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THE DIET OF SPERM WHALES (*PHYSETER MACROCEPHALUS*) CAPTURED BETWEEN ICELAND AND GREENLAND

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(Fig. 1)

The stomach contents of 221 sperm whales were examined at the Icelandic whaling station between 1977 and 1981. Evidence of at least eight species of fish and 22 species of cephalopod was found, together with an assortment of foreign bodies including rock fragments and fishing nets. Fish remains were found in 87% and cephalopods in 68% of the sperm whale stomachs in this area, but quantification of dietary input is complicated by differential rates of digestion and variation in the retention of indigestible remains in the stomach. Prey species are benthic or pelagic in habit and are caught by the whale in waters from 400 m to at least 1200 m in depth. One fish, the lumpsucker *Cyclopterus lumpus*, forms a major part of the diet. Ninety-four per cent of cephalopods are oceanic and neutrally buoyant and 84% of these are ammoniacal. Cranchiids contribute 57% by number and an estimated 25% of the weight, and histioteuthids 26% by number and 38% of the weight of cephalopods eaten. Three species of fish and two of cephalopod have not been previously recorded in sperm whale diets. Comparison with an earlier study shows that the diet is essentially stable over a 14-year period.

INTRODUCTION

The sperm whale is a cosmopolitan species and has a long history of exploitation by man. Whaling operations, particularly during the present century, have facilitated research into the species' anatomy and ecology. It is now clear that sperm whales occurring seasonally at latitudes higher than 45° in both hemispheres are invariably adult males, whereas females and immatures remain in family groups in warmer waters throughout the year. The species is probably the deepest diving of all mammals, and dives of over 60 minutes duration are devoted to feeding (Clarke, 1976; Lockyer, 1977).

Studies of the diet of sperm whales have been reviewed by Kawakami (1980); in most areas cephalopods (squid and octopods) form the bulk of the food. Fish are usually found as a relatively small constituent of the total biomass eaten, but in a few localities the position is reversed and cephalopods assume a lower importance. An earlier study of sperm whale food off Iceland presented by Roe (1969) and Clarke & Macleod (1976) indicated that this stock of animals fell into the second category. Roe (1969) recognized that his findings, from 49 stomachs containing food in two months of the 1967 season, might not have been

representative of the long-term situation in those waters and recommended a further study at a later date. This paper presents the findings from the examination of 221 sperm whale stomachs at the same Icelandic whaling station during the five seasons between 1977 and 1981.

In this study, detailed analysis of the cephalopod component of the diet is based mainly upon collections made in 1977 and 1978, which comprised fewer mandibles (beaks) than in the 1967 sample but considerably more flesh. This has permitted the specific identification of a squid *Teuthowenia megalops*, which is important in the diet but whose family affiliation was not previously known.

MATERIAL AND METHODS

All the sperm whales examined were adult males of between 37 feet (11·3 m) and 56 feet (17·1 m) in total body length. They were killed by steam-powered catcher boats using explosive harpoons in the Icelandic sector of the Denmark Strait, to the west of Iceland, between latitudes 62 and 67° N and longitudes 24 and 30° W (Fig. 1). The sea is between 400 and 200 m deep in this area. Animals were towed to the Icelandic whaling station (marked in Fig. 1) where they were butchered and processed typically between 15 and 40 h post-mortem, averaging $26 \pm 0{\cdot}9$ hours. Examinations were carried out on as many whales as possible in each season without selection.

Reference should be made to Berzin (1972) for a detailed description of the sperm whale stomach. Briefly, it comprises three compartments, the first of which can be considered as an extension of the oesophagus and acts primarily to store and masticate food, since sperm whale teeth do not grind prey. Most flesh was found in this first compartment, where digestion was usually incomplete. The second, main, compartment secretes digestive fluid and is linked to the third, or pyloric, compartment which then joins the ampulla of the duodenum by way of a sphincter. The second compartment usually contained cephalopod beaks, fish bones and perhaps some partially digested flesh. The third, and intestines, often contained little of diagnostic value, but the amount and colour of the contents gave an indication of how much and what type of prey had been taken within the few days prior to death. For most whales, all three stomach compartments and various sections of the intestines were opened and carefully searched. The minimum inspection comprised sectioning and visually checking just the first stomach compartment.

