

THE DIET OF SWORDFISH (*XIPHIAS GLADIUS*) IN AZOREAN WATERS

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ARQUIPÉLAGO



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A total of 132 stomachs were collected in 1992-93 from swordfish caught on drifting longlines near the Azores. Contents were sorted completely into components which comprised all stages of digested fish and cephalopods from complete fish to fragments of muscle, bones, otoliths and beaks of cephalopods. Fish and larger bones which could be identified all belonged to *Capros aper*, *Lepidopus caudatus*, *Pagellus bogaraveo*, myctophids, and the fish used as bait, *Trachurus picturatus*. Flesh of the squids *Todarodes sagittatus*, *Pholidoteuthis boschmai* and the squid used as bait *Illex* sp. was also present. 1249 otoliths and 120 cephalopod lower beaks were identified to genus or species. There was a mean of 3.1 species and 18 animals represented in each stomach. Fish remains occurred in 98.4% of the stomachs and contributed 93.4% of animals in the diet. Cephalopod remains occurred in 37.4% and contributed 5.8% of animals. Estimates of the weights of fish and cephalopods show that cephalopods provide 50.5% and fish species 49.5% of the stomach contents. The most important constituents of the diet by decreasing % estimated weight are *Ommastrephes bartrami* (24.4%), *Lepidopus caudatus* (17.4%), *Pholidoteuthis boschmai* (15.9%), *Capros aper* (14.9%), *Beryx* spp. (5.4%), *Micromesistius poulassou* (4.3%), *Onychoteuthis* sp. (3.9%), *Moroteuthis* sp. (2.7%) and *Pagellus bogaraveo* (2.2%). In all, there are more than 18 species of fish and 22 species of cephalopod in the diet. Size distributions of otoliths and beaks are presented. The species include bottom and midwater forms from both oceanic and near island water and depths. A number of rare species of cephalopods and species not recorded for the Azores are in the diet. Diet does not differ according to the size of swordfish sampled or between female and male swordfish. Preliminary calculations were made on the minimum biomass eaten by the swordfish off the Azores as 7280 - 8680 t per year, approximately half fish and half cephalopods.

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Um total de 132 estômagos de espadarte foram recolhidos durante os anos de 1992/93 em indivíduos capturados em palangre derivante perto do arquipélago dos Açores. Os conteúdos foram completamente separados em componentes que incluíam: todos os estados de digestão de peixes e cefalópodes, desde peixes completos até fragmentos de músculo, ossos e otólitos e bicos de cefalópodes. Os peixes e os ossos maiores, que podem ser identificados, pertenciam todos a *Capros aper*, *Lepidopus caudatus*, *Pagellus bogaraveo*, mictofídeos e o peixe que servia de isco, *Trachurus picturatus*. Músculo das lulas *Todarodes sagittatus*, *Pholidoteuthis boschmai* e a lula que servia de isco *Illex* sp. também foi encontrada. 1249 otólitos e 120 bicos (inferiores) de cefalópodes foram identificados até ao género ou espécie. Encontrou-se uma média de 3.1 espécies e 18 animais representados em cada estômago. 98.4% dos estômagos apresentavam restos de peixes que contribuíam com 93.4% dos animais na dieta. Encontraram-se cefalópodes em 37.4% dos estômagos que contribuíam com 5.8% dos animais. Estimou-se que os pesos dos cefalópodes e peixes

contribuíam respectivamente com 50.5% e 49.5% dos conteúdos estomacais. Os constituintes mais importantes da dieta, determinados por depleção de % peso estimado são *Ommastrephes bartrami* (24.4%), *Lepidopus caudatus* (17.4%), *Pholidoteuthis boschmai* (15.9%), *Capros aper* (14.9%), *Beryx* spp. (5.4%), *Micromesistius poutassou* (4.3%), *Onychoteuthis* sp. (3.9%), *Moroteuthis* sp. (2.7%) e *Pagellus bogoraveo* (2.2%). Ao todo, há mais do que 18 espécies de peixe e 22 de cefalópodes na dieta. Apresentam-se as distribuições por tamanho de otólitos e bicos. Há espécies bentónicas e mesopelágicas de águas oceânicas, costeiras e profundas. Aparecem, na dieta, algumas espécies raras e não registadas para os Açores. As dietas não variam de acordo com a dimensão do espadarte amostrado ou entre sexos. Cálculos preliminares sobre a biomassa mínima consumida pelo espadarte dos Açores apontam para um número entre 7280 a 8680 t por ano, sendo aproximadamente metade peixe e metade cefalópodes.

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INTRODUCTION

The present analysis of swordfish stomach contents from the Azores is the forth part of a continuing programme to analyse the diets of large predators in the food web of Azores waters. Previously, the diets of the cetaceans *Physeter macrocephalus* (CLARKE et al. 1993), one *Kogia breviceps* (MARTINS et al. 1985) and *Loligo forbesi* (MARTINS 1982) have been described from the Azores.

The study of diets of marine fish has previously been attempted by the application of several methods involving greater or lesser complication; the work on swordfish diet is a typical example of progress in this field. Work before 1968 comprised notes of the species occurring in swordfish stomachs, sometimes with reference to the most numerous species (summarised by SCOTT & TIBBO 1968). SCOTT & TIBBO (1968) were the first to provide quantitative data such as occurrence, number of individuals and volumes of the component groups and these were taken from a large sample of 514 swordfish. While the fish species were identified, only the most prolific squid (*Illex illecebrosus*) was identified and that not adequately distinguished from other cephalopods. STILLWELL & KOHLER (1985) also considered only the identifiable specimens of the food organisms and

included both fish and cephalopod species by occurrence, number of individuals and volumes.

Here, the method of voluming was not considered of value since very few cephalopods were represented by flesh and many fish were at an advanced stage of dissolution. Instead of only utilising flesh remains, we also identified otoliths and cephalopod lower beaks and used them to indicate occurrence, numbers and wet weights of the species identified. This was also done, for some of the prey species by MOREIRA (1990), GUERRA et al. (1993) and HERNANDEZ-GARCIA (1995). The use of beaks for such studies is well established and has fewer problems (discussed below and by CLARKE 1986a) than the use of otoliths which has been much discussed and criticised (HYSLOP 1980; JOBLING & BREIBY 1986). Certainly, caution must be exercised in using otoliths because they dissolve at different rates according to their size and species (JOBLING & BREIBY 1986; HERNANDEZ-GARCIA 1995). However, our observations suggest that, with the species occurring here, otoliths can be used to give certain valid conclusions.

Increasing interest in the role of cephalopods in food webs and the use of beaks in its elucidation has led several authors (TOLL & HESS 1981; BELLO 1991; GUERRA et al. 1993; HERNANDEZ-GARCIA 1995) to concentrate on cephalopods and neglect the fish in their diet studies of swordfish.

Previous work was for swordfish caught in the western North Atlantic (SCOTT & TIBBO 1968; STILLWELL & KOHLER 1985; TOLL & HESS 1981), the coast of Portugal (MOREIRA 1990), the eastern North Atlantic (GUERRA et al. 1993; HERNANDEZ-GARCIA 1995), the eastern Mediterranean (BELLO 1991) and the North Pacific (summarised by MARKAIDA 1995). The results show distinct differences depending on the region studied and on the type of analysis employed (see Discussion).

