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Trophic Relations of Lesser Spotted Dogfish (*Scyliorhinus canicula*) and Black Mouth Dogfish (*Galeus melastomus*) in the Benthic and Demersal Communities of the Cantabrian Sea

(Elasmobranch Fisheries – Oral)

by

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Abstract

Scyliorhinus canicula and *Galeus melastomus* are the most abundant squaliforms in the Cantabrian shelf; the ranges of their distribution depths overlap, although they belong to different megabenthic communities. These species are predators and carrion feeders; they feed on megabenthos in several habitats. Their diets according to the size of the predator specimens and to the communities of the continental shelf and slope they belong to are compared in this paper. To examine their feeding strategy, data on the abundance and distribution of the predators, together with the biological knowledge about their most characteristic prey, are analysed. *S. canicula* preys present a high taxonomic diversity, 4.53, than *G. melastomus*, 2.56, and its food habits are also more benthic. The trophic spectra of lesser spotted dogfish and black mouth dogfish were significantly overlapped. The diets of the specimens of both dogfishes caught in the same hauls (zones of coexistence) are also compared.

Key words: dogfish, food habits, Cantabrian Sea, *Scyliorhinus canicula*, *Galeus melastomus*, habitat partitioning.

Introduction

Lesser spotted dogfish (*Scyliorhinus canicula*) and black mouth dogfish (*Galeus melastomus*) are two extremely common elasmobranchs on the northeast Atlantic coasts, and both species are throughout distributed along the continental shelf (Sánchez *et al*., 2002). Lesser spotted dogfish is mostly found at depths ranging from 50 to 500 m, especially between 100 and 300 m (Sánchez, 1993), while blackmouth dogfish is commonly found between 200 and 500 m, but occasionally up to 55 and down to 1 400 m (Compagno, 1984; Carrassón *et al*., 1992). Lesser spotted dogfish is much more abundant than black mouth dogfish and, according to data from surveys (Sánchez, 1993; Sánchez *et al*., 2002), its abundance shows an increasing trend over the last two years (Fig. 2). According to data of the fishery (Fernández *et al*., 2002), landings of lesser spotted dogfish have increased from 195 to 259 tons over the last five years, while there are not available data on landings of black mouth dogfish. These data, however, are not representative because the commercial value of both species has been very little up to now, so landed catches are much lower than discards (Olaso *et al*., 1998; Fernández *et al*., 2002).

So far only food data of lesser spotted dogfish are known; they show characteristics which present this species as a good indicator to monitor the changes in the abundance of species occurring in exploited ecosystems. These changes modify the natural diet of both dogfish species, and they benefit from food provided by discards. Besides, lesser spotted dogfish is usually discarded and returned to its natural state with a survival rate of over 90% (Kaiser and Spencer, 1995; Olaso *et al*., 1998; Rodríguez-Cabello *et al*., 2001; Olaso *et al*., in press). The few, less precise, studies on the feeding of black mouth dogfish (Capapé and Zaouali 1976; Macpherson, 1980; Mattson, 1981) make it possible to suppose it may be also changing its feeding habits due to the supply of energy from fishing activities (discards), but we do not know the vulnerability this species can have to overfishing.

Because all the peculiarities mentioned above, we have been moved to analyse diet composition, intensity and ontogenetic changes of each of these two species and to comp are their food habits.

Material and Methods

Stomach sampling and analysis

5076 lesser spotted and 960 black mouth dogfish stomachs were collected during bottom trawl surveys carried out in October between 1988 and 2001 (Fig. 1), in the north of Spain (ICES Division VIIIc). Surveys were carried out using random sampling stratified by depth, 30-500 m, and geographical areas, following the methodology explained in Sánchez (1993). Ten stomachs of each species were collected from each haul and stomach contents were analysed on board. For each predator specimen, the following data were taken: total length, sex, maturity, and stomach fullness (with food, empty or regurgitated). If a fish had food in its mouth or around the gills, or if its stomach was inverted or flaccid, the fish was categorized as having regurgitated food; in the case of non empty stomachs, the total stomach volume was recorded. The volume (ml) of total prey groups in the stomach was measured using a calibrated measuring instrument we have named trophometer (Olaso, 1990; Olaso *et al*., 1998; Velasco *et al*., 2001). Regarding the prey items data were collected on percentage of the stomach total volume, number, digestion stage and, in the case of fishes, total length or otolith length. Each prey item was classified to the lowest possible taxa for decapod crustaceans and fish; other invertebrates were classified to higher taxonomic levels.

To consider length dependent factors, lesser spotted dogfish in previous studies were divided into length categories to account for ontogenetic shifts in diet (<30 cm; 30-50 cm and >50 cm). Related to the habitat, the depth strata that determine the main species assemblages, <120 m, 120-300 m, >300 m, were also taken into consideration (Olaso, 1990; Sánchez, 1993; Sánchez and Serrano, 2002).

