Diets of thornback ray (*Raja clavata*) and tope shark (*Galeorhinus galeus*) in the bottom longline fishery of the Azores, northeastern Atlantic

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Abstract—Tope shark (*Galeorhinus galeus*) and thornback ray (*Raja clavata*) are the two most captured elasmobranch species by the Azorean bottom longline fishery. In order to better understand the trophic dynamics of these species in the Azores, the diets of thornback ray and tope shark caught in this area during 1996 and 1997 were analyzed to describe feeding patterns and to investigate the effect of sex, size, and depth and area of capture on diet. Thornback rays fed mainly upon fishes and reptants, but also upon polychaetes, mysids, natant crustaceans, isopods, and cephalopods. In the Azores, this species preyed more heavily upon fish compared with the predation patterns described in other areas. Differences in the diet may be due to differences in the environments (e.g. in the Azores, seamounts and oceanic islands are the major topographic features, whereas in all other studies, continental shelves have been the major topographic feature). No differences were observed in the major prey consumed between the sexes or between size classes (49–60, 61–70, 71–80, and 81–93 cm TL). Our study indicates that rays inhabiting different depths and areas (coastal or offshore banks) prey upon different resources. This appears to be related to the relative abundance of prey with habitat. Tope sharks were found to prey almost exclusively upon teleost fish: small shoaling fish, mainly boarfish (*Capros aper*) and snipefish (*Macroramphosus scolopax*), were the most frequent prey. This study illustrates that thornback rays and tope sharks are top predators in waters off the Azores.

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The thornback ray (*Raja clavata* L.), is a shallow water bottom-living elasmobranch found in the Atlantic from Iceland and Norway southwards to South Africa, including Madeira and Azores islands. This species is also found in the Mediterranean, western Black Sea, and southwestern Indian Ocean (Stehmann and Bürkel, 1984). The thornback ray is commercially exploited in several countries. In the Azores it is a bycatch of the bottom longline fishery directed toward demersal and deepwater teleost species. Food and feeding habits of the thornback ray have been intensively studied since the end of the 19th century (e.g. Day, 1880–84) and more recently (e.g. Smale and Cowley, 1992; Ellis et al., 1996; Daan et al.[1]). However, only two studies have been conducted on the thornback ray off Portuguese continental waters (Marques and Ré, 1978; Cunha et al., 1986), and none exists for populations inhabiting waters around the oceanic islands or seamounts in the northeastern Atlantic.

The tope shark (*Galeorhinus galeus* (L.)), is a cosmopolitan species that can be found from about 70ºN to about 55ºS. Distribution of this species includes the Atlantic, Pacific and Indian Oceans (Compagno, 1984). Tope shark is also commercially exploited by several countries around the world, including the Azores, where it is a bycatch of the bottom longline fishery. Compagno (1984) and Olsen (1984) reviewed the biology of this shark; however, there have been relatively few studies on their feeding habits. The diet of tope shark was described by Ford (1921) for individuals landed at Plymouth U.K., by Olsen (1954) in southeastern Australia, and by Ellis et al. (1996) in the northeastern Atlantic Ocean.

Elasmobranchs are among the top predators in marine environments (Ellis et al., 1996); thus they affect the populations of both fish and invertebrates at lower trophic levels. However, feeding studies of elasmobranches in the Azores have been limited to the blue shark (*Prionace glauca*) (Clarke et al., 1996). Tope shark and thornback ray are the two most abundant elasmobranch species landed by the Azorean bottom longline fishery. Information on the feeding habits of these two species contributes to a better understanding of trophic dynamics and food webs—information which is needed as fisheries scientists advance ecosystem principles to fisheries management (Pauly et al., 2000; Pitcher, 2000; Whipple et al., 2000). The purpose of this study was to examine the diet of thornback ray and tope shark, to describe their feeding patterns and the effect of sex, size, depth, and location on their diet.

Materials and methods

Thornback rays and tope sharks were collected between March and May (spring) of 1996 and 1997 during a

[1] Daan, N., B. Johnson, J. R. Larsen and H. Sparholt. 1993. Analysis of the ray (*Raja* spec.) samples collected during the 1991 international stomach sampling project. ICES C.M. 1993/G:15, 17 p.

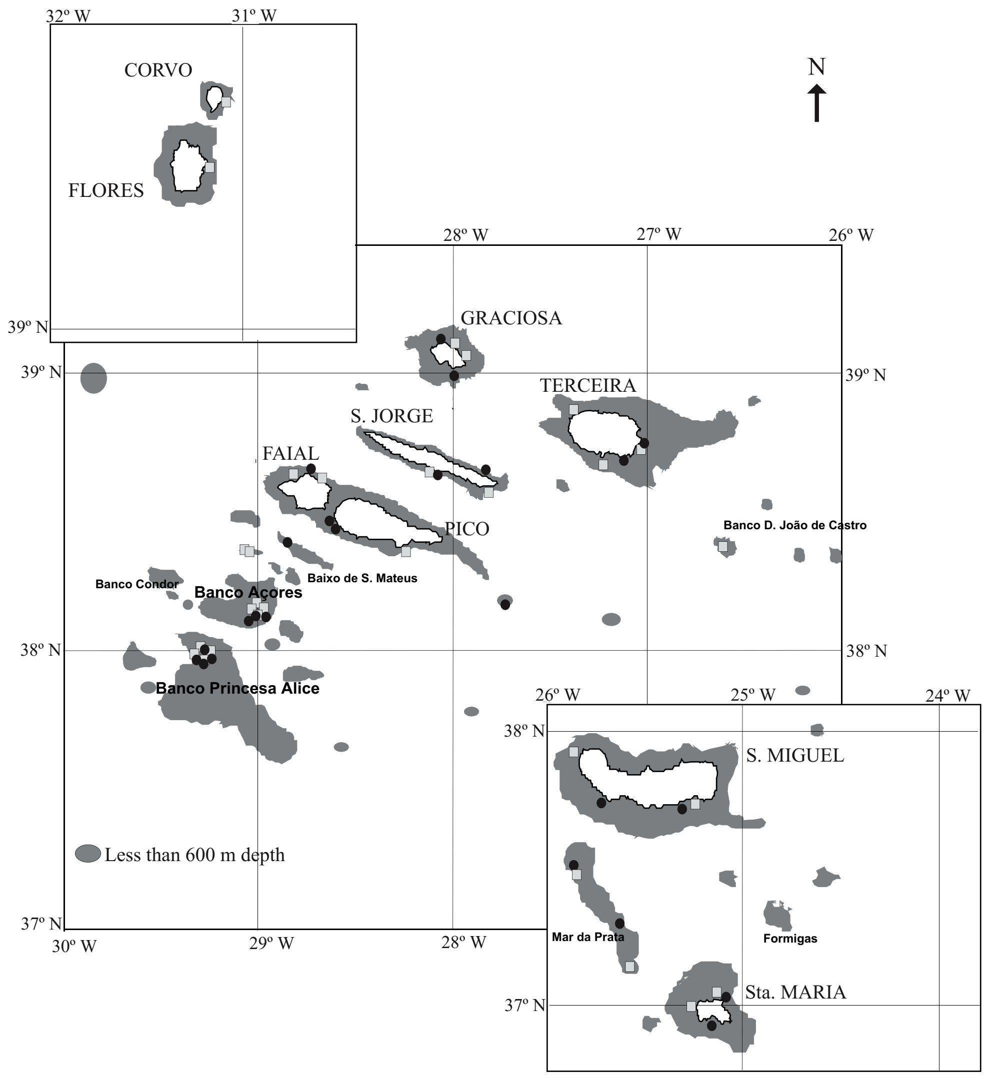

Figure 1

Locations of the longline sets made in the Azores during the spring of 1996 (●) and 1997 (□).