The present work should have value for understanding the role of fish and cephalopods in the foodweb of the Azores as well as for a greater understanding of the diet of the swordfish.

MATERIAL AND METHODS

Stomachs were collected from 132 swordfish, caught by drifting longlines near the surface during commercial (105) and research fishing (27) off the islands of Pico and Faial during the period 25.10.92 - 25.12.93. Line setting began at about 17:00-18:00h and hauling started at about 08:00h the following morning. The sampling area for the research fishing, carried out R.V. "Arquipélago" of DOP, was between the three islands Faial, São Jorge and Pico to the Azores Bank and Princesse Alice Bank. Commercial catches were from the same general area.

Of the 132 swordfish, 113 were collected in October-December 1992 and 19 in February to December 1993. The monthly distribution of the samples was February (2), August (2), October (53), November (33), December (33) which reflects the seasonal presence of the species in the area.

Lower jaw fork lengths of the swordfish were measured from the tip of the lower jaw to the fork of the tail. Stomachs were removed at sea immediately after capture. After being deep frozen, the contents of each stomach were thawed out in the laboratory and weighed; the average weight of the stomach contents was found by deducting the mean of empty stomachs from the mean of stomachs with food. Stomach contents were carefully sifted and sieved for all identifiable

animal remains. Volumes of the major components of the stomach contents were not measured because the variation in condition made such measurements worthless. General identification of flesh and bone remains was followed by examination of otoliths and cephalopod beaks. Where almost complete animals were present their lengths (fork length in the case of fish) were measured, they were weighed and their otoliths were removed for comparative studies. Collection and identification of fishes was aided by help from fish specialists in the Department of Oceanography and Fisheries, University of the Azores, Horta, Faial (DOP, see Acknowledgements). Identification of otoliths (DCC) was achieved by comparison with a collection removed from a variety of local fishes both from catches and from stomach contents and, for myctophids, from the literature (FITCH 1969; GRENFELL 1984; HECHT & HECHT 1987; NOLFE & CAPETTA 1988). Two species were identified by fish and otolith specialists (see Acknowledgements, Smale and Merrett). 1249 otoliths in reasonable condition were identified. 50 (3.8%) were too digested for identification to be possible.

Identification of cephalopod beaks (MRC) was carried out with a large reference collection and methods prescribed by CLARKE (1986a). Seven small lower beaks could not be identified but were probably in three species of small cranchiids.

Estimates of the weights and lengths of *Beryx* species were made from unpublished size relationships supplied by E. Isidro of the D.O.P. Estimates for *Micromesistius poutassou* were taken from $\text{Ln Wt(in g)} = 2.83 \times \text{Ln OL(in mm.)} - 1.29$ (MOREIRA 1990) and $\text{SL} = 23.17 \times \text{OL} - 25.54$ (JOBLING & BREIBY 1986), for *Pagellus bogaraveo* $\text{Wt(g)} = \text{EXP}(\text{Ln}(39.4177) + (1.189 \times \text{Ln(ORadius)}))$ and $\text{Wt(g)} = \text{EXP}(\text{Ln}(0.0124) + (3.137 \times \text{LN(FL in cm)}))$ (derived from KRUG 1989), and for *Trachurus picturatus* $\text{FL (in cm)} = (\text{OL} - 1.759) / 0.224$ and $\text{Log Wt(g)} = \text{Ln } 0.00819 + 3.11 \times \text{Ln(FL in cm)}$ (ISIDRO 1990). A sufficient number of *Capros aper* were present in

the stomachs to relate otolith size to fish weight. This shows considerable variation but several stomachs were dilated with *Capros* in good condition and the total weight and number of fish present showed that *Capros* taken by the swordfish averaged near to 5 g. This agreed with estimates made on fewer fish from otolith length relationships. No weights for myctophids were available but their total weight was calculated from a mean volume of 8.5 ml obtained by data of SCOTT & TIBBO (1968). Other estimates were based on relationships given in SMALE et al. (1995). From the overall totals of food items the sum totals of each species represented in the diet were calculated by adding the number of fish identified from flesh to half the number (rounded up to the next even number) of otoliths, taking account of instances where two otoliths in a stomach only represented a single fish.

Estimates of the weights and mantle lengths (ML) of cephalopods were made from known relationships for the lower beak rostral length or hood length (LRL, LHL) of each species or family found (CLARKE 1986a).

Eye lenses of cephalopods can be distinguished from those of fish by being easily fractured into two unequal hemispheres. This allows digestive fluids to enter between the onion-like layering and the lenses break up under mechanical pressures so that they disintegrate and disappear from the stomachs much more quickly than the fish eye lenses. The ratio between fish and eye lenses does not, therefore, indicate the relation of cephalopods to fish in the diet, as was formerly supposed (CLARKE 1986b; HERNANDEZ-GARCIA 1995).

Two items removed from the stomachs, the horse mackerel, *Trachurus* (12 in 5 stomachs) and the squid *Illex* (one only) were in an undigested state and were almost certain to have been bait used in catching the swordfish. These have been excluded from the calculations. However, where *Trachurus* otoliths alone were present, they were taken to be indicative of *Trachurus* in the diet.

RESULTS

General description of stomach contents

Nine of the total samples were empty except for a few fish eye lenses. The 123 swordfish containing food remains other than fish eye lenses averaged 107 cm in fork length (SD. = 37 cm, range: 49-240 cm) which we calculate to equal 13.4 kg from published relationships (see PALKO et al. 1981). An attempt to categorise the condition of the stomach contents is shown in Fig. 1. The categories show the state of the least digested food in the stomachs; some of the stomachs also contain food in other states of digestion e.g. some have otoliths and debris together with fresh specimens but are placed in the 'good ID' category. The stomach weights plotted against the swordfish fork lengths (Fig. 2) shows that the weights of the stomachs with no identifiable flesh are broadly spread over the size range but there is a suggestion that more swordfish below 100 cm (35.6%) ate less recently than swordfish over 100 cm (25.6%). The stomachs containing remains averaged 518 g in weight. If only the stomachs containing identifiable remains (other than otoliths and beaks) are included, the mean is 739 g. A swordfish of 100 cm (close to the mean FL=107 cm) had a stomach weighing 1660 g which might be taken as an indication of the maximum weight for the mean fish and the mean fish then had about 50% of its stomach capacity filled. Subtraction of the mean weight of stomachs with no contents from the mean weight of stomachs with contents gives a mean weight of 334 g for the stomach contents.

Stomach contents were often bones with macerated fish attached and could be identified as *Capros aper*, *Lepidopus caudatus*, *Pagellus bogaraveo* or myctophid remains. In total, 2189 animals were represented by either flesh, bones, otoliths or beaks in the stomachs (Table 1). A mean of 18.0 animals (SD. 18.0, range: 1-108) (fish, cephalopods or crustaceans) were represented in each stomach. Thirty-nine species of fish and cephalopods were identified from

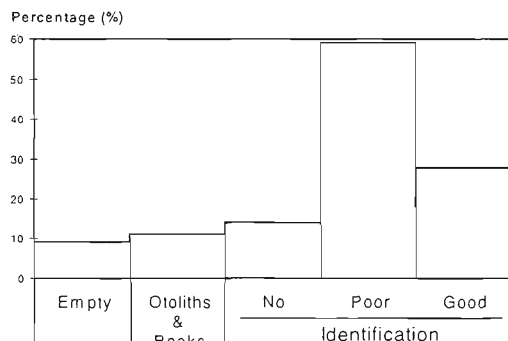


Fig. 1. The percentage of stomachs with contents in a particular stage of digestion. Only the least digested state is shown for each stomach.