Cephalopod flesh could be distinguished from fish flesh, and almost all fish could be identified to the species level either by visual inspection of their shape, size and skin or by closer examination of the underlying skeleton and otoliths. The few fish not recognized on site were photographed and later identified in the U.K. Fish remains often consisted entirely of bones, including otoliths. Such remnants of the more commonly encountered species were easily recognizable and the task of searching for diagnostic bones was made easier by the fact that otoliths and other dense material, such as sand or stones, were often found in discrete aggregations in folds of the stomach lining. Although fish otoliths were common in sperm whale stomachs, and could be used to determine the species and body size of many fish, their use as a diagnostic tool is not straightforward. Otoliths are non-existent in some species, e.g. sharks, and vary greatly in size between others, with the result that they may be retained in a whale stomach for differing lengths of time. This renders them unsuitable as the sole means of finding the relative importance of each fish species in the diet.

One way of overcoming this problem is to look at the occurrence of flesh and to assume that the various species are digested in about the same time. This is not strictly valid in that smaller, soft fish will disappear before larger, tougher sharks, but the occurrence of flesh should provide an approximate ranking of numerical importance among the fish. Because of the difficulties in assessing relative importance in the diet, mentioned above, fish species have only been ascribed to an approximate category of frequency. These are: common (flesh or bones found in more than 25% of stomachs), infrequent (10–25%) and rare (less than 10%).

Entire cephalopods were encountered in only one whale, but crowns (comprising head and limbs) were often found. Samples of cephalopod flesh, from almost all of the whales in which it was discovered, were preserved in 5% formalin for later examination. Most cephalopod remains were in the form of beaks and were found in clusters within a whale's second and third stomachs. While

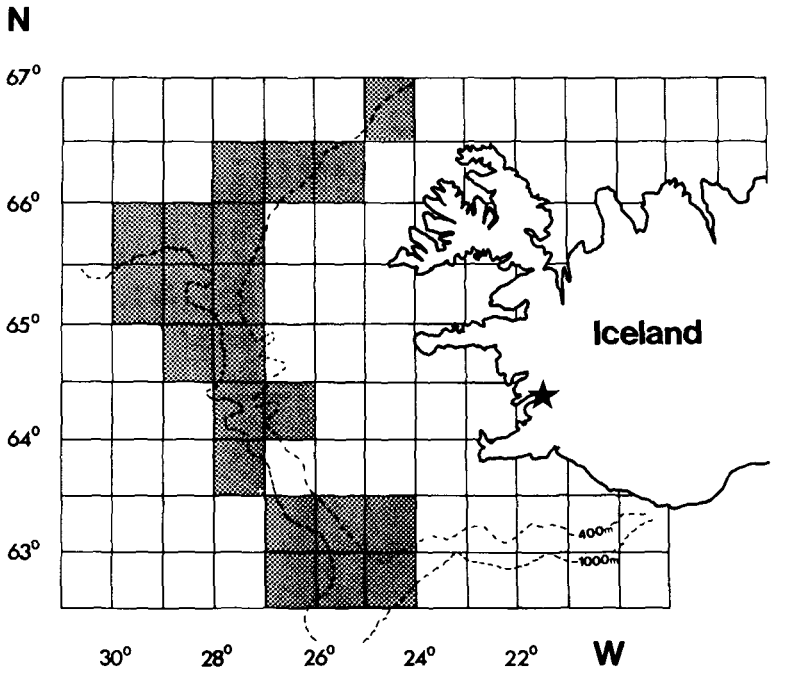

Fig. 1. Geographical distribution of the positions of capture of sperm whales examined during this study (hatched area). The location of the Icelandic whaling station to which all whales were towed for processing and examination is marked *.