study on demersal fisheries in Azorean waters (Fig. 1). Fishes were caught by longline onboard the RV *Arquipélago*. Line setting began before sunrise (approx. 05:00 h) and hauling started about two hours after setting. From the fish sampled, total length (TL, to the nearest cm) was measured, and sex and maturity were determined by macroscopic examination of gonads and claspers with maturity scales, as proposed by Stehmann (1987). Stomachs were removed and classified as either everted, regurgitated, with bait, empty, or with contents. Individuals falling in any of the first three categories, as well as those that had obviously eaten fish hooked on the longline, were excluded from further analysis. Stomachs with contents were placed in plastic bags and frozen (within about 2 h of capture) for subsequent analysis. Stomach contents, which partly consisted of a turbid suspension, were washed with water in a nylon net of approximately 0.5-mm mesh size to allow easier examination. The items were carefully separated, weighed (after removing the surface water by blotting them in tissue paper), and identified to the lowest possible taxonomic level. Individuals of each identified taxon were counted. Whenever fragments were found, the number of individuals was taken as the smallest possible number of individuals from which fragments could have originated.

Precision estimates in diet studies have been advocated and used by several authors (Ferry and Cailliet, 1996; Morato et al., 1999). We used the cumulative trophic diversity, measured with the Shannon-Wiener index [as $H' = -\sum_{i=1}^{n} P_i(\log_e P_i)$, where P_i is the proportion of individuals in the ith species] to measure sample size sufficiency (Hurtubia, 1973). Cumulative numbers of randomly pooled stomachs were plotted against the cumulative trophic diversity. The asymptote of the curve indicates the minimum number of stomachs required. Frequency of occurrence (%O), percentage number (%N), and weight (%W) for each prey type were used to describe the diet of both species (for a review see Hyslop, 1980; Cortés, 1997). Wet weight was used to determine the latter value. The index of relative importance

[IRI=(%N + %W) × %O] (Pinkas et al., 1971) and the %IRI (as %IRI_i = 100 × $IRI_i/\sum_{i=1}^{n} IRI_i$) were calculated for each prey category and used in diet comparisons. Prey taxa occurring in less than five stomachs were grouped into higher taxonomic categories. Ontogenetic differences in the diet of thornback rays were examined by grouping fish into four size classes (49–60, 61–70, 71–80, and 81–93 cm TL). The diet of thornback rays was also analyzed by sex, depth (0–100, 101–200, 201–350 m), and area of capture (coastal areas and offshore banks). No further analyses were performed for tope shark because their diet was dominated by only one prey category (see "Results" section). To determine if the most important preys were similar for different groups of rays, weighted correlation and concordance analyses were used (Zar, 1999). These methods were preferred to conventional rank correlation methods (e.g. Spearman) because they emphasize the high ranking given to the most important prey categories. Differences in the rankings of IRI values for prey categories between three or more groups (e.g. three size classes) were tested for significance with the top-down concordance method (C_T= top-down concordance coefficient) (Zar, 1999). For paired groups (e.g. males and females) the top-down correlation method (r_T= top-down correlation coefficient) was used (Quade and Salama, 1992; Zar, 1999). Schoener's dietary overlap index (Schoener, 1970) (as C_{xy}=1–0.5 $\sum_{i=1}^{n} |P_{xi} - P_{yi}|$, where P_{xi} was the proportion (based on %IRI) of food category i in the diet of x; and P_{yi} was the proportion of food category i in the diet of y) was used to measure the diet overlap between sex, size classes, depth strata, and area of capture.

Cluster analysis was used to describe geographic similarities in the feeding habits of thornback rays. A predator-prey matrix was built from published data. When more than one index was available, the following criteria were used to choose between indexes: IRI or %IRI, %O, %N, %W, %Volume. The number of prey categories included was based on the quality of the description found in the published sources. Eleven different categories were obtained. A distance matrix was then calculated by using Euclidean distance, and the hierarchical form of analysis was applied (Clarke and Warwick, 1994). The grouping of predators was based on the "average linkage method," and a dendrogram was used as a graphic form of representation. Finally, trophic levels (TLv_k) were estimated for each of the samples (k) by using the method proposed by Cortés (1999) [as TLv_k=1+ ($\sum_{i=1}^{n} P_{ik} \times TLv_i$), where TLv_i is the trophic level of each prey category as estimated by the author, P_{ik} is the proportion of prey category i in sample k]. Mean trophic levels were also estimated for groups resulting from the cluster analysis, and differences between them were tested by using one-way ANOVA (Zar, 1999).

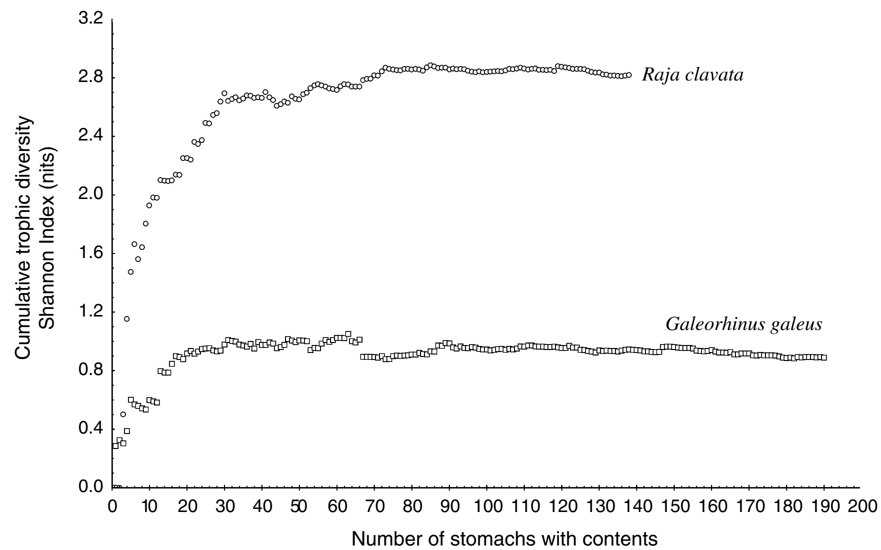

Figure 2

Randomized cumulative trophic diversity curves for thornback ray (*Raja clavata*) and tope shark (*Galeorhinus galeus*).

