

Diets and bathymetric distributions of two bathyal sharks of the Catalan deep sea (western Mediterranean)

M. Carrassón¹, C. Stefanescu², J. E. Cartes²

¹ Unidad de Zoología, Departamento de Biología Animal, Universidad Autónoma de Barcelona, Bellaterra, E-08193 Barcelona, Spain

² Instituto de Ciencias del Mar-CSIC, Paseo Nacional s/n, E-08039 Barcelona, Spain

ABSTRACT: Bathymetric distribution of *Centroscymnus coelolepis* has been studied. This species was restricted to the lower slope (1419 to 2251 m), where it was the only abundant shark. *Galeus melastomus* was abundant below 1000 m but became rare between 1400 and 1600 m, so that there is almost no bathymetric overlap with *C. coelolepis*. Greatest abundance of *G. melastomus* in the Catalan Sea was found in the upper slope. Diets of both species showed a very low overlap which is mainly attributed to the dietary specialization of *C. coelolepis*. Its diet is almost exclusively based on cephalopods. The diet of *G. melastomus* has been analyzed at depths below 1000 m. Its diet is more diverse than that of *C. coelolepis* and cephalopods are not preferential prey. The upper and middle slope specimens of *G. melastomus* have a different diet; this difference may be the consequence of a change in available resources. Finally the trophic position of *Etmopterus spinax*, the third most abundant shark below 1000 m, seems to be more similar to that of *C. coelolepis*. These results suggest that a possible competition is more likely between *C. coelolepis* and *E. spinax* than between *C. coelolepis* and *G. melastomus*. This could explain the bathymetric displacement of *C. coelolepis* in the western Mediterranean as a result of an interaction between species of higher trophic levels.

INTRODUCTION

Information on the distribution and biology of bathyal sharks in the deep Mediterranean Sea (below a depth of 1000 m) is limited and fragmentary.

The bathymetric distribution of *Centroscymnus coelolepis* Bocage & Capello, 1864, the only abundant species at great depths in the Mediterranean Sea, has been partially determined. Subsequent to the synthesis made by Grey (1956), the published data were incomplete (Tortonese 1956, Torchio & Michelangeli 1971, Allué et al. 1985, Della Croce et al. 1988). The trophic habits of this species have been studied in some areas of the Atlantic and Pacific Oceans (Clarke & Merrett 1972, Marshall & Merrett 1977, Sedberry & Musick 1978, Mauchline & Gordon 1983, Yano & Tanaka 1988), but they are completely unknown in the Mediterranean.

There is plentiful information about *Galeus melastomus* Rafinesque, 1810, although it is usually limited to commercial grounds, between 200 and 700 m

(Capapé & Zaouali 1976, 1977, Relini Orsi & Wurtz 1977, MacPherson 1980, Mattson 1981, Mauchline & Gordon 1983, among others). Recently, Golani (1986/87) found this species below 1000 m, off the coast of Israel, and reported preliminary data on its diet at these depths.

Diet analysis allows the study of the trophic overlap among species within a community. This parameter is essential in determining the intensity of the inter-specific interactions (i.e. in marine fish communities: MacPherson 1979, 1981, Blaber & Bulman 1987, among others). For deep-sea sharks, the available data on trophic overlap are scarce. Mauchline & Gordon (1983) discussed some preliminary data at Rockall Trough (NW Ireland); this aspect was also studied by MacPherson (1980) in the upper slope of the Catalan Sea.

Bathymetric distribution, trophic habits and trophic interactions of *Centroscymnus coelolepis* and *Galeus melastomus* are presented in this work. These aspects are analyzed within groups of immature and adult

sizes. The diet of *G. melastomus* is described and compared in 2 bathymetric levels which correspond to the upper and middle slope respectively. Finally, we discuss the possible competitive interactions and the habitat segregation among the most common sharks which inhabit the slope below 1000 m.

MATERIALS AND METHODS

All material was collected from the continental slope of the Catalan Sea (western Mediterranean, 38° 45' to 42° 00' N, 01° 30' to 02° 50' E), during cruises carried out within the framework of the BATIMAR, ABISMAR and PONT'90 projects (1988 to 1990). The specimens were captured with a semi-balloon otter trawl (OTSB14) (cf. Merrett & Marshall 1981) and with longlines. Specimens of *Galeus melastomus* from the upper slope were also obtained from commercial trawls.

To define the bathymetric distribution below a depth of 1000 m, we used records of 76 specimens of *Galeus melastomus* and 62 of *Centroscyrnus coelolepis*, captured exclusively by the OTSB14. We divided the slope sampled (984 to 2251 m) into 6 equivalent bathymetric zones of 200 m each, and calculated the abundance of the species in each zone. Prior to the calculations, data were standardized to number per hour of trawling. In each zone, the number of individuals per hour was determined as the arithmetic mean of the total number of samples taken within these intervals.

A total of 86 specimens of *Centroscyrnus coelolepis* and 99 of *Galeus melastomus* were examined to determine their diet. Moreover, to compare their trophic habits, a few specimens of *Etmopterus spinax* L., 1759 collected with the OTSB14 below 1000 m were analyzed. These data were not included in the results because of the small number of individuals studied. Immediately after capture, specimens were fixed in 10 % formalin. Once in the laboratory, they were measured and dissected for analysis of stomach content.

The food items were identified to the lowest taxonomic level possible. We registered their number and weight to the nearest 0.1 mg, after drying them with blotting-paper to remove surface moisture. In the case of the Foraminifera, we always assigned an abundance of 1 because they were passively ingested (Lagardère 1977).

The quantitative importance of every prey group in the diets of both species was determined by the Index of Relative Importance (Pinkas et al. 1971), which was defined as:

$$IRI = F(N + V)$$

where F = frequency of occurrence of the food item; N = numerical percentage of a food item in the

stomachs, and V = percentage by volume of the food item in the stomachs (Hureau 1970). In our study we used weight (W) instead of volume (V). This index has been expressed as $\%IRI = (IRI / \sum IRI) \times 100$. Prey were sorted in decreasing order according to their $\%IRI$ contribution, and then cumulative $\%IRI$ was calculated. Prey were classified into the 3 following categories according to their contribution to the cumulative $\%IRI$ (Rossetti & Nouaze 1987): preferential prey (those whose cumulative $\%IRI$ attains at least 50 % of the total $\%IRI$); secondary prey (those whose cumulative $\%IRI$, when added to that of preferential prey, attains at least 75 % of the total $\%IRI$); and accidental prey (the remaining prey).

