Feeding ecology of demersal elasmobranchs from the shelf and slope off the Balearic Sea (western Mediterranean)

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SUMMARY: The feeding ecology of eight demersal elasmobranchs, three sharks (*Etmopterus spinax*, *Scyliorhinus canicula* and *Galeus melastomus*) and five batoids (*Myliobatis aquila, Leucoraja naevus, Raja polystigma, R. miraletus* and *R. clavata*), from the Balearic Sea (western Mediterranean) was analyzed. For each species, the diet and feeding habits were characterized by depth strata using quantitative indices such as diet overlap, diet breadth and prey diversity. Diet variation with size and depth were also tested for the most abundant species. For shelf-living species, natantian and reptantian crustaceans together with teleosts were the most important preys. On slope bottoms, euphausiids were the preferential prey for *S. canicula* and *G. melastomus*, while *E. spinax* fed mainly on cephalopods. The most specialist and generalist diet corresponded to *G. melastomus* living on the upper slope and *S. canicula* from the continental shelf, respectively. High overlap was found between all the skates on the continental shelf and the sympatric sharks *S. canicula* and *G. melastomus* on the slope. Significant overlap was also found between *S. canicula* and *R. clavata* on the continental shelf. Size was found to significantly affect the diet of *S. canicula*, *G. melastomus* and *R. clavata*, whereas depth affected exclusively *S. canicula*.

Keywords: Elasmobranch, batoid, shark, feeding habits, diet overlap, niche breadth, Mediterranean.

RESUMEN: ECOLOGÍA ALIMENTARIA DE ELASMOBRANQUIOS DEMERSALES DE PLATAFORMA Y TALUD EN AGUAS DE LAS ISLAS BALEARES (MEDITERRÁNEO OCCIDENTAL). – Se estudia la ecología alimentaria de ocho elasmobranquios demersales, tres tiburones (*Etmopterus spinax, Scyliorhinus canicula* y *Galeus melastomus*) y cinco rayas (*Myliobatis aquila, Leucoraja naevus, Raja polystigma, R. miraletus* y *R. clavata*), del mar Balear (Mediterráneo Occidental). Para cada especie se caracterizó la dieta y la estrategia alimentaria por estratos de profundidad mediante diferentes índices cuantitativos. También se analizó la variación intraespecífica de la dieta con la talla y la profundidad en las especies más abundantes. Las presas más frecuentes en especies de la plataforma continental fueron los peces y los crustáceos natantia y reptantia. En aguas del talud las presas principales de *S. canicula* y *G. melastomus* fueron los eufausiáceos, mientras que *E. spinax* consumió preferentemente cefalópodos. Las especies con la dieta más especializada y más generalista fueron *G. melastomus* del talud superior y *S. canicula* de la plataforma costera, respectivamente. En aguas de la plataforma se detectó solapamiento de dieta entre todas las especies de batoideos, así como entre *S. canicula* y *R. clavata*; el solapamiento fue significativo también entre *S. canicula* y *G. melastomus* del talud. Se observaron cambios ontogénicos en la dieta de *S. canicula*, *G. melastomus* y *R. clavata*, mientras que la única especie que mostró cambios de dieta con la profundidad fue *S. canicula*.

Palabras clave: elasmobranquio, batoideo, tiburón, estrategia alimentaria, solapamiento de dieta, amplitud de nicho, Mediterráneo.

INTRODUCTION

Trophic relationships are fundamental to understanding biological interactions in animal communities and how they respond to human exploitation. Elasmobranchs are top predators playing an important role in the marine ecosystems with a top-down control on the size and dynamics of many species (Wetherbee and Cortes, 2004). Globally, there is increasing evidence that elasmobranchs are more affected than teleosts by fishing exploitation (Stevens *et al*., 2000). Insular areas from the western and central Mediterranean sustain

elasmobranch assemblages with higher diversity and abundance than adjacent mainland areas (Massutí and Moranta, 2003).

Despite the importance of feeding relationships to understand the food structure and dynamics of marine ecosystems, little is known about the feeding ecology of most elasmobranchs (Heithaus, 2004; Wetherbee and Cortes, 2004). This is especially true for batoids, which have received considerably less attention than sharks at a worldwide level (Ishihara, 1990; Motta, 2004). Research on trophic relationships among elasmobranch sympatric species is also scarce in the western Mediterranean, where selachian feeding habits have been studied exclusively with regard to single species and groups of two or three species with similar ecological roles or habitat distribution (Macpherson, 1980, Carrason *et al.*, 1992; Saidi *et al.*, 2009). Furthermore, few studies have focussed on the feeding ecology of batoids individual species in the Mediterranean Sea (Jardas *et al.*, 2004; Romanelli *et al.*, 2007; Saglam and Bascinar, 2008).

