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The diet of sperm whales (*Physeter macrocephalus* Linnaeus 1758) off the Azores

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SUMMARY

Stomach contents from 17 sperm whales, 15 males and two females, caught during commercial activities in 1981–1984 in the Azores region were identified and measured.

A total of 28 738 cephalopods and 16 fish were represented in the collections. In addition, there were tunicates in two whales and man-made products in three whales. None of the stomachs were empty. Flesh was present in 94.1% and indigestible fragments alone, including mandibles (beaks) of cephalopods, were present in 5.9% of the stomachs. Twelve species of cephalopod were represented by flesh and 40 species were represented by lower beaks. The cephalopod families contributing food to the whales in this region are, in order of their contribution by estimated mass, the Octopoteuthidae (39.8%), the Histioteuthidae (32.7%), the Architeuthidae (12.1%), the Lepidoteuthidae (4.5%), the Ommastrephidae (3.4%), the Pholidoteuthidae (2.1%), the Cycloteuthidae (1.9%), the Cranchiidae (1.7%) and eight other families each contributing less than 1% by mass. Presence of *Gonatus* beaks in the stomachs show which whales have migrated southwards to the Azores just prior to capture and the presence of a large *Megalocranchia* species possibly shows which whales have migrated from higher latitudes off Iceland. However, the presence of *Teuthowenia maculata* shows which whales came north from the West coast of Africa, just prior to capture.

The modal mass of cephalopods consumed is 400–450 g which represents 0.00001 of the whales' body mass. 77.5% of the species eaten have luminous organs and 82% of the species are neutrally buoyant. It seems likely that the sperm whale is obtaining 77% of its food by swimming through luminous shoals of slow-swimming, neutrally bouyant squids and only about 23% by chasing faster swimming, larger cephalopods. Cephalopods not previously recorded from the North Atlantic are *Onychoteuthis borealijaponicus*, and *Histioteuthis bonnellii corpuscula*. *Histioteuthis ?miranda* may have been collected by the whales much further south than the Azores. Species not recorded previously in the diet of sperm whales in the North Atlantic are *Ommastrephes bartrami*, *Gonatus steenstrupi*, *Histioteuthis ?miranda*, *H. bonnellii corpuscula*, *H. meleagroteuthis*, *Discoteuthis laciniosa*, *Mastigoteuthis* species, *Chiroteuthis* species, *?Helicocranchia*, *Liocranchia reinhardti*, and *?Liguriella*.

1. INTRODUCTION

Many studies of the diet of the sperm whale (*Physeter macrocephalus*, Linn.) have shown that, except off Iceland (Clarke & MacLeod 1976; Roe 1969; Martin & Clarke 1986) the main food of the whale comprises cephalopods (see Clarke (1980, 1986*b*) for summary). Because the males of these whales can exceed 60 t and females can exceed 30 t they are a major predator of cephalopods (Clarke 1985) and probably consume annually a considerably greater mass of cephalopods than the total mass of all fish caught by man. The species is cosmopolitan and is probably the deepest diving of all mammals regularly diving to depths exceeding 1000 m and sometimes probably to over 3000 m and submerging for over 90 mins (Clarke 1976; Lockyer 1977; M. R. Clarke, unpublished observations).

Many cephalopod species in the diet of sperm whales are rarely, or never, caught by methods devised by man and, from an examination of the cephalopod remains, particularly the beaks, in the diet, much new information on the species, distribution, size ranges, growth, sexual maturity, relative numbers and other aspects of their biology has been obtained. The present collection shows us the relative importance of the families, genera and species in the diet of the whales through the year in the central Atlantic and provides a method by which the migration of sperm whales can be studied in this region. As this is the second largest collection studied it also enables us to check conclusions drawn previously from large collections from the southern hemisphere (Clarke 1980).

Collection of the stomach contents of 17 sperm whales, 15 males and two females, caught during

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Table 1. *Sperm whales of the Azores. Data of the whales sampled and a summary of the stomach contents*
(C = complete sample. 12F = sample from the island of Flores.)

whale no.	1	2	3	4	5	6	7	8	9	10C	11C	12F	13	14	15	16C	17			
sex	M	M	M	M	M	M	M	M	F	M	M	M	M	M	M	F	M	total	mean	mean
month	Jan.	Apl.	May	May	May	Jun.	Jun.	Jly	Aug.	Sep.	Sep.	Sep.	Oct.	Nov.	Nov.	Nov.	Dec.	(mean)	LRL	
day/year	2/83	16/82	23/84	24/82	24/82	7/82	25/82	27/82	11/82	7/81	7/81	21/81	21/81	7/81	16/81	17/81	15/82			
whale length	13.4	9.8	13.2	14.5	13.3	12.6	9.9	11.4	9.3	14.6	14.3	14.9	12.4	11.5	10.0	9.5	15.8	(12.4)		
buccal masses																				
Architeuthis										2							1	3	12.6	
Ommastrephes bartrami						1												1	13.0	
Pholidoteuthis boschmai							1											1	10.6	
Ancistrocheirus lesueuri			3					1										4	6.3	
Taningia danae	3		4			1	2										1	11	18.8	
Octopoteuthis sp.G						1				1	1						1	4	18.5	
Lepidoteuthis grimaldii		1				1			1				1	1	1			6	15.2	
Histioteuthis bonnellii b.	2		6		9	1	2	11	13	10		11	31	47	20	4	20	187	9.2	
Discoteuthis laciniosa		4																4	7.5	
Megalocranchia sp.A.		1	3										1					5	9.4	
Teuthowenia megalops			5													1		6	6.9	
octopod			1															1	40*	
a total buccal masses	5	6	22	0	9	5	5	12	14	13	1	11	33	48	21	5	23	233		13.7
b mass from beaks g	3876	4755	46000		4608	19234	22154	6209	9656	42402	998	5632	19279	27064	13240	2199	38887	266193		16637 (16)
c no. species	2	3	6	0	1	5	3	2	2	3	1	1	3	2	2	2	4	42		2.625 (16)
d monthly totals	5	6			31		10	12	14			25	33			74	23			
e species/month	2	3			7		8	2	2			5	3			6	4			
Beaks																				
f total lower	3217	4887	540	135	111	28	1851	628	2718	1093	2326	885	2130	3237	154	624	3970	28534		1678
g monthly lower	3217	4887			786		1897	628	2718			4304	2130			4015	3970			
h total upper	2726	4873	634	106	165	45	1760	740	2251	1231	2259	832	1574	3097	161	665	3535	26654		
i taxa	17	30			27		26	22	23			25	15			31	16	40		
other																				
Pyrosoma/salps		S	P									P								
elasmobranch					1							1								
fish			1										13							
plastic container	3			1																
netting				present																

commercial activities in 1981–1984 in the Azores region is of particular interest since it is by far the largest collection made in the North Atlantic and complements collections examined from Madeira (Clarke 1962*a*), Spain (Clarke & MacLeod 1974), and Iceland (Martin & Clarke 1986) as well as small collections from the Azores made before methods were developed to identify cephalopod mandibles or 'beaks' (Robert Clarke 1956; Joubin 1895). The chitinous beaks which are not digested, can number over 18 000 in a single whale's stomach, and the specific identification of such collections (Clarke 1986*a*) has greatly extended our knowledge of cephalopod predators' food and migration habits. The present collection comprises 55 184 beaks with no flesh attached and, of these, 28 534 were lower beaks and were identified to genus or species. In addition, there were 233 'buccal masses' (flesh of varying amounts which each contained an upper and a lower beak) and a large octopod.

2. MATERIAL AND METHODS

The first and second stomachs of 17 sperm whales were opened and searched for cephalopod remains during normal commercial whaling activities in the Azores. Sixteen were sampled at San Roque on the island of Pico and one was sampled at Santa Cruz on Flores. Details of the whales from which stomach contents were removed are given in table 1. When possible, the total contents of the stomachs were collected but difficulties in the collection from stomachs, weighing several tonnes, during the commercial process meant that we were only certain that collection was complete for three whales (nos 10, 11 and 16). Samples were roughly sorted on the platform at the whaling station or, when the collection was not a large one, it was sorted at the Department of Oceanography and Fisheries, University of the Azores, Horta. The beaks and smaller specimens were washed and stored in 76% ethyl alcohol. Larger cephalopods, which could not easily be transported from the whaling station, were measured and beaks and statoliths were removed and preserved. At a later stage, in Plymouth, lower beaks were separated from upper beaks, both were counted and then, to avoid duplication of effort, only the lower beaks were identified by methods fully described elsewhere (Clarke 1986*a*). The 'lower rostral lengths' (LRLS) or, for the Octopoda and Vampyromorpha, the 'crest' lengths (LCLS) were then measured to the nearest 0.02 mm with vernier calipers. Where large numbers belonged to one species, a random sample of 200 beaks from each whale was measured. From the rostral or crest lengths, previously published formulae relating these lengths to total masses and mantle lengths (= body lengths) of the animals, according to their families, were used to estimate the total and mean masses and the mean mantle lengths (DMLS) of each taxon identified (Clarke 1986*a*). Dry masses were then estimated for each taxon by applying ratios derived from A. Clarke, *et al.* (1985). Where this is not known for the rarer families we have chosen the ratio which best fits the type of body concerned: e.g. muscular squids such as *Ommastrephes* having a dry mass equal to 0.26 of the wet mass and ammoniacal squid such as *Histioteuthis*, having a dry mass equal to 0.123 of the wet mass. Calorific values have a mean of 20 kJ g^{-1} dry mass. Beaks are ranked in 'importance' from the values of % dry mass multiplied by the % frequency of occurrence. The LRL distributions and the LRLS at which darkening of the wings of the beaks takes place (taken as the interval between the largest LRL at which the beaks have undarkened or no wings and the smallest LRL at which they have darkened wings) are given as a valuable means of comparing samples from different regions. Such comparisons sometimes indicate differences in size of the same species in different regions but often show great similarity and this supports the assumption that sperm whales of the same size sample in the same way at different times and places; this can not be said of any of man's sampling methods. The buccal masses (beaks with muscle attached) and other flesh remains are of particular interest since they represent species which must have been caught by the whales within a few tens of miles from the place at which the whale was killed whereas isolated beaks may have been carried several thousand miles from the place where the whale consumed the cephalopod (Clarke 1980).