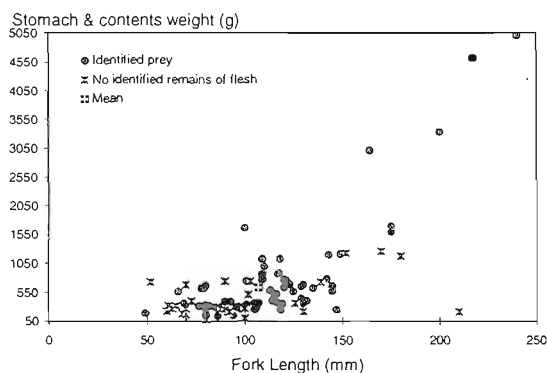


Fig. 2. Weight of stomach including contents plotted against the lower fork length of the swordfish. The mean stomach length is plotted against the mean fork length.

otoliths, beaks, bones and flesh remains (including an unidentified myctophid and excluding 3 very small cephalopod species, probably cranchiids). The state of the crustaceans prevented specific identification but 4 penaeid shrimps, 3 'shrimps', 1 euphausiid and 3 isopods (which may have been parasites off fish) were collected. Crustaceans were too damaged and their weight was too small to be included in calculations of weight.

Fish 'flesh' (including bones with flesh attached and pieces of muscle) occurred in 60.2% of samples and cephalopod flesh in only 2 samples (1.6%) containing food remnants. The fish 'flesh' included recognisable, complete *Capros aper* and the heads and bones of *Lepidopus caudatus*, *Pagellus bogaraveo* and

myctophids. Cephalopod flesh comprised two heads and a body of *Todarodes sagittatus* in one sample and a tentacular crown (with beaks) of *Pholidoteuthis boschmai* in another.

Fish remains occurred in all but two stomachs containing food (98.4%). Cephalopod remains occurred in 37.4% and crustacean remains in only 12.2%. Two samples (1.6%) contained cephalopod but no fish remains. The total number of fish represented by remains was 2045 and cephalopods was 127, a ratio of 16:1. The ratio of fish lenses to cephalopod lenses was 472:1, reflecting the faster digestion and loss of cephalopod lenses compared with those of fish. The number of fish otoliths was 1299 and the number of cephalopod beaks was 263 giving a ratio of 5:1.

Fish comprised 93.4% by number of all animals represented in the stomachs, cephalopods 5.8% and crustaceans 0.8%.

Fish averaged 2.2 species and 16.9 individuals per stomach containing fish and 2.2 species and 16.8 per stomach containing food. Cephalopods averaged 1.81 species and 2.81 individuals per stomach containing cephalopods and 0.78 species and 1.21 individuals per sample with food.

Species contributions

Forty-two species were present (including three cephalopod and one fish species which could not be identified) including 18 species of fish and 24 species of cephalopod and there was an average of 3.2 species per stomach (SD. 1.8, 1-11). The number of individual animals represented in the stomachs averaged 17.9 per stomach.

Fish

Numerical composition of the fish and estimates of the wet weights are shown in Table 2. Otolith length distributions for the commonest species (Fig. 3) show that all species except *Micromesistius poutassou* and *Dirtemus*

Table 1

General information on samples.

	Total (parts)	Mean 1 (n=123)	Mean 2 (no.obs.)	No. of obs.	%	min	max	SD
Swordfish FL			107.2cm	117		49cm	240cm	37
Stomach WT	63692g	518g	631g	101	82.1	80g	5000g	774.8
Content WT.by deduction			334g	101				
Calculated content WT.	56336g	458g	558g	101				
Animals represented	2189	17.9	18	122	99.2	1	108	18.02
No. of species	42	3.16	3.16	123	100	1	11	1.757
Otoliths	1299	10.5	10.5	123	100	0	89	12.63
No. of fish & cephalopods represented by flesh	1279	10.4	17.3	74	60.2	1	95	15.88
Total fish	2045	93.4%		121	98.4			
Total cephalopods	127	5.8%		46	37.4	1	20	3.924
Total crustaceans	17	0.8%			12.2			
Total animals	2189	100%						

FL=fork length; WT= weight; SD=standard deviation; Mean 1=calculated from all stomachs with contents; Mean 2= calculated from number of observations recorded;

Table 2

Numbers and estimated sizes of fishes represented in stomach contents of swordfish.

Family	Genus	Oto- liths	No.o f fish	Mass						Est. lengths			Occur- rence %	Maxi- mum per stomach
				Fish %	%of all	Est. mass	Fish%	all %	mean mass	Min	Max	Mean		
Berycidae	<i>Beryx</i>	25	14	0.68	0.64	2264	8.84	4.02	162	56	231	171	8.1	8
	<i>decadactylus</i>													
	<i>B. splendens</i>	20	11	0.54	0.5	808	3.15	1.43	73	77	225	133	3.3	15
Dirietmidae	<i>Dirietmus</i>	129	68	3.33	3.11	619	2.42	1.1	9	19	106		15.4	25
	<i>argenteus</i>													
Caproidae	<i>Capros</i>	748	1675	81.91	76.52	8375	32.7	14.9	5	45	129	70	72.4	95
Macrorhampho- sidae	<i>Macrorham- phosus</i>	2	2	0.1	0.09	24	0.09	0.04	12	94	96	95	0.8	2
Macrouridae	<i>Coelorhynchus</i> sp.	6	4	0.2	0.18	636	2.48	1.13	159	173	461	305	3.3	2
Trachichthyidae	<i>Hoplostethus</i> sp.	2	2	0.1	0.09	3	0.01	<.01	1.5	42	44	43	0.8	1
Trichiuridae	<i>Lepidopus</i>	22	41	2	1.87	9790	38.23	17.4	239	81	131	108	7.3	19
Gadidae	<i>Micromesistius</i>	68	37	1.81	1.69	2409	9.41	4.28	65	102	134	127	7.3	17
Myctophidae	<i>Diaphus</i>	74	37	1.81	1.69	315	1.23	0.56	9	27	68	46	7.3	48
	<i>Lampanyctus</i>	4	3	0.15	0.14	26	0.1	0.05	9				2.4	2
	<i>Lampanyctus</i>	4	3	0.15	0.14	26	0.1	0.05	9			60	0.8	2
	<i>Nototheniopsis</i>	52	30	1.47	1.37	255	1	0.05	9			55	10.6	13
	<i>resplendens</i>													
	Myctophid sp.	44	80	3.91	3.65	680	2.66	1.21	9			60	1.6	24
Sparidae	<i>Pagellus</i> ot	21	21	1.03	0.96	1266	4.94	2.25	60	95	174	139	4.1	5
Carangidae	<i>Trachurus</i> ot	22	13	0.64	0.59	162	0.63	0.29	12	7.3	13	10	8.1	4
	<i>Epigonus</i> sp.A	5	3	0.15	0.14	120	0.47	0.21	40	82	210	129	2.4	2
	<i>Epigonus</i> sp.B	1	1	0.05	0.05	97	0.38	0.17	97	188	188	188	0.8	1
Total fish		2045				27875	100	49.5	13.6					
Total animals		2189				56336								