Diet analysis

The relative importance of individual prey taxa was assessed by indices of volume (%V), and to compare the diet of the two species caught in the same hauls the index of relative importance, IRI (Pinkas *et al.*, 1971) was applied; this index combines percentage in number, percentage in volume and frequency of occurrence of each prey item. Additionally, in order to compare the feeding intensity of the two species with different size distributions, the fullness index %BV was utilised, that is the wet volume of the stomach contents expressed as percentage of the fish body weight, and it was also calculated as a mean for each species by haul using the regurgitated correction factor.

$$\%BV_i = \frac{\sum_{h=1}^{H}\left[\frac{F+R}{F\times(F+R+E)}\times\sum_{j=1}^{k}\frac{V_{ij}}{Wj}\right]}{H} \qquad \%BV = \sum_{i=1}^{X}\%BV_i$$

where F, R and E are respectively the number of full, regurgitated and empty stomachs of the studied predator species in haul h; V_{ij} is the volume of prey i in the stomach j, with k being the number of stomachs in the haul h; W_j the weight of the predator j; H the total number of hauls in which stomachs of the predator species were analysed, and X the total number of different prey categories consumed by the predator throughout the study. %BV normalise the data of stomach contents in relation to the predator's weight. Furthermore, the percentage of empty stomachs has been studied. All the indices are described by Hyslop (1981).

The measurements of trophic diversity, defined as the width of the feeding niche, was compared by calculating a Shannon-Wiener diversity index, H' (Shannon and Weaver, 1949) and evenness, E (Pielou, 1966):

$$H' = -\sum_{i=1}^{S} p_i \times \log_2(p_i) \qquad \text{and} \qquad E = H'/H\max = H'/\log S$$

where p_i is the proportion of the total sample belonging to ith species, S the total number species found in the stomach sampled, and H_{max} the maximum diversity. These indices were estimated using the number of preys. We were interested in clarifying competitive relationships between both shark species. To do so, we obtained the degree of overlap in the specific diets of the two species by different sizes, using Horn's Overlap Index (Horn, 1966). This index, based on the mean of the volume percentages, which appears to be the most appropriate diet measure (Wallace, 1981), was computed with prey resources defined at the family taxon.

Fishery and survey data

The information and the estimates of the abundance indices obtained during the bottom trawl surveys between 1992-2001, using the methodology of Sánchez *et al*. (2002) have been used in this paper.

Results

Bathymetrical distribution of dogfish species

Lesser spotted dogfish inhabit on the continental shelf, and the maximum abundances are found 30-200 m. The juveniles inhabit deeper grounds than adults, between 150-300 m (Fig. 2a). Black mouth dogfish is found at deep waters on the continental shelf and in the upper margin of the slope at depths ranging from 150 m to 500 m, mainly between 300 m and 500 m. The juveniles inhabit shallower grounds than adults, between 200-350 m (Fig. 2b).

Diet composition and similarity between species

Sampling representativity was studied plotting the number of taxa *vs*. the number of stomachs sampled in each group of diet or both species of dogfish. The size of the samples is sufficient for the description of the prey type, except for *G. melastomus* larger than 50 cm and the specimens caught at less than 120 m deep.

<u>Emptiness and regurgitation percentages</u>

As it is shown in Table 1, the number of empty stomachs is less than 20% in all length groups of both dogfishes; it is, on the average, higher in *G. melastomus* (17%) than in *S. canicula* (14%), being this difference statistically significant (χ^2_1; p=0.012). The emptiness percentage of the two species varies depending on the length groups and depth. In *S. canicula* there are significant differences between the largest size class and the two smaller ones (χ^2_2; p<0.0001), and there are no significant differences between depth classes (χ^2_2; p=0.174); on the contrary, in *G. melastomus* there are no significant differences between size classes (χ^2_2; p=0.454), and there are significant differences between the two well represented depth classes (χ^2_1; p=0.036). The occurrence of regurgitated stomachs is small in both species.

<u>Diet composition in relation to length</u>

Independently of the length of both species, all prey groups identified were present, fish and crustaceans being main preys (Table 2). Crustaceans have a trend to be more important for smaller fish, and this is balanced not only by a higher weight of fish preys of the larger length classes, mainly in black mouth dogfish, but also by a tendency in lesser spotted dogfish to take more cephalopods. Benthic decapods, polychaets, other invertebrates and benthic fishes are more important in lesser spotted dogfish larger than 30 cm, but suprabenthic invertebrates as euphausiids, mysids, benthipelagic shrimps and fishes dwelling in the water column domain prevail in the diet of black mouth dogfish larger than 30 cm (Fig. 3). Dogfishes under 30 cm have a more similar diet, but euphausiids and *Micromesistius poutassou* are more important preys in lesser spotted dogfish. Benthopelagic shrimps (*Pasiphaea multidentata*, *P. sivado*, *Sergestes robustus*) are eaten only by *G. melastomus,* while shrimps closer to the bottom (*Alpheus glaber*, *Solenocera membranacea*) are more important preys for *S. canicula*. Pelagic and mesopelagic fish are more frequent preys of *G. melastomus,* while *S. canicula* feed on a wider variety of benthic and demersal fish.

