The diet of the swordfish *Xiphias gladius* Linnaeus, 1758, in the central east Atlantic, with emphasis on the role of cephalopods

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The swordfish *Xiphias gladius* Linnaeus, 1758, is a mesopelagic teleost with a cosmopolitan distribution between 45°N and 45°S latitude. It is an opportunistic predator feeding mainly on pelagic vertebrates and invertebrates (Palko et al., 1981). The diet of the swordfish has been studied mainly in the western Atlantic Ocean (Tibbo et al., 1961; Scott and Tibbo, 1968, 1974; Toll and Hess, 1981; Stillwell and Kohler, 1985). Earlier reports reflected the importance of fish in the swordfish diet, but recently Stillwell and Kohler (1985) cited squid as the predominant component in the diet of swordfish. Azevedo (1989) and Moreira (1990), reporting from off the Portuguese coast, mentioned fish (principally *Micromesistius poutssou*) and cephalopods as the main prey groups of swordfish. This finding was corroborated by Guerra et al. (1993) from the Northeastern Atlantic where cephalopods were found to be the most important component of the diet. Maksimov (1969) studied the diet of swordfish in the eastern tropical Atlantic Ocean. Cephalopods were a major component of the diet in all areas sampled and although no cephalopod species were identified, the genus *Ommastrephes* was present among the five genera found in stomach contents.

Stomach content analysis is an important tool in ecological and fisheries biology studies. Oceanic vertebrates are often more efficient collectors of cephalopods than any available sampling gear (Bouxin and Legendre, 1936; Clarke, 1966). The purpose of this study was to expand knowledge of the diet of the swordfish from the central east Atlantic Ocean, with special emphasis on the role of cephalopod species.

Material and methods

Sampling areas and capture methods

The stomach contents of 75 swordfish, *Xiphias gladius*, were analyzed. Specimens were caught at night in three different areas of the central east Atlantic Ocean (Fig. 1) from the commercial landings of the Spanish fleet:

Zone A Strait of Gibraltar (35°53'–35°42'N and 6°35'–6°30'W). Thirty five swordfish were caught with drift nets (2.5 miles long × 20 m deep) between 10 and 22 September 1990.

Zone B South of the Canary Islands (23°–26°N and 17°–22°W). Twenty-five swordfish were obtained from a longline vessel between 1 and 15th March 1991 by using mackerel, *Scomber* spp., as bait.

Zone C Gulf of Guinea (3°09'–0°36'N and 26°27'–4°17'W). Fifteen swordfish (standard length [SL] between 140–209 cm) were selected on the basis of the presence of cephalopods in their stomachs. These were taken from catches made by a longliner between May and July of 1991 by using mackerel and squid, *Illex* sp., as bait.

Stomach preservation and analysis

In zones A and B, fish were stored in ice. After landing, fish were measured from the tip of the lower jaw to the fork of the tail (SL). During commercial operations the internal organs were removed before the fish were weighed. The stomach contents of each fish, including all hard parts found in the stomach wall folds (otoliths, very small beaks, and lenses), were weighed (in grams) and preserved in 70% ethyl alcohol. Otoliths were also removed from the fish prey. Nematodes were found in some stomachs in small quantities, but these were assumed to be parasites and were not considered prey. In general, stomach contents showed an advanced level of digestion. A stomach fullness index (*SF*) was calculated as *SF* = (wet weight of the stomach content / wet weight of the swordfish without internal organs) × 100.

In zone C only cephalopods were preserved frozen. Fish were frozen immediately after capture without internal organs. This material was not included in comparative analyses because the main objective was to record the relative proportions of cephalopod species that were preyed upon in this zone.