In the present paper we analyze the diet, feeding habits and trophic interactions for three selachians (*Etmopterus spinax*, *Scyliorhinus canicula* and *Galeus melastomus*) and five batoids (*Myliobatis aquila*, *Leucoraja naevus*, *Raja polystigma*, *R. miraletus* and *R. clavata*) from waters off the Balearic Islands (western Mediterranean).

MATERIALS AND METHODS

The elasmobranch species were taken from the fishery-independent MEDITS bottom trawl surveys conducted around the Balearic Islands (Fig. 1) in early summer from 2007 to 2009. Both sampling scheme and gear (GOC-73) were the same as those used throughout the Mediterranean in the MEDITS programme (Bertrand, 2002). A total of 141 hauls were performed during daylight hours between 45 and 755 m depth. Whenever possible, ten individuals of each elasmobranch species from each haul were separated and their total length, weight and sex were noted. Fresh stomach contents were identified on board to the lowest possible taxonomic level and then all prey items were counted and their volume was measured with a calibrated device used in previous studies (Olaso *et al.*, 1998).

The diet of each elasmobranch species was quantified using the following indices: 1) frequency of occurrence (%F), percentage of stomachs with a specific type of prey in relation to the total number of stomachs containing food; 2) numerical (%N) and volumetric (%V) composition, expressed as the percentage contribution of each prey to the whole content, in number or volume respectively; 3) index of relative importance (IRI=%F(%N+%V), which was standardized following %IRI=(IRI/∑IRI)×100 (Cortes, 1997); 4) vacuity index (*v*), the percentage of empty stomachs; and 5) diet breadth, which was calculated using the Levin's standardized index:
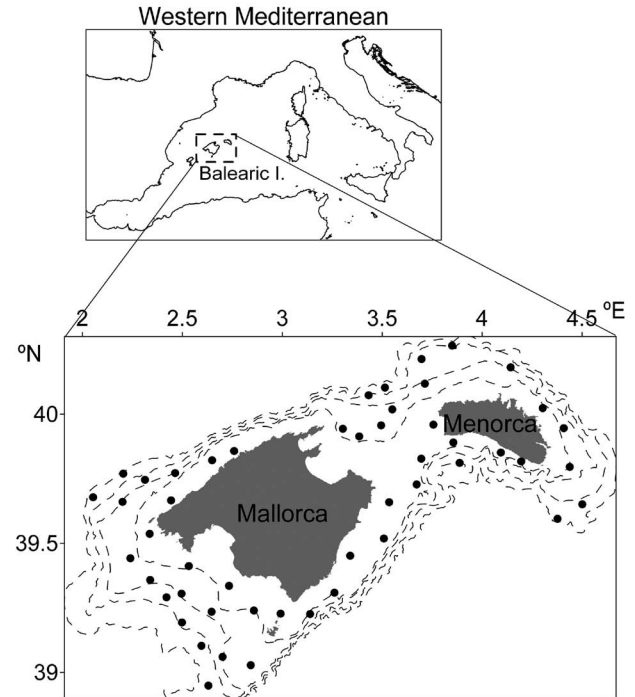

FIG. 1. – Map of sampling sites of the eight elasmobranch species taken in the Balearic Islands (western Mediterranean). The 100, 200, 500 and 800 m isobaths are shown.

$$B_i = \frac{1}{n-1}\left(\frac{1}{\sum_j p_{ij}^2} - 1\right),$$

where p_{ij} is the proportion of diet of predator i that is made up of prey j and n is the number of prey categories. This index ranges from 0 to 1, low values indicating diets dominated by a few prey items (specialist predators) and higher values indicating generalist diets (Krebs, 1999); and 6) species diversity in both prey number (H'_n) and prey volume (H'_v) calculated using the Shannon-Wiener index.

