Comparative feeding ecology of two elasmobranch species, *Squalus blainville* and *Scyliorhinus canicula*, off the coast of Portugal

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Abstract—The small-spotted catshark (*Scyliorhinus canicula*) (Linnaeus, 1758) and the longnose spurdog (*Squalus blainville*) (Risso, 1826) are two species occurring in the European and western African continental shelves with a wide geographical distribution. In this study, the diet of *S. blainville* and *S. canicula* off the Portuguese western Atlantic coast was investigated in 2006 by collecting monthly samples of these two species from local fishing vessels. In the stomachs of both species, crustaceans and teleosts were the dominant prey items, and molluscs, polychaetes, echinoderms, and sipunculids were found in lower abundance. In *S. canicula*, urochordate and chondrichthyan species were also observed in stomachs and were classified as accidental prey items. *Scyliorhinus canicula* consumed a broader group of prey items than did *S. blainville*. A significant diet overlap was observed, despite both species occupying different depth ranges over the continental shelf. *Scyliorhinus canicula* exhibited a consistency in diet composition among seasons, sexes, and maturity stages. Nonetheless, for both adults and juveniles, an increase in relative abundance of teleosts in the diet was observed in the spring and summer. This study provides evidence of the importance of *S. canicula* and *S. blainville* as benthic and pelagic predators along the western Atlantic coast.

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One of the main drawbacks in the assessment and management of elasmobranchs is the lack of biological information and suitable fisheries data (Pawson and Vince, 1999; Herndon et al., 2010). Being at the top of the marine food web, with mean trophic levels similar to marine mammals (Cortés, 1999; Domi et al., 2005), sharks are believed to play a significant role in marine ecosystems (Bowen, 1997). However, even for long and well-studied commercially important species, basic biological information (e.g., growth rates, age structure, reproductive potential, diet) that is essential for developing sound management strategies is still scarce (Stehmann et al., 2009).

In the Central Atlantic and Mediterranean, the small-spotted catshark *Scyliorhinus canicula* (Linnaeus, 1758) and the longnose spurdog (*Squalus blainville*) (Risso, 1826) are common demersal species (Pawson and Ellis, 2005; Froese and Pauly, 2010) and are direct targets for semipelagic longline and trammel fisheries (Coelho et al., 2005). These species also constitute an important bycatch of trawl and artisanal coastal fisheries (Carbonell et al., 2003; Baeta et al., 2010).

The distribution of *S. canicula* covers a wide bathymetric range and spatial area in NE Atlantic Ocean (Norway and British Isles), south to Senegal and the Mediterranean Sea (Whitehead et al., 1986; Froese and Pauly, 2010). *Scyliorhinus canicula* is an oviparous species with a high relative fecundity (Capapé, 1977) and is a broad generalist in its diet (Olaso et al., 2005). In the North Atlantic, this species displays diel vertical migrations: males occupy deeper areas during the day and forage at night in shallow areas, whereas females aggregate in shallow water caves during the day and forage at night in deeper waters (Sims et al., 2006).

The longnose spurdog (*S. blainville*) (Risso, 1826) is an aplacental viviparous shark living in tropical and temperate waters, whose distribution range includes the Mediterranean, the Eastern Atlantic from the Bay of Biscay to South Africa, and the Western Atlantic from the United States to Argentina (Cannizzaro et al., 1995; Froese and Pauly, 2010). It is a demersal species, inhabiting depths from 16 m to about 440 m and may reproduce throughout the year (Cannizzaro et al, 1995; Kousteni and Megalofonou, 2011). References to the diet of this species are scarce, mainly restricted to Tunisian waters (Capapé, 1975)

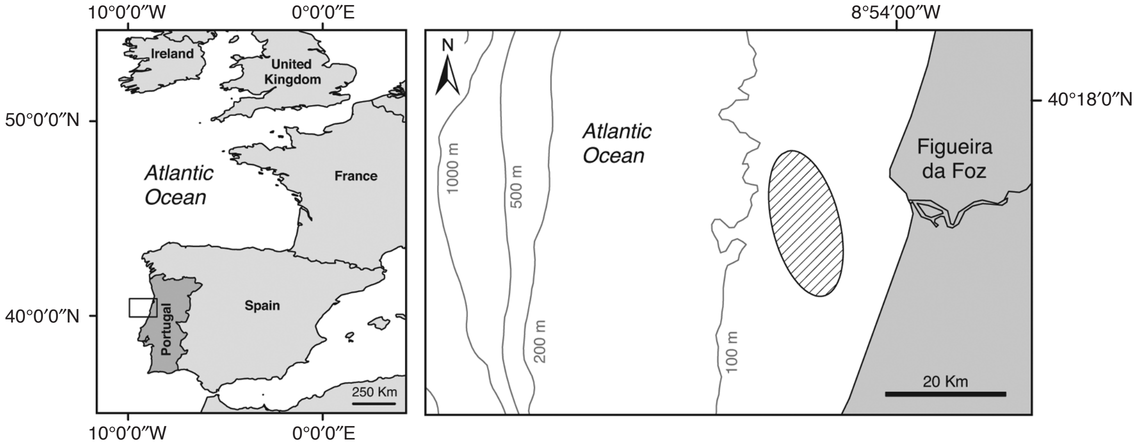

Figure 1

Location of the sampling area (shaded) adjacent to Figueira da Foz harbor off the coast of Portugal, where specimens of *Scyliorhinus canicula* and *Squalus blainville* were collected by commercial fisheries for stomach content analysis in 2006. Gray isolines represent bathymetry (m).

and to its congener *S. acanthias* (Avsar, 2001; Domi et al., 2005).

Studies of stomach contents and feeding ecology have been widely used, mainly for determining the possible competition for food resources (Braccini et al., 2005; Domi et al., 2005), for describing life history patterns (Demirhan and Seyhan, 2007), for determining mean trophic levels of fish species (e.g., Cortés, 1999), and for establishing ecosystem-based models (e.g., Christensen and Pauly, 1992). In this context, changes in the functioning of marine ecosystems, as a consequence of overfishing of elasmobranchs, will, according to Stevens et al. (2000), involve changes in trophic relationships, particularly through selective removal of predators or prey groups, as well as through species replacement and enhancement of food supply by fishery discards. In this study, we tested the hypothesis that *S. canicula* and *S. blainville* have distinct diets, and that possible intraspecific differences in *S. canicula* may be attributed to sexual maturity and seasonal variability in prey resources and habitat use. Therefore, our main objectives were to assess differences in diet composition between *S. canicula* and *S. blainville* captured off the Portuguese Atlantic coast, as well as the consistency between seasons and maturity stages in the feeding ecology of *S. canicula*.

Materials and methods

Acquisition of data

The shark specimens for this study were captured off Figueira da Foz, in the central Atlantic coast of Portugal (ICES Division IXa), in depths up to 70 m (40°10′N, 9°9′W; Fig. 1). Both species were captured between January and December 2006 by local trawl and multigear fishing fleets (mainly trammel and purse-seine nets), and were acquired at the Figueira da Foz Regional Office of Docapesca–Portos e Lotas, Sociedade Anónima, the company in charge of first fish sales along the Portuguese mainland. Sharks were frozen at sea, and the whole fish were transported in ice boxes to the laboratory, to minimize further digestion of stomach contents. In all fish, sex was determined and total length (TL) was measured to the nearest mm.

