denmark (Table 2). In the mass stranding in March 1996, the main prey found was *Gonatus*. *H. bonnellii* and *Teuthowenia megalops* were also present.

Estimated ML of *Gonatus* from the single strandings ranged from 175 to 285 mm (5.00 to 7.74 mm LRL, Fig. 3a). Finally, *Gonatus* size from the mass stranding in March 1996 ranged between 175 and 285 mm ML (5.00 and 7.74 mm LRL), with a single mode at 245 mm (6.72 mm LRL).

The amount of food represented by prey remains recovered from the stomachs surpassed estimated daily food requirements in only 2 of the whales (Table 3). However, it was not possible to examine the whole gastric system and more material may have been present.

The mean estimated weight of the sperm whales from Scotland, Denmark and Belgium during the study period was 26.59 ( $\pm 7.70$ ) t. The estimated average weight of food required daily per sperm whale was 0.86 t. Using Sigurjónsson & Víkingsson's (1992) equation, estimated daily requirements would be 2 501 797 kJ d<sup>-1</sup> (597 544 kca d<sup>-1</sup>). Assuming that all prey had the same energy density as *Gonatus* (a reasonable approximation here since it made up at least 95% of the diet in all the strandings), this is equivalent to 0.66 t d<sup>-1</sup>.

Table 3. *Physeter macrocephalus*. Size, estimated daily food requirements (based on 3.25% of body weight) and stomach contents of stranded sperm whales. Final column shows the number of days feeding represented by beaks in the stomach

Country	Whale	Total length (m)	Estimated weight (t)	Daily food requirements (kg)	Estimated prey weight in sample (kg)	Food present (d)
Scotland	3	12.80	23.6	825	924	1.21
	6	13.40	26.7	935	384	0.44
	9	12.80	23.6	825	4	0.00
	11	12.50	22.1	773	79	0.11
	1	13.70	28.4	993	392	0.43
	302	12.85	23.8	834	18	0.02
	303	12.10	20.2	707	61	0.09
	304	13.75	28.7	1003	362	0.39
	305	13.65	28.1	984	1103	1.21
	306	13.65	28.1	984	97	0.11
Denmark	421	11.85	19.1	668	61	0.10
	422	11.73	18.6	649	1	0.00
	423	13.10	25.1	879	162	0.20
	401	12.80	23.6	825	15	0.02
	405	12.95	24.3	851	25	0.03
	408	11.90	19.3	675	0	0
	412	12.15	20.4	715	248	0.37

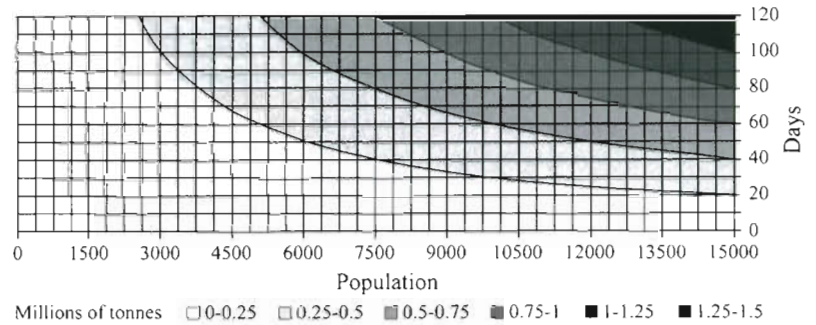


Fig. 4. Estimated consumption of *Gonatus* sp. by sperm whales in the North Atlantic area as a function of the length of the feeding season and the size of the population

Assuming the stomach contents examined were representative of the overall diet composition, sperm whales in the eastern North Atlantic north of 50°N could be consuming as much as 1.5 million t of *Gonatus*, or 1.2 million t, depending on which estimate of daily food intake is used. Making the more conservative assumption that the observed diet refers only to Norwegian waters rather than the entire area, these figures would be reduced to 542 000 and 415 000 t respectively for the 2 estimates. Amounts for the other prey categories are much lower (Table 4). Fig. 4 illustrates the obvious caveat that the amount of *Gonatus* eaten would be much less if (1) not all the whales are present in the area of high *Gonatus* abundance and/or (2) *Gonatus* is available for a shorter period.