The global trophic spectrum comprised 101 prey categories of 10 phyla for *S. canicula* and 50 prey categories in 7 phyla for *G. melastomus*, although it must be taken into account that the number of stomachs analysed is larger for *S. canicula* (table 2). Decapod crustaceans, mainly natantoids and brachiurids, and fish showed the broadest species diversity in the diet of *S. canicula* (Table 3). Dietary diversity was over one third higher in all size groups of *S. canicula* than in those of *G. melastomus*. Horn's index of diet overlap was 0.76 among lesser spotted dogfish and black mouth dogfish, and the values of Horn´s indices between the size groups of the two sharks are very high

(Table 4). Taking into account that the overlap is generally considered biologically significant when the value exceed 0.60 (Zaret and Rand 1971, Mathur 1977), we only found a lower overlap value when comparing *S. canicula* <30 cm and *G. melastomus* >50 cm). The rest of the sizes compared showed significant diet overlap.

Variation in feeding intensity by depth

We have found that more than half of the diet in %BV of *S. canicula* caught at a depth shallower than 120 m is crustacean decapods, and the rest is practically all fish (Fig. 4). Between 120-300 m, it feeds on the same type of food and its feeding intensity increases from 1.6%BV to 1.8%BV, because of a bigger predation on *M. poutassou* and euphausiids. Beyond that depth, where the abundance of the species diminishes clearly, the feeding intensity goes down to 1.5%BV, because it predates much less on decapod crustaceans, although the consumption of *M. poutassou* and cephalopods is higher.

The feeding intensity of *G. melastomus* at a depth less than 120 m is low, 1.3% BV; it must be considered, though, that the stomach contents analysed were few because that depth is the limit of the distribution range of the species. At a depth more than 120 m the feeding intensity increases up to 2%BV, euphausiids and *M. poutassou* being important preys; the consumption of crustacean decapods is reduced. The feeding intensity keeps about 2%BV beyond 300 m; the importance of mysids and euphausiids increases (0.8%BV) and that of decapod crustaceans and *M. poutassou* decreases.

Comparison of the diet of the two species of dogfishes sharing the same area

In order to prevent as far as possible the effects of the conditions of the most frequent habitats of these species, we have investigated the stomach contents of 359 *S. canicula* and 345 *G. melastomus* that lived together at depths between 136 and 382 m (average 262 $\pm$ 20 m); the stomach samples and the emptiness percentages were very similar (Table 5).

The diet was very uniform in specimens less than 30 cm total length; euphausiids were the most abundant prey. Euphausiids, brachiurids and anomurids are major prey items of *S. canicula* 30-50 cm long, but euphausiids are the main prey of *G. melastomus* of the same size, that predate less on brachiurids and anomurids. The largest dogfishes predate on *M. poutassouu* and other fishes; it has been observed that several zoological groups share the importance of the preys of *S. canicula,* whereas fishes, mainly *M. poutassou,* are the basis of the food of *G. melastomus*. Horn's index of diet overlap was 0.83 among lesser spotted dogfish and black mouth dogfish of the same area, and the values of Horn's indices between the size groups of the two sharks are very high.

Discussion

Diets of lesser spotted dogfish and black mouth dogfish

In this paper all the available data on the feeding of the two dogfishes during the autumn have been integrated in order to compare their food habits and the role habitats the latter play in the habitats of these species. We show that previous studies on both dogfishes have provided with information on their feeding in different Atlantic and Mediterranean areas (Matson, 1981; Macpherson, 1981; Lyle, 1983; Carrassón *et al.*, 1992); in the Cantabrian Sea, the diet of these two species have been described for several years (Olaso and Rodríguez-Marín, 1995a; Velasco *et al*., 1996; Olaso *et al*., 1998; Gutiérrez Zabala *et al*., 2001).