To standardize data and to facilitate diet comparisons and analyses, the following twelve major prey categories were established: Polychaeta, Sipuncula, Gastropoda, Bivalvia, Cephalopoda, Euphausiacea, Amphipoda, Isopoda, Mysidacea, Crustacea Reptantia, Crustacea Natantia and Teleostea. Prey categories with frequency of occurrence lower than 3% and unidentifiable remains were excluded from these analyses. Diet overlap between species was calculated using the Schoener index (Hurlbert, 1978), which ranges from 0 (no overlap) to 1 (complete overlap), with values greater than 0.6 representing a significant overlap (Sala and Ballesteros, 1997; Wallace, 1981). In order to compare exclusively coexisting species, all indexes characterizing the diet were analyzed separately for the following four bathymetric strata described in the study area (Ordines *et al.*, 2011): 1) continental shelf (CS: 45-180 m); 2) shelf-break (SB: 180-330 m); 3) upper slope (US: 330-495 m); and 4) middle slope (MS: 495-750 m).

TABLE 1. – General information and diet composition (standardized index of relative importance, %IRI) of eight elasmobranch species caught at different bathymetric strata (CS, continental shelf; SB, shelf-break; US, upper slope; MS, middle slope) in the Balearic Sea (western Mediterranean). N, sample size; TL, total length; WR, weight range; DR, depth range; v, vacuity index; H'$_n$, H'$_v$: Shannon-Wiener diversity in number and volume respectively; and B$_i$, Levin's niche breadth. Values in brackets are the number of taxa in the twelve major taxonomic groups of prey (see Supplementary material Appendix 1). *R.pol.*, *R. polystigma*; *M.aqu.*, *M. aquila*; *L.nae.*, *L. naevus*; *R.mir.*, *R. miraletus*.

	R.pol. CS	*M.aqu.* CS	*L.nae.* CS	*R.mir.* CS	*R. clavata* CS	*R. clavata* SB	*R. clavata* US	*S. canicula* CS	*S. canicula* SB	*S. canicula* US	*G. melastomus* US	*G. melastomus* MS	*E. spinax* MS
N	15	23	27	31	266	48	6	766	66	60	170	167	46
TL (cm)	28-45	51-116	22-52	24-43	18-88	18-77	64-91	11-53	14-46	15-49	14-35	10-63	11-47
WR (g)	91-546	514-4201	59-864	66-421	25-4005	27-2612	1445-4458	11-470	20-336	23-390	7-106	2-628	5-514
DR (m)	63-172	51-63	107-174	58-83	52-174	249-256	355-691	53-174	249-256	355-444	355-450	593-755	597-755
Polychaeta	1.17 (1)	8.07 (1)	0.29 (1)	0.05 (1)	0.08 (1)			22.10 (2)	12.53 (1)	0.5 (1)			0.26 (1)
Sipuncula		1.63 (2)						2.07 (2)					
Gastropoda	0.5 (1)	26.3 (3)			0.08 (1)	0.59 (8)	0.15 (1)	2.38 (6)					
Bivalvia		6.28 (1)				<0.01 (1)		<0.01 (1)					
Cephalopoda	0.5 (1)	0.13 (1)			0.08 (1)	0.59 (6)	0.15 (1)	2.36 (4)	0.60 (1)	0.23 (1)	0.01 (1)	15.93 (8)	64.26 (4)
Euphausiacea						5.13 (2)	1.19 (1)	2.34 (2)	72.38 (2)	77.64 (2)	92.59 (2)	42.97 (2)	0.90 (2)
Amphipoda	1.10 (1)	0.09 (1)	2.78 (1)	3.87 (1)	0.04 (1)	0.24 (1)		0.81 (2)		0.52 (1)	0.32 (2)	0.15 (2)	
Isopoda	7.22 (1)		1.08 (1)	0.04 (1)	3.83 (1)	1.19 (1)		0.51 (1)	1.93 (1)	0.95 (1)		0.01 (1)	0.37 (1)
Mysidacea	6.63 (2)		2.66 (1)	0.36 (1)	2.55 (2)	10.49 (2)		7.40 (2)	0.21 (1)	0.21 (2)	<0.01 (1)	0.01 (2)	
Reptantia	3.35 (3)	81.94 (5)	1.32 (2)	54.88 (2)	29.39 (18)	12.96 (10)	40.61 (3)	34.71 (19)	0.15 (2)	0.53 (5)	0.02 (2)	0.08 (3)	0.08 (1)
Natantia	67.97 (4)	1.10 (2)	50.88 (5)	34.78 (5)	27.19 (8)	31.84 (5)	12.87 (3)	8.62 (11)	5.74 (4)	2.03 (7)	2.60 (7)	14.19 (10)	8.54 (4)
Teleostea	13.51 (2)		40.80 (2)	5.88 (3)	31.08 (18)	41.82 (9)	45.87 (3)	17.85 (16)	5.46 (3)	16.68 (3)	4.42 (5)	25.61 (9)	25.25 (4)
N prey items	15	15	13	15	63	31	11	79	19	25	21	45	16
v (%)	0	4.3	11.1	0	9	10.4	0	20	33.3	18.3	27.7	19.8	45.7
H'$_n$	3.22	2.18	3.05	2.83	3.24	3.95	3.27	4.10	2.16	2.09	2.07	3.50	3.44
H'$_v$	3.23	2.53	2.26	2.69	4.55	3.64	2.86	4.30	3.39	3.12	2.83	3.93	2.97
B$_i$	0.49	0.26	0.36	0.31	0.47	0.49	0.23	0.67	0.49	0.47	0.17	0.43	0.28