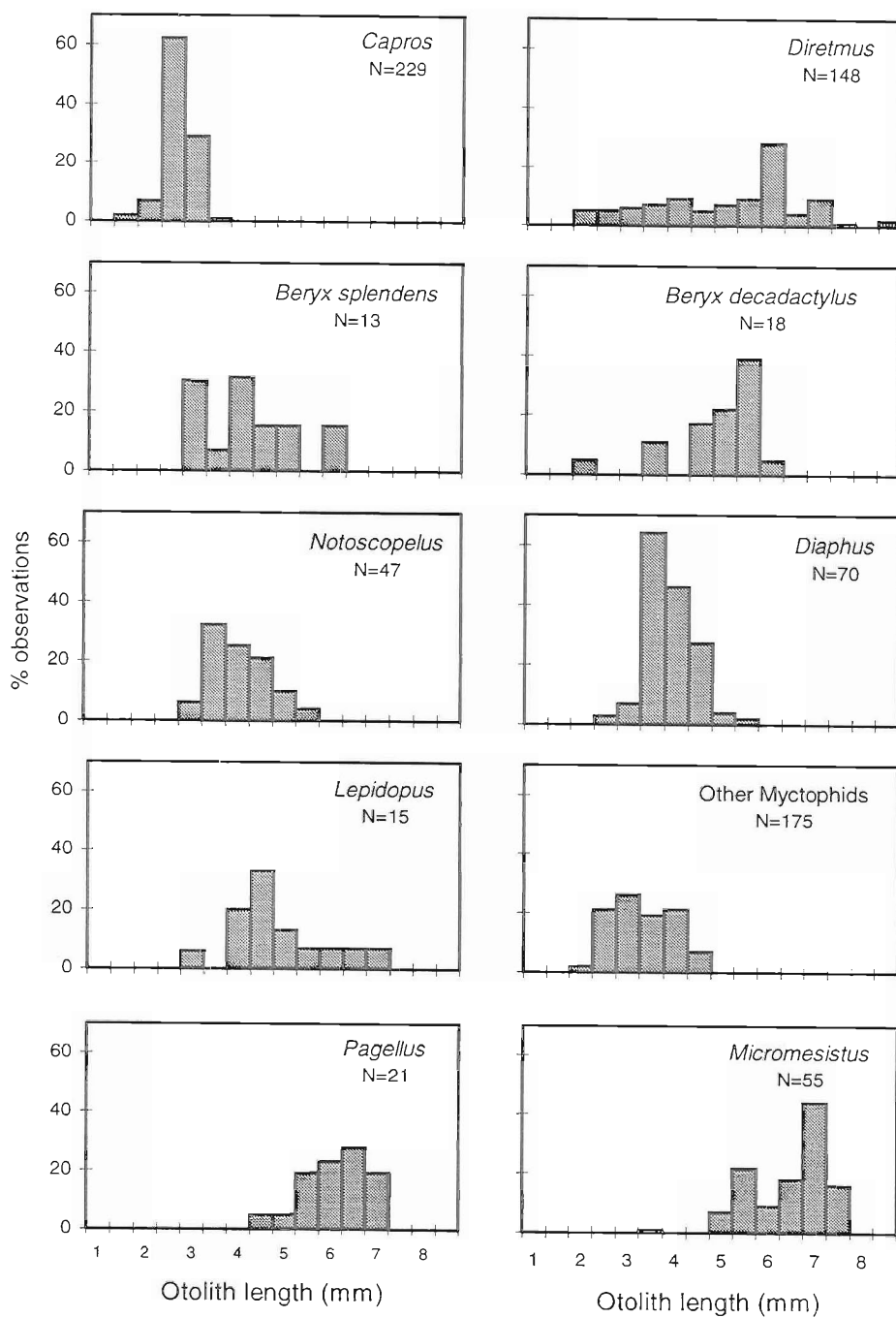


Fig. 3. Otolith lengths of fish identified from swordfish stomachs.

argenteus have distinct unimodal peaks. The smallest species, *Notoscopelus* sp. and *Diaphus* spp., have skewed distributions suggesting that the swordfish selects for the larger fish of these small species.

All the fish in good condition and most of the identifiable poor specimens were *Capros aper* and these had a fork length distribution with a peak at 10-20 mm (Fig. 4).

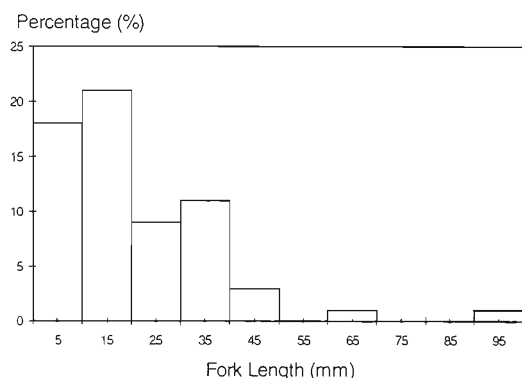


Fig. 4. Histogram of the fork lengths of complete *Capros aper* from stomachs of swordfish.

Diretmus argenteus has previously been regarded as rare in this area.

Four small *Lepidopus caudatus* measured 320-380 mm in length but other specimens were too digested for measurement.

The myctophid otoliths included *Lampadena* sp., *Lampanyctus* sp., *Notoscopelus* sp. and several species of *Diaphus*. Although it is not possible, with material available to us, to estimate their contribution by weight from otolith size, a rough approximation afforded by applying a mean derived from SCOTT & TIBBO (1968) is probably not too far from reality.

No flesh of *Micromesistius poutassou* was found and otoliths were identified by comparison with material of J. Castro (see Acknowledgements). The bimodal peak to the length distribution (Fig. 3) may suggest a second species is included.

The thirteen complete *Trachurus picturatus* in the stomachs are considered to be bait swallowed at the time of capture and their weights are not included in calculations. Because they must have

been in the stomach some time before capture, otoliths are assumed to represent natural food and are used in calculations. However, the heads from which they came may also have been taken off hooks.

Cephalopoda

The pelagic octopods *Argonauta argo*, *Ocythoe tuberculata* and *Haliphron atlanticus* (= *Alloposus mollis*) make a surprisingly large numerical contribution to the cephalopods in the diet (40.1%) but the larger, strong-swimming squids of the Ommastrephidae and the Pholidoteuthidae together contribute 79% of the cephalopods and 41.6% of all the food by weight (Table 3). Another 12.3% of cephalopod weight and 6.5% of the weight of the food is contributed by onychoteuthids, one being *Moroteuthis* sp. which has not been recorded for the North Atlantic but is known to occur here from unpublished data of one of the authors (MRC).

Beak measurements (LRL's and LHL's) are too few to give well-based distributions (Fig. 5) but they do show some grouping in each species.

Very rarely collected genera which are represented are *Discoteuthis*, *Valbyteuthis* and *Grimalditeuthis*.

General

A histogram of estimated mean weights of all the species (Fig. 6) shows that most are less than 100 g in weight and only three species, all cephalopod, are over 400 g.

Figure 7a shows the % weight contributed, of species contributing more than 1%, arranged in descending order of importance. The steep part of the curve includes five fish genera, *Lepidopus*, *Capros*, *Beryx*, *Micromesistius* and *Pagellus* and four cephalopod genera, *Ommastrephes*, *Pholidoteuthis*, *Onychoteuthis* and *Moroteuthis*.