Scomber spp. and *Illex* sp. were not considered prey from zones B

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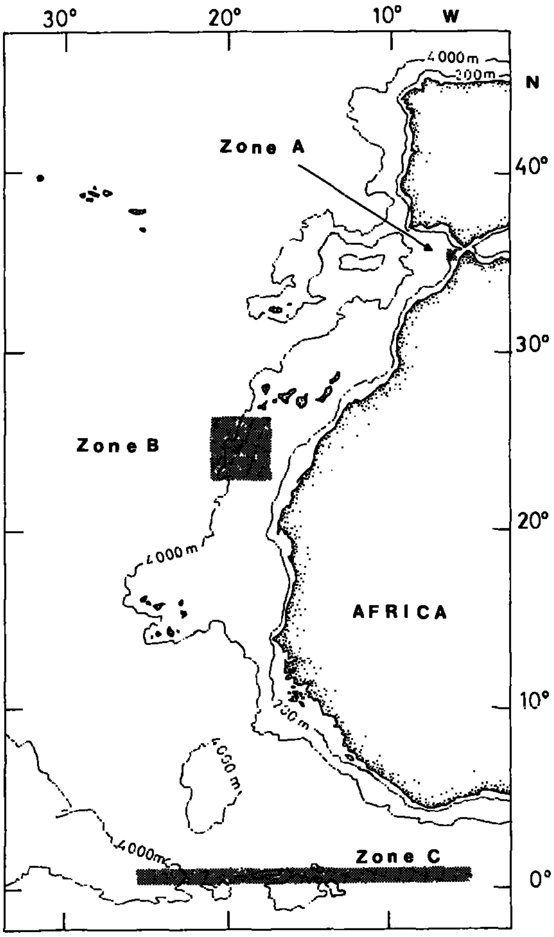

Figure 1
Locations of the swordfish *Xiphias gladius* fishing grounds in the central east Atlantic Ocean where samples were obtained in 1990–91.

and C respectively because they were used as bait. Prey items were identified to the lowest taxonomic category possible. Fish were identified from otoliths and bones (otolith guides of Härkönen (1986), Hecht and Hecht (1979), and author's collection). Crustaceans were classified from external parts of the skeleton (Zariquiey-Alvarez, 1968). Lower beaks (LB) were used as the primary means for classification of cephalopods, and beak identity was established by methods described by Clarke (1962, 1980, 1986a) and supplemented by a collection of cephalopod beaks (including beaks removed from locally caught cephalopods); upper beaks, other morphological characters (Hess and Toll, 1981), and distributional knowledge (Nesis, 1987) were used in some cases as well. Nearly all the beaks collected were fresh. All lower beaks were identified to the lowest taxon possible and the lower rostral length (LRL) or, in the order Sepiida, the hood length (LHL) (defined in Clarke, 1962, 1980) were measured by digital caliper or steroscopic microscope and eyepiece micrometer. Mantle lengths (ML in mm) and weights (W in g) of the cephalopods from which lower beaks came were then estimated from LRL's or LHL's by using relationships published elsewere (Clarke 1962, 1980, 1986a; Pérez-Gándaras, 1983; Wolff, 1982 (cited by Clarke, 1986a), Wolff and Wormuth, 1979).

Despite the advanced state of digestion of stomach contents, an attempt was made to examine the importance of each prey item. Two methods of stomach content analysis were used: percent numerical abundance and percent occurrence (Hyslop, 1980). A coefficient of prey numerical frequency, % No. = $(Ni/Nt) \times 100$, and a coefficient of prey frequency, % occurrence = $(Nsi/Nsf) \times 100$ were calculated; where Ni is the number of prey of each group i, Nt is the total number of prey, Nsi is the number of stomachs containing each group i, and Nsf is the total number of stomachs with food. An index of prey numerical importance (Castro, 1993) was also obtained as % importance = $(\% \text{ No.} \times \% \text{ occurrence})^{1/2} \times 100$.

Comparative analysis of degradation of hard structures

Free hard structures (otoliths, beaks, and eye lenses) were often found in the stomach contents. To estimate the importance of each prey item from the refractory or hard structures, it is important to know the rate of degradation by stomach acids.

Otoliths (sagittae) from four chub mackerel, *Scomber japonicus* (18 to 20 cm SL), similar in size to those found in the swordfish stomachs, and five otoliths of blue whiting, *Micromesistius poutassou*, from head-specimens found in swordfish stomachs were used to determine the rate of otolith degradation. Otolith lengths, taken on the longest axis, were between 3.70 and 4.10 mm for *Scomber* and between 10.81 and 13.53 mm for *Micromesistius*. Beaks from eleven *Illex coindetii* and two *Todarodes sagittatus* were used, with LRL's between 3.90 and 6.19 mm and 7.53 and 8.41 mm, respectively. Degradation of six eye lenses, three belonging to *T. sagittatus* and three belonging to fish species, were also analyzed.