3. RESULTS

A total of 28 767 cephalopods and 16 fish were represented in the collections. In addition, there were tunicates in two whales and man-made products in two whales (table 1). None of the stomachs were empty. Flesh was present in 94.1% and only indigestible fragments including beaks were present in 5.9% of the stomachs. This compares with Robert Clarke's earlier (1956) examination in the Azores in which 95% contained flesh and 5% were empty or contained only beaks and contrasts with Iceland where 36.5% of the stomachs had flesh, 18.4% were empty and 45.1% contained only indigestible fragments.

(*a*) *Cephalopods*

(i) *Flesh*

All but one of the samples contained cephalopod flesh. This was difficult to fully quantify. For example, in one sample there were 50 bodies but not as many heads, in another there were parts of a very large octopod with no head and in some there were buccal masses or 'crowns' of arms but few or no bodies. Although buccal masses did not represent all the cephalopods present, estimation of the masses represented by the beaks in the buccal masses gave a minimum mass for the flesh in each sample (table 1, line b). It should also be remembered that probably most samples did not comprise all the contents of the first and second stomachs.

Species represented by flesh and therefore definitely living in the area of capture were *Architeuthis ?dux*, *Ommastrephes bartrami*, *Pholidoteuthis boschmai*, *Ancistrocheirus lesueuri*, *Taningia danae*, *Octopoteuthis G.* (undes-

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Table 2. *Sperm whales of the Azores. The number of lower beaks in each taxon identified in each month from the stomachs*

species	month (no. of samples) Jan. (1)	Apl. (1)	May (3)	Jun. (2)	Jly (1)	Aug. (1)	Sep. (3)	Oct. (1)	Nov. (3)	Dec. (1)	total (17)	no. of samples with buccal masses
Architeuthis ?dux	17	8	0	1	1	6	62	2	11	27	135	2
Ommastrephes bartrami	1	2	0	1	1	0	1	0	0	0	6	1
Todarodes sagittatus	13	18	1	18	0	82	18	10	173	0	333	0
Onychoteuthis banksi	0	0	0	1	0	0	0	0	1	0	2	0
Onychoteuthis boreali-japonicus	0	17	18	18	15	6	6	0	30	0	110	0
Pholidoteuthis boschmai	2	191	9	20	0	40	3	24	38	3	330	1
Gonatus steenstrupi	185	0	0	0	0	0	185	0	0	8	378	0
Ancistrocheirus lesueuri	3	121	14	19	10	29	1	1	6	0	204	2
Taningia danae	33	607	42	102	1	84	138	36	137	18	1198	5
Octopeuthis sp.G	0	7	10	7	0	2	73	0	14	2	115	4
Octopoteuthis rugosa	2	207	1	44	9	39	2	9	58	0	371	0
Lepidoteuthis grimaldii	34	216	29	50	16	56	34	12	39	35	521	6
Histioteuthis b. bonnellii	2781	1398	262	881	91	1570	3288	1954	2139	3703	18067	14
Histioteuthis arcturi	0	307	113	188	264	168	148	0	785	0	1973	0
Histioteuthis miranda	0	19	33	39	10	181	12	0	21	1	316	0
Histioteuthis b.corpuscula	0	0	8	1	0	10	1	0	0	0	20	0
Histioteuthis meleagroteuthis	0	17	1	6	11	15	1	1	7	0	59	0
Histioteuthis ?celetaria	0	68	22	57	161	36	0	0	82	0	426	0
Histioteuthis reversa	2	3	0	0	0	6	1	0	3	4	19	0
Cycloteuthis akimushkini	0	14	28	24	3	30	29	0	23	1	152	0
Discoteuthis laciniosa	0	1064	1	75	6	124	0	0	21	0	1291	1
Mastigoteuthis sp.A	0	13	2	56	0	12	0	0	0	0	83	0
Mastigoteuthis sp.B	0	1	0	0	0	0	0	0	1	0	2	0
Chiroteuthis joubini	0	0	0	0	1	0	0	0	0	0	1	0
Chiroteuthis sp.B	0	41	2	2	2	2	7	0	6	0	62	0
Chiroteuthis veranyi	0	16	2	1	9	0	2	0	3	0	33	0
Chiroteuthis sp.D	14	9	0	1	0	1	13	29	4	1	72	0
Megalocranchia sp.G	1	0	17	0	1	0	0	0	11	0	30	0
Megalocranchia sp.A (*P. cymoctypus*)	0	127	40	55	7	38	28	2	35	1	333	3
Teuthowenia megalops	12	365	112	206	7	138	49	2	55	38	984	2
Teuthowenia maculata	51	0	0	0	0	0	104	28	291	48	522	0
Teuthowenia sp.	3	0	0	0	0	0	0	0	5	0	8	0
Taonius pavo (small B)	0	2	5	0	0	3	0	1	0	1	12	0
Helicocranchia?	0	0	0	0	1	0	0	0	3	0	4	0
Liocranchia rheinhardti	0	2	1	0	0	0	0	0	1	0	4	0
Liguriella sp.	0	0	0	0	0	0	0	0	1	0	1	0
Vampyroteuthis infernalis	0	4	1	0	0	0	0	0	0	0	5	0
Alloposus mollis	63	22	11	6	1	0	93	19	11	79	305	1
octopodid	0	1	0	0	0	0	0	0	0	0	1	0
unidentified	0	0	0	0	0	40	5	0	0	0	45	0
'Big *Psychroteuthis*'	0	0	1	0	0	0	0	0	0	0	1	0
total	3217	4887	786	1879	628	2718	4304	2130	4015	3970	28534	

cribed species), *Lepidoteuthis grimaldii*, *Histioteuthis bonnellii bonnellii*, *Discoteuthis laciniosa*, *Megalocranchia cymoctypus* and an octopod (table 1). *Histioteuthis bonnellii bonnellii* occurred in 87.5%, *Lepidoteuthis grimaldii* in 37.5% and *Taningia danae* in 31.3% of the 16 stomachs containing flesh. Large specimens of *Lepidoteuthis grimaldii* and *Megalocranchia sp.A* have not been caught by man directly and most of the others have only rarely been caught.

The number of buccal masses per sample ranged from 0 to 48 with a mean of 14 (table 1, line a). These represented up to 46 kg (mean = 16.6 kg) in mass per sample containing flesh and the squids averaged 1142 g. The number of species represented in any sample having flesh ranged from 1 to 6 and variation was not obviously related to the season (line c).

(ii) *Beaks*

A total of 28 534 lower and 26 654 upper beaks were present in the collection (lines f and h). The three complete samples (10, 11 and 16) had 624–2326 (mean = 1348) lower beaks but samples which may not have been complete contained 28–4887 (mean = 1678) lower beaks.

Forty species are represented by lower beaks in this collection (table 1, line i) and the number of species present in each month ranged from 15 to 31 (mean of 23). The number of species is not related to the number of beaks or obviously to the seasons in these samples. The taxa identified from lower beaks were distributed throughout the months according to table 2. Only 24 of the taxa could be confidently given a specific name and there are taxonomic difficulties with some of these (see below). Nearly all the rest of the lower beaks could be identified to genus. Forty-five lower beaks could not be identified, in most cases because of damage.

Beaks of *Taningia danae*, *Lepidoteuthis grimaldii* and *Histioteuthis bonnellii bonnellii* are in all the samples (table 3). Occurrence of beaks (in declining order) of the families is as follows: Histioteuthidae (100% of samples), Octopoteuthidae (100%), Lepidoteuthidae (100%), Cranchiidae (94.1%), Chiroteuthidae (88.2%), Ommastrephidae (82.4%), Pholidoteuthidae (82.4%), Architeuthidae (76.5%), Cycloteuthidae (76.5%), Alloposidae (70.6%), Ancistrocheiridae (70.6%), Onychoteuthidae (52.9%), Mastigoteuthidae (35.3%), Gonatidae (23.5%) and Vampyroteuthidae (11.8%).

The cephalopod families contributing food in the region are, in order of their contribution by estimated mass (table 3), the Octopoteuthidae (39.8%), the Histioteuthidae (32.7%), the Architeuthidae (12.1%), the Lepidoteuthidae (4.5%), the Ommastrephidae (3.4%), the Pholidoteuthidae (2.1%), the Cycloteuthidae (1.9%), the Cranchiidae (1.7%) and eight other families each contributing less than 1% by mass. The ranking by 'importance' in the diet (as estimated from the % dry mass × frequency of occurrence) of the first ten species is (table 3) *Taningia danae* (1), *Histioteuthis bonnellii bonnellii* (2), *Architeuthis ?dux* (3), *Lepidoteuthis grimaldii* (4), *Todarodes sagittatus* (5), *Pholidoteuthis boschmai* (6), *Histioteuthis arcturi* (7), an Octopodid (8), *Teuthowenia megalops* (9), *Discoteuthis laciniosa* (10).