The diets of *S. canicula* and *S. blainville* were studied by examining stomach contents, which were removed and preserved in a 4% buffered formalin solution, for later identification to the lowest possible taxonomical level. Stomach contents were identified by using a set of references for several taxonomic groups: Fauvel (1923; 1927), Crothers (1983), Whitehead et al. (1986), and Hayward and Ryland (1995). All prey items were counted and weighed (wet weight, 0.001 g precision). For statistical comparisons among groups, prey items were grouped into the following major taxonomical groups: Sipuncula, Annelida, Crustacea, Mollusca, Echinodermata, Chondrichthyes, Teleostei, Urochordata, as well as unidentified material.

For *S. canicula*, an elasmobranch species with little sexual dimorphism in total length (Filiz and Taskavak, 2006), individuals of both sexes with TL above 500 mm were considered adults, whereas for *S. blainville*, males above 510 mm and females above 600 mm were considered sexually mature (according to Sion et al., 2003).

Analysis of diet composition

The diet breadth of both species, determined to the lowest taxonomical level possible for each prey item, was compared with two indices: 1) the Shannon-Wiener index (H') as a measure of diversity, which increases with increasing species diversity:

$$H' = -\sum_{i=1}^{S} (p_i \ln p_i), \tag{1}$$

where S = the total number of species; and
p_i =s the frequency of the ith species,

and 2) Pielou's index (J'), which indicates the evenness (i.e., how evenly the individuals are distributed among the different species composing the diet of both species):

$$J' = \frac{H'}{H'_{\max}}, \tag{2}$$

where H' is the number derived from the Shannon-Wiener index and H'_{max} is the maximum value of H'. This last index varies between 0 and 1, when there is an equal distribution in numbers of all species. Adequacy of sample size was assessed by means of cumulative trophic diversity curves (as proposed by Ferry and Cailliet, 1996), measured with the Shannon-Wiener index, by using all prey items, except unidentified ones. The cumulative numbers of 200 randomly chosen stomachs for *S. canicula* and 194 stomachs for *S. blainville* were plotted against the randomized cumulative trophic diversity. This analysis was performed in EstimateS software (Colwell, 2009) with 50 randomizing runs.

The relative importance of each prey item was assessed in three ways by using: 1) the numerical index (NI), i.e, the percentage of each prey item in relation to the total number of prey items (number of individuals of a prey category/total number of individuals among all prey categories)×100; 2) the occurrence index (OI), the percentage of each prey item in all non-empty stomachs, (number of stomachs containing a prey category/total number of stomachs containing prey)×100; and 3) the gravimetric index (GI), the percentage of each prey item regarding the wet weight of all items (weight of individuals of a prey category/total weight of individuals among all prey categories)×100 (Hyslop, 1980). Feeding activity was evaluated by using the vacuity index (VI), the percentage of empty stomachs (number of stomachs with prey/total number of stomachs)×100 (Hyslop, 1980): low feeding activity is considered when high vacuity is observed. Diet overlap was evaluated by Schoener's index (I_S):

$$I_S = 1 - 0.5\left(\sum_{i=1}^{n} | p_{iA} - p_{iB} |\right), \tag{3}$$

where p_{iA} and p_{iB} are the numerical frequencies of item i on the diet of species A and B, respectively (Linton et al., 1981).

Diet overlap was measured by the I_S ranges between 0, when no food is shared, and 1, when there is the same proportional use of all food resources. Although there are no critical levels for this index, Wallace and Ramsey (1983) suggested that values higher than 0.6 should be considered as biologically significant.

To complement the information given by the traditional indices, two mixed methods were also used: 1) the dietary coefficient (QI), adapted by Salgado et al. (2004), defined as:

$$QI = NI \times GI, \tag{4}$$

which considers both the number (NI) and weight (GI) of ingested prey, and classifies them into dominant (QI≥200), secondary (200>QI≥20), or accidental (QI<20) categories; and 2) the index of relative importance (IRI) developed by Pinkas et al. (1971), defined as:

$$IRI = (NI + WI) \times OI, \tag{5}$$

which evaluates the relationships between the different prey items in each species' diet, while considering the number (NI), weight (GI) and occurrence (OI) of each prey item. In order to classify the prey items according to the IRI, the method developed by Rosecchi and Nouaze (1987) was selected, in which the IRI values are ranked. The prey items that constitute 50% of the total sum are considered preferential, the prey items that constitute the next 25% are classified as secondary, and the remaining 25% are considered accessory prey items. The %IRI, defined as

$$\%IRI = 100 * IRI / \sum_{i=1}^{n} IRI, \tag{6}$$

was used to complement the information provided by the QI and IRI indices. For diet comparisons, prey taxa, excluding unidentified items, were grouped into the taxonomical categories referred to previously.

Seasonal and maturity-stage–related variability in the diet of *S. canicula*

Seasonal and sex differences in the diet of *S. canicula* (the most abundant species) were analyzed by grouping fish according to their maturity stage: adults or juveniles, and were presented according to the %IRI. Seasonal changes in diet composition were analyzed by partitioning the sampling period into four periods: winter (January to February), spring (March to May), summer (June to August), and autumn (September to November). Diet compositions of males and females were examined separately, in order to detect possible changes in habitat use. Differences in diet composition and vacuity levels among life stages and seasons were assessed with analysis of variance (ANOVA, α=0.05).

Results

Comparative feeding ecology of *S. blainville* and *S. canicula*

In total, 991 stomachs of *S. canicula* were analyzed. Total lengths ranged from 392 mm to 610 mm in males, and from 378 mm to 595 mm in females. For *S. blainville*, 297 stomachs were analyzed, and total lengths ranged from 401 mm to 600 mm in males, and from 391 mm to 797 mm in females (Fig. 2). In total, the vacuity for *S. canicula* was 13.4%, and for *S. blainville,* 21.6%. The cumulative trophic diversity curves seemed to reach an asymptote, indicating that a sufficient number of