Figure 7b gives the cumulative curve of the same species and shows that these nine species contribute over 91% to the food of the swordfish. This is in contrast to the cumulative curve of numbers in which *Capros* comprises 75% of the number of animals in the diet and only another six species contribute more than 1%.

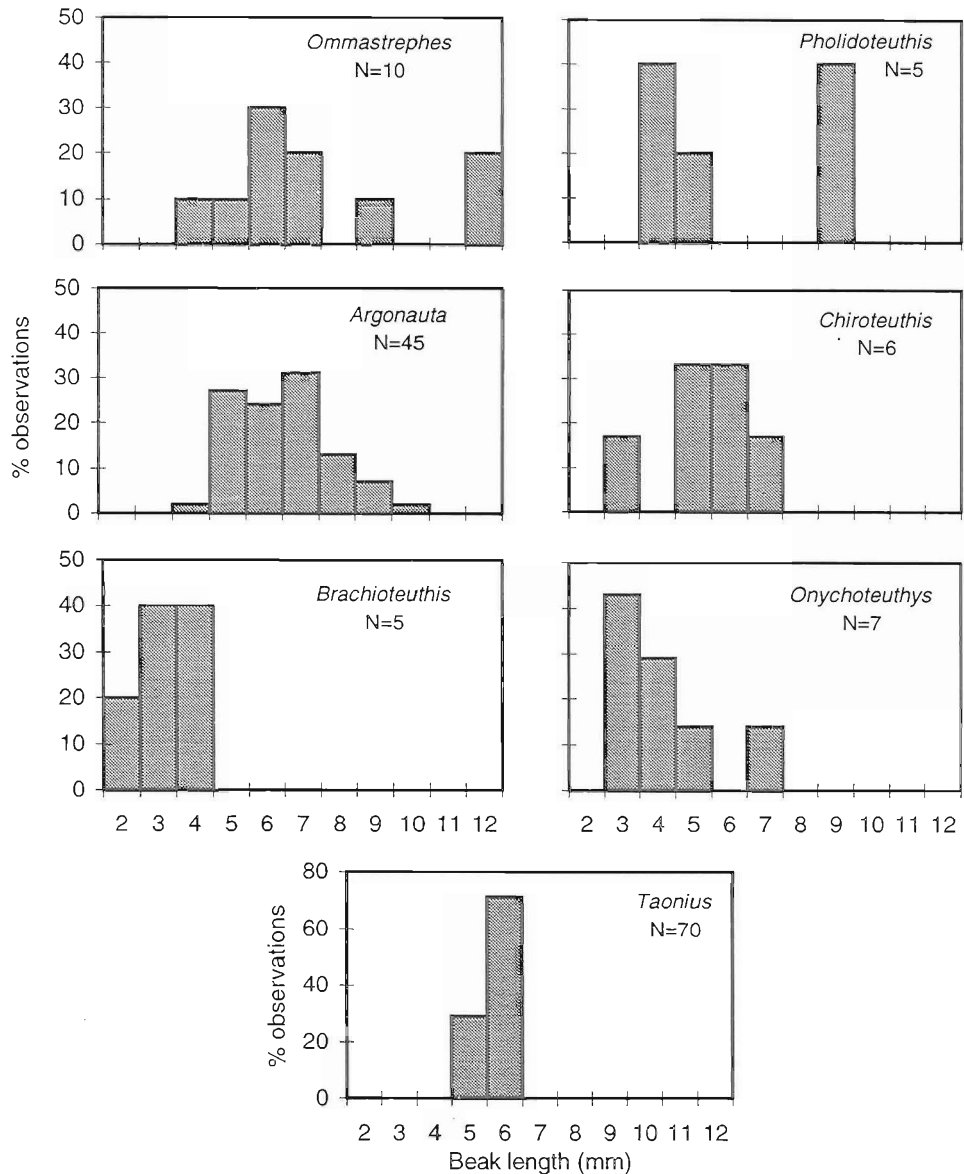


Fig. 5. Lower rostral lengths of the beaks of the commoner cephalopods present in the stomachs of swordfish

Size and habits of prey targeted

Estimates of the mantle and standard lengths of the cephalopods (Table 3) and the fork lengths of some of the fish (Table 2) range between 7 mm and 627 mm. Mantle lengths are not a good

measurement for expressing size of a prey item in the way fork lengths are and a better dimension is the standard length from the tip of the arms to the tip of the mantle. Head and arm lengths can be between 0.4-3.75 times the mantle length according to the species. If the estimates of mean standard lengths from the beaks and fork lengths

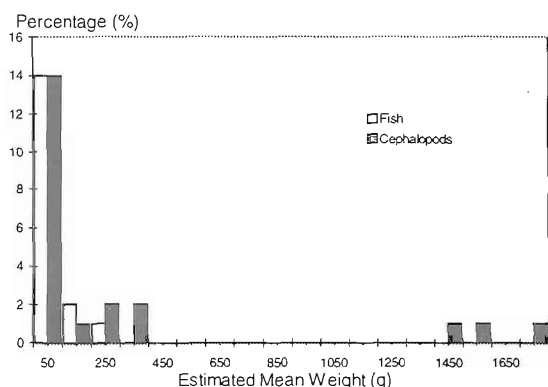


Fig. 6. Histogram showing the estimated mean weights of fish and cephalopods from swordfish stomachs.

from the otoliths are plotted in decreasing values for the fish and cephalopods separately (Fig. 8), it is evident that the mean of no fish exceeds the means of the 7 largest cephalopods. Six of the eight largest cephalopods are muscular, fast swimming and negatively bouyant squids. Seven cephalopods with means between 125 mm and 280 mm are all neutrally bouyant and slow swimming except for *Brachioteuthis*. Five of the 6 smallest genera are negatively bouyant, fast jetters. *Ocythoe* has an air-bladder to control bouyancy.

Influence of swordfish sex on food

Forty-one male and 33 female swordfish were sexed and contained food; 49 were not sexed. The males averaged 102 cm in fork length and the females 121 cm. Stomachs with contents weighed an average of 574 g in the males and 838 g in the females. Females had a mean of 13.6 animals and 2.3 species while males had 21.5 animals and 3.0 species represented in the stomachs. No significant differences between the food species of the two sexes could be detected.

Influence of swordfish length on food

To examine differences in diet attributable to the sizes of the swordfish we compared the samples from 21 fish in each of three size groups with fork lengths less than 80 cm (mean 69 cm), 90-120 cm (mean 100 cm) and over 130 cm (mean 147 cm). Weight of stomach contents were 207 g, 191 g

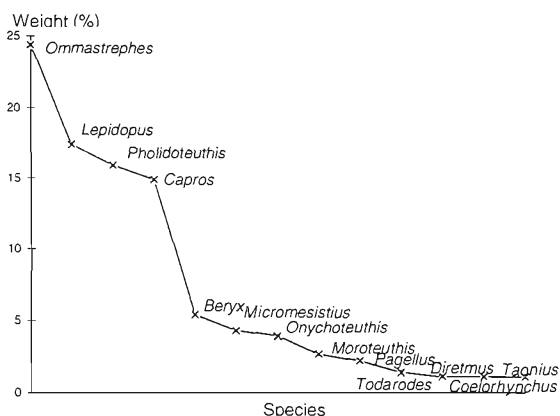


Fig. 7a. The estimated % total weights of species with more than 1% arranged in descending values.