Hard structures were placed in a hydrochloric acid (HCl) solution (pH=1.1; value lower than the range reported by Jobling and Breiby [1986] for fish in which the digestive process had begun), and the temperature was maintained between 18 and 20°C. The experiment was carried out for 48 hours. Old acid solutions were replaced with fresh solutions after 24 hours.

Cephalopod beak digestion (measured as decreasing upper rostral length, lower rostral length, and lower wing length) and eye lens digestion (measured as decreasing lens diameter) were measured every 12 hours. Otolith digestion (measured as decrease of the longest axis length) was measured at intervals of 12 hours for blue whiting, although the third interval was divided into two intervals (measuring each 6 hours). Otolith digestion was measured at intervals of 2.5 or 1 hour for the chub mackerel.

Results

Stomach fullness analysis

Data on fish length (SL), weight (W), and stomach fullness (SF) from zones A and B are given in Table 1. Values of SF in zone A were higher than those in zone B. In the latter area four stomachs were empty whereas in zone A all stomachs had contents.

Stomach contents analysis

Zone A The swordfish diet consisted of fish, cephalopods, and decapods (Table 2). Fish were the most important item by number (93.33%, Table 2), although in 20% of the stomachs analyzed fish were represented by only otoliths and bones. A total of 832 otoliths were collected. Most bone remains could not be identified. Many of them consisted of a large spinal column (as long as 78.5 cm). It was estimated that otoliths and spines belonged to a total of 476 fish. Blue whiting, *Micromesistius poutassou*, was the most important prey species by number (37.81%, Table 3).

Cephalopods were detected in 17.14% of the stomachs sampled, and the number of specimens was estimated as 26 (Table 2). They were always present in those fish with the highest SF. The Ommastrephidae was the most important family by number (35.6%) and *Todarodes sagittatus* was the predominant species (23.4%). The Histioteuthidae ranked second in importance (21.4%) and *Histioteuthis bonnellii* was the dominant species (11.4%, Table 4).

Decapods of the order Natantia were found in the stomach contents of two individuals (Table 2), and a large specimen was identified as *Acanthephyra purpurea*.

Zone B In zone B the swordfish diet consisted of cephalopods and fish. Cephalopods represented the most common food item in this area, revealing the highest index of numerical importance (67.89%, Table 2). A group of six pairs of beaks and one free upper beak with the same shape could not be assigned to any family. These were called "Unknown A." A description and sketches of this beak type (Fig. 2) are given in the Appendix. Ommastrephidae was the

Table 1

Swordfish *Xiphias gladius* data from zones A and B: length (SL) in cm, weight (W) in Kg, and stomach fullness (SF). *n* is the number of fish collected in each zone.

		SL			W			SF		
	n	Range	Mean	SD	Range	Mean	SD	Range	Mean	SD
Zone A	35	103–193	142.4	17.72	20–132	56.95	29.71	0.1–9.0	2.46	2.29
Zone B	25	112–201	153.3	24.54	13–102	40.40	24.36	0–5.3	0.75	1.37

Table 2

Comparison of the dietary importance of the three major forage categories observed in swordfish stomachs from zones A (35 fish) and B (21 fish). Data are given in terms of numerical frequency, frequency of occurrence, and index of numerical importance.

	Zone A				Zone B		
Forage category	% number	% occurrence	% importance	Forage category	% number	% occurrence	% importance
Fish	93.33	100.0	88.78	Fish	28.57	42.85	32.10
Cephalopods	5.09	17.14	8.54	Cephalopods	71.42	76.19	67.89
Decapod crustacea	1.56	5.71	2.66	Decapod crustacea	0.0	0.0	0.0

Table 3

Fish species occurring in the diet of the swordfish *Xiphias gladius* in zones A and B (35 and 9 swordfish stomachs containing fish, respectively) expressed in terms of numerical frequency, frequency of occurrence, and index of numerical importance.