Frequency histograms showing the number of cephalopods at each mass interval (figure 1) show that by far the greatest proportion of cephalopods are 50–700 g but there is an appreciable number over 1 kg and one over 100 kg. Probably some of the smaller beaks are from the stomachs of the larger squids and this may be the reason for the slight asymmetry of the main peak to the left of about 400 g. However, very small, fairly undigested squids of less than 100 g have been collected from the stomachs and their condition suggested they were not eaten by another cephalopod prior to ingestion by the whale. The whales would appear to target cephalopods of around 400–500 g but also take individual larger squids.

(iii) *Species notes*

Architeuthidae

Architeuthis ?dux. Until the genus has been revised it is not possible to be sure of the species name (see Compagno Roeleveld & Lipinski 1991). Four species have been named in the North Atlantic but the only undisputed species in the region is the type species of the genus, *Architeuthis dux* Steenstrup. Beaks occurred in 76.5% of the whales although in small numbers of less than 27 in any single whale. May was the only month sampled in which they did not occur (table 2). Flesh of the species occurred in samples collected in September, December and possibly June (identified

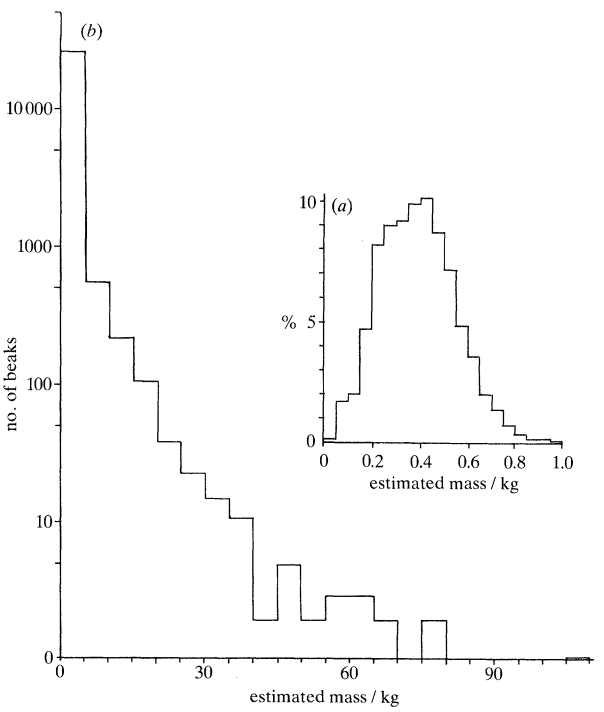

Figure 1. Sperm whales of the Azores. Distribution of the masses of individual cephalopods in the diet estimated from the rostral lengths of lower beaks removed from the stomachs. (*a*) Percentage numbers having masses less than 1 kg. (*b*) Semi-log transformation showing numbers at each mass of all cephalopods represented by lower beaks; $n = 26\,763$.

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Table 3. *Sperm whales of the Azores. The total number and occurrence of lower beaks of each taxon of cephalopod identified from the stomachs of all the 17 whales examined and estimates of wet and dry masses and mean mantle lengths derived from these*

				wet mass total		mean	mean DML	dry mass total		freq.	importance	
		no.	%	kg	%	g	mm	kg	%	(% of whales)	% dry mass × freq.	rank
Architeuthidae	*Architeuthis ?dux*	135	0.5	3189.7	12.10	23627	1159	392.33	10.97	76.5	838.90	3
Ommastrephidae		339	1.2	883.5	3.35			166.98	4.67	82.4	384.58	
	Ommastrephes bartrami	6	0.1	38.2	0.14	6367	486	7.22	0.20	29.4	5.93	
	Todarodes sagittatus	333	1.2	845.3	3.21	2538	484	159.76	4.47	64.7	288.91	5
Onychoteuthidae		112	0.4	96.3	0.37			20.80	0.58	52.9	30.76	17
	Onychoteuthis banksi	2	0.1	0.3		135	166	0.06		11.8		
	O. b.-japonicus	110	0.4	96	0.36	873	317	20.74	0.58	52.9	30.66	18
Pholidoteuthidae	*Pholidoteuthis boschmai*	330	1.2	563.6	2.14	1708	411	121.74	3.40	82.4	280.38	6
Gonatidae	*Gonatus steenstrupi*	378	1.3	29.6	0.11	78	149	5.39	0.15	23.5	3.54	
Ancistrocheiridae	*Ancistrocheirus lesueuri*	2.4	0.7	148.4	0.56	728	230	21.37	0.60	70.6	42.17	12
Octopoteuthidae		1684	5.9	10473	39.72			1508.1	42.15	100	4215.11	
	Taningia danae	1198	4.2	10223	38.77	8533	758	1472.1	41.15	100	4114.73	1
	Octopoteuthis sp.G	115	0.4	121.9	0.46	1060	325	17.55	0.49	70.6	34.64	13
	O. rugosa	371	1.3	127.6	0.48	344	200	18.37	0.51	64.7	33.23	15
Lepidoteuthidae	*Lepidoteuthis grimaldii*	521	1.8	1194.1	4.53	2286	579	146.87	4.11	100	410.52	4
Histioteuthidae		20880	73	8617.6	32.68			1060.0	29.63	100	2962.67	
	Histioteuthis bonnellii b.	18067	63	7424.4	28.16	411	175	913.20	25.52	100	2552.46	2
	H. b. corpuscula	20	0.1	2.5	0.01	123	59	0.31	0.01	35.3	0.30	
	H. arcturi	1973	6.9	917	3.48	465	111	112.79	3.15	58.8	185.37	7
	H. ?miranda	316	1.1	154.8	0.59	490	150	19.04	0.53	64.7	34.43	14
	H. meleagroteuthis	59	0.2	15.8	0.06	267	81	1.94	0.05	58.8	3.19	
	H. ?celetaria	426	1.5	102	0.39	239	91	12.55	0.35	52.9	18.55	20
	H. reversa	19	0.1	1.2		65	52	0.15	0.00	41.2	0.17	
Cycloteuthidae		1443	5.1	490.6	1.86			60.34	1.69	76.5	129.03	
	Cycloteuthis akimushkini	152	0.5	131.1	0.50	862	370	16.13	0.45	70.6	31.82	16
	Discoteuthis lacinosa	1291	4.5	359.5	1.36	278	132	44.22	1.24	41.2	50.92	10
Mastigoteuthidae		85	0.3	13.3	0.05			1.38	0.04	35.3	1.36	
	Mastigoetuthis sp.A	83	0.3	12.8	0.05	154	155	1.33	0.04	29.4	1.09	
	M. sp.B	2		0.5		258	186	0.05		11.8		
Chiroteuthidae		168	0.6	18.9	0.07			1.97	0.05	88.2	4.85	
	Chiroteuthis joubini	1				51	126			5.9		
	C. sp.B	62	0.2	4.1	0.02	66	137	0.43	0.01	47.1	0.56	
	C. veranyi	33	0.1	4.6	0.02	139	177	0.48	0.01	47.1	0.63	
	C. sp.D	72	0.2	10.2	0.04	141	178	1.06	0.03	64.7	1.92	
Cranchiidae		1898	6.7	448.5	1.70			46.64	1.30	94.1	122.68	
	Megalocranchia G	30	0.1	31.8	0.12	1138	817	3.31	0.09	29.4	2.72	
	M. sp.A(=*P.cym*)	333	1.2	105.4	0.40	316	505	10.96	0.31	70.6	21.63	19
	Teuthowenia megalops	984	3.5	202.2	0.77	205	301	21.03	0.59	94.1	55.31	9
	T. maculata	522	1.8	106.2	0.40	203	299	11.05	0.31	41.2	12.72	
	Teuthowenia sp.	8		0.6		74	199	0.06		11.8		
	Taonius pavo (*b*)	12		1.9	0.01	159	412	0.20	0.01	35.3	0.19	
	Helicocranchia?	4		0.1		38	258	0.01		11.8		
	Liocranchia rheinhardti	4		0.3		87	258	0.03		17.7		
	Liguriella	1				14	129			5.9		
Vampyroteuthidae	*Vampyroteuthis infernalis*	5		3.2	0.01	643	104	0.38	0.01	11.8	0.13	
Alloposidae	*Allopsus mollis*	305	1.1	195.7	0.74	642		23.48	0.66	70.6	46.34	11
Octopodidae	Octopodid	1				321		64.2		5.9		
Unidentified		45	0.2							11.8		
	'Big *Psychroteuthis*'	1								5.9		
Totals		28534		26365.8				3577.74				

from notes only). Other specimens of the genus collected in the Azores were recorded by Robert Clarke (1956) including one of 184 kg (1955). The squids from which the beaks came were estimated to have had mantle lengths of 346–1862 mm and to have weighed 221–107 887 g. Compagno Roeleveld & Lipinski (1991) have pointed out that previous estimates of mass and DML (Clarke 1986*a*) from LRL of South African *Architeuthis* are low and the African specimens fit estimates for North Atlantic specimens. These were by far the largest cephalopods in the diet, averaging over 23 kg and a meter in mantle length. Thus, although the genus contributes only 0.5% by number, the total mass represented by beaks is 3190 kg or 12.1% of the total mass of cephalopods represented by beaks (table 3). The wings of the beaks darken at 12.7–14.0 mm compared with 7.0–11.0 in South Africa suggesting that the species of the two regions are distinct. Beaks of this genus were also present in the collections from Madeira, Spain and Iceland although flesh was only found in Madeira.