most cephalopod flesh is easily and quickly digested, the beaks resist chemical attack and are identifiable to at least generic level. Moreover, the size of the beak is proportional to the size of the cephalopod itself (Clarke, 1980, 1986). Complete or partial samples of beaks were taken from many whales and were later sorted and identified. Although beaks provide a valuable record of the genera and sizes of cephalopods eaten in the period prior to the death of the whale, it is not possible to say with certainty how long a beak may have remained within the stomach and thus where the animal from which it came was captured. The identified cephalopod material came from 17 sperm whales caught between 1977 and 1980 (Table 1). Parts of 678 cephalopods were collected. These were mainly identified from the lower beaks with help from the flesh in one species (*Teuthowenia megalops*). The methods used for identification are described elsewhere (Clarke, 1980, 1986). The rostral length (LRL) of all lower beaks was measured with vernier calipers. Estimation of the wet weight of the cephalopods from LRLs was made from relationships published by Clarke (1986).

The temporal spread of stomach examinations across the season and between years is shown in Table 2. Sperm whaling is rarely carried out other than between July and September off Iceland, though the species is undoubtedly present in the Denmark Strait throughout the summer and autumn and may occur year-round.

Throughout this paper the term 'significant' is used solely in the statistical sense of differences significant at the 5% level of probability.

RESULTS

Prey species and relative importance in the diet

Fish

Eight species of fish were identified over the four-year period 1978–1981 (Table 3). Identification of fish remains was not attempted in 1977 and several

Table 1. *Cephalopod remains from stomachs of sperm whales caught off Iceland*

* Whales which contained beaks of squids from lower latitudes.

Year	Log no.	Date	Whale (l)	P.M. time (h)	Beaks		Buccal masses	Crowns +	
					Upper	Lower			
1977	169*	17 Aug.	52	39	100	184	—	63	
	191	31 Aug.	46	29	—	8	—	12	
	240	31 Aug.	46	30	—	—	—	14	
	331	19 Sept.	44	—	—	1	—	7	
	334*	19 Sept.	43	—	—	10	—	—	
	337	22 Sept.	49	—	12	27	—	28	
1978	251	1 Aug.	43	32	25	35	—	18	
	280	14 Aug.	—	—	—	—	—	1	
	293	15 Aug.	43	19	0	5	—	14	
	296*	15 Aug.	46	20	107	120	—	8	
	298*	—	—	—	62	95	—	3	
	320*	27 Aug.	39	22	6	8	7	—	
	334	2 Sept.	46	42	—	—	—	3	
	363	16 Sept.	51	31	—	—	—	3	
1979	267	10 Aug.	—	—	—	—	—	1	
	359	25 Aug.	—	—	—	—	—	1	
1980	329	24 Aug.	46	—	1	2	—	—	
Totals	—	—	—	—	313	495	7	176	678

Table 2. *Number of sperm whale stomachs examined in the course of this study, by year and month*

	July	August	September	Total
1977	14	26	29	69
1978	10	50	14	74
1979	0	36	12	48
1980	1	21	4	26
1981	1	3	0	4
Total	26	136	59	221

lamniform sharks were not identified to species in other years. Four fish species occurred commonly, while the remainder were encountered infrequently or rarely in the diet. Three species (blue whiting *Micromesistius poutassou*, ling sp. (probably blue ling *Molva dypterygia*) and *Scymnorhinus licha* were previously unrecorded from sperm whales.