Diet overlap, niche breadth and diet diversities were calculated using Ecological Methodology software version 7.0 (Krebs, 1999).

Intra-specific trends in the diet related to predator size (total length in cm), and depth (m) of the most abundant species (*S. canicula*, *G. melastomus* and *R. clavata*) were studied applying partial canonical correspondence analysis (pCCA) using CANOCO (ter Braak and Smilauer, 1998). In the pCCA procedure, one explanatory variable (size or depth in this case) was set as a covariable, which allowed the effect of the other one to be tested after the variation explained by the covariable had been factored out. The significance of the explanatory variables was assessed by means of the Monte Carlo permutation-based test. Before the design of the model, the interactions between explanatory variables were analyzed and found to be non-significant.

RESULTS

General information for the eight species studied (e.g. sample size, size and weight range and depth range), the diet composition considering the twelve main major prey categories, and the dietary indexes used (e.g. vacuity, diversity, niche breadth) are shown in Table 1. Total sample sizes were rather unbalanced, ranging from the 15 individuals of *R. polystigma* to about 900 of *S. canicula*. The number of different prey items ranged from 11 in *R. clavata* from the US to 79 in *S. canicula* from the CS. Considering depth strata, sample sizes ranged from 6 individuals of *R. clavata* caught on the US to 766 *S. canicula* individuals from the MS. With the exception of the batoids *M. aquila*

and *R. clavata*, all other species had maximum sizes smaller than 65 cm length. Whereas *S. canicula* and *R. clavata* inhabited all depth strata, the other batoid and shark species were caught exclusively on the shelf and slope, respectively. The percentage of empty stomachs was clearly higher in selachian (18-46%) than in batoid species (0-11%). Globally, the highest dietary diversity was found on the CS, where *S. canicula* and *R. clavata* showed the highest values in terms of numbers (4.10) and volume (4.55) respectively (Table 1). The lowest diversity in numbers was found on the US (~2.1 for both *G. melastomus* and *S. canicula*) but the lowest in weight occurred on the CS (2.3 for *L. naevus*). The most generalist and specialist diets were found in *S. canicula* from the CS (B$_i$=0.67) and *G. melastomus* from the US (B$_i$=0.17). The rest of species had values ranging from 0.26 to 0.49, indicating moderate levels of feeding specialization.

The diet composition of each species is summarized in this paragraph, taking into account both the main prey groups (Table 1) and the lowest identified taxonomic levels (Supplementary material Appendix 1). Beginning with the batoids, natantian crustaceans (68%IRI) followed at some distance by teleosts (13%IRI), isopods (7%IRI) and mysids (7%IRI) were the most important preys of *R. polystigma*. The diet of *M. aquila* was based on anomuran crustaceans (63%IRI) such as *Dardanus arrosor* (18%IRI) and unidentified Paguridae species (11%IRI), molluscs (26%IRI) and polychaetes (8%IRI). The diet of *L. naevus* was almost exclusively based on natantian crustaceans (51%IRI), mainly *Solenocera membranacea* (15%IRI), and teleosts (41%IRI). Brachyuran (55%IRI) and natantian (35%IRI) crustaceans, followed at some distance by

TABLE 2. – Diet overlap (Schoener index, SI) for coexisting elasmobranch species on the continental shelf, shelf break, upper and middle slope of the western Mediterranean. Biologically significant diet overlaps (SI > 0.6) are in bold.