Ommastrephidae

Beaks occurred in 82.4% of the whales although in numbers of less than 173 per whale. December was the only month sampled in which they did not occur (table 2). Two species, *Ommastrephes bartrami* (Lesueur, 1821) (= *O. caroli* (Furtado, 1887) and *Todarodes sagittatus* (Lamarck, 1799) were present. Both species are known to live close to the Azores (Clarke 1966) but only flesh of *Ommastrephes bartrami* occurred and then in only one sample collected in June. The *O. bartrami* were estimated to have had mantle lengths of from 155–751 mm and to have weighed from 108–14 540 g. They averaged over 6 kg and almost 0.5 m in mantle length. The species contributed only 0.1% by number and 0.15% by mass (table 3). Although this species is regularly seen at the sea surface around the Azores (Clarke 1966) and was found there in the stomach contents of the pigmy sperm whale, *Kogia breviceps* (Blainville, 1838) (Martins *et al.* 1985), it has not previously been found in the diet of sperm whales. The fact that it is an extremely fast swimmer is probably not the reason for this since *Dosidicus gigas*, a similarly large and agile squid, is eaten off Peru (Clarke *et al.* 1976); possibly these fast species are only vulnerable when they spawn and *O. bartrami* may spawn on the bottom at a depth or place not accessible to sperm whales. *T. sagittatus* is smaller than *O. bartrami* with estimated mantle lengths of 258–696 mm and masses of 435–6732 g. Even so, they averaged over 2.5 kg and almost 0.5 m in mantle length. The species contributes only 1.2% by number and 3.2% by wet mass to the cephalopods represented by beaks (table 3). The size distribution of the beaks with a peak at 12.0–13.0 mm and a mean of 11.97 mm (figure 2) was similar to those of the same genus in South Africa (peak at 11.5–12.5 mm). The mean mass of 2538 g is larger than for Iceland (1805 g). The largest of these beaks are large for the species suggesting animals weighing over 6.5 kg with mantles of 700 mm.

Onychoteuthidae

Onychoteuthis beaks occurred in 52.9% of the whales and in numbers of less than 30 per whale. They did not occur in October, December or January (table 2). The squids were estimated from LRLS (figure 2) to have had mantle lengths of 154–440 mm and to have weighed 89–2642 g. They averaged 873 g and 317 mm in mantle length. They contribute 0.4% by number and 0.4% by mass to the cephalopods represented by

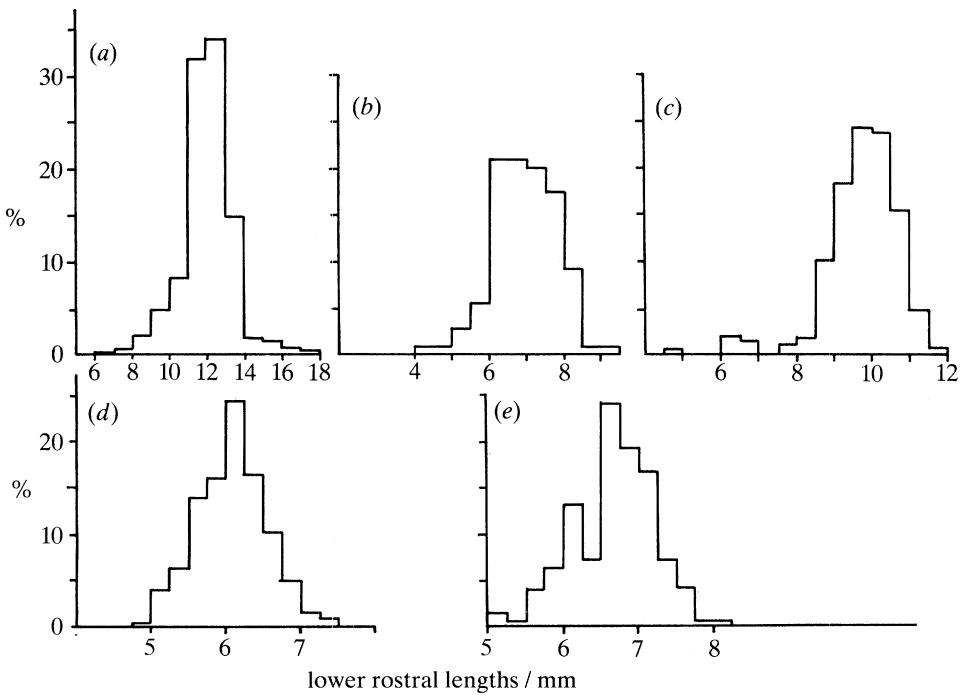

Figure 2. Lower rostral length distributions of cephalopods in the diet of sperm whales caught off the Azores. (*a*) *Todarodes sagittatus*. (*b*) *Onychoteuthis boreali-japonicus*. (*c*) *Pholidoteuthis boschmai*. (*d*) *Gonatus steenstrupi*. (*e*) *Ancistrocheirus lesueuri*.

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beaks (table 3). The wings darken at a LRL of less than 3.0 mm. No flesh was found. Although this genus has been recorded from the Azores (Clarke 1966) it has not previously been found in the diet of sperm whales there. Two species, *O. banksi* (Leach, 1817) and *O. boreali-japonicus* (Okada, 1927) were identified from beaks. *O. banksi* is known to live in the North Atlantic (Clarke 1966) and is smaller than the *O. boreali-japonicus* which had beaks with LRLS with a mean of 6.9 mm and a distribution with a peak at 6.0–7.0 mm. They had estimated masses of 88–2642 g and DMLS of 163–440 mm and averaged 873 g in mass and 317 mm in mantle length. The undigested state of most of the *O. boreali-japonicus* beaks strongly suggest that this is a new record for the North Atlantic. Identical beaks (one from a partly digested head) were found in a whale caught off Madeira (Clarke 1962*a*).

Pholidoteuthidae

Beaks belonging to *Pholidoteuthis boschmai* Adam, 1950 occurred in 82.4% of the whales in numbers between two and 191. They did not occur in July (table 2). Flesh occurred in June. The squids were estimated from LRLS (figure 2) to have had mantle lengths of 196–384 mm and to have weighed 188–2675 g. They averaged 1708 g in mass and 411 mm in mantle length. They contributed 1.2% by number and 2.1% by mass to the cephalopods represented by beaks (table 3). Beaks of the species but no flesh occurred in whales at Iceland and it is probable these squids do not live much further North than the Azores and their presence in the stomachs off Iceland indicates that certain whales travelled North to Iceland from lower latitudes. The wings darken at LRLS of 4.5–7.5 mm. Estimates of DMLS were in the range 196–484 mm and masses in the range 188–2675 g. The size distribution of the beaks (figure 2) with a peak at 9.5–10.5 mm and a mean of 9.7 mm is similar to one of the peaks at Albany, Australia but is at a larger size than in South Africa where the peak is at 8.0–8.5 mm at Durban and 7.5–8.0 mm at Donkergat (Clarke 1980). One buccal mass was found in June.

Robert Clarke (1956) recorded *Tetronychoteuthis* in the diet of sperm whales from the Azores and his specimens were certainly the same species as that from which the present beaks came. This is known from comparisons with one of his specimens and with specimens from South Africa and Australia (Clarke 1980). *Tetronychoteuthis* is very probably a synonym of *Pholidoteuthis* and their taxonomic relationship has been discussed elsewhere (Clarke 1980; Adam 1950; Rancurel 1970; Roper & Lu 1989). Two types of lower beak, A and B, were described from South Africa and most of the Azores beaks belong to type A (Clarke 1986*a*).

Ancistrocheiridae

Beaks belonging to *Ancistrocheirus lesueuri* (Orbigny, 1839) occurred in 70.6% of the whales in numbers between 1 and 121. They did not occur in December (table 2). The squids were estimated from LRLS (figure 2) to have had mantle lengths of 167–285 mm and to have weighed 273–1357 g. They averaged 230 mm ML and 728 g in mass. They contributed 0.7% by number and 0.6% by mass to the cephalopods represented by beaks (table 3). Two samples contained flesh. This widespread species was previously recorded from the Azores by Joubin (1900) from a sperm whale's stomach and beaks have since been collected from the same predator caught off Spain, Madeira and Iceland (Clarke 1962*a*; Clarke & MacLeod 1974, 1976; Martin & Clarke 1986).The wings darken at a LRL of less than 5.1 mm. The LRL distribution has a peak at 6.5–6.75 mm and a mean at 6.7 mm compared with 8.0–8.25 mm in South Africa and 8.4–8.8 mm in the Tasman Sea.

Gonatidae

Beaks belonging to *Gonatus*, occurred in 23.5% of the whales. They only occurred in September, December and January and no flesh was collected (table 2). The mean LRL of the beaks was 5.84 mm in January–December and 6.26 mm in September (figure 2). The squids were estimated to have had mantle lengths of 115–182 mm and to have weighed 41–124 g. They averaged 78 g in mass and 149 mm in mantle length. They contributed 1.3% by number and 0.1% by mass to the cephalopods represented by beaks (table 3). The latitude of the Azores is South of the distribution of either of the two North Atlantic species (Kristensen 1981; Lu & Clarke 1975) and beaks were not found in the same predator caught off Spain and Madeira (Clarke 1974). The four whales in which beaks of *Gonatus* occurred were all male and the presence of this genus (particularly in whale nos. 1 and 12 which contained 185 and 184 beaks respectively) suggests that these whales had migrated from more northerly latitudes immediately prior to being caught. Wings of the beaks darken at less than 4.9 mm which is within the range of those taken from bottlenosed whales stranded at the Faroes which darken at 3.5–5.25 mm. This, and the great similarity of the LRL distributions with a peak at 6.0–6.25 mm and a mean of 6.1 mm (figure 2) strongly suggest the beaks of the two regions are from the same species (Clarke & Kristensen 1980) and, if this is correct, the known range of *Gonatus steenstrupi* will be extended to the Faroes region. These beaks are rather smaller than the beaks of adult *G. fabricii* (Lichtenstein, 1818), best known from Western Greenland, and of *G. antarcticus* Lonnberg, 1898.