Evidence from flesh remains indicates that the number of lumpfish *Cyclopterus lumpus* eaten is about four times that of all other fish species combined, with redfish *Sebastes* sp. (*mentella?*) and angler *Lophius piscatorius* comprising numerically about 10% of the fish component each. Two species, cod *Gadus morhua* and *Micromesistius poutassou* were commonly represented by otoliths but rarely, if ever, by flesh. In the case of *M. poutassou* this may have been due to the small body size of the fish (averaging 0·12 kg as determined from otolith size) or to otoliths being ingested in the gut of larger prey, but we are unable to suggest why

Table 3. *Species of fish represented by remains in stomachs of sperm whales examined during the Icelandic whaling seasons 1978–81*

Species marked thus (*) were also found by Roe (1969) in an earlier study. Depth and habit data are based on Wheeler (1978) and advice from the Marine Research Institute of Iceland.

Species	Occurrence	Evidence from stomachs	Depth (m) and habit	Comments
Lumpsucker* *Cyclopterus lumpus*	Common	Flesh (123 fish), bones	0–500 Bottom/mid-water	Under-represented as indigestible remains. Maximum of 25 fish in one stomach.
Redfish* *Sebastes* sp. (*mentella?*)	Common	Flesh (12 fish), bones, otoliths	100–1000 Mid-water	Range 1–6 kg per fish, average *c.* 2 kg. Sometimes singly, often as groups. Maximum 5 in one whale. Bones very characteristic.
Cod* *Gadus morhua*	Common	Flesh (1 fish) otoliths	0–600 Bottom/Mid-water	Usually as otoliths. Under-represented as flesh. Average weight from otoliths = 3·5–4 kg.
Blue whiting *Micromesistius poutassou*	Common	Otoliths	100–300 Mid-water	Always as otoliths, sometimes hundreds. Average weight from otoliths = 0·12 kg.
Angler* *Lophius piscatorius*	Infrequent	Flesh (11 fish), bones	3–550 Bottom	Always well digested; soft flesh. 1–2 in one stomach. Bones easily distinguished.
Ling sp. *Molva* sp. (*dypterygia?*)	Rare	Flesh (3 fish), otoliths	100–1000 Mid-water	Usually single specimens. Two fish weighed 4 and 7 kg.
Football-fish *Himantolophus groenlandicus*	Rare	Flesh (1 fish)	100–350 Mid-water	Only one found.
Darkie Charlie *Scymnorhinus licha*	Rare	Flesh (1 fish)	100–1000 Mid-water	Only one found.
Sharks (Lamniformes)	Rare	Flesh (4 fish)		Difficult to identify to species. 1–4 in a stomach.

the larger *Gadus morhua* might have been so under-represented by flesh. Taking into consideration the body mass of each species and the known inaccuracies and uncertainties involved in interpreting the evidence, it would only seem reasonable to deduce that *Cyclopterus lumpus* provides at least 50% of the fish biomass consumed by sperm whales off Iceland with *Sebastes* sp., *Lophius piscatorius*, *Gadus morhua*, various sharks and possibly *Micromesistius poutassou* of secondary importance; *Molva* sp. and *Himantolophis groenlandicus* are taken occasionally.

Cephalopods

The following 22 different species were identified from our samples: *Todarodes sagittatus* (Lamarck, 1799), *Kondakovia logimana* (Filippova, 1972), *Onychoteuthis banksi* (Leach, 1817), *Ancistrocheirus lesueuri* (d'Orbigny, 1839), *Gonatus fabricii* (Lichtenstein, 1818), *Brachioteuthis* sp., *Cycloteuthis akimushkini* (Filippova, 1968), *Chiroteuthis* sp., *Lepidoteuthis grimaldii* (Joubin, 1895), two *Octopoteuthis spp.* (A & B in Clarke & MacLeod, 1976), *Histioteuthis bonnellii bonnellii* (Clarke, 1980), *H. dofleini* (Pfeffer, 1912), *H. reversa* (Verrill, 1880), *Teuthowenia megalops* (Prosch, 1847), *Megalocranchia* sp. (previously called *phasmatopsis*), *Taonius pavo*, *Stauroteuthis* sp. and *Alloposus mollis*.