Results

Thornback rays were caught at depths ranging from 10 to 350 m, but primarily (95%) shallower than 250 m. Out of 237 stomachs examined, the contents of four appeared to have been regurgitated (1.7%), seven contained bait only (2.9%), 88 were empty (37.1%), and 138 contained prey (58.2%). Rays with stomachs containing food measured from 49.0 to 93.0 cm TL. All tope sharks were caught between 10 and 150 m depth, except for one individual taken at 300 m. Out of 365 stomachs examined, 174 (47.7%) were empty, seven (1.9%) contained fish hooked on the longline and 184 stomachs (50.4%) contained prey. Sharks with stomachs containing food ranged from 58.0 to 153.0 cm TL. The cumulative trophic diversity curves of both species appeared to reach an asymptote, suggesting that a sufficient number of stomachs were analyzed for both the thornback ray and tope shark (Fig. 2).

Thornback ray

The main diet components of thornback rays were fish (%IRI=81.6) and crustaceans reptants (%IRI=17.4) (Fig. 3). Fish occurred in 84.1% of stomachs that contained food, and represented 78.0% of total prey weight and 50.2% of total prey number (Table 1). Two benthopelagic species, the snipefish (*Macroramphosus scolopax* [%IRI=34.0]) and the boarfish (*Capros aper* [%IRI=26.8]), were by far the predominant fish prey items. However, some pelagic fish

Table 1

Values for percentage by number (%N), weight (%W), occurrence (%O), and index of relative importance (IRI and %IRI) for prey items observed in stomachs (n=138) of thornback rays (*Raja clavata*) caught off the Azores during the spring of 1996 and 1997. Total values are given in bold font.

Prey items	%N	%W	%O[1]	IRI	%IRI
Algae	0.3	0.0	1.5	0.5	0.0
Bivalvia—*Chlamys* sp.	0.1	0.0	0.7	0.1	0.0
Total Cephalopoda	**1.1**	**1.1**	**5.1**	**11.2**	**0.1**
Octopodoidea unidentified	0.1	0.1	0.7	0.1	0.0
Scaeurgus unicirrhus	0.7	0.8	2.9	4.4	0.1
Cephalopoda unidentified	0.3	0.2	1.5	0.8	0.0
Total Polychaeta	**3.4**	**0.8**	**9.4**	**39.5**	**0.8**
Hirudinea	0.1	0.0	0.7	0.1	0.0
Crustacea					
Stomatopoda	0.1	0.0	0.7	0.1	0.0
Total Natantia	**3.1**	**1.0**	**10.1**	**41.4**	**0.3**
Penaeidea unidentified	1.4	0.3	2.9	4.9	0.1
Solenocera membranacea	0.1	0.1	0.7	0.1	0.0
Solenocera sp.	0.1	0.1	0.7	0.1	0.0
Pandalidae	0.3	0.1	0.7	0.3	0.0
Processa intermedia	0.1	0.0	0.7	0.1	0.0
Processa sp.	0.1	0.0	0.7	0.1	0.0
Caridea unidentified	0.1	0.0	0.7	0.1	0.0
Natantia unidentified	0.9	0.4	2.9	3.8	0.1
Total Reptantia	**31.9**	**17.0**	**47.1**	**2303.2**	**17.4**
Anomura unidentified	0.1	0.1	0.7	0.1	0.0
Scyllaridae *Scyllarus arctus*	4.0	0.8	9.4	45.1	0.9
Diogenidae	1.1	1.7	5.8	16.2	0.3
Paguridea	0.3	0.3	1.5	0.9	0.0
Galatheidae *Galathea* sp.	0.3	0.1	1.5	0.6	0.0
Homolidae *Paromola cuvieri*	0.6	0.1	2.9	2.0	0.0
Calappidae *Calappa granulata*	1.8	1.3	7.3	22.6	0.5
Parthenopidae *Parthenope* sp.	2.8	0.7	0.7	2.5	0.0
Portunidae	0.1	0.0	0.7	0.1	0.0
Total *Liocarcinus* spp.	**14.9**	**8.3**	**16.6**	**385.1**	**5.5**
Liocarcinus marmoreus	9.8	5.1	9.4	140.1	2.8
Liocarcinus corrugatus	3.8	2.7	6.5	42.3	0.8
Liocarcinus spp.	1.3	0.5	2.2	4.0	0.1
Brachyura	4.1	2.4	11.6	75.4	1.5
Reptantia unidentified	0.6	0.4	2.9	2.9	0.1
Decapoda unidentified	0.1	0.0	0.7	0.1	0.0
Total Mysidacea	**6.6**	**0.7**	**3.6**	**26.3**	**0.5**
Isopoda	1.6	0.3	5.1	9.7	0.2
Amphipoda–*Vibilia* sp.	0.1	0.0	0.7	0.1	0.0
Crustacea unidentified	1.1	0.8	4.4	8.4	0.2
Total Pisces	**50.2**	**78.0**	**84.1**	**10811.2**	**81.6**
Myctophidae	0.6	0.3	2.2	2.0	0.0
Moridae *Gadella maraldi*	0.1	0.2	0.7	0.2	0.0
Caproidae *Capros aper*	13.7	24.7	34.8	1336.3	26.8
Macroramphosidae *Macroramphosus scolopax*	16.7	19.3	47.1	1695.6	34.0
Sparidae *Pagellus* spp.	1.0	5.4	4.4	28.2	0.6
Mullidae *Mullus surmuletus*	0.1	3.0	0.7	2.2	0.0
Pomacentridae *Chromis limbata*	0.1	0.2	0.7	0.2	0.0
Carangidae *Trachurus picturatus*	0.9	2.6	3.6	12.6	0.3
Scombridae *Scomber japonicus*	0.4	6.0	2.2	14.1	0.3
Pisces unidentified	16.6	16.3	43.5	1431.2	28.7
Rocks	1.0	0.3	5.1	6.6	0.1
Tissue unidentified	0.4	0.8	2.2	2.6	0.1

[1] Because the %O is a nonadditive index (Cortés, 1997) for grouping fish items into higher taxonomic categories (i.e. Pisces, etc), the %O value was recalculated by considering the number of stomachs with the respective higher taxonomic category. This recalculation affects both the IRI and %IRI values.