The wide and great variety of prey items found in the two species in this study implies they are broad generalists in their diets and habitat requirements. In the case of lesser spotted dogfish, the high value of its taxa diversity confirms that is an opportunistic feeder irrespective of size classes, but especially when it is larger than 30 cm, as it has been described previously elsewhere (Lyle, 1983; Olaso *et al*., 1998). As refers black mouth dogfish, although the stomach sampling was not so large because of the smaller abundance of the species, it was appreciated the diet was slightly less diverse than that of lesser spotted dogfish. This apparently lower degree of opportunistic feeding, selecting less varied preys than lesser spotted dogfish, may be influenced by the smaller richness of the fish and crustaceans species living below 300 m (Olaso, 1990; Sánchez, 1993). Black mouth dogfish feeds on a peculiarly low variety of preys in the Norwegian fjords (Mattson, 1981) because, according to this author, it predates on large sized preys, which are less abundant than small preys. Carrassón *et al*. (1992), in specimens from Catalonian (northwestern Mediterranean), consider that the scarcity of the preferred prey and the disappearance of the dominant resources resulted in a diversification in the diet of *G. melastomus* below 1 000 m in all size-classes.

High dietary overlap indices among *S. canicula, G. melastomus* indicate a high potential for resource competition. Diets of two dogfishes smaller than 30 cm were most similar while, diets of the larger specimens were least similar. Such competition may contribute to competitive exclusion of one species or the other, resulting in the decrease of abundance of one of them. In the study done in the coexistence area it has been observed the overlapping of diets is quite high. Thus, resource competition may be more intense between dogfishes under 30 cm total length, that live together in the same zones, but it has a minor effect on the rest of the length classes, since they dwell in different habitats.

We have found that the most intense feeding activity of *S canicula* occurs at a depth less to 300 m, and that of *G. melastomus* beyond that depth, i.e., the optimal feeding options of both species are coincident with the ranges of habitat distribution of juveniles and adults habitats. Young *S. canicula* consume more food than adults in relation to their body size (Sim *et al*., 1994); in the present study we have observed larger feeding intensity occurred at the depth where the abundance of juveniles was the largest.

Resources exploited by S. canicula and G. melastomus

During daytime there are suprabenthic organisms and demersal fish at certain depths (Mauchline and Gordon, 1984, 1991; Gordon *et al*., 1995; Gordon and Mauchline, 1996; Merrett and Haedrich 1997). Although *S. canícula* and *G. melastomus* display nocturnal activity (Carrassón *et al*., 1992; Bello, 1995), the behaviour of both dogfishes allows them to predate on prey from the benthic communities and from midwater; however, *S. canicula* feeding habits are mostly benthic (Lyle, 1979; Olaso and Rodríguez-Marín, 1995a, 1995b) and *G. melastomus* are benthopelagic (Bozzano *et al*., 2001). These authors demonstrated in the Mediterranean Sea that dogfish eyes are considerably important to detect their preys, adapting their retina to the depth they dwell at. *S. canicula*, a more coastal species, adapts to a more variable light intensity and its preys are not bioluminiscent except for the eupausiids; on the contrary, *G. melastomus* has larger eyes, so it can catch a big quantity of bioluminiscent preys. (*Sergestes robustus*, *Pasiphaea* spp.), mysids (*Benthophausia gigas*), fish (*Argyropelecus* spp., myctophids, silver fish). These preys have been beforehand cited in the diet of Mediterranean *G. melastomus* (Bello, 1995), and it has been considered that they make extensive vertical migrations and at least a fraction of the population ascends to the bottom of the near-surface mixed layer (Cartes *et al*., 1993; Bergstad *et al*., 1996); the adaptation of their eyes to depth is highly related to the distribution range of each species. In addition, the visual sharpness increases with age (Bozzano *et al*., 2001). So, young *S. canicula* that feed basically on euphausiids, live at deeper places than adults; on the contrary, young *G. melastomus* are found at less depth than adults, that is to say, they look for habitats where their preys are available.

These dogfishes change their habitat as they grow up from juveniles to adults; *S. canicula* go closer to the shore and *G. melastomus* move further offshore. They adapt their feeding to the animal communities of their new habitats, the variation of their prey species being related to their distribution. So, when the size of predators increases the frequency of capture of euphausiids decreases and the capture of fish increases, as it has been described in other areas (Macpherson, 1980; Relini *et al*., 1975). The consumption of the mesopelagic fish *M. poutassou* is particularly important for both species, and so it is the increase of the catch of cephalopods for *S. canicula*. But for this trophic change, another sensory organ in addition to vision is essential for these dogfishes to detect and catch their preys, the olfactory lobes, which are larger in lesser spotted dogfish. This organ has the ability to sense electric impulses produced by an animal. The detection of lifeless prey by *S. canicula* starts always with an olfactory alarm, and the sharks use this organ to find prey and sense if the animal is dying (Dijkgraaf, 1975). The number of olfactory lamellae in the rosette increases with the fish length (El-Attar, 1998), and squaliforms use this organ to find prey and they feel if the animal is dying (Dijkgraaf, 1975). Moreover, visual sharpness of dogfish increases with age, and this allows them to detect larger prey at a bigger distance (Bozzano *et al*., 2001). This addition of sight and smell makes it possible for *S. canicula* to be scavengers and fishery discards eaters, as it has been described elsewhere (Kaiser and Spencer 1994; Olaso *et al*., 1998 and in press). In the diet of adult *S. canicula*, much of *M. poutassou* in the stomach contents are discards, or are consumed when already dead or damaged (Olaso *et al*., 1998; Olaso *et al*., in press). We assume this is akin in the case of the big quantities of *M. poutassou* consumed by *G. melastomus*, because this mid-water fish is the most important demersal species landed and discarded by the Spanish trawler fleet in the southern Bay of Biscay (Pérez *et al*., 1996).