In addition, beaks of three more species, thought to be *Teuthowenia* or *Galiteuthis* were present. Beaks of one of these were identical to those of *T. maculata* (Leach, 1817) but two crowns were also collected and *T. maculata* is a tropical species (Voss, 1985). Some of these can only be given a generic name either because the genus is currently under taxonomic review or because the beaks of some known species in the genus have not been described.

Of the species collected, *Brachioteuthis* sp. and *Stauroteuthis* sp. have not previously been recorded from sperm whale stomachs. *Onychoteuthis banksi* and *Histioteuthis reversa* have not been recorded from whales caught off Iceland.

The numbers and total wet weights of cephalopods estimated from LRLs of the lower beaks, including those extracted from buccal masses, crowns, etc., are given in Table 4 together with figures for the large sample from a single whale examined in 1967 (Clarke & MacLeod, 1976).

Genera and species within the family which were represented by flesh as well as by beaks were *Teuthowenia megalops* (called 'unknown oegopsid' in Clarke & MacLeod, 1976), of which 166 crowns, heads or whole specimens were collected, *Teuthowenia/Galiteuthis* which is a smaller species represented by 4 heads in poor condition, *Histioteuthis bonnellii* represented by 4 heads and *Todarodes sagittatus* represented by 7 heads and 4 mantles. The largest number of squids represented by flesh in a single stomach was 63 (Table 1), of which 46 were *Teuthowenia megalops*, 12 were *Teuthowenia* A (called *Taonius megalops* by Clarke & MacLeod, 1976 but now recognized as a different species allied to *T. maculata*), two were *Teuthowenia/Galiteuthis* and three were *Histioteuthis bonnellii*. Fifty-three of the *Teuthowenia megalops* heads, many with badly damaged bodies attached, weighed 3·9 kg, giving a mean weight of about 74 g. This compares with a mean weight estimated from beaks of 150 g for the entire, intact squids and confirms that the

Table 4. *Importance by number and weight of cephalopods from stomachs of sperm whales caught off Iceland*

		Beaks (%)			Estimated weights		
				Mean	Total	%	
	No.	1977–8	1967	(g)	(kg)	1977–8	1967
*Architeuthidae	0	0	0·2	0	0	0	3·4
*Ommastrephidae	21	3·1	< 0·1	1,805	38·0	17·1	< 0·1
*Onychoteuthidae	4	0·6	0·8	938	2·8	1·3	6·0
Enoploteuthidae	1	0·1	0·2	1,000	1·0	0·5	< 0·1
*Gonatidae	63	9·3	0·3	331	20·8	9·4	0·1
Pholidoteuthidae	0	0	< 0·1	0	0	—	< 0·1
Brachioteuthidae	3	0·4	0	< 50	0·2	< 0·1	0
Cyloteuthidae	1	0·1	0·6	1,100	1·1	0·5	0·4
Chiroteuthidae	2	0·3	0·1	57	0·1	< 0·1	< 0·1
Lepidoteuthidae	3	0·4	0	5,380	16·1	7·3	0
?Psychroteuthidae	0	0	< 0·1	0	0	0	< 0·1
*Octopoteuthidae	5	0·7	3·4	102	0·5	0·2	25·3
*Histioteuthidae	174	25·7	73·8	490	85·3	38·4	46·5
*Cranchiidae	386	56·9	17·7	141	54·4	24·5	10·7
Alloposidae	11	1·5	2·8	150	1·6	0·7	7·5
Stauroteuthidae	1	0·1	0	< 50	0·2	< 0·1	0
Unidentified	4	0·6	—	—	—	—	—
Totals	679	99·8	—	—	222·1	100·2	100·1

* Asterisked families are represented by beaks of species known to occur in Icelandic waters.

estimate for complete squids is approximately correct. One *Histioteuthis bonnellii* head weighed 717 g.