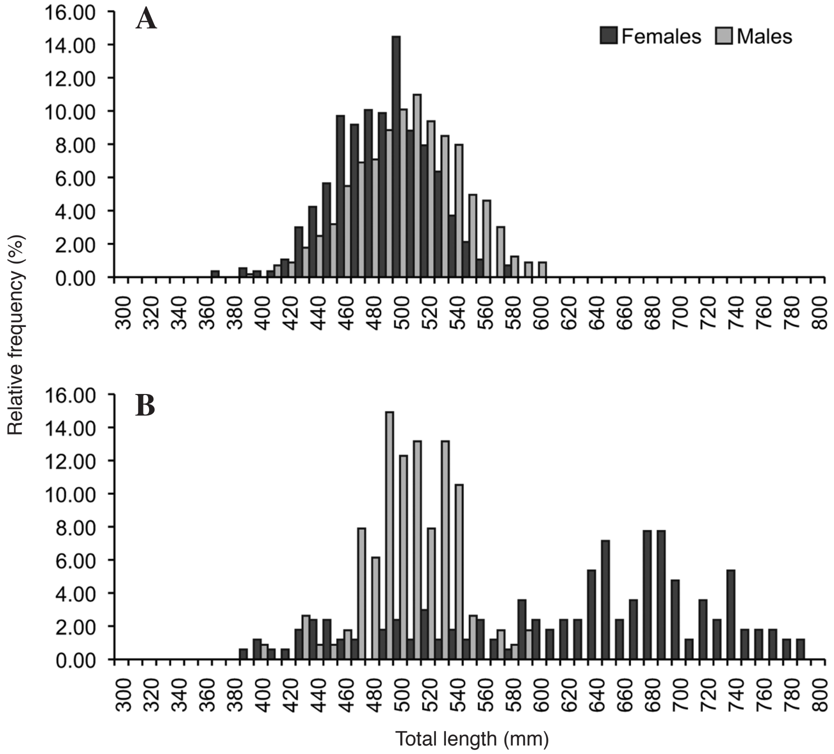

Figure 2

Total length-frequency distributions for (**A**) *Scyliorhinus canicula* and (**B**) *Squalus blainville* collected off the Portuguese coast in 2006 and analyzed for diet composition, separated by sex.

stomachs were used to characterize the diet of both *S. canicula* and *S. blainville* (Fig. 3).

Scyliorhinus canicula exhibited a diverse diet, composed of 63 different taxa, belonging to eight taxonomical groups: Sipuncula, Annelida, Crustacea, Mollusca, Echinodermata, Urochordata, Chondrichthyes, and Teleostei, as well as unidentified materials (Table 1). Crustaceans were by far the most abundant group in the diet of *S. canicula*, according to the numerical and occurrence indices, with values of 49.9% and 66.2%, respectively (Fig. 4). Within this group, the most important prey items were *Pagurus* spp. (including *P. bernhardus*, *P. cuanensis*, and *Pagurus* sp.) and non-identified Decapoda (Table 1). The second and third most abundant prey items in the diet of *S. canicula* according to the NI and OI were Teleostei and Annelida, respectively, although Teleostei contributed more significantly in weight, comprising almost 60% of the total weight of prey items in the stomach contents (Fig. 4A). From this last group, the pelagic fish *Sardina pilchardus* and *Scomber scombrus* were the predominant species. The remaining prey groups—Sipuncula, Mollusca, Echinodermata, Urochordata, Chondrichthyes, and unidentified materials—totaled less than 10% of the diet composition for all indices.

Squalus blainville showed a less diverse diet, composed of 30 different prey item types, grouped into six taxonomical categories: Sipuncula, Annelida, Crustacea, Mollusca, Echinodermata, and Teleostei, as well as unidentified materials (Table 2). The most abundant prey items in the diet of *S. blainville* were crustaceans, according to the NI, OI, and GI (52%, 64%, and 44%, respectively). The most abundant crustacean species were *Polybius henslowii* and *Pagurus* spp., with the first species contributing more than half of the total crustacean prey items in weight (GI=28.5%). The second most abundant prey group for all indices was Teleostei (followed by unidentified materials), although with much lower contribution for the diet composition (Fig. 4B).

In contrast to *S. canicula* where it was nearly 60% by weight, Teleostei comprised only about 30% by weight in *S. blainville*. In *S. blainville*, fish were heavily digested, and it was only possible to distinguish soleids from the remaining fish. Mollusca (mainly Cephalopoda and Gastropoda) played a more secondary role in the diet of *S. blainville* (Table 2), despite their higher proportions when compared to *S. canicula* (see also Fig. 4).

Scyliorhinus canicula had a more diverse diet, feeding on a higher number of prey items (H'=2.61), whereas *S. blainville* had a slightly narrower diet breadth (H'=2.48). In contrast, the diet of *S. blainville* had high-

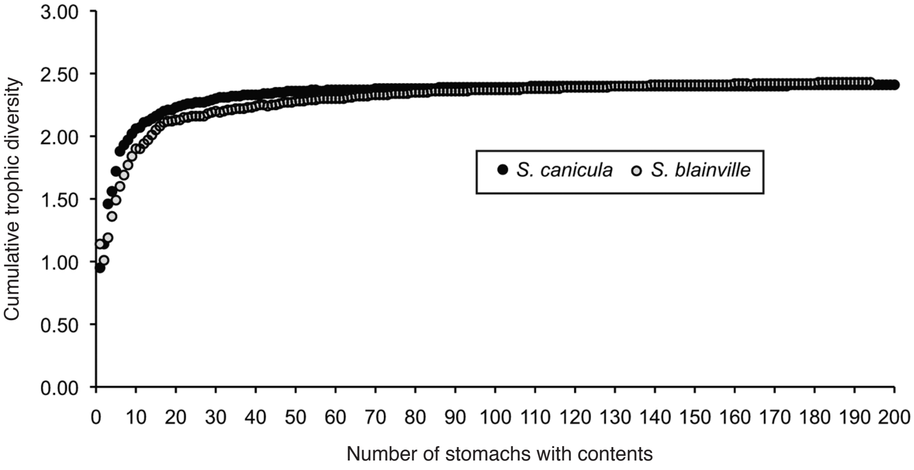

Figure 3

Randomized cumulative trophic diversity curves (Shannon-Wiener index) for *Scyliorhinus canicula* and *Squalus blainville.* The number of stomachs refers to those in which at least one prey item was identified, with the exception of unidentified materials.

er evenness (*J'*=0.73), compared to that of *S. canicula* (*J'*=0.63). Schoener's diet overlap index indicated high overlap (I_S=0.81) between *S. canicula* and *S. blainville*.

The relative importance of each prey group was evaluated by using the dietary coefficient (QI) and the index of relative importance (IRI) (Table 3). For *S. canicula*, Crustacea were considered dominant and preferential by both QI and IRI, respectively, and Teleostei were only considered preferential according to the QI. All other prey items were considered accessory by both classification systems, with the exception of Annelida and unidentified materials, which were considered secondary by the QI. For *S. blainville*, Crustacea and Teleostei were also classified as dominant prey items according to the QI, whereas Mollusca and unidentified materials were considered secondary prey items. According to the IRI, Crustacea were classified as preferential items, Teleostei as secondary, and all other prey groups as accessory prey items (Table 3). The %IRI values were in accordance with these patterns (Table 3).

Seasonal and maturity-stage–related variability in the diet of *S. canicula*

No differences in vacuity levels of *S. canicula* were observed between adults and juveniles for either sex (*F*=2.622; *P*>0.05). Nevertheless, maximum values, which indicate a lower feeding activity, reached ~25% in adult females and ~20% in adult males—all in the autumn (Fig. 5). For juveniles, maximum vacuity was observed in the autumn for females (~17%), and in the summer for males (~16%) (Fig. 5). The higher vacuity values (i.e., lower feeding activity) were observed in adult females.