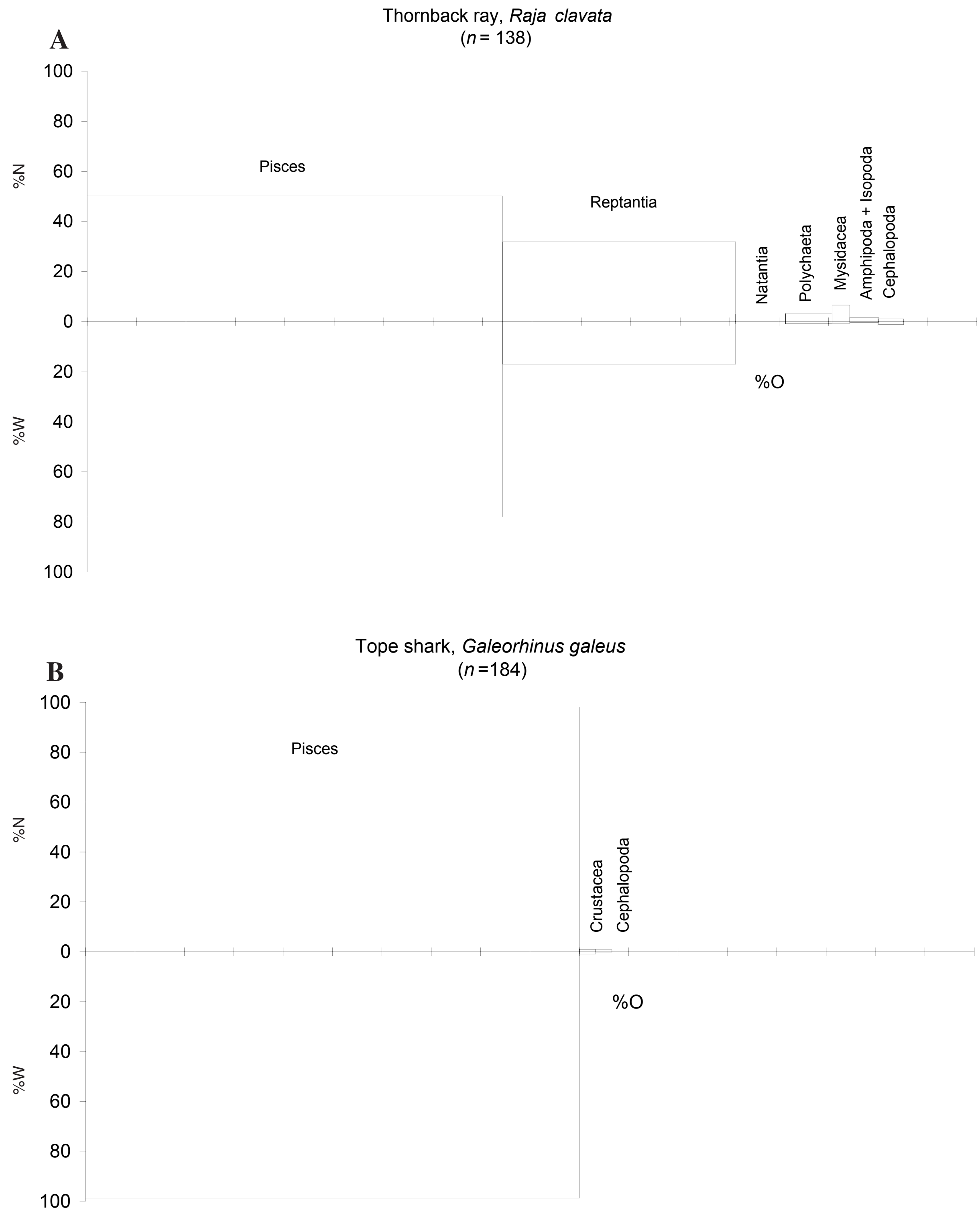

Figure 3

Relative importance of prey categories in the diet of (**A**) thornback ray (*Raja clavata*) and (**B**) tope shark (*Galeorhinus galeus*) ranked from highest IRI values. Where the areas of the boxes are equal to the IRI value [(%N+%W) × %O], %N is the percent number, %W the percent weight, and %O the frequency of occurrence of the prey category. Each tick mark of %O represents 10%.

Table 2

Percentage of relative importance (%IRI) of food categories of *Raja clavata* by sex, total length, depth strata, and areas (coastal and offshore banks). Prey items occurring in less than five stomachs were grouped into higher taxonomic levels. The null hypothesis of not feeding upon the same most important prey categories was tested by using the top-down correlation method (being r_T the top-down correlation coefficient) and the top-down concordance method (being C_T the top-down concordance coefficient). NS = non significant, *P<0.01.

	Sex		Total length (cm)				Depth (m)			Areas	
	F	M	49–60	61–70	71–80	81–93	0–100	101–200	201–350	Banks	Coastal
Cephalopoda	0.52	0.03	1.44	0.00	0.38	0.63	0.03	0.21	5.60	3.48	0.06
Polychaeta	0.62	1.70	0.21	0.43	0.73	6.44	0.54	0.40	15.13	4.23	0.57
Penaeidea	0.34	0.62	0.72	1.32	0.18	0.00	0.19	0.12	14.72	1.41	0.29
Other Natantia	0.10	0.15	0.52	0.11	0.06	0.00	0.48	0.01	0.00	0.08	0.12
Diogenidae	0.07	1.58	1.45	0.00	0.88	0.45	0.69	0.21	0.00	0.00	0.53
Scyllarus arctus	1.54	0.57	1.12	0.25	2.48	0.64	0.76	0.84	4.35	0.91	1.21
Calappa granulata	0.73	0.31	0.45	0.30	0.90	0.36	0.00	1.52	0.00	0.10	0.64
Liocarcinus spp.	8.12	0.60	1.64	3.30	9.49	0.19	10.44	1.43	0.00	0.00	12.30
Other Reptantia	9.20	8.32	1.43	11.88	22.48	0.00	47.44	0.31	0.00	0.52	6.33
Mysidacea	0.68	0.50	0.18	0.62	1.02	0.00	0.00	1.00	2.21	16.79	0.00
Isopoda	0.53	0.00	0.00	0.24	0.30	0.35	0.02	0.47	0.00	0.00	0.31
Capros aper	41.20	24.16	36.26	38.11	23.39	53.34	20.06	38.26	10.63	35.56	32.53
Macroramphosus scolopax	35.15	58.88	53.60	41.65	34.91	37.35	15.81	54.84	36.72	33.50	42.91
Pagellus sp.	0.46	1.07	0.00	1.08	1.24	0.00	0.56	0.19	9.99	2.27	0.43
Myctophidae	0.04	0.12	0.00	0.14	0.09	0.00	0.03	0.04	0.65	1.16	0.01
Trachurus picturatus	0.14	0.57	0.34	0.00	0.87	0.26	1.25	0.01	0.00	0.00	0.40
Other Pisces	0.58	0.82	0.64	0.56	0.61	0.00	1.71	0.15	0.00	0.00	1.36
	r_T=0.70*		C_T=0.74*				C_T=0.51^{NS}			r_T=0.44^{NS}	
Stomachs with contents (n)	89	49	19	47	60	11	47	78	13	24	110

prey were also recorded in the stomachs of thornback rays: the chub mackerel, (*Scomber japonicus* [%IRI=0.3]) and the blue jack mackerel (*Trachurus picturatus* [%IRI=0.3]). Some individuals also fed upon mesopelagic myctophids (%IRI<0.1) and upon shallow water benthic fish such as the red striped mullet (*Mullus surmuletus* [%IRI<0.1]) and the Azorean chromis (*Chromis limbata* [%IRI<0.1]).