Quantity of food in stomachs

Hard parts of prey, principally fish bones and cephalopod beaks, can remain in sperm whale stomachs for several days and possibly weeks (Clarke, 1980), rendering any assessment of dietary input with time, from hard parts alone, very difficult. A further complication is that some whales are known to vomit stomach contents during capture. Table 5 shows the percentage of whales whose stomachs were found to be empty (E), to contain flesh (F) or to contain just indigestible prey remains (I). The proportion of these three categories did not vary significantly between years ($\chi^2 = 13{\cdot}1$, D.F. $= 8$, $P > 0{\cdot}1$). Overall, most whales were not found to have evidence of recent feeding in their stomachs (Table 5). Comparison between the early (before 15 August) and late halves of the season demonstrated very little difference in the ratio of E:I:F between these periods ($\chi^2 = 1{\cdot}0$, D.F. $= 2$, $P > 0{\cdot}5$). A significantly greater proportion of whales from the southern part of the whaling grounds were found to have flesh in their stomach and had thus recently eaten ($\chi^2 = 6{\cdot}1$, D.F. $= 1$, $P > 0{\cdot}02$).

The greatest quantities of flesh found in any whale were 38 kg (28 kg of fish, 10 kg of squid) in a 49 foot (14·9 m) long animal caught on 23 August 1978 and *Ca* 50 kg (all *Cyclopterus lumpus*) in a 50 foot (15·3 m) animal on 20 September 1979.

Table 5. *Percentage of sperm whale stomachs examined, by year, which were found to be empty, to contain flesh or to contain solely the indigestible remains of prey*

	1977	1978	1979	1980	1981	All years combined
n	69	74	48	26	4	221
Empty	26·1	23·0	10·3	0	0	18·4
Flesh	31·9	35·1	39·6	50·0	50·0	36·5
Indigestible remains only	42·0	41·9	50·0	50·0	50·0	45·1
	100·0	100·0	99·9	100·0	100·0	100·0

Table 6. *Percentage of sperm whale stomachs found to contain evidence of cephalopod or fish, by year*

Columns labelled 'F' refer to flesh; those labelled 'I' refer to indigestible remains (cephalopod beaks and fish bones). Whales may be counted in both columns. These values relate to a score of 'present' or 'absent' and do not involve an estimation of relative quantity.

	1977		1978		1979		1980		1981		All years combined		
	F	I	F	I	F	I	F	I	F	I	F	I	F and/or I
n	22	51	26	41	12	27	11	22	0	4	71	145	168
Fish only	59	29	77	34	75	30	82	14	—	0	72	28	32
Cephalopods only	9	18	12	24	17	33	9	14	—	0	11	21	13
Fish and cephalopods	32	53	12	41	8	37	9	73	—	100	17	51	55
Fish (with or without cephalopods)	91	82	89	76	83	67	91	86	—	100	89	79	87
Cephalopods (with or without fish)	41	71	23	66	25	70	18	86	—	100	28	72	68

Ratio of cephalopod to fish

Table 6 gives the percentage of stomachs containing food remains in which were found flesh of fish, cephalopods or a mixture of the two prey classes. Most squid were ammoniacal and, as such, had soft bodies which would probably be digested more quickly than fish. Certainly, most squid flesh encountered comprised the muscular crown (head and limbs) alone. The only complete squid seen, with the skin intact, were three *Todarodes sagittatus* (a non-ammoniacal species of the Ommastrephidae) from one sperm whale stomach.

The ratio of the number of stomachs containing fish flesh to those containing squid flesh was 63:20 in our sample, giving 76% fish and 24% squid (see Discussion for interpretation).

The relative frequency of occurrence of fish and cephalopod flesh did not vary significantly between years ($\chi^2 = 1{\cdot}32$, D.F. = , $P > 0{\cdot}7$), so either the ratio of cephalopods and fish available remains constant or, if it varies, prey selectivity also changes in response.