In *S. canicula* males, Crustacea were the dominant prey items in both adults and juveniles, with %IRI values between 44.3% and 69.7% in adults, and between 56.4% and 92.4% in juveniles (Fig. 6). Teleostei were, in general, the second most important prey group for both adults and juveniles according to the %IRI, but higher in the spring and summer. In the autumn, both adults and juveniles relied more on crustaceans, with also a marked increase in the presence of sipunculid worms. This finding, however, was more evident in juveniles. During the winter, the importance of Annelida (namely Polychaeta) for the diet of adults was noticeable (%IRI=17.4), but the reliance on this group was reduced in the subsequent seasons.

For *S. canicula* females, the seasonal dietary patterns were similar to those of males (Fig. 7). Likewise, crustaceans composed the majority of the diet in juveniles (%IRI between 43.6% and 91.5%) and adults (%IRI between 32.3% and 57.4%) across seasons. For adult females, Teleostei were also an important part of the diet in spring and summer (%IRI=39.0% and 64.8%, respectively). In juveniles, the increase in importance of Teleostei during the same period was even more marked (%IRI=5.2% and 42.7%, respectively) (Fig. 7). As with adult males, *S. canicula* adult females had a more equally distributed diet between the main prey items in the winter, in contrast with the rest of the year. However, no significant differences were found between maturity stages for each sex and season after taking into account the diet composition evaluated by the %IRI (ANOVA; *P*>0.05).

Diet overlap was measured with Schoener's index (I_S). With a comparison of the different maturity stages, sexes, and seasons, a significant overlap was observed for all possible combinations (Table 4). The exception,

Table 1

Stomach contents of *Scyliorhinus canicula*, according to the numeric (NI), occurrence (OI), and gravimetric (GI) indices. Numbers in parentheses are the number of each prey item (NI), the number of non-empty stomachs where each prey item occurred (OI), and the weight (g) of each prey item (GI), respectively. Total number of stomachs=991; total number of stomachs with prey=858; total number of prey items=1749; total weight of prey items=3039.96 g.

Prey item	NI	OI	GI
Sipuncula	1.20 (21)	1.86 (16)	1.68 (51.04)
Siphonosoma sp.	1.03 (18)	1.63 (14)	1.17 (35.69)
Sipuncula	0.17 (3)	0.23 (2)	0.50 (15.34)
Annelida	19.44 (340)	19.81 (170)	1.45 (44.10)
Oligochaeta	3.03 (53)	0.35 (3)	0.02 (0.59)
Diopatra neapolitana	0.29 (5)	0.23 (2)	0.01 (0.16)
Diopatra sp.	0.06 (1)	0.12 (1)	0.001 (0.03)
Nothria sp.	1.43 (25)	0.35 (3)	0.12 (3.79)
Sternaspis scutata	0.06 (1)	0.12 (1)	0.01 (0.24)
Polychaeta	14.58 (255)	18.65 (160)	1.29 (39.29)
Crustacea	49.91 (872)	66.20 (567)	25.43 (773.14)
Ampelisca brevicornis	0.29 (5)	0.35 (3)	0.003 (0.11)
Amphipoda	0.17 (3)	0.23 (2)	0.003 (0.10)
Alpheus glaber	0.29 (5)	0.47 (4)	0.17 (5.16)
Pasiphaea sp.	0.11 (2)	0.12 (1)	0.02 (0.48)
Solenocera membranacea	0.69 (12)	0.82 (7)	0.47 (14.31)
Natantia	1.37 (24)	1.63 (14)	0.88 (26.82)
Anapagurus sp.	0.46 (8)	0.70 (6)	0.80 (24.41)
Atelecyclus sp.	0.06 (1)	0.12 (1)	0.03 (0.12)
Diogenes pugilator	0.11 (2)	0.23 (2)	0.16 (5.01)
Diogenes sp.	0.06 (1)	0.12 (1)	0.04 (1.33)
Ebalia granulosa	0.06 (1)	0.12 (1)	0.02 (0.53)
Gonepax rhomboides	1.09 (19)	2.10 (18)	0.98 (29.92)
Jaxea nocturna	0.06 (1)	0.12 (1)	0.01 (0.38)
Liocarcinus sp.	0.06 (1)	0.12 (1)	0.02 (0.60)
Lophogaster typicus	0.69 (12)	0.47 (4)	0.21 (6.32)
Pagurus bernhardus	0.11 (2)	0.23 (2)	0.22 (6.55)
Pagurus cuanensis	0.06 (1)	0.12 (1)	0.03 (0.78)
Pagurus spp.	3.14 (55)	4.66 (40)	4.22 (128.40)
Polybius henslowii	0.17 (3)	0.35 (3)	0.46 (14.04)
Polybius sp.	0.06 (1)	0.12 (1)	0.03 (0.81)
Thia scutellata	0.06 (1)	0.12 (1)	0.08 (2.58)
Upogebia sp.	0.06 (1)	0.12 (1)	0.02 (0.54)
Diogenidae	0.06 (1)	0.12 (1)	0.10 (2-94)
Paguridae	0.17 (3)	0.35 (3)	0.19 (5.77)
Portunidae	1.03 (18)	1.40 (12)	2.07 (62.80)
Pasiphaeidae	0.17 (3)	0.12 (1)	0.12 (3.72)
Reptantia	0.51 (9)	0.82 (7)	0.48 (14.49)
Decapoda	8.75 (153)	12.47 (107)	3.61 (109.84)
Euphausiidae	5.49 (96)	0.23 (2)	0.03 (0.96)
Mysidacea	0.11 (2)	0.12 (1)	0.01 (0.19)
Eurydice sp.	0.17 (3)	0.23 (2)	0.02 (0.51)
Isopoda	0.23 (4)	0.47 (4)	0.07 (2.07)
Crustacea	23.96 (419)	36.36 (312)	9.86 (299.77)
Mollusca	3.09 (54)	4.78 (41)	2.78 (84.58)
Haliotis tuberculata	0.06 (1)	0.12 (1)	0.001 (0.02)
Gastropoda	0.34 (6)	0.58 (5)	0.24 (7.42)
Loligo vulgaris	0.11 (2)	0.23 (2)	0.33 (10.12)
Sepia officinalis	0.06 (1)	0.12 (1)	0.11 (3.30)
Octopodidae	0.11 (2)	0.23 (2)	0.70 (21.28)
Cephalopoda	2.40 (42)	3.50 (30)	1.40 (42.45)
Echinodermata	2.17 (38)	3.96 (34)	2.43 (74.00)
Asteroidea	0.06 (1)	0.12 (1)	0.02 (0.74)
Cucumariidae	0.17 (3)	0.35 (3)	0.33 (10.13)
Holoturoidea	1.89 (33)	3.38 (29)	2.03 (61.82)
Echinodermata	0.06 (1)	0.12 (1)	0.04 (1.31)
Urochordata	0.06 (1)	0.12 (1)	0.24 (7.44)
Ascidiacea	0.06 (1)	0.12 (1)	0.24 (7.44)
Chondrichthyes	0.17 (3)	0.35 (3)	0.18 (5.45)
Rajidae	0.06 (1)	0.12 (1)	0.11 (3.30)
Chondrichthyes	0.11(2)	0.23 (2)	0.07 (2.16)
Teleostei	17.78 (311)	32.75 (281)	57.14 (1736.90)
Callionymus sp.	0.23 (4)	0.12 (1)	0.67 (20.36)
Hippocampus ramulosus	0.06 (1)	0.12 (1)	0.01 (0.17)
Sardina pilchardus	0.46 (8)	0.93 (8)	5.50 (167.26)
Scomber scombrus	0.57 (10)	1.05 (9)	6.66 (202.50)
Trachurus trachurus	0.17 (3)	0.23 (2)	3.37 (102.49)
Trisopterus luscus	0.06 (1)	0.12 (1)	0.80 (24.20)
Pleuronectidae	0.11 (2)	0.23 (2)	0.27 (8.19)
Teleostei	16.12 (282)	29.95 (257)	39.86 (1211.783)
Unidentified material	6.23 (109)	12.70 (109)	8.67 (263.54)