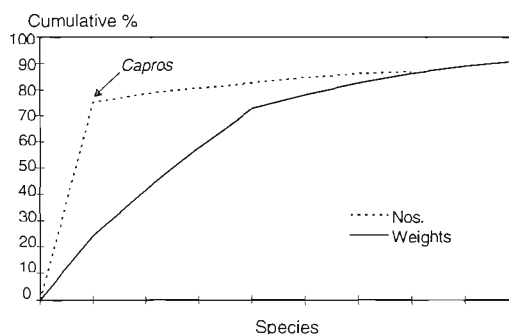


Fig. 7b. Cumulative % weights of the species in 7a and cumulative numbers of species in descending value showing *Capros aper* as the first species.

and 608 g respectively for the smallest to the largest fish. As one might expect from this, the weight of *Capros aper* flesh (the main component by bulk of the contents) increased from a mean of 4.4 g through 8.8 g to 10 g but no other trends were evident in fish or cephalopods.

DISCUSSION

Methodology

Although otoliths in diet studies must be used with care, we believe that the present work demonstrates their value and justifies their use. If only identifiable flesh were used for identification, only five instead of 18 species of fish and two instead of 21 species of cephalopod would have been recognised. If size and number

Table 3

Numbers and estimated sizes of cephalopods represented in swordfish stomachs by lower beaks. (No.-number; ML- mantle length; Std l- standard length; Occ.-occurrence)

Family	Genus	No.				Mass		Mean	Min.	ML		Std l	Occ.
		No	%	% all	total	%	% all wt			Max.	Mean	Mean	%
Argonautidae	<i>Argonauta</i>	45	35.4	2.05	297	1.04	0.55	6.6	16	58	36	80.64	18
Ocythoidae	<i>Ocythoe</i>	5	3.94	0.22		0	0	0	18	55	38	88.54	3
Alloposidae	<i>Haliphron</i>	1	0.8	0.05	300	1.05	0.55	300	62	62	62	279	1
Sepiolidae	<i>Heteroteuthis</i>	1	0.8	0.05	2	<.01	<0.01	2	17	17	17	34	1
Loliginidae	<i>Loligo</i>	1	0.8	0.05	356	1.25	0.66	356	244	244	244	341.6	1
Ommastrephidae	<i>Ommastrephes</i>	12	9.45	0.54	13188	46.3	24.39	1099	160	378	245	382.2	6
	<i>Todarodes</i>	3	2.36	0.13	668	2.35	1.24	222	136	229	168	283.9	3
Onychoteuthidae	<i>Onychoteuthis</i>	8	6.3	0.36	2089	7.34	3.86	261	124	337	180	313.2	5
	<i>Moroteuthis</i>	1	0.8	0.05	1438	5.05	2.66	1438	343	343	343	627.7	1
Pholidoteuthidae	<i>Pholidoteuthis</i>	5	3.94	0.22	8621	30.3	15.94	1724	160	465	296	455.8	3
Brachioteuthidae	<i>Brachioteuthis</i>	6	4.72	0.27	31	0.1	0.06	5	53	79	66	135.3	5
Enoploteuthidae	<i>Abraliopsis</i>	2	1.57	0.09	6.7	0.02	0.01	3	35	35	35	81.55	2
Pyroteuthidae	<i>Pyroteuthis</i>	2	1.57	0.09	10	0.04	0.02	5	39	39	39	74.88	2
Histiotteuthidae	<i>Histio A</i>	2	1.57	0.09	246	0.86	0.45	123	52	83	68	216.2	2
	<i>Histio B</i>	2	1.57	0.09	92	0.32	0.17	46	36	46	41	130.4	2
Discoteuthidae	<i>Discoteuthis</i>	6	4.72	0.27	61	0.21	0.11	10	85	107	97	234.7	4
Chiroteuthidae	<i>Chiroteuthis</i>	6	4.72	0.27	319	1.12	0.59	53	75	175	129	474.7	5
	<i>Valbyteuthis</i>	3	2.36	0.13	21	0.07	0.04	7	51	51	51	120.9	3
Grimalditeuthidae	<i>Grimalditeuthis</i>	1	0.8	0.05	56	0.19	0.1	56	109	109	109	190.8	1
Mastigoteuthidae	<i>Mastigoteuthis</i>	1	0.8	0.05	37	0.12	0.07	37	94	94	94	194.6	1
Cranchiidae	<i>Taonius</i>	7	5.51	0.31	595	2.09	1.1	85	282	344	313	406.9	6
	3 unidentified sp	7	5.51	0.31	28	0.1	0.05	4					5
TOTALS		127	100	5.8	28462	99.9	50.521	224					
Upper beaks		136											
Total animals		2189			56336								

of otoliths and beaks had been ignored, *Capros aper* would have been considered the overwhelmingly most important food species instead of providing only 14.9% of the food. Such computations from beak and otolith size must be considered rough estimates but are much better than relying on weights of partially and variably digested stomach contents.

In determining the relative importance of fish and cephalopods from flesh, or beaks and otoliths, various problems arise. The flesh of many cephalopod species is digested much more rapidly than fish flesh; cephalopods have no bones, which take longer to digest than flesh. On the other hand, beaks are not digested in the stomach while some otoliths take only a few hours to digest (JOBLING & BREIBY 1986; HERNANDEZ-GARCIA 1995). These factors would clearly make comparisons meaningless if the time in the

stomach was appreciably longer than the time taken to dissolve otoliths; the counts would be biased towards cephalopods.

The conclusion drawn below that the food has been in the stomachs for less than 12 hours makes it unlikely that many of the otoliths have dissolved completely in stomach juices (JOBLING & BREIBY 1986; HERNANDEZ-GARCIA 1995) and this is supported by there being few halves of *Capros* otoliths which are small and easily break into two. Thus, we consider the ratios between the otoliths are meaningful for determining diet.

As pointed out by JOBLING & BREIBY (1986) reduction of the lengths of otoliths after a short time in the stomach could materially affect estimates of body lengths and weights of the fish. For the commonest fish, *Capros aper*, the estimates from the better otoliths gave similar results to direct weighing and measuring of intact