Reptants occurred in 47.1% of the stomachs examined and represented 17.0% by weight and 31.9% by number of the total prey found (Fig. 3A). Swimming crabs (*Liocarcinus* spp. [%IRI=5.5]), which include both *L. marmoreus* (%IRI=2.8) and *L. corrugatus* (%IRI=0.8), were the most important reptant prey item in the diet of thornback ray (Table 1). Other important reptants included the lesser locust lobster (*Scyllarus arctus* [%IRI=0.9]), the shamefaced crab (*Calappa granulata* [%IRI=0.5]), as well as some unidentified Diogenidae (%IRI=0.3) and brachyura (%IRI=1.5).

Polychaetes (%IRI=0.8) were the third most important prey category and occurred in 9.4% of the stomachs with food (Fig. 3A). Mysids (%IRI=0.5), natants (%IRI=0.3), isopods (%IRI=0.2), and cephalopods (%IRI=0.1) also occurred in stomachs of thornback rays sampled in the Azores (Table 1).

A comparison of thornback ray's diet in relation to sex, length, depth and area of capture (Table 2) suggests that *C. aper* and *M. scolopax* were by far the most important prey for all subgroups examined. The diets of both sexes were significantly correlated (r_T=0.70, P<0.01), indicating a high degree of similarity in the diets of males and females. Both sexes fed primarily upon two benthopelagic fish species (*M. scolopax* and *C. aper*) and reptants (Table 2). Schoener's diet overlap index between males and females was 0.72, also indicating a high level of similarity between diets.

Significant concordance (C_T=0.74, P<0.01) was displayed among thornback rays of different size classes (49–60, 61–70, 71–80 and 81–93 cm TL). Prey categories had similar %IRI values for the different size classes (Table 2), with the exception of reptants (both *Liocarcinus* spp. and "other reptants"), which were more important in the diet of the two middle size classes. Schoener's index also suggested a high degree of overlap (>0.60) among all size classes (Table 3).

Examination of depth-related differences was limited by the small sample size of rays from deeper waters ($n_{201–350m}$=13). However, the top-down concordance coefficient suggested that individuals captured at different depths (0–100, 101–200, and 201–350 m) do not feed upon the same most important prey categories (C_T=0.52, P>0.05). Reptants (both *Liocarcinus* spp. and "other reptants") and the fish species *T. picturatus* were more important in the diet of rays captured in shallow waters (0–100 m); whereas

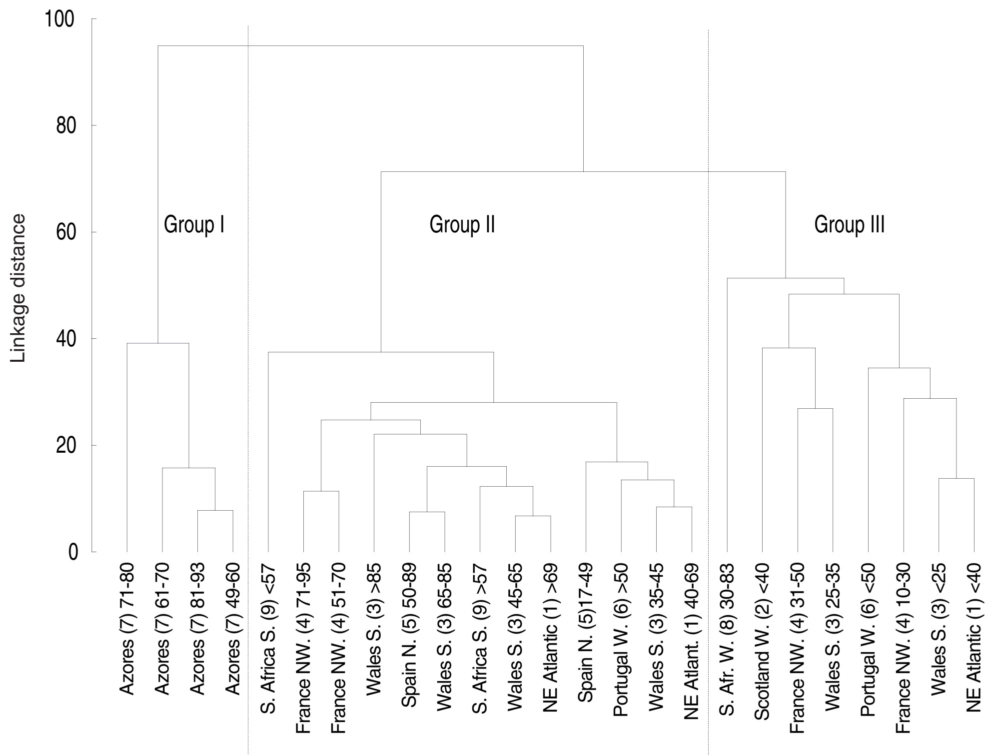

Figure 4

Dendrogram of the cluster analysis (Euclidean distance, average linkage method) for geographic patterns of feeding habits of *Raja clavata*. In parentheses is given the authorship of the studies: 1 = Ellis et al. (1996); 2 = Gibson and Ezzi (1987); 3 = Ajayi (1982); 4 = Quiniou and Andriamirado (1979); 5 = Olaso and Rodríguez-Marín (1995); 6 = Cunha et al. (1986); 7 = the present study; 8 = Ebert et al. (1991); 9 = Smale and Cowley (1992).

polychaetes, cephalopods, penaeids, mysids, seabreams (*Pagellus* sp.), and myctophids were consumed more by rays caught in deeper waters (Table 2). Schoener's overlap index for individuals captured at different depth intervals (Table 3) indicated low overlap (=0.50), supporting the results of the top-down concordance coefficient analysis.

Finally, the diet of rays caught in coastal areas and offshore banks were not significantly correlated (C_T=0.44, P>0.05), indicating that thornback rays feed upon different prey depending on the environment. The Diogenidae, *Liocarcinus* spp., "other reptants," and "other Pisces" were more important prey for rays in coastal areas, whereas polychaetes, penaeids, cephalopods, mysids, seabreams (*Pagellus* sp.), and myctophids were more important for rays caught at offshore banks (Table 2). However, Schoener's index showed a high level of overlap (0.69) between the diets of rays caught in the different locations—most likely due to the high dominance of two benthopelagic fishes in their diets (75.4% and 69.1% for coastal areas and offshore banks, respectively).