Species	SI
Continental shelf	
R. clavata vs M. aquila	0.28
R. miraletus vs R. clavata	**0.73**
R. miraletus vs M. aquila	0.47
L. naevus vs M. aquila	0.16
L. naevus vs R. miraletus	**0.65**
L. naevus vs R. clavata	**0.74**
R. polystigma vs R. clavata	**0.76**
R. polystigma vs R. miraletus	**0.65**
R. polystigma vs L. naevus	**0.83**
S. canicula vs M. aquila	0.57
S. canicula vs R. clavata	**0.71**
S. canicula vs R. miraletus	0.58
S. canicula vs L. naevus	0.51
S. canicula vs R. ploystigma	0.59
Shelf break	
S. canicula vs R. clavata	0.42
Upper slope	
S. canicula vs G. melastomus	**0.73**
S. canicula vs R. clavata	0.37
G. melastomus vs R. clavata	0.31
Middle slope	
E. spinax vs G. melastomus	**0.67**

TABLE 3. – Results of the partial canonical correspondence analysis (pCCA) testing the effects of predator size (total length, cm) and depth (m) on the volumetric contribution of the diets of the sharks *Scyliorhinus canicula* and *Galeus melastomus* and the skate *Raja clavata*. The percentage of variance explained (VE), the F-ratio, and the *P*-value are shown (ns: non-significant effect).

| Predator species | Size | | | Depth | | |
	VE	F-ratio	*P*	VE	F-ratio	*P*
S. canicula	4.12	4.25	<0.01	7.42	7.65	<0.01
G. melastomus	9.63	8.37	<0.01	2.13	1.88	n.s.
R. clavata	11.54	15.64	<0.01	1.40	1.85	n.s.

teleosts (6%IRI), were the most important preys of *R. miraletus*. The skate *R. clavata* preyed on teleosts (31%IRI), natantian (27%IRI) and reptantian (29%IRI) crustaceans on the CS, but on teleosts (42%IRI) and natantians (32%IRI) on the SB; teleosts (46%IRI) and reptantians (41%IRI) were the main preys on the US, although these values must be taken with caution owing to the small sample size (N=6). Concerning the sharks, *S. canicula* preyed on reptantians (35%IRI), polychaetes (22%IRI) and teleosts (18%IRI) on the CS; euphausiids were the most important prey on both the SB (72%IRI) and US (78%IRI), followed by polychaetes (12%IRI) and teleosts (17%IRI), respectively. The catshark *G. melastomus* preyed almost exclusively on euphausiids on the US (93% IRI), but on a mixture of euphausiids (43%IRI), teleosts (26%IRI), cephalopods (16%IRI) and natantians (14%IRI) on the MS. Finally, the diet of *E. spinax* consisted primarily of cephalopods (64%IRI) and teleosts (25%IRI), followed at some distance by natantian crustaceans (9%IRI).

Diet overlap was biologically significant (>0.6) in 9 of the 19 coexisting species (Table 2). In other four cases, however, the overlap remained close to the cut-off value of significance (0.51-0.59). Diet overlap was significant among different pairs of skate species and between the shark *S. canicula* and *R. clavata* on the CS. Overlap also existed between the sharks *S. canicula* and *G. melastomus* on the US and between *E. spinax* and *G. melastomus* on the MS.

Considering intra-specific trends for the three most abundant species, size was found to significantly affect the diet of all of them, whereas depth affected exclusively the shark *S. canicula* (Table 3). There existed a gradient of increasing prey size with increasing predator size in all three species, ranging from small-sized

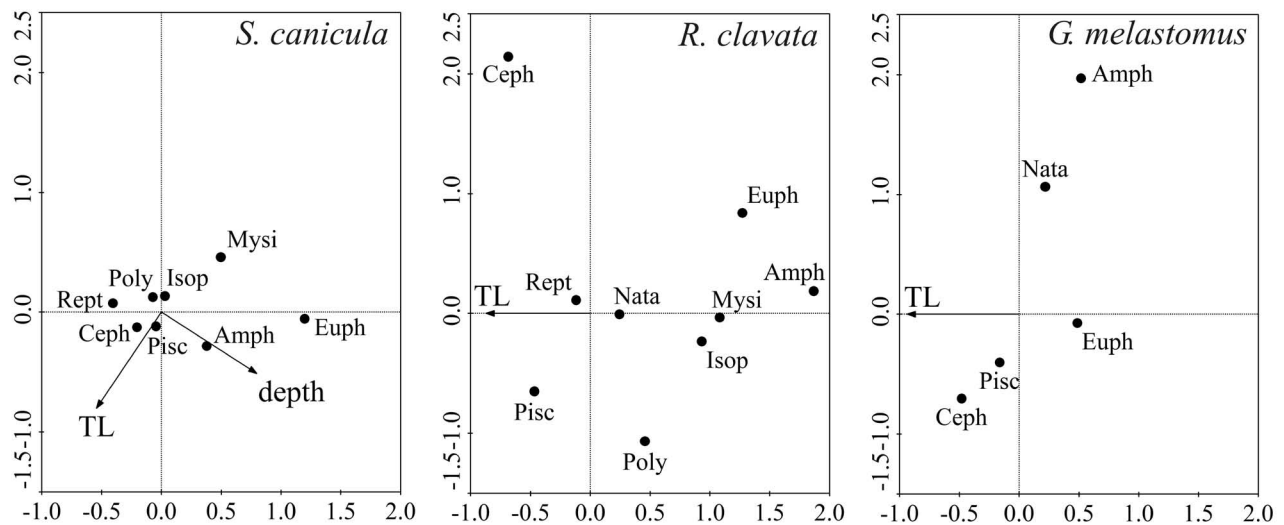FIG. 2. – Partial canonical correspondence analysis (pCCA) biplots of the explanatory variables predator size (total length, cm) and depth of capture (in m) and nine different prey categories for the sharks *Scyliorhinus canicula* and *Galeus melastomus* and the skate *Raja clavata*. Euph, euphausiids; Amph, amphipods; Mysi, mysids; Isop, isopods; Poly, polychaetes; Nata, natantia; Rept, reptantia; Ceph, cephalopods; Pisc, pisces.