Octopoteuthidae

Beaks belonging to the family occurred in 100% of the whales (table 2). They belong to three species, *Taningia danae*, *Octopoteuthis rugosa* and *Octopoteuthis* sp.G.

Taningia danae Joubin, 1931 beaks were present in all samples. These squids were estimated to have had mantle lengths of 180–1587 mm and to have weighed 1028–39 603 g. They averaged 8533 g in mass and 758 mm in mantle length. They contributed 4.2% by number and 38.8% by mass to the cephalopods represented by beaks (table 3). Flesh was collected from sperm whales in the Azores previously by both Joubin (1900) and Robert Clarke (1956) as *Cucioteuthis*

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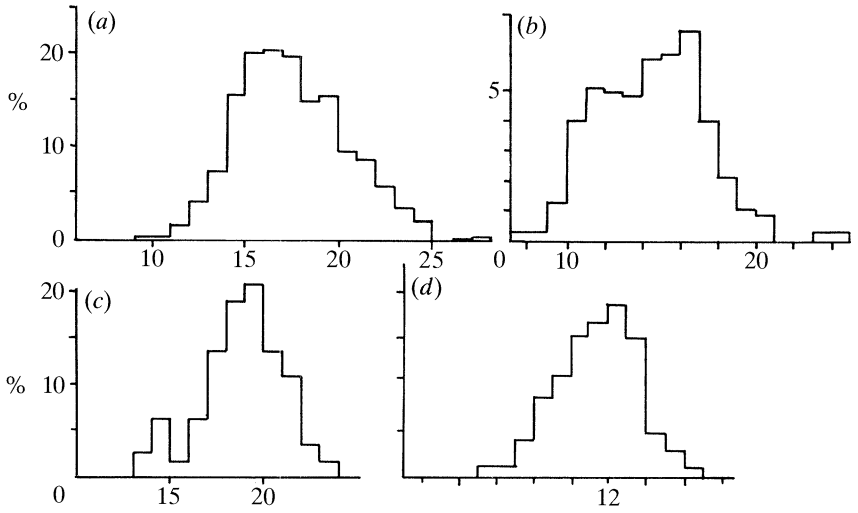

Figure 3. Lower rostral length distributions of cephalopods in the diet of sperm whales caught off the Azores. (*a*) *Taningia danae*. (*b*) *Lepidoteuthis grimaldii*. (*c*) *Octopoteuthis* sp.G. (*d*) *Octopoteuthis rugosa*.

unguiculatus (Molina). *T. danae* was also an important part of the diet of the same predator caught off Spain and Madeira (Clarke & MacLeod 1974). The LRL distribution (figure 3) was more symmetrical than in South Africa and had a mode at 15–18 mm with a mean of 17.6 mm as opposed to modes at 11–12 mm at Durban and Donkergat and 20–21 mm in Western Australia (Clarke 1980). Wings darkened at 15.9–18.3 mm.

Some octopoteuthid beaks, which are very similar to those of *Taningia danae* but are even larger (figure 3), are called here *Octopoteuthis* sp.G. They are identical to those from a very large specimen of a new, undescribed species trawled from the bottom of the North Atlantic (see 'Giant *Octopoteuthis*, p. 116 in Clarke (1986*a*) for photograph of beak). Beaks identical to the beaks of this specimen were discovered in whales' stomachs from the Tasman Sea (Clarke & MacLeod 1982) and were formerly referred to as 'Big *Octopoteuthis* sp.'. The squids were estimated to have had mantle lengths of 230–412 mm and to have weighed 468–1794 g. They averaged 1060 g in mass and 325 mm in mantle length. They contributed 0.4% by number and 0.5% by mass to the cephalopods represented by beaks (table 3). Buccal masses were collected from four whales. LRLs had a mean of 17.6 mm and a distribution with a peak at 19.0–20.0 mm

The *Octopoteuthis rugosa* Clarke, 1980 were estimated to have had mantle lengths of 133–247 mm and to have weighed 132–553 g. They averaged 344 g in mass and 200 mm in mantle length. They contribute 1.3% by number and 0.5% by mass to the cephalopods represented by beaks (table 3). No flesh was collected. Beaks came from 64.7% of the samples and were collected in all months except December. Neither the beaks nor the animals have previously been collected from the North Atlantic. The LRL distribution (figure 3) had a mode at 12.0–12.5 mm and a mean of 11.6 mm compared with a peak at 10–11 mm off South Africa.

Lepidoteuthidae

Lepidoteuthis grimaldii Joubin, 1985 were estimated to have had mantle lengths of 306–1024 mm and to have weighed 260–11 867 g. They averaged 2286 g in mass and 579 mm in mantle length. They contributed 1.8% by number and 4.5% by mass of the cephalopods represented by beaks (table 3). Beaks were present in 100% of the samples spread throughout all months of the year (table 2). Flesh was collected from six samples spread throughout the year (table 1). The size distribution of beaks has two peaks (figure 3). In one sample taken in May most of the beaks were much smaller (LRL = 8.1–12.4) and mainly had undarkened wings and these could belong to another, undescribed species. The LRLs have a mean of 14.4 mm and a distribution with the peak at 16.0–17.0 mm is about the same as off South Africa (Clarke 1980). This species was first described from sperm whale stomachs examined in the Azores (Joubin 1900) and Madeira (Clarke & Maul 1962) and flesh has since been collected from the same predator as far south as 40°S and in all oceans (Clarke & MacLeod 1982). Only young specimens have been caught directly by man (Clarke 1964).

Histioteuthidae

Beaks of this family are very abundant in these samples and seven species are represented by lower beaks although one subspecies, *Histioteuthis bonnellii bonnellii* is very much more abundant than the other species. The *Histioteuthis bonnellii bonnellii* (Ferussac, 1835) were estimated to have had mantle lengths of 78–291 mm and to have weighed 82–1111 g. They averaged 411 g in mass and 175 mm in mantle length. The LRL distribution for the species is unimodal with a peak at 8.5–9.0 mm (figure 5). Darkening of the wings took place at an LRL of 7.7–9.5 mm. The whales are largely taking squids with undarkened beaks i.e. they are immature (Clarke 1962*b*). Figure 4 shows that small male sperm whales with lengths less than 10 m eat much smaller members of the species than large

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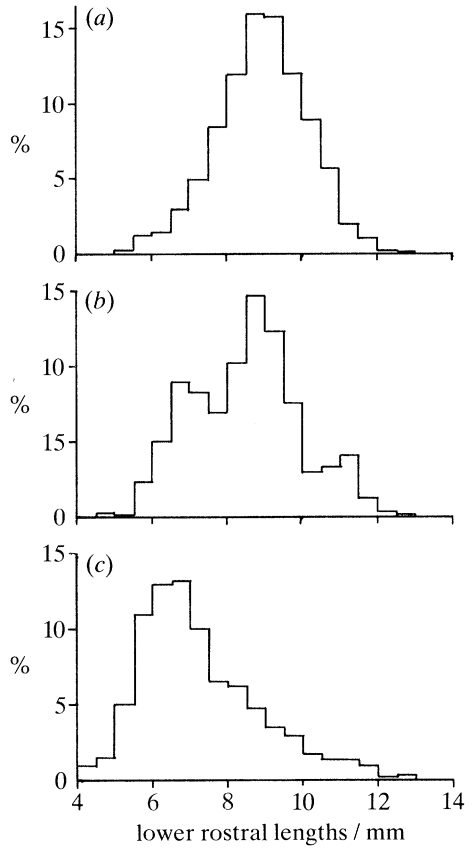

Figure 4. Lower rostral length distributions of *Histioteuthis bonnellii bonnellii* in the diet of: (*a*) large male sperm whales greater than 13 m long; (*b*) female whales; and (*c*) small male whales less than 10 m long.

males of over 13 m. Large males on the other hand, are mainly sampling squids which are approaching maturity or are sexually mature. Females, on the other hand, eat a mixture of the two size groups sampled by males and both may be found in a single female's stomach (e.g. whale no. 9). The species contributed 63.3% by number and 28.2% by mass to the cephalopods represented by beaks (table 3). Flesh was collected from 82% of the samples. The species was previously recorded from sperm whales in the Azores by Robert Clarke (1956) and from the pigmy sperm whale, *Kogia breviceps* (Blainville, 1838) by Martins *et al.* (1985). The species is also an important part of the diet of the same predator caught off Spain (5.6% by mass), Madeira (36.1%, Clarke & MacLeod 1974) and to the West of Iceland where flesh was also found (Martin & Clarke 1986).

Histioteuthis bonnellii corpuscula Clarke, 1980 was represented by only 20 lower beaks. The squids were estimated to have had mantle lengths of 41–65 mm and to have weighed 48–151 g. They contribute only 0.1% by number and 0.01% by mass to the cephalopods represented by beaks (table 3). Beaks were present in four samples from May to September. The LRL distribution (figure 5) has a peak at 5.0–5.25 mm with a mean of 4.7 mm which is close to the peak of beaks of the same species from South African samples (4.8–5.2 mm, Clarke 1980). Flesh was not present in any samples. The sub-species has not been recorded previously from whales in the Azores, Spain or Madeira (Clarke 1974) although they have been caught by trawl in the North Atlantic (M. R. Clarke, unpublished observation). While the validity of this sub-species is questionable (N. A. Voss, K. N. Nesis & P. G. Rodhouse, personal communication) there is no doubt that the lower beaks are distinct from those of *H. bonnellii bonnellii* in shape, in size and in the degree of darkening at any particular size. Thus there must be two populations even if they do not fulfill the criteria necessary for sub-species.