Published information on the diet of thornback rays is summarized in Table 4. Estimations of mean trophic levels vary from 3.1, for the smallest size class (South Wales: <25 cm TL), to 4.2 for the Azorean thornback ray (this study; size classes 49–60 and 81–93 cm TL). The arbitrarily chosen cutoff in the cluster analysis was set at 60% dissimilarity, which divided the dendrogram into three groups with similar feeding patterns (Fig. 4). Cluster group I grouped the Azorean populations (all size classes) and had an estimated trophic level of 4.14 (±0.09 SD). Cluster group II contained all other medium and large size classes (i.e. >40 cm TL), with the exception of small rays from the Cantabrian Sea, North Spain (17–49 cm TL), and one small- to

Table 3

Schoener's diet overlap index for thornback rays (*Raja clavata)* size classes and for different depth strata.

	Depth (m)			Total length (cm)		
	101–200	201–350		61–70	71–80	81–93
0–100	0.40	0.29	49–60	0.83	0.66	0.76
201–350		0.50	61–70		0.77	0.77
			71–80			0.62

Table 4

Categorized diets of thornback ray in different geographic locations. Estimation of trophic level (TL) following Cortés (1999) is also presented. Abbrevations of prey categories: POL= Polychaeta; BIV= Bivalvia; ECH = Echinodermata; CEP = Cephalopoda: ISO = Isopoda; AMP = Amphipoda; MYS = Mysidacea; STO = Stomatopoda; NAT= Natantia; REP = Reptantia; PIS = Pisces. PM is the point method (Hyslop, 1980). Numbers in the reference (Ref.) list represent the following studies: 1 = Ellis et al. (1996); 2 = Gibson and Ezzi (1987); 3 = Ajayi (1982); 4 = Quiniou and Andriamirado (1979); 5 = Olaso and Rodríguez-Marín (1995); 6 = Cunha et al. (1986); 7 = present study; 8 = Ebert et al. (1991); 9 = Smale and Cowley (1992). TLv = trophic level.

Location		Size class (cm TL)	Index	Prey categories POL	BIV	ECH	CEP	ISO	AMP	MYS	STO	NAT	REP	PIS	Ref.	TLv
NE Atlantic		<40	PM	5.20	0.50	0.00	4.50	0.20	2.70	2.90	0.00	52.40	16.30	2.60	1	3.2
NE Atlantic		40–69	PM	4.70	3.50	0.00	1.60	0.70	3.70	0.80	0.00	17.00	60.90	5.70	1	3.5
NE Atlantic		>69	PM	3.00	2.90	0.30	0.60	0.00	0.00	0.00	0.00	7.10	73.60	11.30	1	3.6
Scotland	West Coast	<40	%IRI	2.40	0.00	3.60	0.00	0.00	32.90	10.50	0.00	27.90	16.10	0.00	2	3.2
Wales	South Coast	<25	%W	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	63.65	16.15	2.88	3	3.1
Wales	South Coast	25–34.9	%W	3.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	42.12	38.30	8.68	3	3.4
Wales	South Coast	35–44.9	%W	3.80	0.00	0.00	0.00	0.00	0.00	0.00	0.00	22.23	64.21	3.98	3	3.4
Wales	South Coast	45–64.9	%W	3.90	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.68	72.88	13.76	3	3.4
Wales	South Coast	65–84.9	%W	1.40	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.22	85.41	1.33	3	3.3
Wales	South Coast	>85	%W	1.73	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	67.12	25.08	3	3.5
France	NW Coast	10–30	%CN	0.00	2.34	0.00	0.00	0.00	12.50	22.46	0.00	55.97	2.42	0.00	4	3.3
France	NW Coast	31–50	%CN	0.00	3.75	0.00	0.00	0.00	19.35	0.81	0.00	27.02	42.94	0.00	4	3.3
France	NW Coast	51–70	%CN	0.00	16.53	0.00	0.00	0.00	2.02	0.00	0.00	9.27	70.56	0.00	4	3.4
France	NW Coast	71–95	%CN	0.00	21.45	0.00	0.00	0.00	0.00	0.00	0.00	0.32	75.16	0.00	4	3.4
Spain	N Coast	17–49	%V	2.26	0.00	0.00	0.00	0.00	0.00	2.26	0.00	33.87	58.39	0.00	5	3.4
Spain	N Coast	50–89	%V	0.00	0.00	0.00	4.70	0.00	0.00	0.00	0.00	4.41	84.64	6.52	5	3.6
Portugal	West Coast	<50 [1]	%Q	0.01	0.00	0.00	0.01	0.17	0.09	1.83	0.00	86.38	3.36	7.63	6	3.6
Portugal	West Coast	>50 [1]	%Q	0.03	0.00	0.00	0.52	0.00	0.00	0.00	0.00	24.66	73.23	1.52	6	3.5
Portugal	Azores	49–60	%IRI	0.21	0.00	0.00	1.44	0.00	0.00	0.18	0.00	1.24	6.09	90.84	7	4.2
Portugal	Azores	61–70	%IRI	0.43	0.00	0.00	0.00	0.24	0.00	0.62	0.00	1.43	15.73	81.54	7	4.1
Portugal	Azores	71–80	%IRI	0.73	0.00	0.00	0.38	0.30	0.00	1.02	0.00	0.24	36.23	61.11	7	4.0
Portugal	Azores	81–93	%IRI	6.44	0.00	0.00	0.63	0.35	0.00	0.00	0.00	0.00	1.64	90.95	7	4.2
South Africa	West coast	30–86	%IRI	0.00	0.00	0.00	0.00	0.00	0.00	1.13	20.75	41.01	3.01	34.10	8	3.7
South Africa	Cape South	<57	%IRI	0.00	0.00	0.00	0.08	0.00	0.00	20.86	12.39	10.59	47.84	8.23	9	3.5
South Africa	Cape South	>57	%IRI	0.21	0.00	0.00	0.31	0.00	3.21	1.33	5.71	10.72	72.80	5.71	9	3.5

[1] TL was estimated from disk width (DW) and by using the length-length relationship for the Azores; DW=0.1087+0.7002TL (unpubl. data).

Table 5

Values for percentage by number (%N), weight (%W), occurrence (%O), and index of relative importance (IRI and %IRI) for prey items observed in stomachs of tope shark (n= 184), *Galeorhinus galeus*, caught off the Azores during the spring of 1996 and 1997. Number (No.) and percent occurrence (%O) of fish lenses, fish remains, and otoliths found in stomach, are also presented. Total values are given in bold font.