preys such as amphipods, euphausiids and mysids to large-sized preys such as cephalopods and teleosts (Fig. 2). In the case of the bathymetric effect on *S. canicula*, the separation along the depth axis seems to be related to preferences for prey such as polychaetes and reptantian crustaceans in the shallow populations and euphausiids in the deeper populations.

DISCUSSION

To our knowledge, this is the first study in the Mediterranean dealing with the trophic ecology (e.g. diet composition, diet diversity, niche breadth, diet overlap) of such a large number of elasmobranchs, since we have analyzed data of the most abundant demersal species from our study area. In total, three shark species (*Etmopterus spinax*, *Scyliorhinus canicula* and *Galeus melastomus*), and five batoid species (*Myliobatis aquila*, *Leucoraja naevus*, *Raja polystigma*, *R. miraletus* and *R. clavata*) inhabiting the shelf (CS: shelf and SB: shelf break) and the slope (US: upper slope and MS: middle slope) were analyzed. Other studies in the Mediterranean analyzed at most three elasmobranch species (Macpherson, 1980).

The vacuity index was clearly higher in sharks (18-46%) than in batoids (0-10%), which could be related to the well-known decrease in trophic resources with increasing depth (Carrasson *et al*., 1992; Olaso *et al*., 2005). Fittingly, the shark *E. spinax,* which only inhabits the deepest stratum (MS), had nearly half of their stomachs empty. The fact that *E. spinax* feeds preferentially on cephalopods, which in general have high nutritional values and low non-edible remains (Boyle and Rodhouse, 2005), may also influence such a high vacuity index. With the only exception of *S. canicula* from the CS, which showed the most generalist diet (0.67), and *G. melastomus* from the US, which showed the most specialist behaviour (0.17), all other species had niche breadth values between 0.26 and 0.49 that might be associated with moderate levels of specialization. Such moderate levels could be related to the high species richness and biomasses of shelf benthic ecosystems from the Balearic Islands (Massutí and Reñones, 2005; Ordines and Massutí, 2009). Lower niche breadths on the slope than on the shelf might also be related to the already mentioned decrease in trophic resources with depth. As pointed out by Carrasson *et al*. (1992), the decrease in the number of prey per stomach and the trophic diversity with depth are indicative of the increasing resource scarceness along the depth gradient in the western Mediterranean. On the CS, diet overlap was biologically significant among all the batoid species, except *M. aquila*, and between the skate *R. clavata* and the shark *S. canicula.* The lack of significant dietary differences among comparably-sized shelf skates suggests that inter-specific resource competition was not intense (Bizzarro *et al*., 2007). High values of overlap do not necessarily imply competition, except when resources are in short supply (Macpherson, 1977;

Cartes, 1998). The coexistence between species with similar trophic habits and a narrow niche breadth might be due to the abundance of food resources (Collwell and Futuyma, 1971). As mentioned above, this would be the case on the rich shelf bottoms of our study area. Otherwise, species that are spatially segregated are not driven to differentiate their diets and may easily converge in the use of resources overlapping areas (Ross, 1977). Elasmobranch species from the Balearic Islands showed different optimum depths (Ordines *et al*., 2011), which could indicate a sort of fine-tuned bathymetric segregation, though they coexisted on shelf and slope bottoms.