## DISCUSSION

The present work represents the first large-scale study of sperm whale diet in the North Atlantic since the cessation of commercial whaling in the early 1980s and demonstrates that squid, primarily *Gonatus* (probably *G. fabricii*), form a major part of the diet. Comparison of these results with the earlier work of Martin & Clarke (1986), based on commercially caught whales, which indicated that cephalopods formed only 24% of the diet, raises some important questions: (1) Have sperm whale diets in the North Atlantic changed substantially over the last 2 decades? and (2) Do results from strandings provide a true picture of the diet?

The earliest studies on sperm whale diets in the Northeast Atlantic often

Table 4. *Physeter macrocephalus*. Estimates of consumption of different prey species by sperm whale populations in the eastern North Atlantic (t). Calculations are based on the overall average diet for whales sampled in this study and 2 estimates of daily energy intake. Estimate A is based on the whales eating food equivalent to 3.25% of body weight daily, Estimate B is based on estimated energetic requirements and the calorific density of the main prey (see text). Figures were derived for Norwegian waters, Icelandic waters and both areas combined

Species	% weight	Norway Estimate		Iceland Estimate		Combined Estimate	
		A	B	A	B	A	B
<i>Haliphron atlanticus</i>	1.64	8896	6813	16403	12563	25300	19376
<i>Eledone cirrhosa</i>	0.02	108	83	200	153	309	236
<i>Gonatus</i> sp.	95.96	520545	398673	959788	735079	1480333	1133752
<i>Histioteuthis bonnellii</i>	1.21	6564	5027	12102	9269	18666	14296
<i>Loligo forbesi</i>	0.01	54	42	100	77	154	118
<i>Teuthowenia megalops</i>	0.34	1844	1413	3401	2604	5245	4017
<i>Todarodes sagittatus</i>	0.43	2333	1786	4301	3294	6633	5080
<i>Pollachius virens</i>	0.39	2116	1620	3901	2988	6016	4608
Total	100.00	542460	415457	1000196	766026	1542656	1181484

reported only general qualitative information on the prey. Haldane (1905) found a skate, cephalopod beaks, the jawbone of an anglerfish and the head of a shark in the stomach of a sperm whale captured in 1904 off Shetland. Millais (1906) noted 'remains of predacious fish and cuttlefish beaks', and also fish hooks, in a sperm whale killed in 1904 off Shetland. Murray & Hjort (1912) reported the presence of squid beaks and fish bones in the stomach of a sperm whale killed in 1903 off the east coast of Iceland. Hamilton (1914) examined the stomachs of 6 sperm whales captured in 1913 off the west coast of Ireland and found an almost complete specimen of *Architeuthis* in one whale and remains of fish in a second, while the remaining 4 whales had only cephalopod beaks in the stomachs.

The first of several more detailed studies was carried out by Roe (1969), who examined stomachs of 57 male sperm whales caught in July and August off Iceland. This author found demersal fish (lumpsucker *Cyclopterus lumpus*, redfish *Sebastes* sp. and monkfish *Lophius piscatorius*) to be the most important prey, as well as some cephalopods (later analysed by Clarke & MacLeod 1976). The cephalopods found in these samples were (in order of importance by number) *Histioteuthis bonnellii*, an unidentified oegopsid, *Haliphron atlanticus* and *Gonatus fabricii*. Clarke & MacLeod (1974) identified *H. bonnellii* and *Taningia danae* as the most numerous prey in the stomach of a male sperm whale captured off Vigo (NW Spain) in 1966. Martin & Clarke (1986) analysed 221 stomach contents from sperm whales taken off Iceland between 1977 and 1981. Their results corroborated Roe's finding that fish was the most important prey (*C. lumpus*, *Sebastes* sp. and *L. piscatorius* were again the most numerous species, along with cod *Gadus morhua* and various sharks). Squid of the families Histioteuthidae and

Cranchiidae were the most common cephalopod prey, and *Todarodes sagittatus* and *G. fabricii* were also found.

The most recent studies have all been based on strandings. González et al. (1994) found *Mastigotheuthis* sp., *Teuthowenia megalops*, *Histioteuthis* sp., *Chiroteuthis* sp. and *Octopus vulgaris* in the stomach of a juvenile sperm whale stranded in Galicia (NW Spain). Lick et al. (1995) recorded mainly *Gonatus* beaks along with small numbers of beaks of *Haliphron atlanticus* and *Histioteuthis bonnellii* in the stomach of a sperm whale stranded in Germany in November 1994. Clarke (1997) also recorded mostly *Gonatus* beaks in stomachs of 3 sperm whales stranded in Holland in the same month. In this case the only other species recorded was *H. atlanticus*. These 2 most recently published studies are thus in agreement with the results of the present study.