Prey items	%N	%W	%O[1]	IRI	%IRI
Total Crustacea	**1.0**	**1.0**	**3.3**	**6.5**	**0.03**
Isopoda	3.6	1.1	2.7	12.8	0.3
Crustacea unidentified	1.2	0.0	1.1	1.3	0.0
Total Cephalopoda	**0.8**	**0.2**	**3.3**	**3.2**	**0.02**
Octopodidae	0.6	0.3	0.5	0.5	0.0
Cephalopoda unidentified	3.0	0.0	2.7	8.1	0.2
Total Pisces[2]	**98.2**	**98.8**	**100.0**	**19,700.4**	**99.95**
Sternoptychidae unidentified	0.6	0.2	0.5	0.4	0.0
Synodontidae *Synodus* sp.	0.6	11.5	0.5	6.5	0.2
Trichiuridae *Lepidopus caudatus*	0.6	0.0	0.5	0.4	0.0
Macrouridae unidentified	0.6	0.0	0.5	0.3	0.0
Phycidae *Phycis phycis*	1.2	0.0	1.1	1.4	0.0
Caproidae *Capros aper*	65.0	25.6	38.6	3494.6	93.2
Macroramphosidae *Macroramphosus scolopax*	11.2	2.7	8.2	113.5	3.0
Carangidae *Trachurus picturatus*	2.4	7.6	2.2	21.6	0.6
Total Sparidae	**6.5**	**32.0**	**4.4**	**169.7**	**4.5**
Pagellus acarne	2.4	5.8	1.6	13.3	0.4
Pagellus bogaraveo	2.4	14.4	1.6	27.3	0.7
Pagellus spp.	1.2	11.7	1.1	14.1	0.4
Pagrus pagrus	0.6	0.1	0.5	0.4	0.0
Sparidae unidentified	0.6	0.5	0.5	0.6	0.0
Scombridae *Scomber japonicus*	2.4	18.4	1.6	33.8	0.9
	No. of	%O			
Pairs of fish lenses	493	103			
Otoliths unidentified	118	75			
Fish remains	3	2			

[1] Because the %O is a nonadditive index (Cortés, 1997), when grouping fish items into higher taxonomic categories (i.e. Pisces, etc) the %O value was recalculated considering the number of stomachs with the respective higher taxonomic category. This recalculation will affect both the IRI and %IRI values.

[2] Including unidentified fish, pairs of lenses, otoliths, and fish remains.

medium-size class of South Wales (35–45 cm TL). Cluster group III grouped small rays from several geographic regions, from South Africa (which also includes some large individuals) to NE Atlantic. Estimates of trophic levels were 3.46 (±0.84 SD) for the rays of the cluster group II (i.e. medium and large), and 3.35 (±0.21 SD) for the rays composing cluster group III (i.e. small). The estimated trophic levels for the three cluster groups were significantly different (P<0.001).

Tope shark

The diet of tope shark consisted almost exclusively of fish (%IRI=99.95), along with a few crustaceans (%IRI=0.03) and cephalopods (%IRI=0.02) (Fig. 3B). Recognizable prey from 14 different taxa were identified (Table 5). The boarfish (*C. aper*) was the most important prey item (%IRI=93.2), accounting for 65.0% of food by number (%N), 25.6% by weight (%W), and occurred in 38.6% of stomachs that contained food (%O). The second most important prey item was the snipefish (*M. scolopax* [%IRI=3.0]), which represented 11.2% of food by number and 2.7% by weight. Some commercially important fish species were also found in the stomachs of tope shark; sparids (%IRI=4.5, which included *Pagellus acarne*, *P. bogaraveo,* and *Pagrus pagrus*), the chub mackerel (*S. japonicus* [%IRI=0.9]), and the blue jack mackerel (*T. picturatus* [%IRI=0.6]). These species were more important by weight than by number or occurrence. The stomachs of tope sharks also contained 493 pairs of eye lens and fish that were heavily digested, as well as unidentifiable otoliths.

Discussion

In general, the percentage of empty stomachs for thornback rays and tope sharks was relatively high compared to the percentage from literature reports. The percentage of empty stomachs for tope shark was 47.7%—much higher than the 4.3% observed by Ellis et al. (1996). The percentage of empty thornback ray stomachs was high (37.1%) when compared to values reported for the North Sea (9%, Daan et al.[1]; and 3.7%, Ellis et al., 1996), Carmarthen Bay, South Wales (4.5%, Ajayi, 1982), west coast of Southern Africa (4.5%, Ebert et al., 1991; and 2.6%, Smale and Cowley, 1992) and the Portuguese mainland coast (2.5%, Cunha et al., 1986). We attribute the high percentage of empty stomachs found in our study to the use of longlines to catch the fish in the Azores (trawls were used in the other studies). Longlining is a passive fishing method, which suggests that fish that feed to satiation have a reduced response to bait odor (Løkkeborg et al., 1995), meaning that fish with full stomachs tend not to eat the bait and be caught. Thus, only those fish with empty stomachs or partial stomach fullness were caught.

Thornback rays captured by longline in the Azores during the spring of 1996 and 1997 fed upon a wide variety of organisms. Fishes (81.6 %IRI) and reptants (17.4 %IRI) dominated the diet, which also consisted of polychaetes, mysids, natants, isopods, and cephalopods. In general, thornback rays in the Azores preyed more heavily upon fish in comparison with the predation patterns described in other studies. Ajayi et al. (1982) reported a predominance of crustaceans (83%W) for all size classes and a low importance of fish (11.6%W) in the diet of thornback rays in Carmarthen Bay, Bristol Channel. They also reported amphipods, polychaetes, and some natants as food items. Using the points method of Hyslop (1980), Ellis et al. (1996) reported that thornback rays from the North Sea fed primarily on crustaceans (78.9%) compared to mollusks (10.2%) and fish (7.3%). Several others have also reported a dominance of crustaceans and low importance of fish in the diet of thornback ray (Fitzmaurice, 1974; Marques and Ré, 1978; Quiniou and Andriamirado, 1979; Cunha et al., 1986; Gibson and Ezzi, 1987; Smale and Cowley, 1992; Olaso and Rodríguez-Marín, 1995; Daan et al.[1]; Ebeling[2]). Polychaetes (Holden and Tucker, 1974; Marques and Ré, 1978), bivalves (Quiniou and Andriamirado, 1979), holothurians (Ebeling[2]), and cephalopods (Holden and Tucker, 1974; Marques and Ré, 1978; Smale and Cowley, 1992; Olaso and Rodríguez-Marín, 1995) that were considered important prey items in the other studies mentioned were not recorded or were insignificant in our samples.