Non-food items found in stomachs

A variety of non-food objects was found in stomachs; most of these were either fragments of rock or floating debris. The latter were usually of plastic or wood and 0·2 m or less in length. Plastic drinking cups, children's toys, small pieces of tree branches and a newspaper were typical of this category. The rock fragments, both basalt and granite were all small, weighing less than 0·02 kg, but up to 0·1 kg of rock were found in some stomachs. The presence or absence of non-food items was not always recorded, but fewer than 10 % of whales were found to have them at death.

The only large items discovered were five discarded fishing nets. The largest of these weighed 63 kg and was firmly stuck in the constriction between the second and third stomach compartments. It is possible that such a blockage could lead to death of the whale through starvation, but the smaller items could easily be voided with the bones and squid beaks at periodic regurgitations. Varying quantities of unidentified parasitic nematodes were found in most stomachs.

DISCUSSION

This study supports Roe's (1969) conclusion that, unlike most stocks elsewhere in the world (Kawakami, 1980), the sperm whales occurring between Greenland and Iceland probably eat more fish than cephalopods. Furthermore, the dominance of fish remains constant from year to year and one species, *Cyclopterus lumpus*, may provide almost half of the total biomass taken by sperm whales in this area.

The four fish most commonly encountered in this study, *C. lumpus*, *Sebastes* sp., *Lophius piscatorius* and *Gadus morhua*, were all recorded as being of major importance by Roe (1969), suggesting that the major components of the diet are substantially constant over a period of a decade or more. However, the rarer species (Table 3) were not observed by Roe, and four fish recorded by Roe were not seen between 1978 and 1981.

The relative importance of the various species of cephalopod and fish in the diet cannot be calculated directly from flesh remains. Although most prey items will leave diagnostic 'indigestible' remnants, they are not comparable between the two prey classes or even between all fish species, so they alone are not a sufficient measure of relative importance. The estimate derived from the occurrence of flesh alone (76 % fish and 24 % squid) does not rely on an assessment of relative quantity in each stomach but assumes that squid crowns and fish remain identifiable for equal periods of time after ingestion. This assumption may not hold, because squid crowns are small and thus possibly digested more quickly than the much larger entire fish. If so, cephalopods would be under estimated in the diet. A bias in the technique itself is that the less common prey in a stomach with both fish and cephalopods present receives equal weighting with the dominant type. This can lead to underestimation of the latter when

determining the relative importance of the two components overall. If cephalopods are less important than fish, the effect of this bias is opposite to that caused by any error in the assumption of equal digestion rate. Taking into consideration the possible biases, the evidence of flesh in stomachs can only be advanced as a strong indication that fish provide a greater proportion of the diet than do cephalopods.

Ninety-four per cent of the cephalopods are neutrally buoyant, mid-water oceanic animals; 84% of these are ammoniacal and 9% have a low-density oil. Only about 12% of the cephalopods (ommastrephids and gonatids) are muscular and would resist digestion to the same extent as most fish species. While detailed differences between the 17 squid samples from 1977 to 80 and the large complete 1967 sample probably only reflect the particular diet of the 1967 whale prior to capture, certain comparisons are useful. Thirteen cephalopod families were present at both times and six families were only present at one or other time. Three families, the Architeuthidae, the Pholidoteuthidae and the ?Psychroteuthidae were present in 1967 and were not represented in 1977–80. Three families, the Brachioteuthidae, Lepidoteuthidae and Stauroteuthidae were represented in 1977–80 but not in 1967.

The cephalopod families Histioteuthidae and Cranchiidae are the most numerous in both samples although their numerical importance is reversed in 1977–80 (Table 4). The Gonatidae and Ommastrephidae were more numerous in 1977–80 than in the 1967 sample. In the recent material the Histioteuthidae (38·4%) and the Cranchiidae (24·5%) are the most important by weight, with the Ommastrephidae (17·1%) and the Gonatidae (9·4%) being of secondary importance. The Lepidoteuthidae almost certainly only live in much lower latitudes, and their apparent importance by weight (7·3%) reflects their large size and retention in the stomachs of whales which had migrated north prior to capture.