Diet was studied according to the different size-classes in both species. We considered 2 size-groups which generally corresponded with the immature specimens (total length <40 cm) and mature specimens (total length \geq 40 cm). The maturity size of *Galeus melastomus* was previously determined in the study area by MacPherson (1980). Maturity length of *Centroscyrnus coelolepis* was determined from personal observations.

The diet of *Galeus melastomus* was determined for 2 different bathymetric strata (371 to 667 m and 984 to 1584 m), which approximately correspond to the upper and middle slope. All of *Centroscyrnus coelolepis* specimens were captured in the lower slope (1729 to 2251 m).

We determined the cumulative trophic diversity curves in the same way as Mauchline & Gordon (1985). The Shannon-Wiener index (Shannon & Weaver 1949) was calculated on the abundance values of prey for each specimen. The asymptotic stabilization of the curves indicates the minimum number of stomachs that have to be analyzed in order to get reliable enough results.

Degree of overlap in the diet of both species, by different sizes and bathymetric levels, was determined using the quantitative Schoener index (Schoener 1974) and the semi-quantitative Spearman correlation coefficient (Sokal & Rohlf 1969). Trophic diversity (H') was calculated using the $\%IRI$ values and the Shannon-Wiener index.

RESULTS

Bathymetric distributions

Centroscyrnus coelolepis

The bathymetric preferences of *Centroscyrnus coelolepis* in the Catalan Sea (which has a maximum depth of about 2400 m) are represented in Fig. 1 This

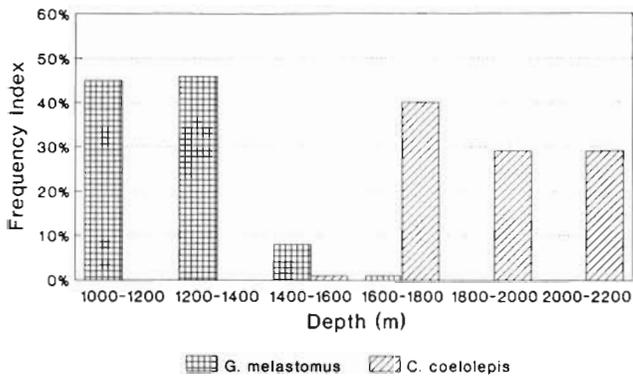


Fig. 1 *Galeus melastomus*, *Centroscymnus coelolepis*. Bathymetric distribution of 2 bathyal sharks in the Catalan Sea below a depth of 1000 m

species is found almost exclusively on the lower slope, where it is the only common shark; the upper limit is about 1419 m, although it is a very rare species at depths less than 1600 m. The complete absence of this shark in the upper and middle slope is corroborated by the absence of published records in an area where intensive sampling of the demersal fauna has been carried out.

Fig. 2 represents the bathymetric distribution of all specimens by size and sex. There is a possible trend in sexual and ontogenetic segregation by depth although

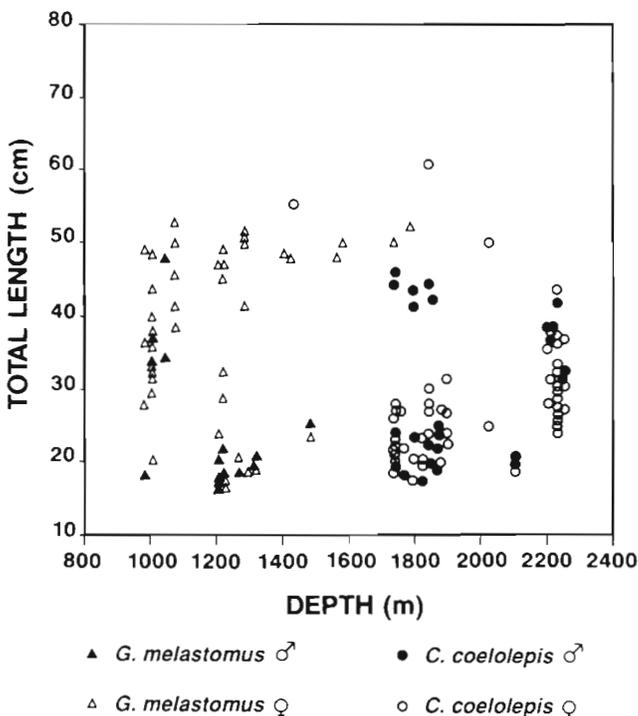


Fig. 2 *Galeus melastomus*, *Centroscymnus coelolepis*. Bathymetric distribution by sizes and sex of 2 bathyal sharks in the Catalan Sea below a depth of 1000 m

more data would be required to confirm this. Adult males and females (length ≥ 40 cm) were found between 1700 and 1900 m, as were immature males and females (20 to 30 cm). The largest specimens of both sexes were not present at the greatest depths. Below a depth of 2000 m sharks of intermediate size (30 to 40 cm) prevailed.

Galeus melastomus

In the western Mediterranean, *Galeus melastomus* is the most abundant demersal shark on the upper and middle slope (Relini Orsi & Wurtz 1977, Allué 1985, Bauchot 1987a).

In our study, we found that *Galeus melastomus* was abundant from 1000 m to as deep as 1400 m. Below that depth, numbers declined very sharply and it became rare (Fig. 1).

Bathymetric distribution of *Galeus melastomus* by size and sex is shown in Fig. 2. At the limit of the bathymetric range adult males disappear and only immature males of 10 to 20 cm total length are found. On the other hand, immature and adult females of about 10 to 61 cm are present at the greatest depths.