In accordance with previous studies carried out in both the Mediterranean (Romanelli *et al*., 2007; Saglam and Bascinar, 2008) and the Atlantic (Ellis *et al*., 1996; Gomes *et al*., 1998; Farias *et al*., 2006), the dominant prey taxa in all the batoid species, except *M. aquila*, were natantian crustaceans and teleosts. However, the diet of *M. aquila* was highly specialized in anomuran crustaceans and non-cephalopod molluscs (mainly bivalves), two prey groups that, with the exception of anomurans in *S. canicula*, were barely present in the rest of species; *M. aquila* was also characterized by being the only species that did not prey on teleosts and by the moderate importance of polychaetes. Such important differences would explain the lack of diet overlap between *M. aquila* and the rest of the elasmobranch species. In general, other authors mentioned the same food preferences for *M. aquila* in the Mediterranean (Azouz and Capapé, 1971; Capapé and Quignard, 1974; Capapé, 1976; Jardas *et al*., 2004) but differed with regard to such a specialized diet based in anomuran crustaceans. The diet of *R. miraletus* differed slightly from that of the other skates, as it preyed mainly on a mixture of brachyuran crabs and natantian crustaceans and displayed a narrow niche breadth. In accordance with previous studies (Farias *et al*., 2006; Saglam and Bascinar, 2008), the skate *R. clavata* based its diet on teleosts and reptantian and natantian crustaceans, showing no trend with depth.

The shark *S. canicula* inhabiting the CS showed the highest diversity of all species-strata, having a diet composed of a mixture dominated by reptantian crustaceans, polychaetes, teleosts and natantians. Prey diversity, however, decreased with depth, mainly because the shark changed to a diet based on euphausiids in deeper waters. Secondary preys were polychaetes and teleosts on the SB and US, respectively. To our knowledge, the importance of polychaetes in the diet of *S. canicula* has not been reported previously. Polychaetes were also found in all the batoids analyzed, but they only constituted accessory preys. In the Cantabrian Sea, Serrano *et al*. (2003) found that polychaetes preyed by *S. canicula* belonged to surface and subsurface mobile families. As Olaso *et al*. (1998) pointed out, referring to the presence of subsurface species in the diet of *S. canicula*, high consumption rates of polychaetes might indicate the availability of endobenthic preys that are

exposed to predation because of the physical effects of trawling.

The diets of the catsharks *S. canicula* and *G. melastomus* overlapped on the US, where both species preyed mainly on euphausiids. The shark *G. melastomus* displays a marked bathymetric segregation of populations in the study area, with recruits and adults inhabiting the US and MS, respectively (Massutí and Moranta, 2003). Consequently, competition for resources on the US, namely euphausiids, occurs between adults of *S. canicula* and recruits of *G. melastomus*. However, it is also possible that competition is lessened by a sort of size selection of preys owing to the marked size differences between the small-sized *G. melastomus* and the adults of *S. canicula*. The occurrence of euphausiids in the diet of a large number of species inhabiting the SB and US may be due to the high abundance of these organisms in those strata (Cartes *et al.*, 2009).

The diets of the sharks *E. spinax* and *G. melastomus,* which were the only species coexisting on the MS, showed both similarities and notable differences. The similarities were that both species had comparatively low to moderate values of natantian crustaceans (8-14%IRI) and high values of teleosts (25%IRI). The differences appeared in the relative importance of euphausiids and cephalopods, which showed an inverse pattern in the two species: while cephalopods were the most important prey (64%IRI) and euphausiids only vestigial (1%IRI) for *E. spinax*, values in *G. melastomus* were inverted (16 and 43%IRI, respectively). Given that both species showed significant diet overlap, this inverse pattern would be a mechanism to lessen competition on the MS. In agreement with this, Macpherson (1980) found that the diet overlap between these two species was significant for all size classes and seasons in the western Mediterranean. Both sharks consumed mesopelagic preys that were typical inhabitants of the Benthic Boundary Layer (BBL) (Angel and Boxshall, 1990), such as myctophids, euphausiids (e.g. *Meganycthyphanes norvegica*) and cephalopods (e.g. *Histioteuthis* spp.). These mesopelagic preys would be caught when the BBL remains close to the bottom, indicating the high dependence of slope demersal elasmobranchs on the pelagic ecosystem (Bizzarro *et al.*, 2007; Rinewalt *et al.*, 2007). A high dietary overlap between these two species was also reported in the Cantabrian Sea (Preciado *et al.*, 2009) but, in contrast with the preference of *E. spinax* for cephalopods in our samples, that population preyed mainly on euphausiids.