Differences in diet composition of several predators may reflect the geographic peculiarities in fauna composition (e.g. Smale and Cowley 1992), but when comparing diets based on higher taxonomic levels (such as fish, reptants, and natants categories), such geographic differences should not be so obvious. Our geographic analysis (see Fig. 4) distinguished three major groups: I) the Azorean individuals; II) other large individuals; and III) other small individuals. Further, the estimated mean trophic levels for these three major groups were significantly different: 4.14 (±0.09 SD) for the Azores; 3.46 (±0.84 SD) for other large rays; and 3.35 (±0.21 SD) for smaller rays. The higher trophic level for the Azores is a result of a higher degree of piscivory in this region and an increased consumption of decapods and fish by larger rays, compared with small rays. Notwithstanding the difference in sampling methods (longline *vs.* trawl caught), it appears that the Azores can be considered a separate group. In other studies, predator size played the major role in controlling feeding patterns.

The diet of the thornback ray in the Azores consists of a greater proportion of fish than in any other area and may reveal differences in the function of different environments, because seamounts and oceanic islands are the major topographic feature of the Azores region and the other studies were conducted on continental shelves. The general function of oceanic seamount environments is still not completely understood but they are characterized by substantial enhancement of primary production due to topographic effects on local hydrographic conditions (Genin and Boehlert, 1985). However, evidence for enhanced primary production leading to concentrations of fish over seamounts is sparse (Rogers, 1994). Additionally, the availability and relative abundance of the two most important fish prey items found in our work (the benthopelagic species *C. aper* and *M. scolopax*) vary considerably both seasonally (Granadeiro et al., 1998) and annually. Therefore, the high degree of piscivory in the Azores may result from environmental features and exceptional fish prey availability during the sampled years or seasons.

Thornback rays also fed on pelagic fish, as indicated by the presence of chub mackerel and jack mackerel in stomachs—a finding that confirms previous suggestions (see Daan et al.[1]; Ebeling[2]) that thornback rays are active predators and able to feed semipelagically. The most important reptants in the diet, *Liocarcinus* spp., were also reported as the main prey item for thornback rays by Ellis et al. (1996). The level of importance of isopods and amphipods, mysids, cephalopods, and polychaetes in the diet of thornback rays in the Azores was similar to values reported by other authors (Ellis et al., 1996; Daan et al.[1]; Ebeling[2]).

Differences in the dentition of females and males were reported by Quiniou and Andriamirado (1979) but we and Smale and Cowley (1992) observed no differences in the major prey consumed between sexes. Therefore, sexual dimorphism in dentition does not appear to be manifested in dietary preferences between sexes, as was initially expected.

Several studies have demonstrated differences in predation patterns for rays of different size classes—primarily a decrease in importance of crustaceans and an increase of fish with size (e.g. Smale and Cowley, 1992; Ellis et al., 1996; Daan et al.[1]; Ebeling[2]). Some authors attribute these differences to the ability of large predators to prey upon larger prey (Smale and Cowley, 1992); others suggest the difference is due to a pronounced shift from a benthic to a benthopelagic feeding behavior (Skjæraasen and Bergstad, 2000; Ebeling[2]) or the reverse (Quiniou and Andriamirado, 1979). We found no significant size-related differences in diet. Quiniou and Andriamirado (1979) reported shifts in diet at a size of 30 to 40 cm TL but we could not verify these conclusions because our sample included only rays larger than 49 cm.

[2] Ebeling, E. 1988. A brief survey of the feeding preferences of *Raja clavata* in Red Wharf Bay in the Irish Sea. ICES C.M. 1988/G:58, 5 p.

There have been few data indicating dietary differences between thornback rays collected at different depths. Smale and Cowley (1992) reported that bottom type used by rays varies with depth and predicted that the prey spectrum would thus also vary, but no depth-related analyses of diet composition were preformed in their study. Despite similarities in size (i.e. no differences in the mean size by depth strata; Menezes[3]), we found that rays inhabiting different depths prey upon different resources. The decreasing consumption of *Liocarcinus* spp., "other reptants," and *T. picturatus*, and the increasing consumption of penaeids, seabreams, and myctophids with depth of capture of rays, appears to be in general agreement with the relative abundance of prey with depth. Therefore, such depth-related variations in diet may simply reflect differences in prey availability. It is not clear, however, why *Scyllarus arctus*, a species with a known depth distribution of 4 to 50 meters (e.g. Alvarez, 1968; Castellón and Abelló, 1983), appears in stomachs of thornback rays caught between 201 and 350 meters (see Table 2). There is no evidence of vertical migrations of thornback ray associated with feeding activity; therefore this prey was likely eaten at deep water. Thus, the depth distribution range of *S. arctus* in the Azores may be significantly greater than what was previously known. The only study that could corroborate this hypothesis (Fransen, 1991) reported one *S. arctus* caught between 420 and 700 meters depth in the Canary Islands.

Our comparisons between areas (coastal and offshore banks) were unable to clearly separate the influence of depth because nearly all coastal samples were obtained from shallow waters, and offshore bank samples were collected from much deeper waters. Hence, we were incapable of determining whether the high level of polychaetes, penaeids, cephalopods, mysids, seabreams, and myctophids in the diet of rays caught at offshore banks reflects the availability of these prey in these areas, or in deeper waters, or both. Nevertheless, our findings indicate that coastal rays have different diets from rays taken in offshore banks.

Tope sharks preyed almost exclusively upon teleosts, along with very few crustaceans and cephalopods. Previous observations on the feeding behavior of this species suggested that fish and cephalopods are the main prey categories (Ellis et al., 1996; Olsen, 1954). The diet of tope shark in the Azores consists of fewer species (mainly small shoaling fish, mainly boarfish and snipefish) compared to the diet of tope shark documented in previous studies. These two fish were also important diet components of other piscivorous species around the Azores between 1993 and 1997, namely cephalopods (Pierce et al., 1994), elasmobranchs (Clarke et al., 1996), fishes (Clarke et al., 1995; Morato et al., 1999, 2000, 2001) and seabirds (Granadeiro et al., 1998; Ramos et al., 1998a, 1998b). The role of these two small shoaling fish in the marine food web of the Azores is not yet fully understood. The fact that these prey may exhibit strong variation in abundance, raises the question of how well predators can adapt to extensive changes in their availability.

Stomach-content data offer a good snapshot of the feeding habits of fish species, but diets may vary substantially with food availability, depth, location, and season. Caution is, therefore, required when drawing conclusions about the trophic ecology of marine predators. The trophic role of thornback rays and tope sharks in the Azores could be further clarified by year round sampling and by an analysis of stable isotopes (Gu et al., 1996; Jennings et al., 1997; Pinnegar and Polunin, 2000), which could provide a less biased average estimate of predator trophic level.

[3] Menezes, G. 1995–97. Unpubl. data. Department of Oceanography and Fisheries, University of the Azores. Cais de Santa Cruz, PT9901-862 Horta, Portugal.

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