Diet

Centroscymnus coelolepis

Table 1 shows the results of stomach content analysis for 86 specimens. The high percentage of empty stomachs (41.2 %) is an obstacle to conclusions in the case of mature individuals (Fig. 3). In general the diet consisted almost exclusively of cephalopods, decapods and fishes. This low diversity can be seen in Table 2c.

The relative importance of the different prey groups is shown in Fig. 4. It emphasizes the dominant role of the cephalopods, in which the combination of frequency and great abundance together with their high weight results in a %IRI of 87.2. Decapods and fishes can be considered as casual prey groups. The contribution of the remaining prey was minimal (%IRI ≤ 0.3).

Important ontogenetic changes in the diet are evident in Table 1. The low value of overlap between both size-groups (27.6) corroborates this (Table 2b).

In both size-groups, cephalopods were always the preferred prey. Natantia decapods made an important contribution to the diet of the immatures. There was an obvious preference for the caridean *Acantheephyra eximia* (%IRI = 12.4), which is by far the most abundant decapod in the Mediterranean deep sea (Cartes 1991). There was a total absence of decapods in the adult diet.

Table 1 *Centroscymnus coelolepis*. Qualitative and quantitative composition of diet by size-classes. *F*: frequency; *N*: percentage by number; *W*: percentage by weight

	1729–2251 m							
	19–39 cm				40–75 cm			
	<i>F</i>	<i>N</i>	<i>W</i>	%IRI	<i>F</i>	<i>N</i>	<i>W</i>	%IRI
Foraminifera	–	–	–	–	10.0	8.3	0.6	0.8
Planktonic Foraminifera	–	–	–	–	10.0	8.3	0.6	2.8
Decapoda Natantia	38.6	31.6	4.6	14.9	–	–	–	–
<i>Acantheephyra eximia</i>	25.0	19.3	2.8	12.4	–	–	–	–
<i>Acantheephyra pelagica</i>	9.1	7.0	1.8	1.8	–	–	–	–
Decapoda unid.	6.8	5.3	•	0.8	–	–	–	–
Cephalopoda	65.9	50.9	62.4	79.6	70.0	58.3	87.7	92.4
<i>Heteroteuthis dispar</i>	2.3	1.8	0.7	0.1	–	–	–	–
<i>Histiototeuthis</i> sp.	2.3	1.8	0.2	0.1	–	–	–	–
<i>Todarodes sagittatus</i>	2.3	1.8	0.8	0.1	20.0	16.7	40.1	34.8
<i>Ommastrephes bartrami</i>	–	–	–	–	10.0	8.3	29.4	11.6
Ommastrephidae unid.	2.3	1.8	41.4	2.2	–	–	–	–
Theuthoidea unid.	2.3	1.8	•	0.1	10.0	8.3	16.6	7.6
Cephalopoda unid.	54.5	42.1	19.3	75.3	30.0	25.0	1.6	23.0
Pisces Osteichthyes	13.6	12.3	20.0	4.7	20.0	25.0	5.7	5.5
<i>Chauliodus sloani</i>	–	–	–	–	10.0	8.3	3.4	3.7
<i>Bathypterois mediterraneus</i>	2.3	1.8	16.3	0.9	–	–	–	–
Osteichthyes unid.	13.6	10.5	3.7	4.4	20.0	16.7	2.3	11.9
Cetacean blubber	–	–	–	–	10.0	8.3	6.8	4.6
Plastic	2.3	1.8	1.1	0.1	–	–	–	–
Unidentified tissues	4.5	3.5	11.7	1.6	–	–	–	–
No. fish examined		69				17		
% Empty stomachs		36.2				41.2		
No. prey items (average)		58 (1.3)				21 (2.1)		
Total weight (average)		110.2 (2.5)				212.3 (21.2)		

Galeus melastomus

Table 3 shows the results of the stomach analysis of 99 individuals. The percentage of empty stomachs was very low (10.2 % in the middle slope and null in the upper slope). In all size-groups we studied, diets were

determined with sufficient accuracy (Fig. 3). Three prey groups (Natantia decapods, fishes and cephalopods) mainly dominated the diet on the middle slope (Fig. 4C). On the upper slope, euphausiids and Macrura decapods were also seen. Differences were also noted between the size-classes in each bathymetric zone.

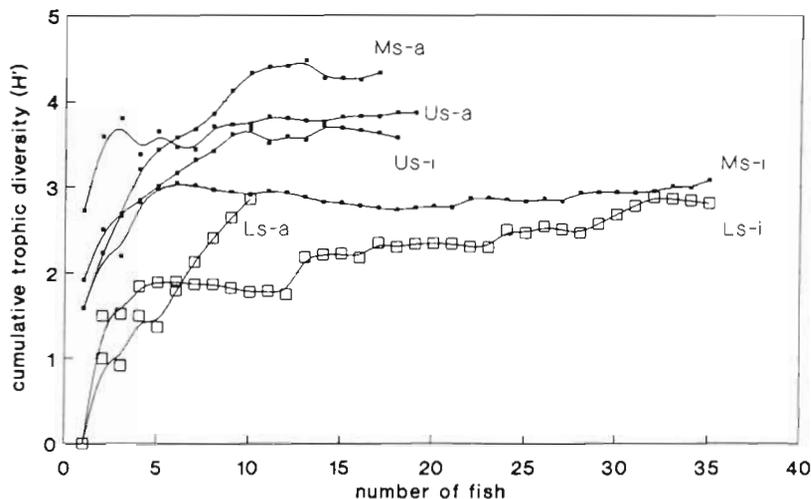


Fig. 3. *Galeus melastomus*, *Centroscymnus coelolepis*. Cumulative trophic diversity curves for different size and bathymetric groups for (•) *G. melastomus* and (□) *C. coelolepis*. Us: upper slope; Ms: middle slope; Ls: lower slope; a: adults; i: immatures