	Zone A				Zone B		
Species	% number	% occurrence	% importance	Species	% number	% occurrence	% importance
Micromesistius poutassou	37.81	80.00	38.61	*Diaphus* sp.	16.66	22.22	18.35
Scomber japonicus	3.78	22.85	6.53	*Thunnus* sp.	5.55	11.11	7.49
Capros aper	2.10	8.57	2.97	Not identified	77.77	77.77	74.16
Lepidopus caudatus	1.47	20.00	3.80				
Trachurus sp.	1.26	14.28	2.97				
Merluccius merluccius	0.84	5.71	1.53				
Thunnus sp.	0.21	2.85	0.54				
Not identified	52.52	71.42	43.00				

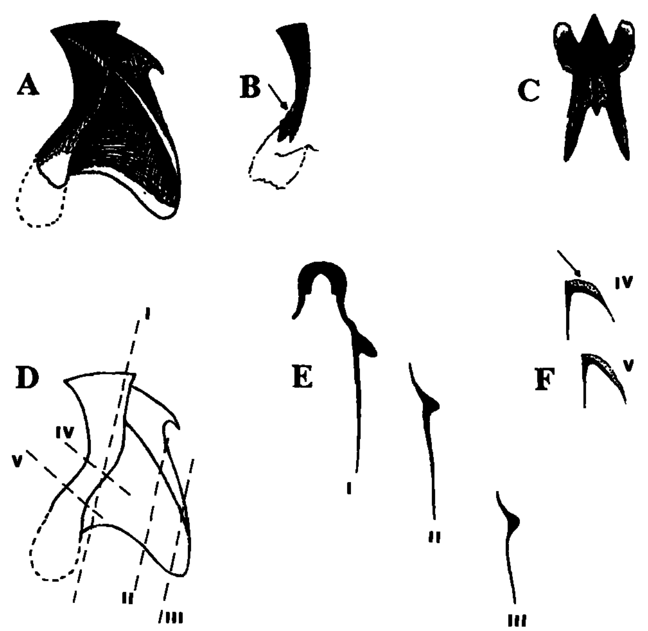

Figure 2

Illustration of the characteristic, unidentified, lower beak (called "Unknown A"). Lower rostral length = 3.4 mm. (**A**) profile of the beak; (**B**) profile of the anterior part with one side removed to show the shoulder and the anglepoint; (**C**) top view; (**D**) outline of the beak showing the positions of sections shown in E and F; (**E**) three sections of the crest and one lateral wall taken at positions indicated in D to show thickening; and (**F**) two sections of the wing and shoulder region at positions shown in D. Cartilage is indicated by arrows and dotted area.

Table 4

Cephalopods in the diet of the swordfish *Xiphias gladius* from zones A, B, and C (6, 16, and 15 swordfish with cephalopod remains, respectively). Number of cephalopods (*n*), index of numerical importance (IN), range of lower rostral length (LRL), range of estimated mantle length (ML), and range of estimated body weight (W) in each zone. The percentage by number of each species in all areas together is also given. The equation used is given under the symbol (A) (a = Clarke, 1962; b = Clarke, 1980; c = Clarke, 1986; d = Pérez-Gándaras, 1983; e = Wolff and Wormuth, 1979; f = Wolff, 1982). A specimen identified and counted from upper beaks is indicated by an asterisk (*). Broken beaks are indicated by (R).