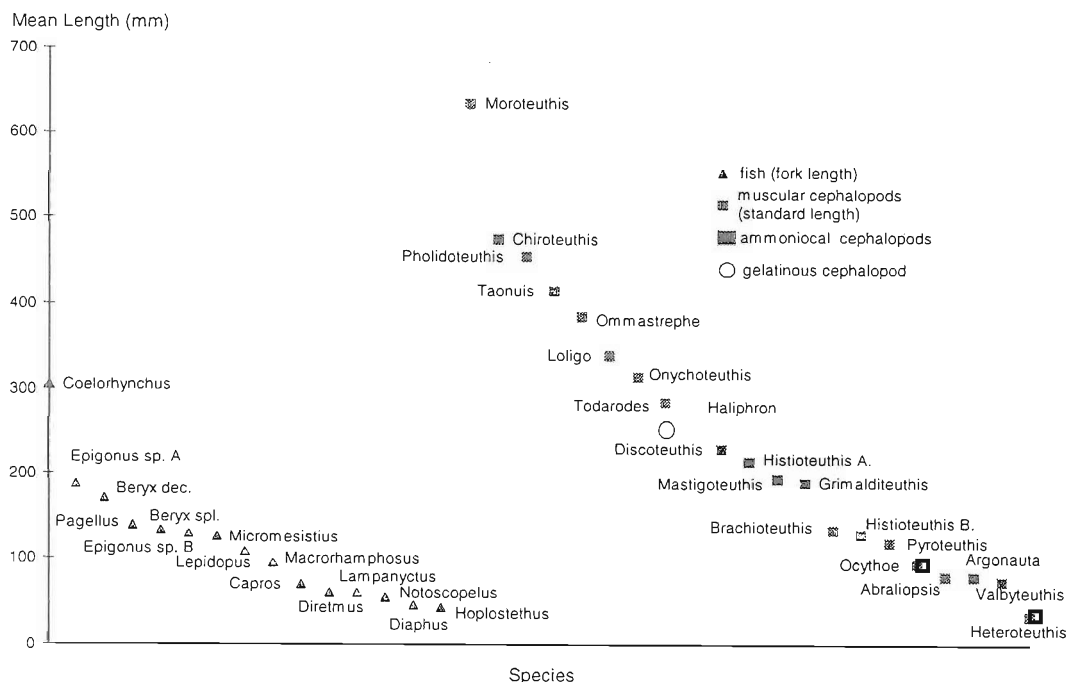


Fig. 8. Estimated mean fork lengths for fish and standard lengths for cephalopods arranged in descending values, fish and cephalopods plotted separately. Square points are ammoniacal squids.

fish from the stomachs. In other species the weights were estimated from the better otoliths or, where appropriate the mean, and multiplied by the total number of otoliths present. Cephalopod estimates depend upon beaks whose rostral lengths do not reduce with digestion. The main limits to accuracy for cephalopod estimates are imposed by the limited accuracy of body weight and length to LRLs relationships. For the species occurring here, most relationships are reasonably accurate except for *Ocythoe*, *Haliphron*, *Discoteuthis*, *Valbyteuthis* and *Grimalditeuthis*, together only comprising 9.6% of the number of beaks.

Other possible errors in this kind of analysis are acquisition of food organisms from the stomachs of the food targeted by swordfish. This could be the source of the smallest beaks, and should be borne in mind when species are considered, but this is not likely to be a cause of error in considering the commonest and larger cephalopods. Evidence from flesh showed that

Todarodes and *Pholidoteuthis* were eaten directly by the swordfish but that is also highly likely for all species but the smallest such as *Heteroteuthis*, *Abraliopsis*, *Pyroteuthis*. Flesh was identified from the smallest fish, *Capros aper* and the myctophids.

Regional comparisons

Comparisons with other studies on swordfish from the Atlantic are summarised in Table 4. Oceanic samples showed a numerical dominance of cephalopods in the diet and samples near or on the Continental shelves showed a dominance of fish. The difference in this respect between the results of SCOTT & TIBBO (1974) and STILLWELL & KOHLER (1985), from much the same region was explained by the latter as a result of the increase in squid in the time between the sampling years. It could also partly be explained by the difference in latitude and depth of water of the main areas of sampling.

Table 4

Comparison of general results with the literature. (No.-number; Occ.-occurrence; Vol-volume; wt-weight; Sw-swordfish; S.-same; F-Fish; C- Cephalopod; f-family; g- genera).

Region	group	No.%	Occ.%	Vol/wt%	Main food	No.Sw	L/Wt.Sw	% empty	S. taxa as here	No spp	Author
Azores	fish	93.1	98.4		<i>Lepidopus</i>	132	107cm	7		14	This paper
	cephalopods	6.1	37.4		<i>Ommastrephes</i>					22	
	crustacea	0.8	12.2								
N.E.Atl. (oceanic)	fish		12			113		13			GUERRA et al.
	cephalopods		84		Ommastrephids				10Cg	17	
	crustacea		3								
Equator (oceanic)	fish				selected for C	15					HERNANDEZ- GARCIA
	cephalopods		100		<i>Sthenoteuthis</i>				3Cg	9	
	crustacea										
Portugal	fish	69		54	<i>Micromesistius</i>	37	140- 209cm		1Ff	9+	MOREIRA
	cephalopods	31		44	<i>Illex</i>				5Cf		
	crustacea		3								
Str.Gib.	fish	93	100		<i>Micromesistius</i>		103- 193		4Fg		HERNANDEZ- GARCIA
	cephalopods	5	17		<i>Todarodes</i>	35			5Cg	20+	
	crustacea	2	6								
W.Afr.	fish	29				25	112- 201cm		1Fg		HERNANDEZ- GARCIA
	cephalopods	71			<i>Sthenoteuthis</i>				6 Cg	14+	
	crustacea	0									
N.W.Atl	fish		94	78	<i>Scomber</i>	514			0	31	SCOTT & TIBBO
	cephalopods		61.5	16	<i>Illex</i> (Mar-Oct)						
	crustacea										
N.W.Atl.	fish	9.4	52.3			65	118- 218cm				TOLL & HESS
	cephalopods	90.6	100		<i>Illex</i> ; <i>Histioteuthis</i>				5Cf, 4Cg	14	
	crustacea	0.1	9.2								
N.W.Atl.	fish	17	53		<i>Merluccius</i>	168		10	2Ff	20	STILLWELL & KOHLE
	cephalopods	82	82	67	<i>Illex</i>				5Cf	12	
	crustacea										
E.Med	fish										BELLO
	cephalopods				<i>Todarodes</i>	38	80- 170cm				
	crustacea						8-90kg				
W.Baja. Calif	fish	11.4				84	90- 233cm		2Fg 7Cg	30	MARKAIDA
	cephalopods	85	96	90	<i>Sthenoteuthis</i>						
	crustacea										
N.Baja Calif	fish	62	65	84	<i>Trachipterus</i>	75			2Fg	21	MARKAIDA
	cephalopods	38		16						?	

The specific composition of fish and cephalopods in the samples varies greatly between areas, particularly for the fish. The closest similarity to the Azores region is, not surprisingly, the area between the Azores and Spain (GUERRA

et al. 1993) which share 9-11 species (or genera) of 28 named species/genera recorded in the two studies. The most notable difference, *Sthenoteuthis pteropus*, which is the most numerous in the Spanish samples and does not

occur in the Azores samples has a usual northern limit to the South of the Azores and this is reflected in the samples. The abundance of *Argonauta argo* in the present samples may reflect an unusual abundance in the year or possibly the time of year (the months of sampling were not recorded by GUERRA et al. 1993) sampled off the Azores as they did not occur in the Spanish samples. However, they did occur in swordfish off Portugal (MOREIRA 1990) showing that they are probably a regular part of the diet. In all regions, species in the Ommastrephidae were the most important cephalopods by number and, where measured, by weight or volume.

Predator comparisons

Twelve of the 40 species of cephalopods from stomachs of sperm whales caught near the Azores (CLARKE et al. 1993) also occurred in the swordfish diet of the area which comprised 21 identified species. Genera eaten by swordfish but not found in stomachs of sperm whales in the region are *Argonauta*, *Ocythoe*, *Moroteuthis*, *Loligo*, *Heteroteuthis*, *Brachioteuthis*, *Abraliopsis*, *Pyroteuthis*, *Valbyteuthis* and *Grimalditeuthis*. Squids of the last six genera are all too small to be likely targets of the whales. The first two genera may live too near the sea surface to fall within the whale's normal sampling depth range. As explained above, *Moroteuthis* is a new record for the area and may be extremely rare here. *Loligo* lives close to the edge of what little shelf is present off the Azores islands and may be too close to the islands to be a regular prey of the whales. Considering the importance of octopoteuthids to sperm whales (5.9% by number) it is surprising they were not found in the diet of swordfish although they are eaten elsewhere in the eastern North Atlantic (MOREIRA 1990; GUERRA et al. 1993; HERNANDEZ-GARCIA 1995).