when no diet overlap was observed, occurred during the winter between juvenile and adult males, adult females and juvenile males, and adult females and juvenile males.

Discussion

A comparison of the generic diet of *S. canicula* and *S. blainville*

The *S. canicula* specimens captured in 2006 had a broad diet spectrum, which is in agreement with several published studies of this species (Ellis et al., 1996; Olaso, 1998; Serrano et al., 2003; Domi et al., 2005; Olaso et al., 2005). In the present study, the main dietary items of *S. canicula* were Crustacea, Teleostei, and Mollusca (essentially cephalopods), with Polychaeta also as an important food item but in lower magnitude. The most abundant crustaceans belonged to the order Decapoda, which were the dominant prey items in the diet of this species in number, occurrence, and weight. Within this group, the benthic crabs *Pagurus* spp. and *Goneplax rhomboides* were the most abundant species, indicating the ability of *S. canicula* to forage in benthic habitats. Effectively, this species has been described as an active benthic feeder that uses a range of active senses for finding prey (e.g., Olaso et al., 2005; Kimber et al., 2009). In the Bay of Biscay, high prey diversity enabled its classification as a generalist feeding species (Serrano et al., 2003). This species has also been considered an opportunistic scavenger (Olaso et al., 1998; 2005), taking advantage of the discards from local trawling fisheries.

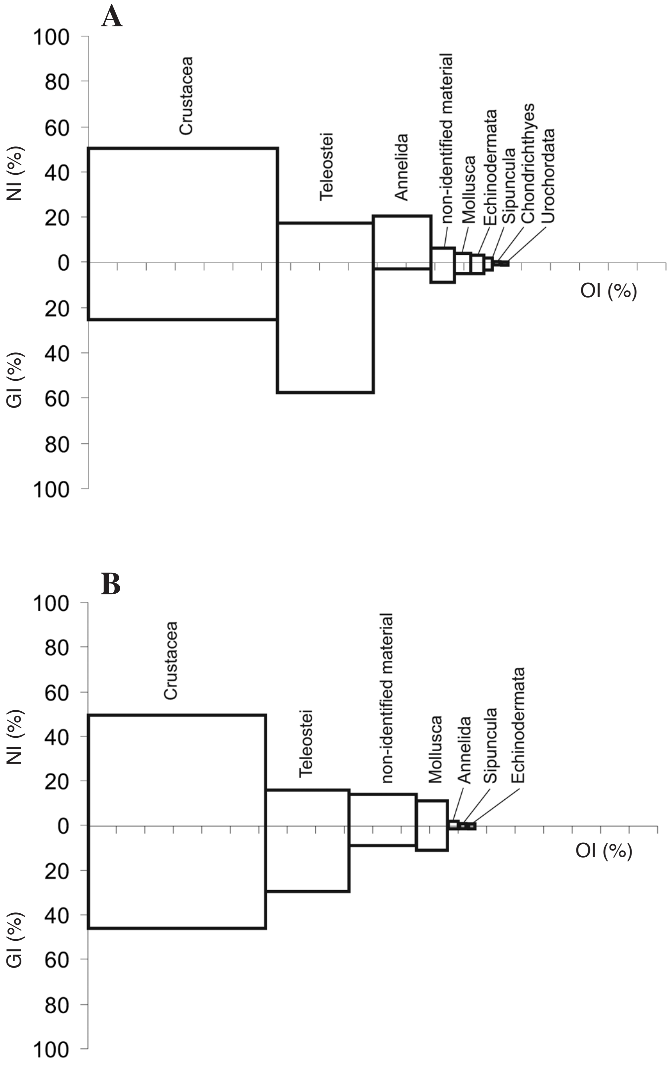

Figure 4

Relative importance of each prey category for (**A**) *Scyliorhinus canicula* and (**B**) *Squalus blainville* determined by using the combined values of the percent number (numerical index, NI), percent weight (gravimetric index, GI), and frequency of occurrence (occurrence index, OI). Each tick mark along the OI axis represents 10%.

The presence of pelagic fish such as *Sardina pilchardus*, *Trachurus trachurus*, and *Scomber scombrus* in the stomach contents of *S. canicula* is also evidence of this species as a pelagic predator. These and other pelagic fish species have also been reported to be an important part of the diet of *S. canicula* captured off the Cantabrian coast of Spain (see Olaso et al., 2005). The presence of Chondrichthyes (apart from Rajidae) in the diet of *S. canicula* may, up to some point, indicate the possibility of cannibalism, as observed in other areas of the Atlantic (Olaso et al., 2005).

For *S. blainville*, as stated previously, information on its diet composition is limited to that supplied by Capapé (1975), who classified it as a voracious species. In the present study, the major prey groups of *S. blainville* were Crustacea (mainly Paguridae and Portunidae decapods), Teleostei (Soleidae), and to a lesser extent, Mollusca (mostly Cephalopoda), all of which (except Teleostei) denote the ability of this species to forage near the seabed, targeting preferentially benthic prey. In the Mediterranean, Teleostei were the most ubiquitous prey items in *S. blainville*, and there was a lower, but similar, occurrence of Mollusca, Sipuncula, and Crustacea (see Capapé, 1975). The differences in diet composition may be attributed to distinct foraging areas, food availability, and depth that characterize the Mediterranean and Atlantic habitats. Ultimately, the diet composition of *S. blainville* likely reflects the availability of prey items in the environment. A congener species, *Squalus acanthias*, captured off Patagonian waters, Argentina, was determined to be a fairly indiscriminate predator (Alonso et al., 2002) as was S. *blainville* in our study. As with *S. canicula*, the compiled indices also revealed

Table 2

Stomach contents of *Squalus blainville*, according to the numeric (NI), occurrence (OI), and gravimetric (GI) indices. Between parentheses is the number of each prey item (NI), the number of nonempty stomachs where each prey item occurred (OI) and the weight (g) of each prey item (GI). Total number of stomachs=297; total number of stomachs with prey=233; total number of prey items=391; total weight of prey items=1420.58 g.