Seventy-three per cent of the cephalopod species and 87% of the cephalopods represented in the collection have photophores, so they would be detectable by sperm whales by sight in the dark depths or at night. Species represented by beaks which are known to live south of 45° S but not known to live off Iceland are *Onychoteuthis banksi*, *Brachioteuthis* sp., *Cycloteuthis akimushkini*, *Lepidoteuthis grimaldii*, *Histioteuthis dofleini*, *H. reversa*, *Megalocranchia* sp., *Stauroteuthis* sp. and *Alloposus mollis*. These may be used as 'markers' of whales which had travelled north prior to being caught off Iceland. Four such whales were caught in August and one was caught in September (Table 1).

From existing knowledge of the habits of the cephalopods and, especially, fish found as flesh in this study, we can deduce that sperm whales in the Denmark Strait typically feed either in mid-water or at the sea-bed in waters 400–1200 m in depth. The species is very rarely seen in shallower waters off Iceland but may extend its range to water depths of 2000–3000 m, beyond the reach of the Icelandic catcher boats.

Similar studies elsewhere have shown that sperm whales are often benthic or

bathypelagic feeders (e.g. Betesheva & Akimushkin, 1955; Clarke, 1976, 1980; Gaskin & Cawthorn, 1967; Nemoto & Nasu, 1963) and the extraordinary duration of dives undertaken by this species, together with evidence from sonar traces and entanglements in submarine cables, support this conclusion. Nevertheless, some of the prey taken off Iceland, as elsewhere, is probably obtained in mid-water and some may even be taken from near the sea surface at night (e.g. ommastrephids). The presence of positively buoyant objects such as pieces of wood and plastic in some stomachs demonstrates that whales do swallow items from the surface.

The occurrence of non-food items in the stomach is consistent with observations made on sperm whales elsewhere (Nemoto & Nasu, 1963). There can be little doubt that most of these items are regurgitated with the indigestible hard-parts of prey at intervals of days or weeks (Clarke, 1980). Thus the proportion of animals in which these objects were found at death will probably be a gross underestimate of the proportion which swallow such items at some time in their lives. The ingestion of stone is likely to be accidental during foraging at the sea-bed. Certainly, insufficient quantities were found in this study to indicate that they were used to masticate food.

Comparison with other studies, e.g. the Azores (Clarke, 1956), South Africa (Clarke, 1980; Gambell, 1972), New Zealand (Gaskin & Cawthorn, 1967) suggests that Icelandic-caught sperm whales had, on average, stomachs which were more often empty, less often contained flesh and, when flesh was present, contained a smaller quantity than elsewhere. The length of time between whale capture and examination, and thus post-mortem digestion, was similar in these studies. The contrast between the situation in the Azores and that in Iceland is particularly interesting, since it is known that some whales occurring off Iceland also spend time in Azorean waters (Martin, 1982). Only 5% of the stomachs of males examined in the Azores between July and September by Clarke (1956) were either empty or contained only indigestible remains (compared with 63·5% off Iceland), 95% contained flesh (36·5% off Iceland) and the first stomachs of 41·8% of the Azorean whales were 'stuffed with food', a description which could not apply to a single animal examined at the Icelandic station.

If it really is the case that male sperm whales in the Denmark Strait are eating less well than their counterparts around the Azores, the question arises as to why they undertake the journey to higher latitudes at all. Given that the females all stay nearer the equator, that energy requirements to maintain the body in colder waters are greater than those needed in warmer seas and that the journey to and from Iceland must be energetically costly, it has previously been assumed that the benefits of moving into high latitudes must be considerable. However, unless there are benefits to be gained other than food, or the results of this study are misleading, it seems that the sperm whales occurring off Iceland might gain by remaining all year in lower latitudes

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