Table 2. *Centroscymnus coelolepis*, *Galeus melastomus*. (a) Spearman correlation coefficient between the different groups established (*significant at $p \leq 0.05$). (b) Overlap Schoener index. (c) Trophic diversity (H'). All calculations were made using %IRI. CCI: Immatures of *C. coelolepis*; CCA: adults of *C. coelolepis*; GMIU: immatures of *G. melastomus* (upper slope); GMAU: adults of *G. melastomus* (upper slope); GMIM: immatures of *G. melastomus* (middle slope); GMAM: adults of *G. melastomus* (middle slope)

a. Spearman correlation					
	CCA	GMIU	GMAU	GMIM	GMAM
CCI	0.08	-0.56*	-0.35	-0.05	0.30
CCA	-	-0.46*	-0.30	-0.16	0.02
GMIU	-	-	0.47	0.03	-0.12
GMAU	-	-	-	0.05	-0.10
GMIM	-	-	-	-	0.14

b. Overlap Schoener index					
	CCA	GMIU	GMAU	GMIM	GMAM
CCI	27.6	5.7	5.8	28.6	23.6
CCA	-	9.5	21.6	34.8	31.3
GMIU	-	-	23.6	20.5	16.1
GMAU	-	-	-	58.9	43.4
GMIM	-	-	-	-	51.4

c. Trophic diversity	
	H'
CCI	1.34
CCA	2.48
GMIU	1.78
GMAU	2.57
GMIM	2.48
GMAM	3.47

Upper slope. We identified 45 prey from a total of 60 stomachs. Natantia decapods and euphausiids were the preferred prey, fishes and Macrura decapods were secondary and cephalopods and the rest were accidental (Fig. 4B). At the species level *Calocaris macandreae* and *Pasiphaea multidentata* were the most exploited prey; both species are predominant elements of the benthic and benthopelagic fauna in the upper slope of the Catalan Sea (Abelló et al. 1988).

There were important differences between the diets of immature and adult specimens. These differences are shown by low values in the overlap (Table 2b). *Calocaris macandreae*, which is the preferential prey of the immatures (%IRI = 62.8), is only a casual prey in the adults (%IRI = 4.1). The importance of euphausiids is also considerably reduced. On the other hand fishes and *Pasiphaea multidentata* are more common in the adults. The cephalopods, which hardly appear in the diet of the immatures, are a secondary prey in the adults.

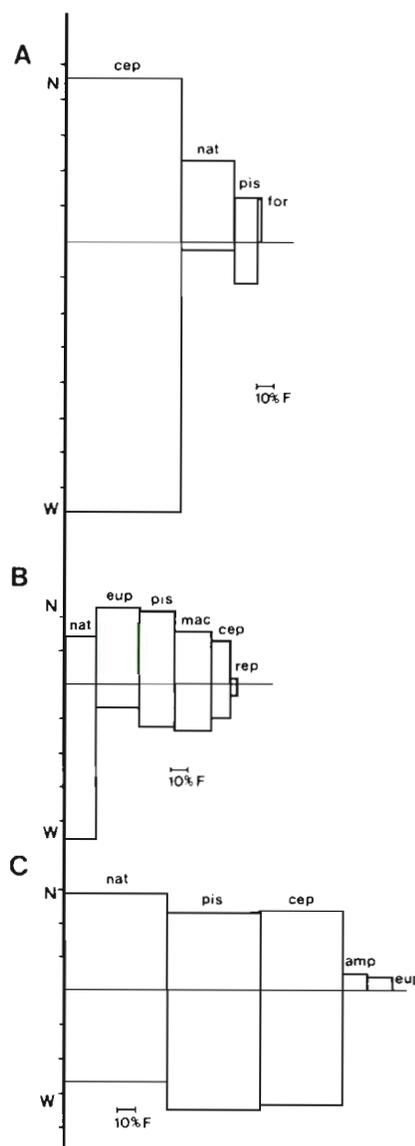


Fig. 4. Relative importance of prey groups to (A) *Centroscymnus coelolepis*, (B) *Galeus melastomus* (upper slope), and (C) *Galeus melastomus* (middle slope). Areas of rectangles are proportionate to the IRI. F: Frequency in % of a prey group (width of rectangle); N: percentage by number of a prey group; W: percentage by weight of a prey group; cep: Cephalopoda; nat: Decapoda Natantia; pis: Pisces; for: Foraminifera; amp: Amphipoda; eup: Euphausiacea; mac: Decapoda Macrura; rep: Decapoda Reptantia

Middle slope. 43 prey items were identified from a total of 39 stomachs examined. In the large size-class, diversity was low because Natantia decapods, fishes and cephalopods were preferred prey (%IRI = 97.7). *Pasiphaea multidentata* was the most abundant prey species; its weight was less than other prey items such as *Todarodes sagittatus* or *Mora moro*, but it was much more frequently captured.

Table 3 (continued)