We suppose that the morphological characteristics of the eyes and olfactory lobes of both dogfishes must cause differences in the search for and catch of preys in the two species. The best sight and worse smell of black mouth dogfish favours the hunting and capture of preys which are found in the water column. On the contrary, the worse sight and better smell in lesser spotted dogfish explain that this species is more adapted to consume benthic preys and other organisms that are in the seafloor. In conclusion, despite competition for food resources, *G. melastomus* seems to be able to coexist with *S. canicula* possibly through habitat segregation and avoidance of antagonistic encounters. On one hand, the supletory food introduced by fishing activity, offal and discard, implies that their populations might be positive affected by the same external factors, and on the other hand that their abundances have increased in the last years.

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Table 1. Percentages of empty and regurgitated stomachs per length ranks and depth strata for *Scyliorhinus canicula* and *Galeus melastomus.*

S. canicula	Length Ranges (cm)			Depth strata (m)		
	7 - 29	30-49	50-75	< 120	120 - 299	> 299
% Empty	11.46	12.85	16.60	14.04	14.28	8.97
% Regurgitated	0.46	0.09	0.41	0.29	0.28	0
% Full	88.08	87.07	82.99	85.67	85.44	91.03
Total number	864	2242	1970	1026	3894	156
Mean length (cm)	24.09	39.35	56.23	48.09	41.75	50.69

G. melastomus	Length Ranges (cm)			Depth strata (m)		
	13 - 29	30-49	50-77	< 120	120 - 299	> 299
% Empty	15.81	19.06	18.38	38.46	14.32	19.42
% Regurgitated	0	0	0.74	0	0	0.21
% Full	84.19	80.94	80.88	61.54	85.68	80.38
Total number	525	299	136	13	468	479
Mean length (cm)	22.17	38.39	60.07	32.85	27.40	37.65

Table 2. Diet (% volume) of Scyliorhinus canícula and Galeus melastomus by size-class (cm). Only the prey with at least more than 1% in one length range are shown.

	Diet of *Scyliorhinus canicula*				Diet of *Galeus melastomus*			
	< 30	30-50	>50	Total	< 30	30-50	>50	Total
Crustacea	68.6	48.9	35.2	42.3	64.5	47.8	25.7	39.1
Decapoda	46.7	44.8	33.0	38.3	23.6	27.1	18.2	21.8
Munida spp.	3.3	2.4	1.3	1.9				
Pagurus prideaux	5.7	8.0	7.1	7.4	0.1	4.3	0.5	1.6
Goneplax rhomboides	1.1	0.8	0.4	0.6	0.0	0.0	0.2	0.1
Liocarcinus depurator	2.0	3.0	2.2	2.5	0.0	0.1	0.0	0.0
Polybius henslowi	3.6	8.0	5.3	6.3	0.1	2.1	0.6	0.9
Alpheus glaber	3.6	4.3	2.2	3.1	1.4	0.4	0.6	0.7
Pasiphaea multidentata					0.3	0.6	2.4	1.5
Pasiphaea sivado					5.2	13.3	9.8	10.1
Processa spp.	3.3	2.0	0.8	1.4	3.4	0.2	0.0	0.6
Sergestes robustus	0.0	0.0	0.0	0.0	0.0	0.0	1.5	0.8
Solenocera membranacea	2.7	1.8	1.4	1.6	0.9	0.6	0.2	0.4
Other Decapoda	21.3	14.6	12.4	13.7	12.3	5.3	2.5	5.0
Euphausiacea	14.5	1.8	1.1	2.1	36.1	14.1	5.5	13.4
Isopoda	1.5	0.3	0.3	0.4	0.1	0.1	0.1	0.1
Mysidacea	2.4	0.7	0.2	0.5	0.9	3.4	1.0	1.7
Other crustacea	3.6	1.3	0.5	1.0	3.8	3.1	0.9	2.1
Mollusca	3.9	4.2	7.6	6.1	4.1	0.8	2.7	2.4
Cephalopoda	3.9	4.1	7.6	6.0	4.1	0.7	2.7	2.3
Other mollusca		0.1		0.1		0.1		0.1
Polychaeta	7.1	4.3	2.1	3.2	1.1	0.4	0.0	0.3
Other invertebrata	2.1	2.8	1.7	2.1	0.0	1.3	3.2	2.2
Fish	18.3	39.9	53.4	46.3	29.9	49.7	68.8	56.3
Gadiculus argenteus	1.2	0.4	0.3	0.4	2.0	1.6	0.0	0.8
Micromesistius poutassou	5.6	16.7	22.6	19.4	9.7	28.7	22.1	21.9
Merluccius merluccius					0.0	2.6	0.0	0.8
Xenodermichthys socialis					0.0	0.0	2.0	1.1
Scomberesox saurus					0.0	0.8	8.8	4.9
Argyropelecus spp.					0.0	0.0	1.1	0.6
Mycthophid					1.2	1.9	0.4	1.0
Trachurus trachurus	0.4	0.6	2.1	1.4	0.0	1.9	9.3	5.4
Cepola rubescens	0.0	0.7	3.2	2.1	0.0	0.0	0.0	0.0
Scomber scombrus	0.0	0.9	2.2	1.6		0.1	0.0	0.0
Other fish	11.1	20.5	23.0	21.4	17.0	12.3	25.2	19.8
Stomachs with food	761	1952	1635	4348	442	242	110	794
Average length (cm)	24.09	39.35	56.23	43.3	22.17	38.39	60.07	32.59
No. of phyla	7	9	8	10	5	6	4	7
No. of taxa	43	79	74	101	36	33	29	50