Histioteuthis arcturi (Robson, 1948) beaks were not in samples from October, December and January but were numerous in other months (table 2). The squids were estimated to have had mantle lengths of 83–130 mm and to have weighed 213–687 g. They averaged 465 g in mass and 111 mm in mantle length. They contributed 6.9% by number and 3.48% by mass to the cephalopods represented by beaks (table 3). The LRLs have a mean of 7.1 mm and a distribution with a main mode at 7.0–7.75 mm (figure 5) which is close to measurements for this species from the South Atlantic (7.0–8.0 mm, in Clarke (1980) as *H. dofleini* (Pfeffer, 1912)). Flesh was not present in any samples and it is probable that this species was collected by the whales well to the South of the Azores. The species has not been recorded previously from sperm whales in the Azores, Spain or Madeira (Clarke & MacLeod 1974). Specimens have been reported from *Alepisaurus* stomachs from Madeira; the northern boundary of its distribution in the North Atlantic is thought to be 36°N (Voss 1969).

Histioteuthis meleagroteuthis (Chun, 1910) was represented by 59 lower beaks. The squids, were estimated to have had mantle lengths of 52–96 mm and to have weighed 60–453 g. They contributed only 0.2% by number and 0.06% by mass to the cephalopods represented by beaks (table 3). Small numbers of beaks were present throughout the year except in December and January (table 2). Flesh was not present in any samples. The LRL distribution has a double peak at 4.0–4.75 mm and a mean at 4.3 mm (figure 5). The species has not been recorded previously from whales in the Azores, Spain or Madeira (Clarke 1974) although its limit of distribution in the North Atlantic is thought to be about 35°N (Voss 1969).

Histioteuthis reversa (Verrill, 1880) was represented by only 19 lower beaks. The squids were estimated to have had mantle lengths of 44–61 mm and to have weighed 37–100 g. They contribute only 0.1% by number and less than 0.01% by mass to the cephalopods represented by beaks (table 3). Small numbers of beaks were present throughout the year but not in all months (table 2). Flesh was not present in any samples. The LRL distribution has a peak at 3.0–3.25 mm and a mean of 3.2 mm (figure 5). Wings darken at a LRL of 2.7 mm. The species has not been recorded previously from sperm whales in the Azores, Spain or Madeira (Clarke & MacLeod 1974) although beaks were found in a *Kogia breviceps* stomach in the Azores (Martins, 1985). Its northern limit of distribution in the North Atlantic is 55°N (Voss 1969).

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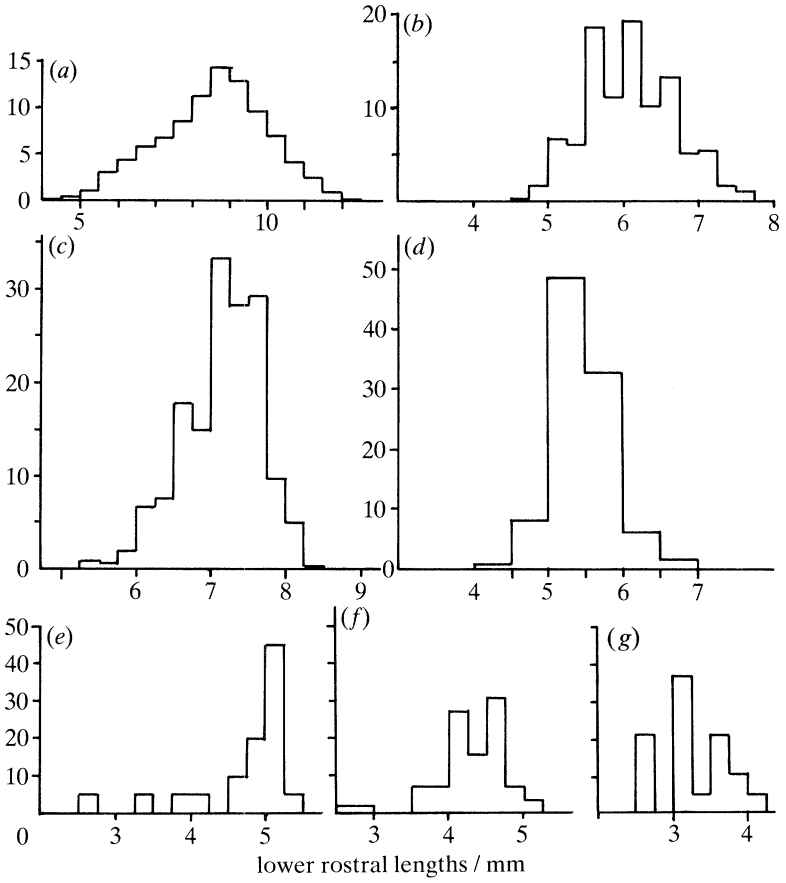

Figure 5. Lower rostral length distributions of cephalopods in the diet of sperm whales caught off the Azores. (*a*) *Histioteuthis bonnellii bonnellii*. (*b*) *H. ?miranda*. (*c*) *H. arcturi*. (*d*) *H. ?celetaria*. (*e*) *H. bonnellii corpuscula*. (*f*) *H. meleagroteuthis*. (*g*) *H. reversa*.

At least two further species of *Histioteuthis* beaks are present but neither can be positively identified. We shall call these *Histioteuthis ?celetaria/corona* and *H. ?miranda* although there are considerable doubts about both; about the first because of its variation and about the second because of its known distribution.

Histioteuthis ?celetaria (Voss 1960)/*corona* (Voss & Voss 1962) was represented by 426 lower beaks. These beaks may comprise two species, one having beaks rather like small *H. bonnellii bonnellii* and one like small *H. arcturi* but with some intermediates making a clear separation impossible. The squids were estimated to have had mantle lengths of 75–133 mm and to have weighed 120–425 g. They contribute only 1.5% by number and 0.4% by mass to the cephalopods represented by beaks. Small numbers of beaks were present throughout the year but not in all months (table 2). The LRL distribution has a narrow peak at 5.0–5.5 mm with a mean of 5.4 mm (figure 5). Flesh was not present in any samples. These beaks have not been recorded previously from whales. The distributions of both *H. celetaria* and *H. corona* extend into the North Atlantic (Voss 1969).

The *Histioteuthis ?miranda* (Berry, 1918) were estimated to have had mantle lengths of 112–189 mm and to have weighed 246–836 g. They averaged 490 g in mass and 150 mm in mantle length. They contributed 1.1% by number and 0.6% by mass to the cephalopods represented by beaks (table 3). Beaks were in 64.7% of samples from all months except October and January. Flesh was not present in any samples. These beaks have a particularly high wing fold, are similar to those described as *Histioteuthis* 'A3' from Durban (Clarke, 1980) and possibly 'species A' from Iceland (Clarke & MacLeod, 1976) and closely resemble *H. miranda* of the Pacific which has not been recorded in the North Atlantic. The LRL distribution has a peak at 5.5–6.75 mm and a mean at 6.1 mm (figure 5), being at a smaller size than 'A3' beaks from South Africa with a mode at 6.7–7.2 mm (Clarke 1980).

Cycloteuthidae

The *Cycloteuthis akimushkini* Filipova, 1968 were estimated to have had mantle lengths of 189–505 mm and to have weighed 225–1530 g. They averaged 862 g in mass and 370 mm in mantle length. They contributed 0.5% by number and 0.5% by mass to the cephalopods represented by beaks (table 3). They were present in 70.6% of the samples spread thinly throughout the year except in January and October (table 2). The LRL distribution (figure 6) with the main peak at 10.0–15.0 mm and a mean of 11.9 mm is similar to peaks of the species from South Africa and Western Australia (Clarke 1980). Flesh was not present. Wings darkened at a LRL of 9.9–10.7 mm. *Cycloteuthis sirventi* was described by Joubin (1919) and later redescribed by Young & Roper (1969) from the North Atlantic. The present beaks are identical to

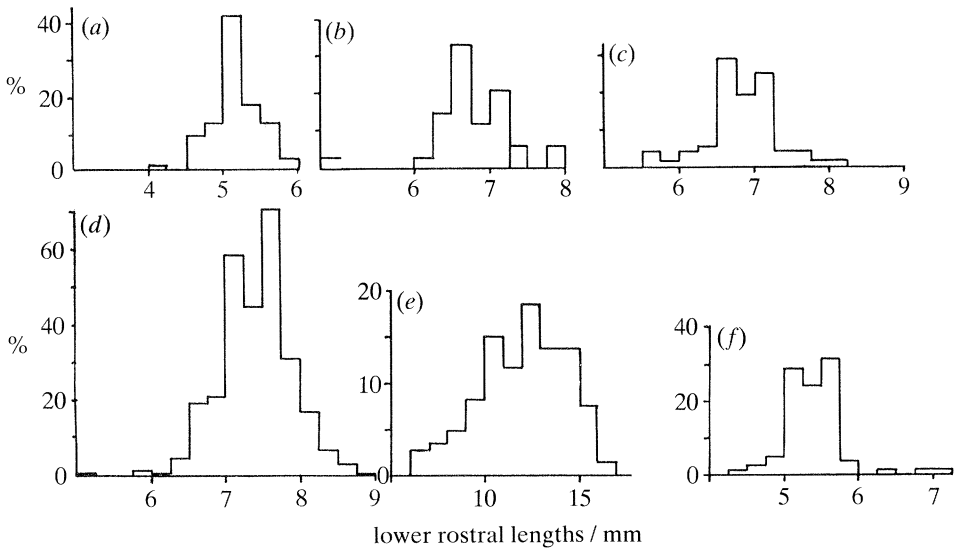

Figure 6. Lower rostral length distributions of cephalopods in the diet of sperm whales caught off the Azores. (*a*) *Chiroteuthis* sp.B. (*b*) *Chiroteuthis veranyi*. (*c*) *Chiroteuthis* sp.D. (*d*) *Discoteuthis laciniosa*. (*e*) *Cycloteuthis akimushkini*. (*f*) *Mastigoteuthis* sp.A.

beaks from South Africa described as *C. akimushkini* by Clarke (1980) who pointed out the possibility that the latter was a synonym of *C. sirventi*. The present beaks make it more likely that the large individuals extend into the North Atlantic and that the two nominal species are the same.