	Zone A					Zone B					Zone C					All zones	
Group or Species	*n*	% IN	LRL (mm)	ML (mm)	W (g)	*n*	% IN	LRL (mm)	ML (mm)	W (g)	*n*	% IN	LRL (mm)	ML (mm)	W (g)	%	A
Family Spirulidae																	
Spirula spirula						1	2.6	0.7	20.4	1.0						0.9	c
Family Sepiidae																	
Sepia officinalis	1	5.0	4.0	97	34											0.9	d
Family Loliginidae																	
Loligo vulgaris						2	3.7	3.9–4.2	286–311	437–542						1.7	c
Family Ancistrocheiridae																	
Ancistrocheirus lesueuri	1	5.0	5.6	186	379						1	3.0	—	170	—	1.7	b
Family Octopoteuthidae																	
Octopoteuthis rugosa	1	5.0	12.4	215	401											0.9	b
Family Onychoteuthidae																	
Onychoteuthis A						3	6.5	3.2–4.5	166–245	132–466	1	3.0	6.6	373	1,923	3.5	f
Onychoteuthis B											1	3.0	3.0	154	105	0.9	f
Onychoteuthis C											6	17.2	3.0–4.4	154–243	109–451	5.3	f
Family Gonatidae																	
Gonatus sp. ?	1*	5.0	—	—	—											0.9	—
Family Histioteuthidae																	
Histioteuthis bonnellii	5*	11.4	6.4–7.9	74–88	247–377											4.4	b
Histioteuthis dofleini	1	5.0	7.0	128	435						3	8.3	5.4–6.9	95–121	235–435	3.5	bf
Histioteuthis A	1	5.0	2.8	48	53											0.9	b
Family Brachioteuthidae																	
Brachioteuthis sp.						1	2.6	1.6	48	3						0.9	c
Family Ommastrephidae																	
Todaropsis eblanae	2	7.2	R–4.3	R–141	R–189											1.7	d
Todarodes sagittatus	7*	23.4	4.4–6.9	172–274	149–517	2*	5.6	6.5	260	448						8.0	ba
Ommastrephes bartrami	1	5.0	8.5	303	1,383	3	8.0	4.5–8.1	180–289	185–1,170						3.5	a
Sthenoteuthis pteropus						10*	20.6	8.1–12.9	336–531	787–7.508	22*	41.6	5.3–10.8	218–442	375–4,052	28.3	e
Ommastrephid species						1	2.6	1.6	—	—						0.9	—
Family Thysanoteuthidae																	
Thysanoteuthis rhombus						4	7.5	3.3–7.6	252–727	670–8,613	4*	11.8	4.2–5.9	351–543	1,402–4,052	7.0	c
Family Mastigoteuthidae																	
Mastigoteuthis sp.	1	5.0	5.6	—	—											0.9	—
Family Grimalditeuthidae																	
Grimalditeuthis bomplandi											1	3.0	3.9	—	—	0.9	—
Family Cranchiidae																	
Teuthowenia megalops	1	5.0	4.1	179	56											0.9	c
Teuthowenia sp.											1	3.0	2.8	—	—	0.9	—
Megalocranchia sp.						2	5.3	5.1–5.4	276–297	—						1.7	b
Family Argonautidae																	
Argonauta sp.	1*	5.0	—	—	—	6	13.0	3.8–7.2	—	—						6.2	—
Unknown A						7*	14.0	3.0–4.4	—	—						6.2	—
Not identified	2	7.2	—	—	—	3	8.0	—	—	—	2	5.9	—	—	—	6.2	—

most important family by number (36.8%), and the orangeback squid, *Sthenoteuthis pteropus*, was the most important species (20.6%, Table 4).

Eighteen fish were counted from spinal columns and otoliths with an index of numerical importance of 32.10% (Table 2). Fish were found together with cephalopods in 19.0% of the stomachs containing food. In zone A the numbers of free lenses of fish and cephalopods were similar. However, only 32 cephalopod lenses were found in zone B; fish lenses were not found.

Zone C A total of 46 cephalopods were found in stomachs from zone C. The family Ommastrephidae, represented solely by *Sthenoteuthis pteropus*, was the most important species by number (41.6%) and estimated weight (Table 4). The Onychoteuthidae ranked second in importance by number but not by weight.

In the combination of all three zones, the Ommastrephidae, Onychoteuthidae, Histioteuthidae, and Thysanoteuthidae were the most important cephalopod families by number in swordfish diet (67.9%); other families are probably occasional prey. The most important species was *Sthenoteuthis pteropus* (28.3%, Table 4). The *S. pteropus* collected were mostly females, as evidenced by their large ML's (females can reach 650 mm ML and males 280 mm ML, Zuev et al., 1985) and by the presence of large oviducts. Moreover of the "Unknown A" species, five cephalopod species (*Brachioteuthis* sp., *Grimalditeuthis bomplandi*, *Megalocranchia* sp., *Octopoteuthis rugosa*, and *Spirula spirula*) were identified for the first time in swordfish stomach contents.

Comparative analysis of hard structure degradation

Otoliths (sagittae) of *Scomber japonicus* were dissolved after an average time of 6 hours and 47 minutes (% decrease of otolith length=2.121 + 14.424T, SD=5 min; Fig. 3). Otolith length decreased significantly over a period of one hour (ANOVA, df=14, $P=5.0425 \times 10^{-5}$).