	371–667 m								984–1584 m							
	15–30 cm				40–60 cm				10–39 cm				40–61 cm			
	F	N	W	%IRI	F	N	W	%IRI	F	N	W	%IRI	F	N	W	%IRI
Cephalopoda	7.3	2.1	0.4	0.2	73.7	21.1	17.0	19.5	38.9	22.2	5.2	12.2	52.9	25.0	36.6	30.6
<i>Heteroteuthis dispar</i>	-	-	-	-	5.3	0.5	5.6	0.4	-	-	-	-	-	-	-	-
<i>Chiroteuthis veranyi</i>	-	-	-	-	-	-	-	-	5.6	2.2	0.3	0.3	5.9	1.3	0.6	0.4
<i>Galiteuthis armata</i>	-	-	-	-	-	-	-	-	-	-	-	-	5.9	2.6	1.0	0.7
<i>Histhioteuthis</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	5.9	2.6	1.0	0.7
<i>Todarodes sagittatus</i>	-	-	-	-	10.5	1.1	7.5	1.0	-	-	-	-	5.9	1.3	29.5	5.9
Ommastrephidae unid.	-	-	-	-	-	-	-	-	-	-	-	-	11.8	3.9	1.4	2.0
Teuthoidea unid.	2.4	0.7	0.1	0.1	47.4	15.8	3.6	10.0	-	-	-	-	11.8	3.9	0.5	1.7
<i>Bathypolypus sponsalis</i>	-	-	-	-	-	-	-	-	-	-	-	-	5.9	1.3	0.4	0.3
Cephalopoda unid.	4.9	1.4	0.3	0.1	21.1	3.7	0.4	1.0	38.9	20.0	5.2	24.2	29.4	7.9	1.9	9.3
Brachiopoda	-	-	-	-	-	-	-	-	-	-	-	-	5.9	1.3	0.8	0.1
<i>Gryphus</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	5.9	1.3	0.8	0.4
Tunicata	-	-	-	-	15.8	1.6	1.7	0.4	-	-	-	-	5.9	1.3	0.2	0.1
Pyrosomida	-	-	-	-	-	-	-	-	-	-	-	-	5.9	1.3	0.2	0.3
Salpidae	-	-	-	-	15.8	1.6	1.7	0.6	-	-	-	-	-	-	-	-
Pisces Osteichthyes	41.5	13.5	2.8	7.4	89.5	27.4	13.2	25.2	55.6	24.4	58.3	52.3	52.9	22.4	32.7	27.5
<i>Chauliodus sloani</i>	-	-	-	-	-	-	-	-	-	-	-	-	11.8	2.6	3.2	2.2
<i>Stomias boa boa</i>	-	-	-	-	5.3	0.5	0.6	0.1	-	-	-	-	-	-	-	-
<i>Symbolophorus veranyi</i>	-	-	-	-	5.3	0.5	3.1	0.2	-	-	-	-	-	-	-	-
<i>Notolepis rissoi</i>	-	-	-	-	5.3	0.5	0.3	0.1	-	-	-	-	-	-	-	-
Mesopelagic fishes	-	-	-	-	-	-	-	-	-	-	-	-	5.9	1.3	3.0	0.8
<i>Coelorhynchus coelorhynchus</i>	-	-	-	-	5.3	0.5	0.3	0.1	-	-	-	-	-	-	-	-
<i>Antonogadus megalokynodon</i>	-	-	-	-	-	-	-	-	5.5	4.4	55.6	8.2	-	-	-	-
<i>Mora moro</i>	-	-	-	-	-	-	-	-	-	-	-	-	11.8	2.6	26.3	11.0
Osteichthyes unid.	41.5	13.5	2.8	9.3	89.5	25.3	8.8	33.3	50.0	20.0	2.7	28.0	29.4	15.8	0.3	15.3
Scales	4.9	1.4	0.1	0.1	-	-	-	-	-	-	-	-	-	-	-	-
Chicken leg	2.4	0.7	26.5	0.9	-	-	-	-	-	-	-	-	-	-	-	-
Coal	-	-	-	-	-	-	-	-	-	-	-	-	11.8	2.6	1.2	1.5
Plant debris	4.9	1.4	0.1	0.1	-	-	-	-	-	-	-	-	-	-	-	-
Remains of carton	-	-	-	-	-	-	-	-	-	-	-	-	5.9	1.3	1.4	0.5
Plastic	-	-	-	-	5.3	0.5	1.5	0.1	-	-	-	-	5.9	1.3	1.1	0.5
Synthetic fibres	-	-	-	-	5.3	0.5	0.1	0.1	-	-	-	-	-	-	-	-
Unidentified tissues	14.6	4.2	1.5	1.2	-	-	-	-	-	-	-	-	5.9	1.3	0.1	0.3
No. fish examined	41				19				21				18			
% Empty stomachs	0.0				0.0				14.3				5.6			
No. prey items (average)	141 (3.4)				190 (10.0)				45 (2.5)				76 (4.5)			
Total weight (average)	18.1 (0.4)				72.4 (3.8)				11.7 (0.7)				112.3 (6.6)			

Immature fish had a high diversity diet; there were some prey types such as hyperiid amphipods and mysids, which did not appear in the diet of the adults. In this group we could distinguish between the preferred prey (fishes, %IRI = 52.3), secondary prey (Natantia decapods, %IRI = 27.8) and the accidental prey (cephalopods, amphipods and euphausiids). In the diet of adults we can only distinguish between the preferred prey (Natantia decapods, cephalopods and fishes, with a Σ %IRI = 98.1) and the accidental prey. In both groups, *Pasiphaea multi-dentata* was the dominant prey item, but the relative importance of other prey changed from one case to the other. The overlap between both size groups showed an intermediate value and there is no correlation in the order of importance of prey items (Table 2a, b).

DISCUSSION AND CONCLUSIONS

In this work, the distribution of *Centroscyrnus coelolepis* has been accurately determined. This species was exclusive to the lower slope (1500 to 2250 m, *sensu* Haedrich & Merrett 1988), where it was the only abundant shark. In the rest of the western Mediterranean Sea it presumably shows the same preferences, although extending to abyssal grounds over 2500 m. Grey (1956) analyzed the data of 42 individuals (1350 to 2718 m) and concluded that its center of distribution was below 2000 m.

The records of this species from 200 to 400 m (cf. Bauchot 1987b, Fredj & Maurin 1987) are probably incorrect. They may be a consequence of the extrapolation of the bathymetric range shown in the Atlantic Ocean. In Atlantic waters *Centroscyrnus coelolepis* is

common from the middle slope to the upper rise (Haedrich & Merrett 1988) and off the Japanese coast it is captured between 100 to 1500 m (Yano & Tanaka 1984, 1988). Though in the western Mediterranean there is a substantial amount of information related to the ichthyofauna of the upper slope (e.g. see Allué (1985) and references cited therein), *C. coelolepis* has never been sited in this bathymetric zone.

This preference for deeper waters in the Mediterranean cannot be explained by hydrographic factors such as temperature or salinity, because they remain constant (about 13 °C and 38.4 ppm, respectively) from 200 m downwards (Salat & Cruzado 1981). A possible reason could be a displacement of the spatial niche of *Centroscymnus coelolepis* to avoid competing against other species with similar trophic habits such as *Galeus melastomus*.

Galeus melastomus was abundant below 1000 m but it suddenly became rare between 1400 to 1600 m, so that there is almost no bathymetric overlap with *Centroscymnus coelolepis*.