The Discoteuthis laciniosa Young & Roper, 1969 were estimated to have had mantle lengths of 98–155 mm and to have weighed 131–417 g. They averaged 278 g in mass and 132 mm in mantle length. They contributed 4.5% by number and 1.4% by mass to the cephalopods represented by beaks (table 3). They were present in 41.2% of the samples spread thinly throughout the year except in April when they numbered 1064 or 24% of the lower beaks (table 2). Flesh was collected from the same sample. This family was revised by Young & Roper (1969) on the basis of very few specimens. *D. discus* Young & Roper, 1969 and *D. laciniosa* are warm water species of the North Atlantic; the former extends North to 15°N and the latter to about the latitude of Madeira at 33°N. The present beaks are identical to beaks from South Africa described as *?Discoteuthis* by Clarke (1980) and more recent material has confirmed the specific identity. The LRL distribution (figure 6) has a peak at 7.0–7.75 mm and a mean of 7.4 mm which is much the same as for samples from South Africa (Clarke 1980). Wings darkened at a LRL of less than 5.9 mm. On the basis of the known distribution and recent material collected in South Africa the species is certainly *D. laciniosa* although it is not possible to confirm this from the meagre flesh found.

Mastigoteuthidae

All but two of the beaks belonging to this family closely resemble those described as *?Mastigoteuthis* A by Clarke from South Georgia (1980) but the LRLs have a mean of 5.4 mm and a distribution (figure 6) with a peak at 5.0–5.75 mm is at a smaller size than for the beaks from the Antarctic and it is probably a different species. The squids were estimated to have had mantle lengths of 126–202 mm and to have weighed 85–325 g. They averaged 155 mm in mantle length and 154 g in wet weight. They contribute 0.3% by number and 0.05% by mass to the cephalopods represented by beaks (table 3). They were present in 29.4% of the samples and occurred from April to August (table 2). No flesh was collected. Two beaks had shorter crests and do not appear to belong to the same species. The genus requires revision as there are few specimens in collections which approach the size shown by the large beaks.

Chiroteuthidae

The *Chiroteuthis* were estimated to have had mantle lengths of 109–207 mm and to have weighed 33–216 g. They contribute 0.6% by number and 0.07% by mass to the cephalopods represented by beaks (table 3). They were present in 88.2% of the samples and occurred in all months sampled (table 2). No flesh was collected. Although the taxonomy of the family is in great need of revision and naming species even from flesh is often difficult, we can be sure that there are four types of lower beak which belong to *Chiroteuthis* species. Two kinds can be identified, *Chiroteuthis joubini* Voss, 1967 ('species A' of Clarke 1980) and *Chiroteuthis veranyi* (Ferrusac, 1835) ('type C' of Clarke 1980). Both these species are known to occur in the North Atlantic. A third type of beak in this collection ('type B') was also described by Clarke from whales caught off South Africa (1980). *Chiroteuthis* 'D' has not previously been described and cannot be named. Only one other *Chiroteuthis* species is known to occur in the North Atlantic, *C. capensis* Voss, 1967 and either 'B' or 'D' may be that species. The LRL distributions with peaks at 5.0–5.25 mm and a mean of 5.2 mm for species B, with a peak at 6.5–6.75 mm and a mean at 6.8 mm for species C and with a peak at 6.5–7.25 mm

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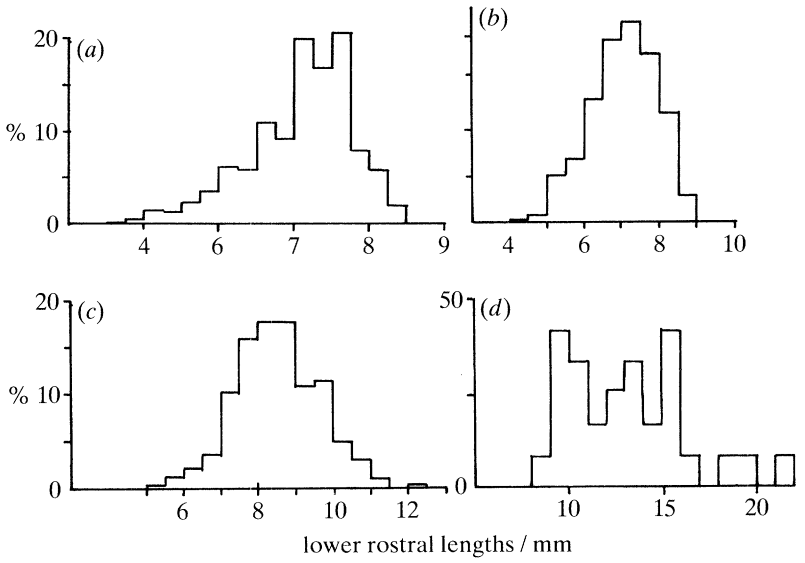

Figure 7. Lower rostral length distributions of cephalopods in the diet of sperm whales caught off the Azores. (*a*) *Teuthowenia megalops*. (*b*) *Teuthowenia* sp.B. (*c*) *Megalocranchia* sp.A (=*P. cymoctypus* Clarke). (*d*) *Megalocranchia* sp.G.

and a mean of 6.8 mm for species D are shown in figure 6; nearly all the beaks in South African samples lay at 5.0–7.5 mm.

Cranchiidae

This family contributes little to the diet (6.7% by number and 1.7% by mass) but six genera are represented in the beak collection.

There is a large and a small species of *Megalocranchia*. Members of the large species were estimated to have had mantle lengths of 495–1408 mm and to have weighed 289–3988 g. They averaged 1138 g in mass and 817 mm in mantle length. They contributed 0.1% by number and 0.1% by mass to the cephalopods represented by beaks (table 3). The same type of beak was also collected off Iceland and was mistakenly thought to be *Kondakovia* which it resembles except for its lack of a step below the jaw angle (Clarke & MacLeod 1976). However, less damaged beaks now make the present identification more likely although we must await the discovery of specimens to be sure of the generic identity of this unknown species. They were present in 29.4% of the samples (table 2). Flesh was not collected. The LRLs had a mean of 13.0 mm and are grouped at 9.0–16.0 mm (figure 7). The LRLs of beaks collected near Iceland were similar (Clarke & MacLeod 1976). The wings darkened at an LRL of 12.4–15.5 mm.

Squids of the smaller species, *Megalocranchia* sp.A of Voss (Clarke 1986*a*) were estimated to have had mantle lengths of 283–692 mm and to have weighed 81–656 g. They averaged 316 g in mass and 505 mm in mantle length. They contributed 1.2% by number and 0.4% by mass to the cephalopods represented by beaks (table 3). They were present in 70.6% of the samples (table 2). Flesh was collected from three whales. These beaks were the same as those referred to as *Phasmatopsis cymoctypus* de Rochbrune, 1884 by Clarke (1962*c*, 1980) but later considered by Voss as the same as her unnamed species of *Megalocranchia* sp.A (see Clarke 1986*a*). The LRLs have a mean at 8.45 mm and a distribution (figure 7) with a peak at 8.0–9.0 mm which is at the same size as the same species in South African samples (Clarke 1980). The wings darkened at an LRL of 6.9–7.8 mm

Teuthowenia megalops (Prosch, 1849) were estimated to have had mantle lengths of 204–355 mm and to have weighed 78–302 g. They averaged 301 mm in mantle length and 205 g in mass. They contributed 3.5% by number and 0.8% by mass to the cephalopods represented by beaks (table 3). They were present in 94% of the samples (table 2). Flesh was present in two samples. According to Voss (1985) this is the only species of *Teuthowenia* known to live in the Azores region. Identical beaks have been described elsewhere as *Teuthowenia*/*Galiteuthis* sp.A (Clarke 1986*a*). The LRLs have a mean of 7.1 mm and a skewed distribution with a peak at 7.0–7.75 mm (figure 7). The wings darkened at an LRL of 5.8–7.2 mm.

Teuthowenia maculata (Leach, 1817) which is limited to an area to the west of Africa north to 20°N (Voss 1985) is probably the second species of the genus represented by beaks. These were estimated to have had mantle lengths of 192–371 mm and to have weighed 67–337 g. They averaged 299 mm in mantle length and 203 g in mass. They contribute 1.8% by number and 0.4% by mass to the cephalopods represented by beaks (table 3). They were present in 41.2% of the samples collected only in the months from September to January (table 2). As one would expect from knowledge of the geographic distribution, no flesh was present in the samples. The LRLs have a mean at 7.0 and a distribution with a peak at 7.0–7.5 mm (figure 7). The wings darkened at an LRL of 5.1–7.3 mm.