Prey distribution

The fish eaten by swordfish include species from all the ecological niches near these oceanic islands. Species living in island-influenced waters such as the near surface shoaling species *Capros*

aper, *Micromesistius poutassou* and *Trachurus picturatus*, near bottom species such as *Pagellus bogaraveo* and slope species such as *Coelorhynchus* and midwater slope species such as *Lepidopus caudatus*. The myctophids are oceanic shoaling species and share the same water between 200 m and 1000 m with many of the neutrally bouyant squids also found in the swordfish stomachs. Most of these have diel vertical migrations bringing them into the top 200 m at night so that their presence in the diet does not contradict the conclusion that the swordfish is a nocturnal feeder. *Heteroteuthis* is particularly associated with sea mounts. Thus, the swordfish appears to search all the sea around the islands and the adjacent sea mounts for a wide diversity of prey, perhaps having little preference except for size.

It would clearly be to the swordfish's advantage to select for the largest prey items but its adaptability in accepting a large variety of species, large and small, ammoniacal as well as muscular, mesopelagic as well as epipelagic assures it of an ample food supply when large species are scarcer. The mean weights of the cephalopods in the diet is 224 g and for the fish it is 13.6 g.

Food consumption

Finding the time taken for a swordfish to eat the estimated mean stomach contents cannot be done directly. If food is eaten more or less continuously and leaves the stomach continuously, we might expect to find all stomachs to be in more or less the same state of balance between the constituents. This is clearly not so (Fig. 1). Such a system would have the problem of clearing bones and beaks from the stomach in a regular manner with the fine breakdown products, without losing recently eaten food at the same time. More likely, is that a feeding bout of some duration is accompanied by, and followed by, reduction of all the muscle food to a particulate state followed by expulsion of the harder tissues before the next feeding bout begins. The variation of our samples supports this. Such a natural break could be night and day and work by CAREY & ROBISON (1981)

shows that swordfish spend nights near the surface and days at considerable depths in cold water where they may be far less active and may, indeed, feed less. As the present samples were all collected from fish caught at night and many have fresh fish and identifiable, deteriorating fish, they, at least, must be assumed to be that night's food intake. We might conclude that the night's feeding bout, is followed by a daylight period of digestion and an emptying of the stomach prior to the swordfish's migration to shallower depths at dusk. JOBLING & BREIBY (1986) suggested that marine mammals and birds may have an interdigestive migrating myoelectric complex (IMMC) of muscular activity as in terrestrial mammals. To quote from them: "This cyclic pattern of contractions includes a series of powerful bursts of contractions which pass from the stomach to the upper intestine and serve to sweep any indigestible remains from the stomach." The present work suggests a similar mechanism in swordfish and that beaks and otoliths are therefore not held up in the stomach. However, we cannot rule out the possibility that the clearout of food remains is not totally effective and some beaks and otoliths may remain from the previous night's feeding.

If some holdup takes place a clue to the magnitude of this may be obtained by reviewing the contents of stomachs with no flesh but only otoliths and or beaks. From these stomachs 200 otoliths (15.5% of all otoliths) and 29 lower beaks (22.8% of all lower beaks) were collected. These otoliths represent 1360 g and the lower beaks 6489 g of the food represented in the stomachs. If the total, 7849 g, is subtracted from the total food represented in the stomachs, 56336 g, the weight left for the average feed is 382 g. This compares with 458 g if one assumes no otoliths or beaks are carried over from one feeding period to the next. A rough weight for the mean stomach contents is derived from subtracting the mean weight for empty stomachs from the mean weight of the stomachs containing food and is 334 g. The difference between this and the estimates of 382 g and 458 g can be accounted for by loss of digestive products from the stomachs but this is so small as to suggest that most loss is not a

continuous process but is more an explosive process after one feeding and before the next.

We believe the estimated weight of the stomach contents are most likely to be the product of only one night's feeding because, if the food remains had been obtained in two nights, one might expect the otoliths, beaks and the unidentifiable slurry to be the product of the first night's feeding and to have, on average, much the same constituents as the second night. This is clearly not so. In addition, the work on disappearance of otoliths due to digestion is sufficiently fast to remove all traces of the smallest otoliths, *Caprus* and myctophids, from a previous night's feeding period.

As the mean swordfish weight, calculated from the mean fork length is 13.4 kg, in one day the average swordfish would eat 2.8-3.4% of its body weight per day and 10.4-12.4 times its body weight annually. This is higher than the estimate of 3.4-5.8 times derived by STILLWELL & KOHLER (1985) using digestion time intervals of sharks, although it is below estimates for some other fish.

From knowing the annual requirement of food and the proportion of the components of the diet, it is possible to estimate the minimum mass of each component eaten by swordfish in various regions (STILLWELL & KOHLER 1985; HERNANDEZ-GARCIA 1995). In the Azores region about 344 t of swordfish are landed annually. As these are probably three years old (OVCHINNIKOV 1970) and the catch has been sustained over a number of years, our sample might be expected to represent a population at least 3 times as many and weighing at least twice as much. However, the catches suggest they may only spend three months in the region. The consumption of the 700 t of swordfish would consume while in the Azores region over 7280-8680 t. This would include, for example, something in the region of 1387 t of *Lepidopus caudatus* and 435 t of *Beryx*, tonnages considerably exceeding those taken commercially (=255 t and 176 t respectively). The 2045 t of ommastrephids also eaten by swordfish shows the importance of these squids in a region where they are not caught commercially. Such computations should not be carried through to other years since

we have no idea of the inter-year stability of the diet until the work is repeated.

Future

While several papers now show the considerable regional variation in the species eaten by swordfish, there is no evidence for annual changes or their magnitude in any one place. Assessing the stability and reproducibility of the results of such analyses is of crucial importance in assessing their value for prediction and must involve collections made in as precisely similar ways as possible at different times. Comparisons should not only involve species composition of whole specimens but should include both flesh, otoliths and beaks and their size distributions.

As more species are treated in the same way as here, it is hoped that well based modelling of the foodwebs in this area will be possible. Seeing changes in the ecostructure may then be practical by monitoring the changes in diet composition of a few selected, high predators in the system. It is our conviction that such monitoring will be much more effective and a much cheaper way of observing change than collection with nets from oceanographic vessels; such will give direct information of the interaction of animals by means of rather few samples including a good spread of species and sizes.

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History Museum identified *Epigonus* otoliths and confirmed several other species identifications. Dr. Vicente Hernandez-Garcia and Dr. José Castro of the University of Las Palmas, Canary Islands kindly let us examine their collections of otoliths. To all the above, we are most grateful. Our special thanks are given to Carmelina Leal whose energy and thoroughness in the unenviable task of sorting the total stomach contents into Classes and sometimes Genera, counting, measuring and note-taking has made the final analysis possible.

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