As with *Centroscymnus coelolepis*, there are some differences in the bathymetric distribution of *Galeus melastomus* in the Mediterranean Sea and in the Atlantic Ocean. According to the literature this species occurs between 55 and 1000 m (Compagno 1984), preferably at the 200 to 500 m level. In Mediterranean waters, Bauchot (1987a) and Fredj & Maurin (1987) quote the same range. Later, Golani (1986/87) reported on the exceptional capture of 2 individuals at 1440 m, off the coast of Israel.

The greatest abundance of this species in the Catalan Sea is found in the upper slope (Allué 1985), but we can state that it is frequent to 1400 m. Below that depth it quickly becomes rare. Its lower bathymetric limit is extensive as indicated by the capture of 2 females at 1739 and 1794 m respectively. In the rest of the western Mediterranean, *Galeus melastomus* is probably common to 1400 m, and not to 1000 m as was earlier believed.

The diets of *Centroscymnus coelolepis* and *Galeus melastomus* showed a very low overlap which was mainly due to the dietary specialization of *C. coelolepis*. This species almost exclusively consumes cephalopods, which accounts for the low value of its trophic diversity ($H' = 1.34$ to 2.48). The Mediterranean data suggest that *C. coelolepis* is not a species of strong scavenger habits, as has been indicated in the Atlantic populations (Clarke & Merrett 1972, Sedberry & Musick 1978, Mauchline & Gordon 1983). In the Catalan Sea it is an active predator on pelagic organisms (cephalopods and, in immatures, decapod crustaceans), which are known to have important migratory habits (Foxton 1972, Roper 1972). The presence of some remains that could be attributable to a scavenging

activity (e.g. cetacean blubber) was rare in both size-groups. Also, the maximum size which has been recorded in the Mediterranean (about 70 cm) is much less than that found in the Atlantic and Pacific Oceans (Compagno 1984). Moreover, because there are some ontogenetic variations in the diet, the results of this work are not comparable with those obtained elsewhere.

For the first time, the diet of *Galeus melastomus* has been analyzed at depths between 1000 and 1600 m. Its diet was more diverse ($H' = 1.78$ to 3.47) than *Centroscymnus coelolepis*. Cephalopods did not represent a large portion of the diet of *G. melastomus*. It consumed epibenthic and/or benthopelagic species throughout its whole bathymetric range. On the upper slope, the immatures captured mainly *Calocaris macandreae* and secondarily euphausiids while the adults preferred the benthopelagic species (Ommastrephidae, mesopelagic fishes and *Pasiphaea multidentata*). This tendency remained in the middle slope for all sizes.

The diets of upper- and middle-slope specimens were different and may be the consequence of a change in available resources. The small contribution of *Calocaris macandreae* to the diet of the middle slope immature individuals parallels the scarceness of this species below 1000 m (authors unpubl.). Something similar occurs with the mesopelagic prey: the euphausiid *Meganyctiphanes norvegica* (the species that reaches the greatest depths in the Mediterranean) is only abundant to 1000 m (Lagardère 1977). Moreover, it is accepted that 1000 m is the lower limit of the diel mesopelagic fish migration (Goodyear et al. 1972, Marshall 1979).

The scarcity of the preferred prey and the disappearance of the dominant resources resulted in a diversification in the diet of *Galeus melastomus* below 1000 m in all size-classes. In general, the ontogenetic differences could be attributed to the fact that most of the adults select large-size prey (cephalopods, *Mora moro*, *Geryon longipes*, *Pagurus alatus*), rather than amphipods, mysids and euphausiids. There was also evidence (pieces of prey too large in relation to the predator's size) which perhaps implies that adult *Galeus melastomus* hunt in groups, as Springer (1967) already suggested for the small sharks.

As in the case of *Centroscymnus coelolepis*, *Galeus melastomus* only occasionally acts as a scavenger species.

Diets of these 2 sharks have been shown to be different as revealed by both the Spearman correlation coefficient and the overlap Schoener index. These values must be carefully interpreted. The level of prey identification (especially cephalopods and fishes) is not the same in all cases. In large measure it depends on the

advanced level of digestion. Moreover, differences in resource availability in the bathymetric ranges occupied by both species undoubtedly increase such low values of overlap.

If *Centroscymnus coelolepis* and *Galeus melastomus* had the same bathymetric distribution, it is possible that their diets would be more similar. It is interesting to note that the adult specimens of *G. melastomus* that inhabit greater depths (exclusively females, see Fig. 2), and whose bathymetric range overlaps with that of *C. coelolepis*, show a tendency to take cephalopods as their preferred prey (observations of 2 individuals captured between 1500 and 1584 m, Table 3).

The trophic position of *Etmopterus spinax*, the third most abundant shark below 1000 m, seems to be more similar to that of *Centroscymnus coelolepis* than of *Galeus melastomus*. The diet of *E. spinax* has been carefully studied in Mediterranean waters, but only on the upper slope (Wurtz & Vacchi 1978, MacPherson 1980). This species shows a preference for cephalopods, especially the adult specimens which inhabit the greater depths (Wurtz & Vacchi 1978).

In this study it was not possible to obtain a sufficient number of samples of *Etmopterus spinax* because of its strong pelagic habits (Grey 1956, MacPherson 1980). However, personal observations verify the size increase with depth, and its specialization in the capture of cephalopods. Nineteen individuals which were collected between 984 and 1488 m were exclusively adults over 30 cm length. This bathymetric range coincides with the range of *Galeus melastomus* and does not overlap with the range of *Centroscymnus coelolepis*. Cephalopods were found in the stomachs of 4 individuals ($F = 100\%$). This suggests a trophic strategy which is parallel to that of *C. coelolepis*.

These results suggest that competition is more likely between *Centroscymnus coelolepis* and *Etmopterus spinax* than between *C. coelolepis* and *Galeus melastomus*. This could explain the bathymetric movement of *C. coelolepis* in the western Mediterranean as a result of the vertical ranges along the depth gradient being more compressed by interspecific competition between members of higher trophic levels (Rex 1977).

Finally it is interesting to note the variations in the percentage of empty stomachs, the average of prey per stomach and the diversity of the diet. The percentage of empty stomachs increases with depth, reaching a very high value in the case of *Centroscymnus coelolepis*. In the same way, the average number of prey per stomach decreases with depth (from 5.5 in *Galeus melastomus* of the upper slope to 1.3 in *C. coelolepis*). The trophic diversity is also less in this species.