In clear contrast to the results from whales killed during whaling activities off Iceland (Roe 1967, Clarke & MacLeod 1976, Martin & Clarke 1986), very few fish remains were found in any of the stranded whales from the North Sea (González et al. 1994, Lick et al. 1995, Clarke 1997, this study). It is true that samples from strandings are usually incomplete, but this should not, in itself, necessarily result in any bias in evaluating diet composition.

The fact that no flesh was found in any of the samples in the present study seems to indicate that the whales had not been feeding immediately prior to stranding. Cephalopod beaks, which are relatively indigestible (except at the growing margins) and tend to become entrapped in the folds of the stomach lining, may accumulate until they are regurgitated, whereas fish remains could be retained for a shorter time in the stomach and/or digested more quickly. Bigg & Fawcett



(1985) record that squid beaks can remain in Northern fur seal stomachs 24 h longer than fish bones. Thus, the importance of cephalopods in the diet of stranded whales would tend to be overestimated. However, some fish remains can also spend a long time in predator stomachs and be retained in the folds (especially robust otoliths, Hernández-García 1995a). Eye lenses of both taxa should be equally likely to survive intact. Furthermore, squid flesh is digested faster than fish flesh (Bigg & Fawcett 1985, Hernández-García 1995b). Interestingly, Martin & Clarke (1986) acknowledge that they could have underestimated the importance of cephalopods, 'because squid crowns are small and thus possibly digested more quickly than the much larger entire fish'.

In the present study some trace fish remains were present, and the dominance of cephalopods is consistent with the findings of Lick et al. (1995) and Clarke (1997). However, we cannot rule out the possibility that larger quantities of fish had been eaten and their remains digested.

A serious challenge to the use of cephalopod beaks in stomach contents to interpret the diet of sperm whales was made by Clarke et al. (1988). These authors argued that the fleshy remains of the large squid *Dosidicus gigas* in the stomachs of sperm whales caught in the Southeast Pacific represented the main prey, whereas the beaks (mainly of other species) described from the same samples by Clarke et al. (1976) were ingested secondarily in the stomachs of *D. gigas*. Clarke et al. (1993) reply to this, pointing out that flesh of the small squids was also found, suggesting direct ingestion by the sperm whales. There have been similar arguments about whether grey seals *Halichoerus grypus* eat sandeels *Ammodytidae*. Prime & Hammond's (1987) answer to this question is pertinent here: when sandeel otoliths were encountered in large numbers in faecal samples there were usually no other prey remains present and direct feeding on sandeels is the most likely interpretation. In faecal samples containing larger otoliths, a few sandeel otoliths were often also present and could represent secondary ingestion. In the present study there was no evidence at all of predation on larger squids and we believe that it is reasonable to assume that the beaks found are those of the prey of sperm whales. A possible additional bias is that smaller beaks may pass through the intestine, while larger beaks are retained in the stomach and subsequently regurgitated. In the present study most of the beaks found were of relatively similar sizes, although a few small beaks were found.

Aside from questions about differential digestion/retention and secondary ingestion, information from strandings can be biased because sick or injured whales are more likely to be stranded than healthy

individuals (Pierce & Boyle 1991, Sekiguchi et al. 1992). In the context of the present study, there is some evidence of ill-health in sperm whales stranded in the North Sea, although it is not thought that this would have directly contributed to the stranding event. The only detailed pathological studies were those carried out on 4 whales stranded in Belgium in November 1994 and 3 whales stranded in The Netherlands in January 1995 (Jauniaux & Coignoul 1996, Jauniaux et al. 1996, 1998), none of which had food remains in the stomach (Jauniaux pers. comm., Smeenk pers. comm.). Jauniaux and co-authors found that some of the whales were underweight and recorded the presence of various lesions. Levels of trace metals, organochlorine pesticides, their metabolites and chlorobiphenyl congeners in tissue samples from sperm whales stranded on North Sea coasts were generally within the range of values previously reported in the literature (Law et al. 1996, Bouquegneau et al. 1997, Joiris et al. 1997, McKenzie et al. 1997). However, high cadmium concentrations were found in the 4 Belgian sperm whales stranded in November 1994. One of the Orkney (1994) whales had a large part of its lower jaw missing. The wound had long since healed and the whale had a blubber thickness similar to that of other whales (R. J. Reid pers. obs.).