Prey items	NI	OI	GI
Sipuncula	0.77 (3)	1.29 (3)	0.94 (13.32)
Siphonosoma sp.	0.26 (1)	0.43 (1)	0.08 (1.08)
Sipuncula	0.51 (2)	0.86 (2)	0.86 (12.23)
Annelida	1.79 (7)	3.00 (7)	0.06 (0.81)
Polychaeta	1.79 (7)	3.00 (7)	0.06 (0.81)
Crustacea	51.66 (202)	63.52 (148)	44.30 (629.29)
Alpheus glaber	0.26 (1)	0.43 (1)	0.08 (1.16)
Anapagurus laevis	0.26 (1)	0.43 (1)	0.10 (1.48)
Pagurus bernhardus	0.26 (1)	0.43 (1)	0.11 (1.49)
Pagurus spp.	2.81 (11)	3.00 (7)	1.32 (18.71)
Paguridae	0.77 (3)	0.86 (2)	0.28 (3.98)
Polybius henslowii	9.72 (38)	9.87 (23)	28.50 (404.90)
Portunidae	3.84 (15)	3.86 (9)	4.31 (61.25)
Palaemonidae	0.51 (2)	0.43 (1)	0.12 (1.74)
Reptantia	0.26 (1)	0.43 (1)	0.62 (8.81)
Natantia	3.58 (14)	3.00 (7)	0.34 (4.84)
Decapoda	10.23 (40)	14.59 (34)	5.02 (71.28)
Eurydice affinis	0.51 (2)	0.86 (2)	0.03 (0.36)
Eurydice sp.	0.26 (1)	0.43 (1)	0.01 (0.12)
Isopoda	0.77 (3)	1.29 (3)	0.03 (0.36)
Crustacea	17.65 (69)	23.61 (55)	3.44 (48.83)
Mollusca	11.25 (44)	15.88 (37)	13.02 (185.01)
Calliostoma sp.	0.26 (1)	0.43 (1)	0.01 (0.21)
Gastropoda	4.60 (18)	6.44 (15)	1.17 (16.63)
Haliotidae	0.51 (2)	0.43 (1)	0.03 (0.47)
Bivalvia	0.26 (1)	0.43 (1)	0.12 (1.69)
Loligo vulgaris	0.26 (1)	0.43 (1)	1.33 (18.87)
Sepia officinalis	0.77 (3)	0.86 (2)	1.13 (16.02)
Octopodidae	0.77 (3)	1.29 (3)	4.03 (57.30)
Cephalopoda	3.84 (15)	5.58 (13)	5.20 (73.82)
Echinodermata	0.26 (1)	0.43 (1)	0.07 (0.99)
Holoturoidea	0.26 (1)	0.43 (1)	0.07 (0.99)
Teleostei	18.16 (71)	30.04 (70)	30.51 (433.47)
Soleidae	0.26 (1)	0.43 (1)	1.56 (22.18)
Teleostei	17.90 (79)	29.61 (69)	28.95 (411.28)
Unidentified material	16.11 (63)	26.61 (62)	11.10 (157.61)

that crustaceans and teleosts are the most important prey items in the diet of *S. blainville*.

This study also provided important information regarding the potential for resource competition, given the high level of diet overlap between both species. Other than the fact that competition and predation are important features structuring the distribution of marine organisms, little is known about how competition and predation may influence the distribution of elasmobranch fishes (Papastamatiou et al., 2006). From a management point of view, it is important to determine the preferential prey items and feeding habitats of elasmobranchs in order to assess resource partitioning and competitive segregation among species that coexist in similar areas. In fact, given that both species were captured roughly at the same areas, competition should be more intense if both species use these habitats throughout their whole life-cycle. Olaso et al. (2005) observed in the Cantabrian Sea (Spain) a high diet similarity between two scyliorhinid sharks, whose depth range overlaps to some degree.

Nevertheless, the potential for resource competition may be diminished by depth segregation, because *S. blainville* has been recognized to inhabit deeper water than *S. canicula*. The absence of larger *S. blainville* males in the sampled areas may also be an indication of sexual segregation, which to some degree may reduce intraspecific competition. In *S. acanthias*, the onset of sexual maturity has been proposed as one reason for habitat segregation between sexes, triggered by changes in energetic needs, feeding habits, and consequently, habitat use (Alonso et al., 2002).

Seasonal and maturity-stage–related variability in the diet of *S. canicula*

In this study, both adults and juveniles of *S. canicula* exhibited a common trend in their dietary seasonal variations, with Crustacea being the dominant prey items, and Teleostei becoming more important as a food source during spring and summer months. A similar pattern has been observed in the Bay of Biscay (Serrano et al., 2003).

Compared with juveniles, adults showed a higher number of Teleostei in their diet. According to Olaso (1998) and Rodríguez-Cabello et al. (2007), as sharks grow, the consumption of crustaceans is slightly reduced and teleosts become more important as a food source. Although the increase in teleost abundance was somewhat small, the present results are in agreement with those of previous authors. Rodríguez-Cabello et al. (2007) also observed a diet shift from immature to mature stages, which can possibly be influenced by the onset of maturity, and may be related to changes from pelagic to more demersal habitat use (Alonso et al., 2002), as well as reduced handling times and higher foraging success rates for larger prey (Juanes et al., 2001) by older and more experienced foragers. This higher success rate could indicate that adult sharks show some degree of selective feeding, favoring fish instead of invertebrates.

Being a species with a broad spectrum diet, *S. canicula* likely takes advantage of available prey, which have seasonally abundant cycles. Sousa et al. (2005) observed seasonal variations in the composition and abundance of demersal assemblages off the Portuguese Atlantic coast, which can be linked to upper trophic-level predators, such as elasmobranchs. A high abundance of annelid worms was observed in the diet of both juveniles and adults of this species during the winter, which may constitute alternative prey items, given the seasonal reduction in crustaceans and teleosts.

A significant diet overlap was observed throughout the year among all four groups: juvenile males, adult males, juvenile females, and adult females. This overlap would indicate that both sexes and maturity stages share a common habitat. An exception was observed in the winter, during which there was no overlap between adults and juveniles from both sexes, as well as between juvenile and adult males. Such differences in prey composition can be attributed to morphological (i.e., mouth gape) and behavioral traits, such as habitat segregation (Sims et al., 2006), differential habitat use, and reproductive behavior amongst males and females (Sims et al., 2001; Rodríguez-Cabello et al., 2007).

Table 3

Classification of each prey group for *Scyliorhinus canicula* and *Squalus blainville* according to the dietary coefficient (QI, adapted by Salgado et al., 2004) and the index of relative importance (IRI, Rosecchi and Nouaze, 1987). For the QI, prey groups are classified as dominant if QI≥200, secondary if 200>QI≥20, or accidental if QI<20. IRI prey items that constitute 50% of the IRI total sum are considered preferential, prey items that constitute the next 25% are secondary, and the remaining 25% are accessory prey items. %IRI is also shown. Dominant and preferential prey items are highlighted in bold.