In our opinion, these factors are indicative of the increasing resource scarceness along the depth gradient in the western Mediterranean (Thiel 1983, Pérès 1985,

personal observations on the decapod crustacean and fish biomass), which causes a change in the life strategy of both sharks. This tendency is also noticed in other aspects of their biology. *Centroscymnus coelolepis* shows a conservative life history, which is reflected in low fecundity and long periods of gestation of the embryos (Yano & Tanaka 1988). This species seems to be better adapted to a poorer environment (lower slope) than to the upper and middle slope, which is occupied by *Galeus melastomus*, an oviparous species with a higher fecundity (Capapé & Zaouali 1977).

Acknowledgements. For their help in identifying food items, we thank Dr M. Durfort (Departament Biologia Cel·lular, Universitat de Barcelona) and F. Giró (Departament Medi Ambient, Generalitat de Catalunya); Dr D. Lloris and P. Rubiés (Institut Ciències del Mar ICM-Barcelona) who identified mesopelagic fishes; F. Pagès (ICM), who identified Hydrozoa; and R. Villanueva and Dr P. Sánchez (ICM), who identified cephalopods. We also thank Drs J. Retana (CREAF, Facultat de Ciències, UAB), P. Abelló (ICM) and J. D. M. Gordon (Dunstaffnage Marine Laboratory, Oban) for their comments on the manuscript; Mrs. María Codorniu for the English translation, and J. M. Anguita for drawing the figures. Thanks are due to all the members of the research programs BATIMAR, ABISMAR and PONT'90 for their collaboration, specially to Drs J. Rucabado, D. Lloris, J. Matallanas and F. Sardà. BATIMAR project was financed by CSIC and CAICYT (reference PAC 86-008/ID 821). ABISMAR and PONT'90 projects were financed by CSIC. This study was also supported by 'Fundació Caixa de Barcelona: Ajuts a la Recerca, 1989, Ambit Pesca'

LITERATURE CITED

- Abelló, P., Valladares, F. J., Castellón, A. (1988). Analysis of the structure of decapod crustacean assemblages off the Catalan coast (North-West Mediterranean). *Mar. Biol.* 98: 39–49
- Allué, C. (1985). Composición y estructura de la comunidad de peces demersales frente a Barcelona (Años 1980-1981). *Thalassas* 3(1): 57–90
- Allué, R., Allué, C., Rucabado, J., Lloris, D. (1985). Ichthyofaune des eaux profondes dans la Mer Catalane. *Rapp. P.-v. Réun. Comm. int. Explor. scient. Mer Méditerran.* 29(8): 111–114
- Bauchot, M.-L. (1987a). Scyliorhinidae. In: Fischer, W., Bauchot, M.-L., Schneider, M. (eds.) Fiches FAO d'identification des espèces pour les besoins de la pêche (Révision 1). Méditerranée et Mer Noire. Zone de pêche 37. Vol. 2. FAO, Rome
- Bauchot, M.-L. (1987b). Squalidae. In: Fischer, W., Bauchot, M.-L., Schneider, M. (eds.) Fiches FAO d'identification des espèces pour les besoins de la pêche (Révision 1). Méditerranée et Mer Noire. Zone de pêche 37. Vol. 2. FAO, Rome
- Blaber, S. J., Bulman, C. M. (1987). Diets of fishes of the upper continental slope of eastern Tasmania: content, caloric values, dietary overlap and trophic relationships. *Mar. Biol.* 95: 345–357
- Capapé, C., Zaouali, J. (1976). Contribution à la biologie des Scyliorhinidae des côtes tunisiennes. V. *Galeus mela-*