The sperm whale which stranded in the Firth of Forth in 1997 continued to swim up the Firth of Forth despite twice being grounded and efforts to persuade it to swim out of the Firth. It may be suggested that the whales are aware of the direction in which they need to travel, but have difficulty navigating once they enter the unfamiliar and shallow waters of the North Sea. Smeenk (1997) has commented that the North Sea may be regarded as a 'sperm whale trap'.

The main prey found in the 17 sperm whale stomachs containing food remains was the oceanic squid *Gonatus* [probably *G. fabricii* (Lichtenstein), given its distribution (Kristensen 1983)]. *G. fabricii* is an oceanic species considered to be the most abundant squid in the Arctic and Sub-arctic area of the North Atlantic (Kristensen 1983). Juveniles (ML  $\leq$  50 mm) are caught in the surface layers but, at a length of 50 to 70 mm, *G. fabricii* disappears from the surface, probably moving to deeper waters (Bjørke 1995). Squids of 80 to 250 mm ML have been caught at depths of 200 to 550 m with deep pelagic and bottom trawls (Wiborg et al. 1982, 1984). Off West Greenland, males are thought to mature at a ML of about 200 mm (probably aged 2 yr), with females maturing at a ML larger than 200 mm (aged 2 to 3 yr) (Kristensen 1983). The ML estimated for the majority of *Gonatus* in the sperm whale stomachs varied between 205 and 245 mm (Fig. 3a), which corresponds with the size of mature squid (Wiborg et al. 1982, Kristensen 1983).

The main spawning period for *Gonatus fabricii* in the Norwegian Sea is from December to April (Bjørke 1995). However, very few mature specimens or egg masses have ever been found (the first record of putative egg masses, taken in a pelagic trawl, is in Bjørke et al. 1997), which led Kristensen (1984) to suggest that spawning probably takes place at depths greater than 200 m. Areas of spawning have not been definitely identified but Wiborg (1979) considers that they may coincide with localities where bottlenose whales *Hyperoodon ampullatus* Forster were abundant (off Møre and Vesterålen, west of Svalbard and between Iceland and Jan Mayen, Fig. 1). This is supported by the finding of squid spermatophores in the stomach of a bottlenose whale which had fed exclusively on *G. fabricii* (as indicated by beaks representing more than 1 t of squid) (Lick & Piatkowski 1998).

Moiseev (1991) collected data on the vertical distribution of *Gonatus fabricii* using manned underwater vehicles. He observed squid along the North-Atlantic Ridge (at 49° and 59° N and in the Sea of Irminger) from July to September 1986. During the day, squid were found between 420 and 1200 m depth, while at night they occurred at depths from 350 to 1200 m. He concluded that, because of the considerable overlap in distribution between day at night, the daily vertical migration of *G. fabricii* was probably insignificant.

The high number of *Gonatus* beaks found in stomachs, and the fact that most of them were from large squid, suggests the possibility that the sperm whales had been feeding on shoals of adult squid. Akimushkin (1955) suggested that, because squid beaks of each species in the food of sperm whales tended to be of similar size, this was an indication of squids living in shoals of individuals of similar age. Gaskin & Cawthorn (1967) also noted the regularity in the sizes of beaks recovered from stomachs of sperm whales caught in New Zealand.

Most squid species aggregate in dense concentrations to mate and lay eggs (e.g. Hanlon & Messenger 1996). Females typically die after spawning and, in some cases, so do the males, although it is believed that male *Gonatus* could survive to breed again (Kristensen 1984). Clarke (1980) pointed out that if the whales were feeding on spawning aggregations, they would be eating dense concentrations of incapacitated and dying squids at their maximum size. The timing of the strandings (between the end of December to March) broadly coincides with the spawning period for *Gonatus* (December to April). If the sperm whales were feeding on spawning aggregations, it would explain the high numbers and uniform sizes of beaks found in some of the stomachs.