Other cranchiids comprised eight beaks of another species close to *Teuthowenia* with LRLs 3.9–5.3 mm with wings darkening at 3.9–4.3 mm, twelve beaks of *Taonius pavo* (Lesueur, 1821) of a type previously

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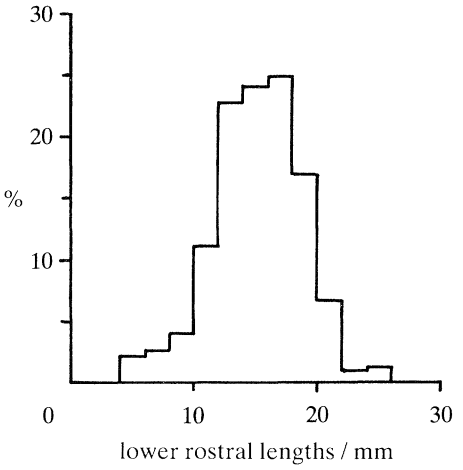

Figure 8. Lower hood length distribution of *Alloposus mollis*.

termed '*Taonius* small B' (=Taonius sp.B of Voss; Clarke 1986*a*) and with darkened wings and LRLS 4.1–8.5 mm, four beaks of *?Helicocranchia* (which could possibly be *Leachia*) with LRLS of 3.2–3.9 mm, four beaks of *Liocranchia reinhardtii* (Steenstrup, 1856) with LRLS of 2.6–3.6 mm and one beak with an LRL of 2.3 mm closely resembling the beaks of the southern genus *Liguriella*.

Unidentified squids

One beak with an LRL of 8.1 mm belongs to an unidentified species previously referred to as 'Big *Psychroteuthis*' (Clarke 1986*a*).

Forty-five lower beaks could not be identified to family.

Vampyromorpha. Vampyroteuthidae

Five *Vampyroteuthis infernalis* Chun, 1903 were estimated to have had mantle lengths of 96–129 mm and to have weighed 453–1264 g. They averaged 104 mm in mantle length and 643 g in mass and they contributed less than 0.01% to both the number and the mass of cephalopods represented by beaks (table 3). They were present in 11.8% of the samples collected and only in April and May (table 2). Lower Hood lengths were 4.5–25.8 mm.

Octopoda. Alloposidae

Alloposus mollis Verrill, 1880 were estimated to have weighed 109–1371 g. They averaged 642 g in mass and contributed 1.1% to the number and 0.7% to the mass of the cephalopods represented by beaks (table 3). The LRLS have a mean at 15.1 and a distribution with a peak at 12.0–18.0 mm (figure 8). They were present in 70.6% of the samples and in all months except August (table 2). Flesh was present in the May sample.

Octopodidae

One lower beak with a hood length of 7.9 mm could not be further identified.

A very large octopod body in whale no.1 could not be identified.

(*b*) *Fish*

On 24 May a male whale measuring 13.3 m contained very little except a skeleton resembling that of a ray. Another elasmobranch skeleton was present in whale no. 12 caught off Flores. A third fish from another whale caught in May was probably *Alepisaurus*, a deep-living midwater species. A whale in October contained 13 unidentified teleost skeletons. A male whale (not otherwise examined or listed) caught in August contained a rare angler fish, *Himantolophius* which was recorded previously by Robert Clarke (1956) from the same predator and location (1956).

(*c*) *Other animals*

A 9.8 m long male whale contained a large number of salps, some of which were strawberry-coloured and *Pyrosoma* was present in two stomachs.

(*d*) *Man-made objects*

On 24 May a male measuring 14.5 m had a stomach distended with water which contained only 135 lower and 106 upper beaks, a large part of a fisherman's trawl and a plastic jug. Course trawl netting was also collected from a male caught in August but otherwise not examined.

4. DISCUSSION

Cephalopod beaks from this collection, not previously recorded from the diet of sperm whales in the North Atlantic, are *Ommastrephes bartrami*, *Onychoteuthis ?boreali-japonicus*, *Gonatus steenstrupi* (may have been confused with *G. fabricei* previously), *Histioteuthis ?miranda*, *H. bonnellii corpuscula*, *H. meleagroteuthis*, *Discoteuthis laciniosa*, *Mastigoteuthis* species, *Chiroteuthis* species, *Helicocrancha-Leachia*, *Liocranchia reinhardti*, and *?Liguriella*. Because *Gonatus* does not extend to lower latitudes than about 45°N the males (Kristensen 1981; Lu & Clarke 1975), from which these beaks were collected, had migrated from the north of the Azores, prior to being caught. Thus, whale no. 1 in January and whale no. 12 in September (table 2) had probably moved south from colder waters prior to capture. On the other hand, the presence of *Teuthowenia maculata* in whales from September to January probably means that, during this period, most of the whales had travelled north to the Azores from West Africa.

The regularity in occurrence of so many species which are only caught or seen rarely by man is surprising. In particular, the high importance of *Taningia danae* (ranking 1), *Lepidoteuthis grimaldii* (4), *Pholidoteuthis boschmai* (6), is particularly surprising since very few of any of these have been caught directly by man.

The estimated mass of cephalopod flesh represented by the 28 534 beaks is over 26 t giving a mean mass per cephalopod of 923 g. Plots of the estimated masses of the cephalopods represented by beaks (figure 1) shows the enormous range of size sampled. R. Clarke *et al.* (1988), on the basis of further observations in

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later years, claimed that many of the smaller squids recorded by M. Clarke *et al.* (1976) in sperm whales off Peru were probably ingested by the larger squids prior to being eaten by the whales. However, this ignored the fact that three small species in the genera *Histioteuthis*, *Chiroteuthis* and *Ancistrocheirus*, comprising 68% of the number of beaks represented, did have flesh present and we feel that this is good evidence to suggest that, at the time of our investigation, these small species were important in the diet of sperm whales and were not mainly derived from the stomachs of the large squids, *Dosidicus gigas*. It seems more likely that the difference in findings was due to oceanographic changes between the years of collection. Similarly, in the Azores region, flesh was present in 12 species including ten gelatinous species, the digestion of which would probably be rapid. In addition, previous evidence from dissecting stomachs of squids from sperm whales (Clarke 1980) suggests that stomach contents of the larger food is not the major source of the small beaks. We feel confident that the whales are sampling squids from less that 100 g to over 100 000 g. Previous observations of large squids being vomited from sperm whales show they eat even larger cephalopods of perhaps as much as 400 000 g. Thus, the range sampled spans four orders of magnitude. The modal mass is 400–450 g which represents 0.00001 of the whales' body mass. This is comparable to a 90 kg man aiming to sample food the size of a walnut and swallowing anything between the size of a pea and a half pound steak. Clearly the whales' tactics for attacking the two ends of the size range must be different. Presumably, the smaller squids are scooped up as the whale swims through a shoal while the larger ones, of perhaps over 800 g or so, may be chased individually.

Of the species eaten 77.5% have luminous organs including all species with mean masses under 1200 g; there is only one (*Gonatus steenstrupi*) non-luminous species of that size (Clarke *et al.* 1979). Only one luminous species, *Taningia danae*, has a mean mass above 1200 g. Eighty-two per cent of the species are neutrally buoyant and these include all those with a mean mass under 1200 g as well as two larger species, *Architeuthis ?dux* and *Lepidoteuthis grimaldii*. From these features, it seems likely that the sperm whale is obtaining 77% (by mass) of its food by swimming through shoals of slow-swimming, luminous, neutrally bouyant squids and only about 23% by chasing faster swimming, larger cephalopods, some or all of which, shoal. The former may require sonar for detection at distances greater than two or three hundred metres, below which they could be seen, while the latter may require sonar during capture at greater depths than 600 m where they could not be seen and most of them are caught (Clarke 1980). Recent speculation that sperm whales need a sound-stunning device to kill squid is largely based upon the belief that the squids caught are large and fast-swimming. This is not true of most of the cephalopods eaten at the Azores or, indeed, elsewhere (Clarke 1986*b*).

As discussed previously (Clarke 1988), sperm whales eat different sized cephalopods according to the whale's sex and size. This is confirmed for *Histioteuthis bonnellii* in this study (figure 4). Small male whales, ate smaller *H. b. bonnellii* than did large male whales. Females, which dive and feed with young males, by themselves or with large males take a mixture of small and large *H. b. bonnellii*. As the small males also eat much larger squids of other species, this sampling difference is likely to be a reflection of the depth distribution of the cephalopod and the lesser diving capacity of the smaller whales rather than of the selection by size by the different sizes of whale. Many species of cephalopod descend to greater depths as they grow (Clarke & Lu 1974; Lu & Clarke 1975).

This collection provides data on the consumption of whales which can be usefully compared with similar data from South Africa (Clarke 1980). Taking the mean body mass of the whales sampled as about 38 t and the requirement as 2–3.5% body mass per day these whales would have required 760–1330 kg per day. Assuming that the number of buccal masses in a sample represents the intake in the last dive prior to capture, the mean weight of flesh represented by buccal masses (17 kg) suggests that the whales would have to make 45 dives during each day to fulfill its needs. However, they cannot do this because the dive cycle usually takes about one hour in whales of this size (Clarke 1976). Even if the maximum mass of flesh found (46 kg) is taken, 17 dives per day would be necessary. This is possible but it is more likely that fewer dives are made and that the mean consumption is greater than our maximum estimate. A likely 12 dives per day would require a consumption of 64 kg per dive. As the mean mass of cephalopod represented by buccal masses and lower beaks is estimated at 1142 g and 923 g respectively a mean of 1 kg per cephalopod can be taken. The number of cephalopods consumed per day would be 760–1330 kg or about 1000. The beaks in the samples therefore represent less than five day's food with a mean of 1.7 days. This compares closely with the conclusions based on previous samples (Clarke 1980).

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