Table 3. Number of taxa of the most important prey groups, for size-class of *Scyliorhinus canícula* and *Galeus melastomus*

	Taxa of *S. canicula*			Taxa of *G. melastomus*		
	< 30 cm	30-50 cm	>50 cm	< 30 cm	30-50 cm	>50 cm
Anomura	4	8	7	4	4	2
Brachyura	5	9	5	1	2	2
Macrura	1	3	2	1	1	1
Natantia	8	12	11	9	8	6
Euphausiacea	1	1	1	1	1	1
Mysidacea	1	1	2	2	2	1
Ot crustacea	3	3	3	3	2	2
Cephalopoda	5	9	7	3	3	1
Other invertebrata	12	19	15	5	6	3
Fish	8	23	28	10	7	11
Taxa diversity (prey number)	3.48	4.59	4.67	2.10	2.57	2.96
Evenness (prey number)	0.60	0.70	0.72	0.39	0.49	0.58
Number of stomachs	761	1952	1635	442	242	110
Taxa diversity (prey volume)	3.76	3.63	3.42	2.95	3.37	3.32
Evenness (prey volume)	0.87	0.79	0.76	0.68	0.73	0.74

Table 4. Horn's Overlap Index values for total volume of prey consumed by size-classes of lesser spotted dogfish and black mouth dogfish.

		Scyliorhinus canicula			*Galeus melastomus*		
		< 30 cm	30-50 cm	>50 cm	< 30 cm	30-50 cm	>50 cm
Scyliorhinus canicula	< 30 cm	-	0.87	0.76	0.81	0.79	0.57
	30-50 cm		-	0.95		0.77	0.65
	>50 cm			-		0.65	0.69
Galeus melastomus	< 30 cm				-	0.83	0.65
	30-50 cm					-	0.79
	>50 cm						-

Table 5. Percentages of empty and total stomachs per length ranges, by *Scyliorhinus canicula* and *Galeus melastomus* that habit in the same places

Scyliorhinus canicula	Length Ranges (cm)		
	< 30 cm	30-50 cm	> 50 cm
% Empty stomach	15.6	11.3	20.5
Total number of stomach contents	96	97	166

Galeus. melastomus	Length Ranges (cm)		
	< 30 cm	30-50 cm	> 50 cm
% Empty stomach	16.1	11.7	8.7
Total number of stomach contents	211	111	23