The majority of the other cephalopod remains found in the stomachs were also from oceanic species. Of the

3 other oceanic squids eaten, *Todarodes sagittatus* is the best-known, having been the object of a directed fishery in several northern countries, most importantly in Norway (Sundet 1985, Borges & Wallace 1993). All 3 species are widely distributed in the Atlantic, extending into Arctic waters, and are reported from a wide range of water depths (Voss 1969, Kristensen 1980, Nixon 1983, Voss 1985, Guerra 1992). The biology of *Histioteuthis bonnelli* is relatively poorly known. However, there is information on size at maturity in *T. sagittatus* and *T. megalops* (Nixon 1983, Wiborg & Beck 1984), and both species are known to undertake daily vertical migrations (Lu & Clarke 1975, Hanlon & Messenger 1996), although the latter comes to the surface by day rather than at night. The size of the *T. megalops* eaten by sperm whales in the present study (145 to 315 mm ML) spans the previously reported size ranges for juveniles (70 to 180 mm) and adults (260 to 352 mm). *T. sagittatus* shows a marked sexual dimorphism in body size as well as a wide range of size at maturity. The size and pigmentation of the lower beaks found in the sperm whale stomachs were consistent with mature or maturing squid.

The octopus *Haliphron atlanticus* is a cosmopolitan bottom-living species recorded from depths up to 3180 m (Clarke & Lu 1975, Guerra 1992). However, Collins et al. (1995) reported an immature female (estimated weight 11.5 kg) captured by a bottom trawler in Shetland at a depth of around 180 m. Based on a comparison of beak sizes, the octopuses taken by the sperm whales were all smaller than those recorded by Collins et al. (1995).

The other cephalopod prey found (*Loligo forbesi* and *Eledone cirrhosa*) are both mainly coastal species, although they are also caught offshore (e.g. at Rockall, off Scotland, Pierce et al. 1994). Only 1 beak of each species was found, in samples from Cruden Bay (Scotland) in 1994. The presence of these beaks, along with 2 skate egg capsules among the food remains in samples from Scotland and the saithe bone recorded from Denmark, provides the only tentative evidence of feeding in coastal waters.

Of the 25 sperm whales stranded in the North Sea area for which stomach contents were examined, food remains were found only in the Scottish and Danish whales, with the largest amount of remains being present in stomachs from Scotland. No prey remains were found in the whales stranded in Belgium in 1994, although 2000 beaks were found in a whale stranded in The Netherlands in 1994 (Clarke 1997). The sperm whale that stranded in the Firth of Forth in 1997 also had an empty stomach. It had spent at least 11 d in the Firth of Forth (R. J. Reid pers. obs.) and no food remains were found in the stomach.

From the evidence available, it appears that the sperm whales were feeding in deep waters off Norway on spawning concentrations of oceanic squids. After entry into the North Sea, little further feeding took place. An obvious inference is that sperm whales do not enter the North Sea to feed: they may normally feed little while in transit or the food available in the North Sea may be unsuitable.

Although large numbers of beaks were found in some of the stomachs, at most they represented little more than a single day's food requirements (Table 3). Of course, it was never certain that the entire stomach contents were recovered. Clarke (1980) estimated that an average female sperm whale would retain beaks in the stomach for 2.1 to 2.5 d while the average male would retain them for 1.2 to 1.6 d. Beaks are probably then regurgitated.

Estimates of daily food requirements differ depending on which source is used: Sergeant (1969), Lockyer (1981) or Sigurjónsson & Víkingsson (1992). The latter estimate is expressed as energy rather than weight, requiring an explicit assumption to be made about the calorific density of the prey. The value we used, for *Gonatus*, derives from Clarke et al. (1985). The family Gonatidae is characterised by the presence of large amounts of low density oil in the liver, which allows the squids to be neutrally buoyant (Clarke et al. 1979). The values given by Clarke et al. (1985) refer to juveniles and the authors acknowledge that, in mature specimens, the presence of oil would increase the calorific value. This would lead to reductions in our estimates of the total weight of squid consumed.