- stomus* Rafinesque, 1810. Régime alimentaire. Archs Inst. Pasteur Tunis 53(3): 281–292
- Capapé, C., Zaouali, J. (1977). Contribution à la biologie des Scylliorhinidae des côtes tunisiennes. VI. *Galeus melastomus* Rafinesque, 1810. Répartition géographique et bathymétrique, sexualité, reproduction, fécondité. Cah. Biol. Mar. 18: 449–463
- Cartes, J. E. (1991). Análisis de las comunidades y estructura trófica de los crustáceos decápodos batiales del mar Catalán. Ph.D. thesis, Univ. Politécnica de Catalunya
- Clarke, M. R., Merrett, N. R. (1972). The significance of squid, whale and other remains from the stomachs of bottom living deep-sea fish. J. mar. biol. Ass. U.K. 52: 599–603
- Compagno, L. J. V. (1984). FAO species catalogue. Vol. 4. Sharks of the world. An annotated and illustrated catalogue of sharks species known to date. Part 1. Hexanchiformes to Lamniformes. FAO Fish. Synop. (125) Vol. 4, part 1
- Della Croce, N., Drago, N., Flocchini, G. (1988). Ricerche biologiche e geofisiche. Campagna oceanografica N/R 'Minerva' (14–31.8.1987). Università di Genova, Istituto di Scienze Ambientali Marine, Rapp. Tecnico 24
- Foxton, P. (1972). Observations on the vertical distribution of the genus *Acanthephyra* (Crustacea: Decapoda) in the eastern North Atlantic, with particular reference to species of the 'purpurea' group. Proc. R. Soc. Edinb. 73(30): 301–313
- Fredj, G., Maurin, C. (1987). Les poissons dans la banque des données MEDIFAUNE. Application à l'étude des caractéristiques de la faune ichtyologique méditerranéenne. Cybium 11(3): 219–299
- Golani, D. (1986/87). On deep-water sharks caught off the Mediterranean coast of Israel. Israel. J. Zool. 34(1-2): 23–31
- Goodyear, R. H., Zahuranec, B. J., Pugh, L. W., Gibbs, R. H. Jr (1972). Ecology and vertical distribution of Mediterranean midwater fishes. In: Mediterranean Biological Studies, Final Report, Part 3. Smithsonian Institution, Washington
- Grey, M. (1956). The distribution of fishes found below a depth of 2000 m. Fieldiana, Zool. 36(2): 75–183
- Haedrich, R. L., Merrett, N. R. (1988). Summary atlas of deep-living demersal fishes in the North Atlantic Basin. J. nat. Hist. 22: 1325–1362
- Hureau, J.-C. (1970). Biologie comparée de quelques poissons antarctiques (Nototheniidae). Bull. Inst. océanogr. Monaco 68(1391): 1–250
- Lagardère, J.-P. (1977). Recherches sur la distribution verticale et sur l'alimentation des crustacés décapodes benthiques de la pente continentale du golfe de Gascogne. Analyse des groupements carcinologiques. Bull. Cent. Étud. Rech. scient., Biarritz 11(4): 367–440
- MacPherson, E. (1979). Ecological overlap between Macro-urids in the western Mediterranean Sea. Mar. Biol. 53: 149–159
- MacPherson, E. (1980). Regimen alimentaire de *Galeus melastomus* Rafinesque, 1810, *Etmopterus spinax* (L., 1758) et *Scymnorhinus licha* (Bonnaterre, 1788) en Méditerranée occidentale. Vie Milieu 30: 139–148
- MacPherson, E. (1981). Resource partitioning in a Mediterranean demersal fish community. Mar. Ecol. Prog. Ser. 4: 183–193
- Marshall, N. B. (1979). Developments in deep-sea biology. Blandford Press Ltd, Poole, Dorset
- Marshall, N. B., Merrett, N. R. (1977). The existence of a benthopelagic fauna on the deep-sea. Deep Sea Res. 24 (Suppl.): 483–497
- Mattson, S. (1981). The food of *Galeus melastomus*, *Gadiculus argenteus thori*, *Trisopterus esmarkii*, *Rhinonemus cimbricus* and *Glyptocephalus cynoglossus* (Pisces) caught during the day with shrimp trawl in a west Norwegian fjord. Sarsia 66: 109–127
- Mauchline, J., Gordon, J. D. M. (1983). Diets of sharks and chimaeroids of the Rockall Trough, northeastern Atlantic Ocean. Mar. Biol. 75: 269–278
- Mauchline, J., Gordon, J. D. M. (1985). Trophic diversity in deep-sea fish. J. Fish Biol. 26: 527–535
- Merrett, N. R., Marshall, N. B. (1981). Observations on the ecology of deep-sea bottom living fishes collected off northwest Africa (08°–27° N). Prog. Oceanog. 9: 185–244
- Péres, J. M. (1985). History of the Mediterranean biota and the colonization of the depths. In: Margalef, R. (ed.) western Mediterranean. Pergamon Press, New York
- Pinkas, L., Oliphant, M. S., Iverson, I. L. K. (1971). Food habits of albacore, bluefin tuna and bonito in California waters. Calif. Fish Game Fish. Bull. 152: 1–105
- Relini Orsi, L., Wurtz, M. (1977). Patterns and overlap in the feeding of two selachians of bathyal fishing grounds in the Ligurian sea. Rapp. P.-v. Réunion. Comm. int. Explor. scient. Mer Méditerran. 24(5): 89–93
- Rex, M. A. (1977). Zonation in deep-sea gastropods: the importance of biological interactions to rates of zonation. In: Keegan, B. F., Ceidigh, P. O., Boaden, P. J. S. (eds.) Biology of benthic organisms. Pergamon Press, New York
- Roper, C. F. E. (1972). Ecology and vertical distribution of Mediterranean pelagic cephalopods. In: Mediterranean biological studies, Final Report, Part 5. Smithsonian Institution, Washington
- Rosecchi, E., Nouaze, Y. (1987). Comparaison de cinq indices alimentaires utilisés dans l'analyse des contenus stomacaux. Rev. Trav. Inst. Pêches. marit. 49(3-4): 111–123
- Salat, J., Cruzado, A. (1981). Masses d'eau dans la Méditerranée occidentale: Mer Catalane et eaux adjacentes. Rapp. P.-v. Réunion. Comm. int. Explor. scient. Mer Méditerran. 27(6): 201–209
- Schoener, T. W. (1974). Resource partitioning in ecological communities. Science 185: 27–39
- Sedberry, G. R., Musick, J. A. (1978). Feeding strategies of some demersal fishes of the continental slope and rise off the mid-Atlantic coast of the USA. Mar. Biol. 44: 357–375
- Shannon, C. E., Weaver, W. (1949). The mathematical theory of communication. University of Illinois Press, Urbana
- Sokal, R. R., Rohlf, F. J. (1969). Biometry: the principles and practice of statistics in biological research. W. H. Freeman and Co., San Francisco
- Springer, S. (1967). Social organization of sharks populations. In: Gilbert, R. F., Matheuson, R. F., Rall, D. P. (eds.) Sharks, skates and rays. John Hopkins Press, Stanford
- Thiel, H. (1983). Meiobenthos and nanobenthos of the deep sea. In: Rowe, G. T. (ed.) Deep-sea biology. The sea. Vol. 8. John Wiley & Sons, New York
- Torchio, M., Michelangeli, M. (1971). Prima segnalazione in acque italiane di uno squalidae del genere *Centroscymnus*. Natura, Milano 62/3: 241–245
- Tortonese, E. (1956). Leptocardia, Ciclostomata, Selachii. In: Fauna d'Italia. 2. Calderini, Bologna
- Wurtz, M., Vacchi, M. (1978). Ricerca di cicli nittimerali nell'alimentazione di Selaci batiali. Quad. Lab. Tecnol. Pesca 3 (Suppl.): 155–164
- Yano, K., Tanaka, S. (1984). Some biological aspects of the deep sea squaloid shark *Centroscymnus* from Suruga Bay, Japan. Bull. Jpn Soc. Fish. 50(2): 249–256
- Yano, K., Tanaka, S. (1988). Size at maturity, reproductive cycle, fecundity, and depth segregation of the deep sea squaloid sharks *Centroscymnus owstoni* and *C. coelolepis* in Suruga Bay, Japan. Nippon Suisan Gakkaishi 54(2): 167–174