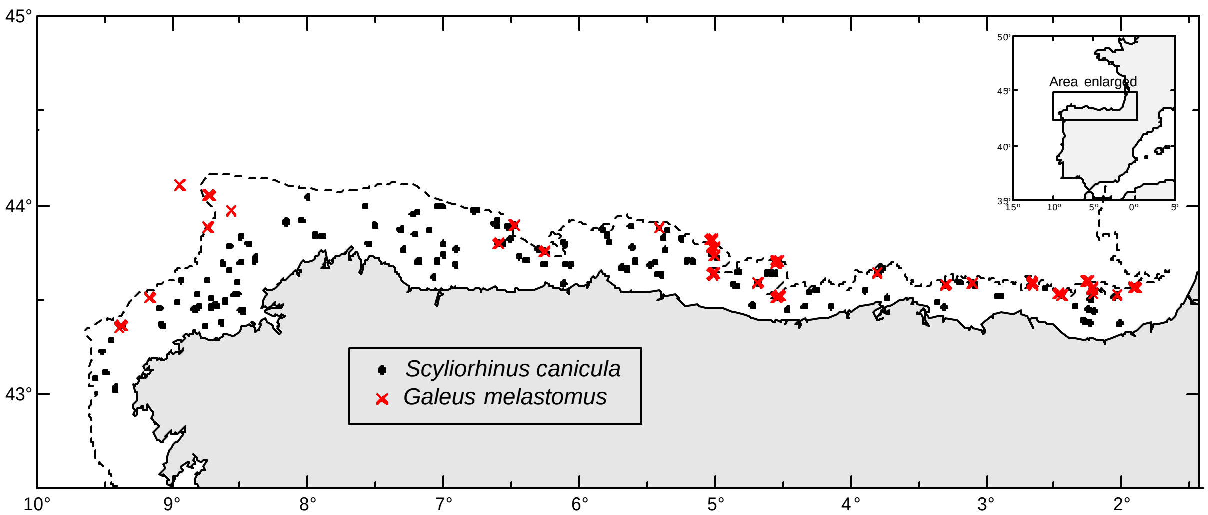

Fig. 1. Location of the study area (Cantabrian Sea; north of Spain) and hauls used in the diet analysis of each species.

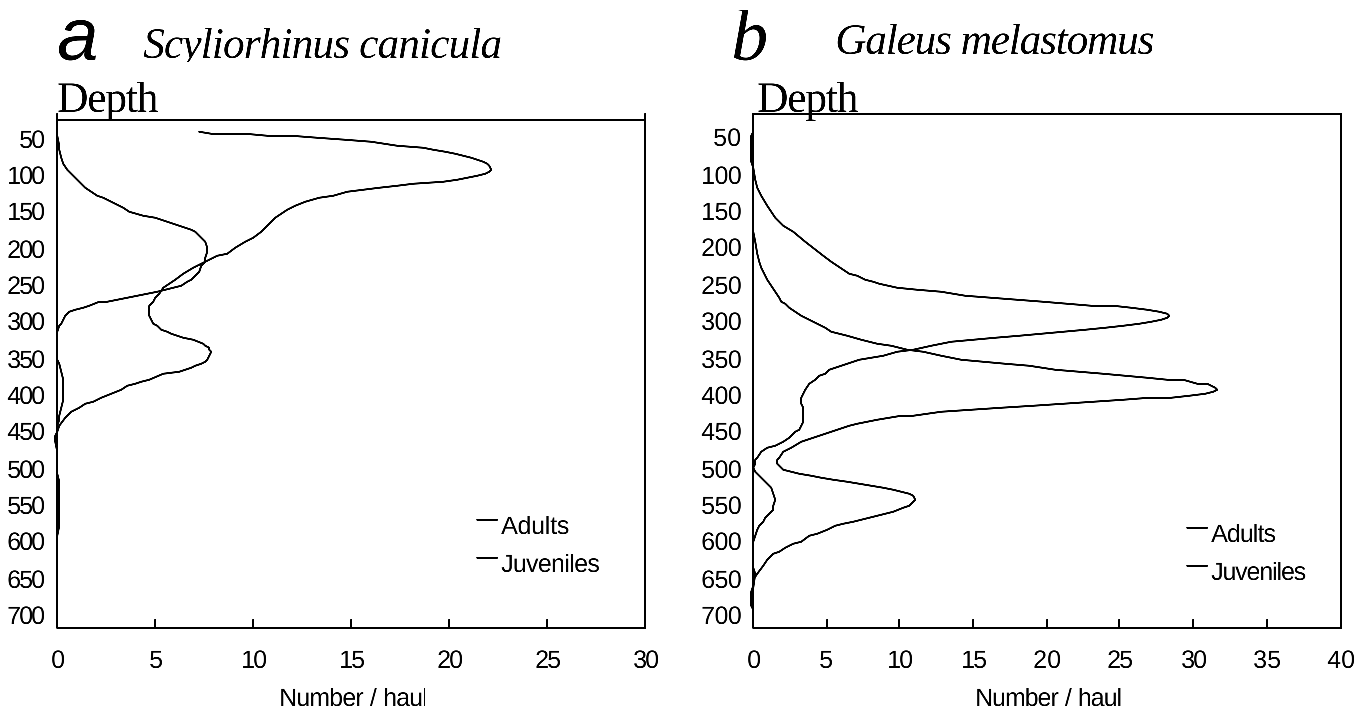

Fig. 2. Bottom trawl surveys biomass indices (kg/30 min. haul) of *S. canicula* and *G. melastomus.*