Our crude calculations indicate that sperm whales in the eastern North Atlantic could take up to 1.5 million t of squid during the feeding season, mostly *Gonatus fabricii*. This obviously involves a series of assumptions, the first of which is that the stomach contents were representative. We have already noted that studies on whales caught off Iceland indicated predation on fish as well as cephalopods. Although most recent studies agree that cephalopods are the main prey, they have been based on stranded whales. If the whales in the present study had eaten fish and cephalopods in the proportions suggested by Martin & Clarke (1986), i.e. 24% of the diet being cephalopods, the estimate of consumption of *Gonatus* would come down to 370 000 t at most. Furthermore, *Gonatus* might be taken only during the spawning period, and only by whales in the spawning area. Hence the number of days of feeding and the population size assumed might both have been unrealistically large.

We have also implicitly assumed that the whales stranded in the North Sea were of the same average size as the population as a whole and that daily feeding rate is constant. In fact, if the whales are building up

energy reserves for breeding, feeding rates may be considerably higher during the period spent in northern waters.

The total sperm whale population in the North Atlantic is presently unknown, hence we used estimates by Christensen et al. (1992) and Sigurjónsson & Víkingsson (1992) based on a survey in 1989. The time period over which these whales remain in northern waters is also uncertain. Sightings and strandings of sperm whales occur all year round, suggesting that at least some whales remain in the area during the winter months (Christensen et al. 1992, Smeenk 1997). Whitehead & Arnborn (1987), working on sperm whales off Galapagos, suggested that mature male sperm whales do not breed every year but, because of energetic or other limitations, remain in the cold water areas where they feed.

The only previous estimate for the amount of cephalopods eaten by sperm whales for this area (Sigurjónsson & Víkingsson 1992) used dietary data from Martin & Clarke (1986). The resulting figure, approximately 33 000 to 40 000 t of cephalopods eaten per year in Icelandic waters (north of 60°N), is not directly comparable to our estimate since we considered all whales in the eastern North Atlantic (north of 50°N (i.e. a total population of 14 876 whales rather than 2456 whales, based on their figures). Scaling up their figures would give a maximum estimate of around 242 000 t of cephalopods eaten, and much of the remaining difference is then attributable to the differing estimates of dietary importance for cephalopods.

Of the species eaten by sperm whales in the North-east Atlantic, only *Todarodes sagittatus* has been the object of a significant directed fishery, mainly in Norway (Sundet 1985). The main prey species, *Gonatus fabricii*, although thought to be very abundant, has never been the object of a directed fishery. Juvenile squid stranded in autumn on the Norwegian coast are used as bait (Wiborg et al. 1982) and there is also a substantial by-catch in shrimp trawls off West Greenland (Piatkowski & Wieland 1993). It has been proposed as a possible fishery resource (Wiborg 1979, Wiborg et al. 1982, 1984, Piatkowski & Wieland 1993) but fishing experiments with pelagic trawls have been unsuccessful, due to the lack of knowledge on the location of adults and spawning aggregations (Wiborg et al. 1982). Bjørke (1995) estimated the stock of juvenile *Gonatus* in the Norwegian Sea in July 1994 as 2 to 3 million t. He noted that this could be an underestimate due to inefficiency of the gear. *Gonatus* is eaten by a variety of predators including the bottlenose whale, narwhal *Monodon monoceros*, beluga *Delphinapterus leucas*, Sowerby's beaked whale *Mesoplodon bidens*, pilot whale *Globicephala melas*, Northern fur

seal *Callorhinus ursinus*, hooded seal *Cystophora cristata*, harp seals *Phoca groenlandica*, herring *Clupea harengus*, salmon *Salmo salar*, blue ling *Molva byrke-lange*, Greenland halibut *Reinhardtius hippoglossoides*, cod *Gadus morhua*, rat-tails *Coryphaenoides* spp., and redfish *Sebastes marinus* (Murray & Hjort 1912, Hjort & Ruud 1929, Grimpe 1933, Nesis 1965, Benjaminsen & Christensen 1979, Wiborg 1979, Clarke & Kristensen 1980, Lear 1980, Wiborg et al. 1982, 1984, Kristensen 1983, Lydersen et al. 1991, Bjørke 1995, Martin & Christiansen 1997, Lick & Piatkowski 1998). If sperm whales take as much as 1.5 million t of *Gonatus* annually from the North Atlantic, then it is likely that Bjørke's estimate of *Gonatus* abundance is a very conservative one. If, in the future, *Gonatus* becomes a fishery resource, the effect on the sperm whale population would need to be carefully monitored.

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