	S. canicula					*S. blainville*				
Prey group	QI	Prey type	IRI	%IRI	Prey type	QI	Prey type	IRI	%IRI	Prey type
Sipuncula	2.02	Accidental	5.37	0.07	Accessory	0.72	Accidental	2.19	0.03	Accessory
Annelida	23.88	Secondary	376.36	4.78	Accessory	0.10	Accidental	5.55	0.07	Accessory
Crustacea	**1269.47**	**Dominant**	**4988.03**	**63.31**	**Preferential**	**2288.55**	**Dominant**	**6095.35**	**76.66**	**Preferential**
Mollusca	12.96	Accidental	36.92	0.47	Accessory	146.55	Secondary	385.50	4.85	Accessory
Echinodermata	5.29	Accidental	18.26	0.23	Accessory	0.02	Accidental	0.14	0.002	Accessory
Chondrichthyes	0.03	Accidental	0.12	0.002	Accessory	0.00	—	—	—	—
Teleostei	**1015.97**	**Dominant**	2453.59	31.14	Secondary	**554.08**	**Dominant**	1462.24	18.39	Secondary
Urochordata	0.01	Accidental	0.04	0.0004	Accessory	0.00	—	—	—	—

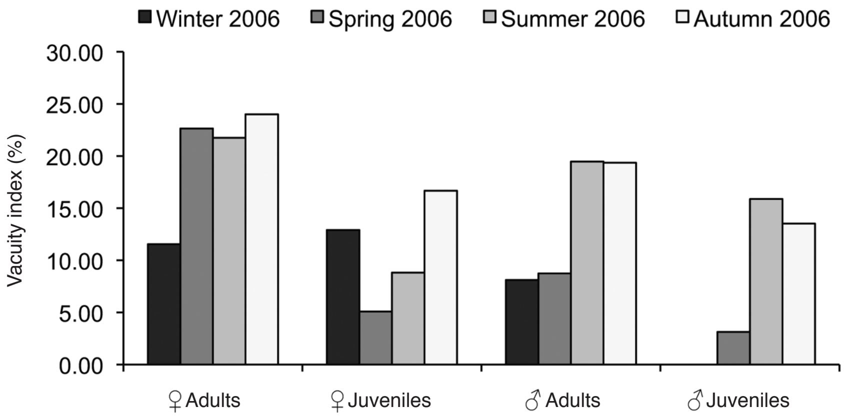

Figure 5

Seasonal variation in the vacuity index (given as the percentage of empty stomachs) for *Scyliorhinus canicula*, separated by sex (females, males) and maturity stage (juveniles, adults).

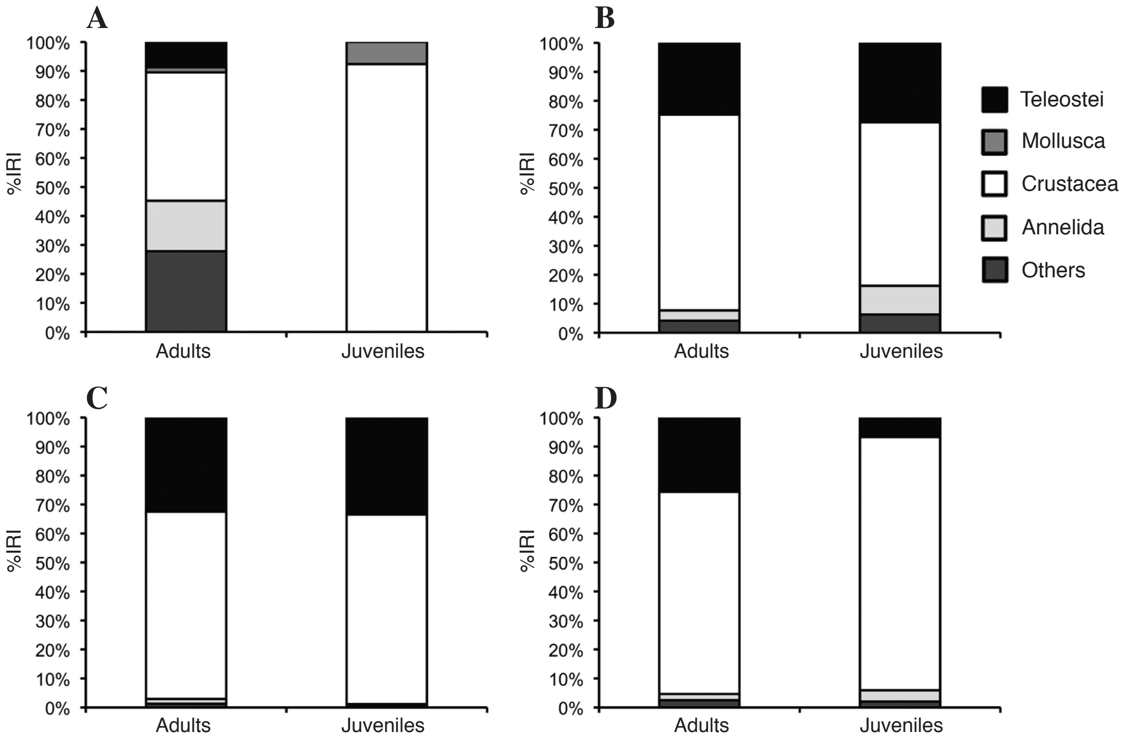

Figure 6

Seasonal variation in diet composition of *Scyliorhinus canicula* males according to the %IRI (% of the index of relative importance), separated according to the maturity stage for (**A**) winter 2006; (**B**) spring 2006; (**C**) summer 2006; and (**D**) autumn 2006. The category "others" represents Echinodermata, Sipuncula, Chondrichthyes, Urochordata, and unidentified material.

The feeding activity was generally higher in the spring and summer, which matches the period of higher abundance of benthic invertebrates and fish. In general, low vacuity was observed in *S. canicula* during the study period, suggesting a more continuous feeding activity, contrary to that observed by Braccini et al. (2005). An exception was observed for *S. canicula* adult females, whose lower feeding activity in spring