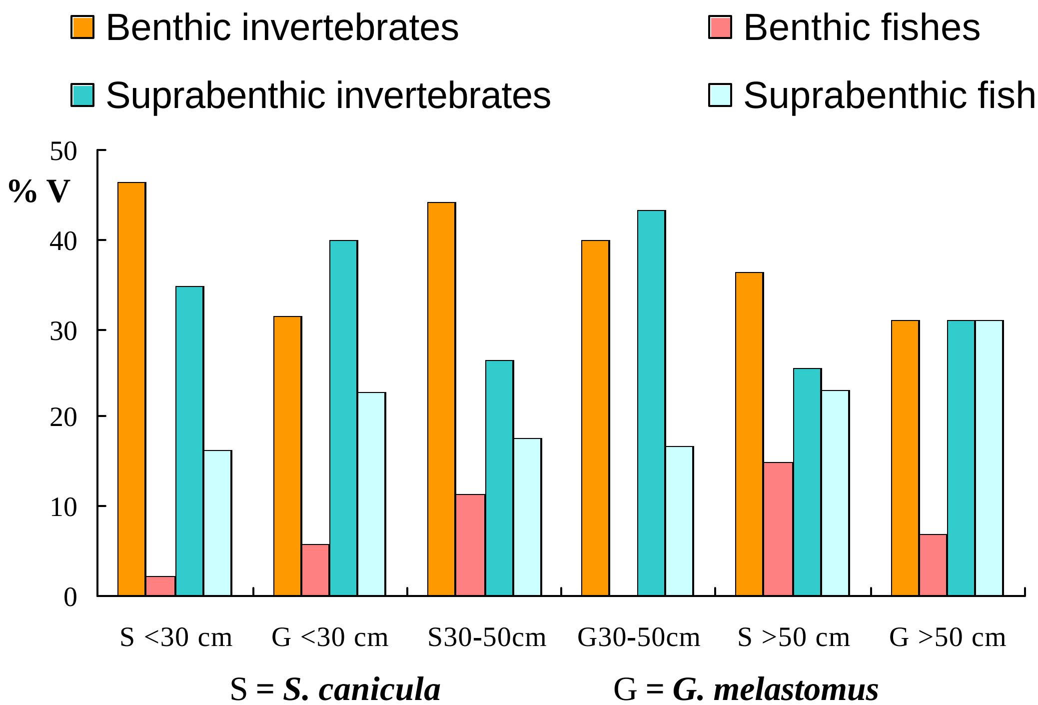

Fig. 3. Differences in importance of the type of prey available in *Scyliorhinus canícula* and *Galeus melastomus*, by size classes; data in volume percentages.

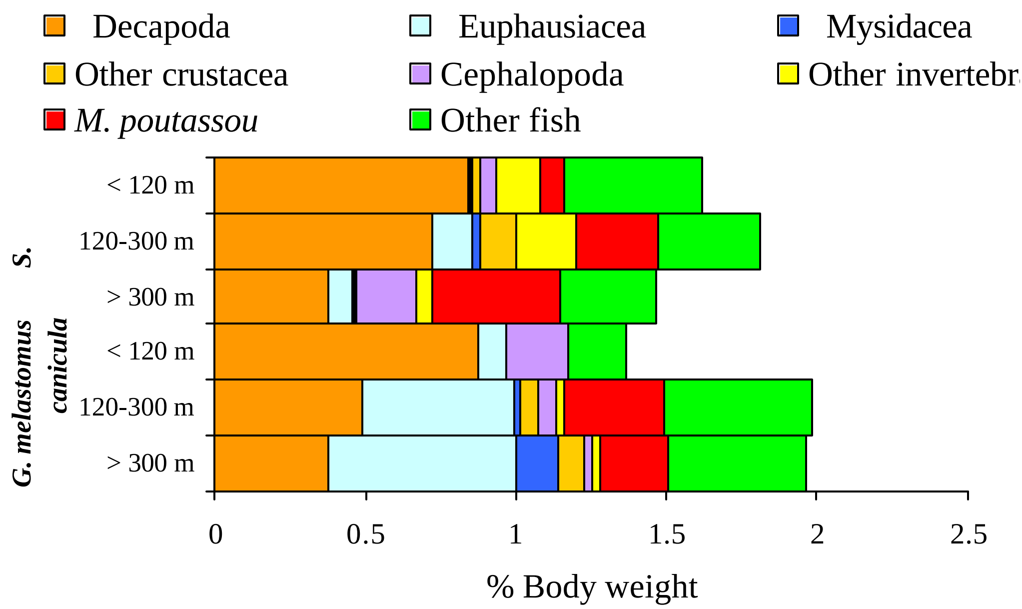

Fig. 4. Comparison of the feeding intensity by depth strata, between *Scyliorhinus canícula* and *Galeus melastomus*.