Otoliths of *Micromesistius poutassou* showed a significant decrease in length after an interval of 12 hours (ANOVA, df=8, $P=1.7605 \times 10^{-2}$). After 48 hours, they had lost 40% of their length (% decrease of otolith length=1.932 + 0.843T, Fig. 3) but still maintained their original shape.

Lower rostral length and upper rostral length did not differ significantly after 48 hours in acid (ANOVA, df=24, P=0.95588 and df=24, P=0.93221, respectively). In addition, wing length of the lower beak did not differ significantly after 48 hours (ANOVA, df=24, P=0.97319). No significant differences were found for fish and cephalopod eye lense diameter after 48 hours (ANOVA, df=4, P=0.50454 and df=4, P=0.89424, respectively).

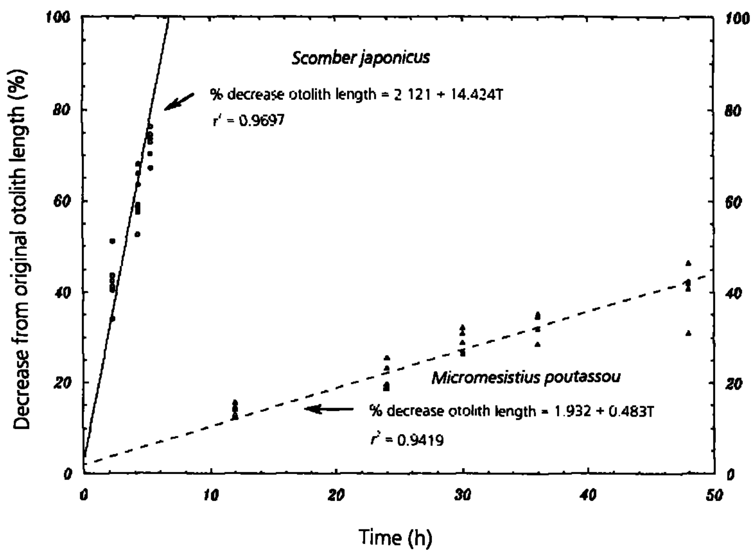

Figure 3

Decrease in otolith length of chub mackerel, *Scomber japonicus*, and blue whiting, *Micromesistius poutassou* (measured on the longest axis) after immersion in hydrochloric acid (pH=1.1) for 48 hours.

Discussion

Commercial longline fishing generally lasts for 12–14 hours and the fish caught can remain alive for many hours (Boggs, 1992); thus digestion of stomach contents is continuous. Moreover, regurgitation regularly occurs (Tibbo et al., 1961). This may bias values of stomach fullness. The period of study was limited in each area and sample sizes were not large, precluding statistical analysis. However, the diet of swordfish appeared to show substantial variation between areas. In neritic areas (zone A) swordfish preyed upon pelagic and benthic species of fish and squids, whereas in oceanic areas (zone B) they preyed mainly on squids (Table 2). This pattern was also observed by Maksimov (1969). In addition, Carey and Robison (1981) showed that in neritic areas swordfish have a different ecology and migration pattern from that found in oceanic waters. In neritic areas, swordfish are found near the bottom during the daylight, feeding mainly on benthic species (i.e. *Capros aper* and *Merluccius merluccius* in this study, Table 3); at night, they move offshore to feed actively on squid and other migrating fauna concentrated near the surface (i.e. *Todarodes sagittatus* in this study, Table 4). In oceanic waters, swordfish undergo a diel vertical migration reaching about 600 m at noon and ascending to shallow waters at night; they can prey actively on oegopsid squids at both ends of the migration (Carey and Robison, 1981). The mean number of cephalopods per stomach was 0.7 in zone A, similar to data reported by Moreira (1990). In zone B (oceanic waters) the mean was 1.8, similar to the value of 2.1 calculated from data obtained by Guerra et al. (1993). In zone C, the mean number of cephalopds per stomach was 3. Bane (in Fonteneau and Marcille, 1991) also showed that cephalopod-prey are more important in oceanic waters than inshore for yellowfin tuna, *Thunnus albacares*.