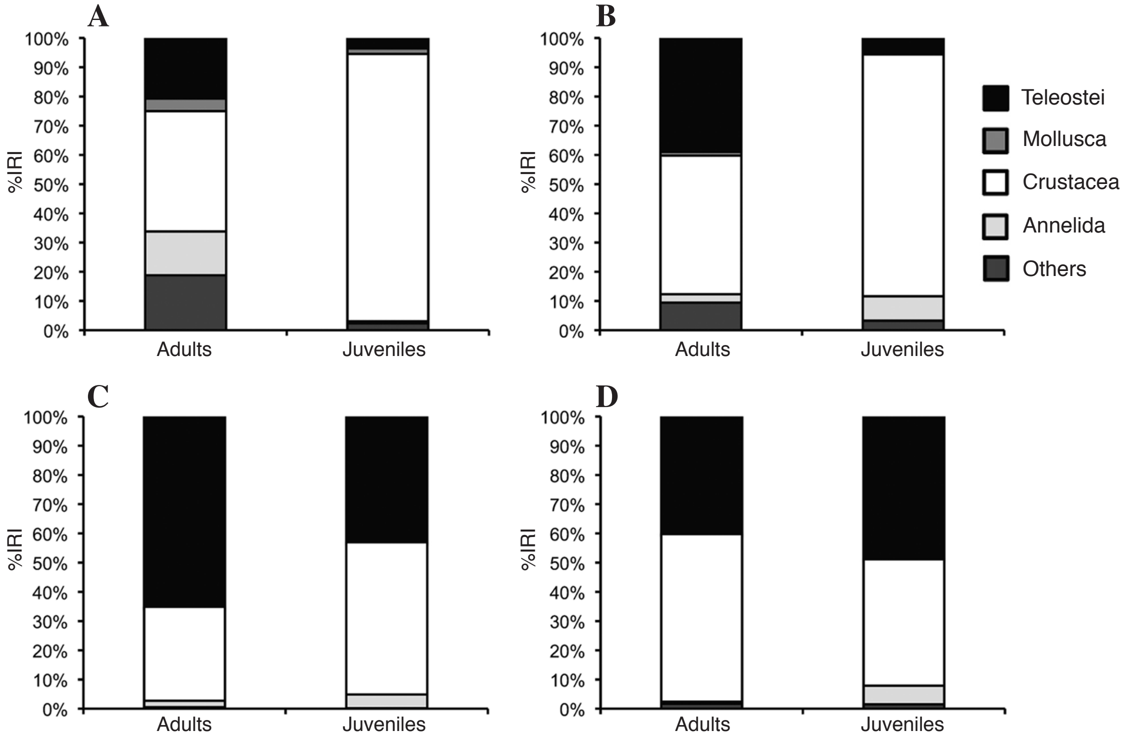

Figure 7

Seasonal variation in diet composition of *Scyliorhinus canicula* females according to the %IRI (% of the index of relative importance), separated according to the maturity stage for (**A**) winter 2006; (**B**) spring 2006; (**C**) summer 2006; and (**D**) autumn 2006. The category "others" represents Echinodermata, Sipuncula, Chondrichthyes, Urochordata, and unidentified material.

Table 4

Seasonal Schoener index (I_S) values for *Scyliorhinus canicula*, in a comparison of diet overlap between males and females by life stage: juvenile and adult. Values above 0.60 (marked with *) are considered a significant diet overlap, according to Wallace and Ramsey (1983).

	♀ Adults ♀ Juveniles	♂ Adults ♂ Juveniles	♀ Adults ♂ Adults	♀ Juveniles ♂ Juveniles	♀ Adults ♂Juveniles	♂ Adults ♀ Juveniles
Winter 2006	0.60*	0.31	0.88*	0.72*	0.37	0.55
Spring 2006	0.71*	0.77*	0.78*	0.78*	0.85*	0.91*
Summer 2006	0.79*	0.88*	0.83*	0.87*	0.75*	0.89*
Autumn 2006	0.86*	0.85*	0.89*	0.83*	0.76*	0.85*

and summer may also be linked to their reproductive cycles (see Capapé, 1974), during which females may reduce feeding activity in favor of courtship and reproduction. This lower feeding activity during higher reproductive activity was also observed by Capapé et al. (2008) along the Mediterranean coast of France and by Craik (1978) for waters off the coast of England. This linkage between reproductive activity, feeding ecology, and differential habitat selection is therefore a critical issue for future research on elasmobranchs.

Variation in feeding ecology of *S. blainville* and *S. canicula* along the Atlantic and Mediterranean waters

When comparing the diet composition of *S. blainville* and *S. canicula* from the present results with diet composition from other studies from the Mediterranean and Atlantic waters, several differences can be observed (Table 5). In general, Mollusca, Crustacea, and Teleostei were the most abundant prey items in the study by

Table 5

Comparison of diet composition of *Scyliorhinus canicula* and *Squalus blainville* in different geographical areas. Values for the prey items are values determined with the occurrence index (OI) (the percentage of each prey item in all nonempty stomachs), except where marked with an asterisk, which are presented as % volume. Superscripts refer to the source study: [1]Olaso et al. (1998), [2]Serrano et al. (2003), [3]present study, [4]Capapé (1974), and [5]Capapé (1975).

	S. canicula				*S. blainville*	
Geographical location	Atlantic, Bay of Biscay (Spain) [1,*]	Atlantic, Bay of Biscay (Spain) [2,*]	Atlantic (Portugal) [3]	Mediterranean (Tunisia) [4]	Atlantic (Portugal) [3]	Mediterranean (Tunisia) [5]
Size range (total length, cm)	14.0–70.0	12.0–68.0	21.5–61.0	Juveniles and adults	32.6–79.6	Juveniles and adults
Mollusca	6.7	3.18	4.78	20.9	26.3	39.0
Polychaeta	4.2	—	19.46	4.9	3.4	0.0
Sipuncula	0.9	—	1.86	0.0	1.3	39.0
Crustacea	31.5	45.61	66.20	38.5	58.8	32.0
Echinodermata	0.0	0.21	3.96	0.0	0.9	0.0
Teleostei	54.6	48.20	32.75	33.7	31.9	72.0
Others	0.0	2.79	13.17	2.0	0.0	3.0

Capapé (1975) and in the present one, with Sipuncula also present in significant amounts in Mediterranean waters. For *S. canicula*, a wider distributional range (from the Atlantic Ocean [Bay of Biscay: Olaso et al., 1998; Serrano et al., 2003] to the Mediterranean Sea [Tunisia: Capapé, 1974]) was obtained from the literature than that determined for *S. blainville*. For *S. canicula*, Crustacea and Teleostei were always among the most abundant prey items, but with high variability in species composition between areas (see Table 5). Polychaeta and Mollusca were also important in the diet of the southernmost populations. As observed previously, given the wide range of items that both species prey on, their diet may reflect the available fauna at each distinct habitat.

Understanding the feeding ecology of sharks is important because changes in diet composition are good indicators of changes in fishery-exploited ecosystems. In fact, fishing activities such as trawling may induce changes in the benthic environment, by modifying the abundance of prey items, as well as increasing the availability of discards, which may constitute alternative food sources for these species (e.g., Olaso et al., 1998; 2005; Stevens et al., 2000). In addition, given the current rate of global exploitation and mortality of sharks (see Herndon et al., 2010 for in-depth details), it becomes imperative to identify their main life-history traits in order to design and implement sustainable management plans for these species.

Conclusions

The present results show that the dietary composition of both species in the study area is quite similar: at a broad taxonomical level, both species feed mostly on crustaceans and teleosts, and therefore the potential invertebrate and fish prey resources are, to a considerable extent, partitioned among these important predators. Although both species feed on a wide range of prey items, changes in crustacean and finfish abundance due to trawling activities and an increase in fishing effort and fishing depth may introduce changes in predator-prey relationships and should be considered when developing management plans for sustainable coastal fisheries. Further work should also include continued interseasonal and interannual sampling, in order to detect the possible influence of fishing activities on benthic organisms and on the diet composition of top predators such as elasmobranchs, as well as on other life-history parameters, such as age and length structure, age at maturity, and, ultimately, stock identification.

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