From analysis of degradation, otoliths were strongly eroded by acid; large, thick otoliths dissolved more slowly than small, thin ones. Cephalopod beaks and eye lenses and fish eye lenses were not affected by acid. Fish were the item with the highest index of numerical importance (Table 2) in zone A. However, the value obtained must be treated with caution because the otoliths of *Micromesistius poutassou* may accumulate owing to the structure of the stomach wall and the time necessary to dissolve them (Fig. 3). The otoliths of *Scomber japonicus* were not found free, a feature that accords with the results of the analysis of degradation. Therefore, if evaluation of fish biomass is based on the presence of otoliths, biomass may be overestimated for fish with large and dense otoliths (i.e. *M. poutassou*). Fish with smaller and weak otoliths may be underestimated as was observed by both da Silva and Neilson (1985) and Jobling and Breiby (1986). However, the rate of degradation of otoliths in this study may be overestimated because the acidity was greater than the value reported in general for fish stomach acids (pH=2.0–3.0) after the digestive process has begun. Because cephalopod eye lenses and fish eye lenses are not affected by acid, as noted by Clarke (1986b), the number of lenses found in a stomach may be a means of estimating the relative importance of cephalopods and fish in the diet. However, the percentage of occurrence of fish (counted from whole fish and free otoliths) was similar to that obtained by Azevedo (1989) and Moreira (1990) in areas nearest to zone A. In zone B, if eye lenses of fish and cephalopods are considered, both of which experience a similar rate of digestion, the relative importance of fish in the diet is less than what was indicated by data from the otoliths.

The importance (based on % number) of *Sthenoteuthis pteropus* in zone C is not surprising given the large abundance of this species at these latitudes (Voss, 1966; Zuev et al., 1985). The preferred temperature range for swordfish is from 25° to 29°C (Ovchinnikov, 1970) which is nearly the same as that for adult squid females (24°–30°C, Zuev et al., 1985). These temperatures are almost constant at these latitudes throughout the year. Around zone C, there is a complex system of currents and frontal zones where there is a high biomass (Blackburn, 1965; Ovchinnikov, 1970): in addition, high swordfish CPUE values have been obtained in these areas by the Spanish fishing fleet (Mejuto et al., 1991) and the Japanese longline fishery (Palko et al., 1981). Therefore, the availability of prey may be partially responsible for the distribution of swordfish in these waters.

Guerra et al. (1993) found that *Sthenoteuthis pteropus* was the most common species in the swordfish diet in the Northeastern Atlantic; this species is possibly one of the unidentified ommastrephid species found by Maksimov (1969). *Todarodes sagittatus* and *Ommastrephes bartrami* were also found. These three species ascend to the upper epipelagic layer and feed actively on myctophids and small squid at night (Nigmatullin et al., 1977; author, unpubl. data). During the day, *S. pteropus* descend to 350 or 400 m (Moiseyev, 1988). These ommastrephids have a high growth rate and their life span is no longer than 1.5 years (Arkhipkin and Mikheev, 1992; Rosenberg et al., 1980; Ishii, 1977). Therefore, squid may be an efficient means of energy transfer in oceanic food webs.

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Appendix

Description of the "unknown A" lower beak

Terms and measurement used to describe the characteristic beak (the "Unknown A") are the same as those used by Clarke (1980, 1986a). The beak (Fig. 2) belongs to an unidentified species of oegopsid, and its general shape is similar to the beak of *Discoteuthis*. It is taller than it is long (Fig. 2A) and although five of them had digested wings, the largest beak (lower rostral length=4.4 mm) had a full wing with an isolated spot.

The rostrum is distinctly shorter than deep (g/a=0.67, where g is the hood length in the midline and a is the length of the rostral edge visible in profile) and narrow (i/j=2.8, where i is the LRL and j is the distance between the jaw angles). There is no hook in the rostral edge, but rather this is sharp-edged and thickened. The crest is short and has a notch in the lateral wall to the side of the crest (Fig. 2, A and C). The hood does not lie close to the crest. The surface of the hood has a very soft fold. The jaw angle is obtuse and a sharp anglepoint is present (Fig. 2B). Jaw angle is obscured from the side by a very low wing fold (Fig. 2, A, B, and F) which is covered by cartilage (dotted area). A distinct lateral wall ridge forms a fin (Fig. 2, E, I), similar to *Histioteuthis* beaks (type A) described by Clarke (1980). This runs toward the midpoint of the posterior edge of the lateral wall (Fig. 2, E, III). The beaks of *Discoteuthis* lack this ridge.