The three most abundant elasmobranch species (*R. clavata*, *G. melastomus* and *S. canicula*) showed ontogenetic variations in diet. The trend was the same in the three species, with small individuals preying mainly on crustaceans but changing to a diet based on fishes in large-sized individuals. Such ontogenetic shifts have already been reported in other areas for both the two catsharks (Macpherson, 1980; Olaso *et al.*, 2005) and the skate (Holden and Tucker, 1974; Ellis *et al.*, 1996; Saglam and Bascinar, 2008). However, results

of some studies focusing on *R. clavata* do not agree with this trend, such as the shift from benthic shrimps to pelagic crabs reported by Farias *et al.* (2006) and the lack of differences with size found by Morato *et al.* (2003). Ontogenetic shifts in diet are generally related to higher metabolic requirements of larger individuals (Carlson *et al.*, 2004) or to resource partitioning (Werner and Gilliam, 1984). The metabolic explanation would apply to *S. canicula*, because juvenile and adult populations live on different bathymetric strata in the Mediterranean (D'Onghia *et al.*, 1995; Massutí and Moranta, 2003). Given that there is no bathymetric segregation of size classes either in *R. clavata* or in the populations of *G. melastomus* living on the MS in our study area (Massutí and Moranta, 2003), the observed ontogenetic shift might be a way of avoiding intraspecific competition.

To conclude, the present work is a comprehensive study on the feeding ecology of the most abundant demersal elasmobranchs, including both shark and batoid species, from an insular area geographically separated from the mainland in the western Mediterranean. Our results represent an important step forward in the knowledge of the trophic interactions among these elasmobranchs, but further studies of aspects not dealt with here, such as seasonal variations in diet, prey availability and diet of the coexisting teleost community, are needed to improve the assessment of the role played by these species on the marine food webs from this area.

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SUPPLEMENTARY MATERIAL

The following Appendix is available through the web page
http://www.icm.csic.es/scimar/supplm/sm75n4633sm.pdf

Appendix 1. – Diet composition to the lowest possible taxon of eight elasmobranch species (five skates and three sharks) from the Balearic Islands (western Mediterranean).

Feeding ecology of demersal elasmobranchs from the shelf and slope off the Balearic Sea (western Mediterranean)

MARÍA VALLS, ANTONI QUETGLAS, FRANCESC ORDINES and JOAN MORANTA

Supplementary material

APPENDIX 1. – Diet composition to the lowest possible taxon of eight elasmobranch species (five skates and three sharks) from the Balearic Islands (western Mediterranean). Frequency of occurrence (%F), the percentage of stomachs with a specific type of prey in relation to the total number of stomachs containing food; volumetric composition (%V), expressed as the percentage contribution of each prey in volume to the whole content; standardized index of relative importance (%IRI=(IRI/∑IRI)×100), where IRI=%F(%N+%V) and %N is the numeric composition or the percentage of each prey in number to the whole content. Unid. stands for unidentified.

Prey items	R. polystigma %F	%V	%IRI	M. aquila %F	%V	%IRI	L. naevus %F	%V	%IRI	R. miraletus %F	%V	%IRI	R. clavata %F	%V	%IRI	S. canicula %F	%V	%IRI	G. melastomus %F	%V	%IRI	E. spinax %F	%V	%IRI
ALGAE																1.27	0.16	0.02	0.39	0.12	<0.01			
Phyllophora nervosa																0.14	0.01	<0.01						
Posidonia oceanica																0.14	<0.01	<0.01						
Algae unid.																0.85	0.15	0.01	0.39	0.12	<0.01			
POLYCHAETA	13.33	4.18	1.17	36.36	4.87	8.07	4.17	0.17	0.29	3.23	0.09	0.05	4.81	0.35	0.09	31.90	12.38	22.45				4.00	0.16	0.26
Aphroditidae																1.56	0.49	0.04						
Polychaeta unid.	13.33	4.18	1.17	36.36	4.87	8.07	4.17	0.17	0.29	3.23	0.09	0.05	4.81	0.35	0.09	30.34	11.90	20.55				4.00	0.16	0.26
SIPUNCULA				13.64	8.02	1.63										7.65	6.30	2.02						
Sipunculidae				9.09	2.54	0.61										7.51	6.14	1.94						
Sipunculus nudus				4.55	5.47	0.24										0.14	0.15	<0.01						
NEMERTEA																0.28	0.25	<0.01						
MOLLUSCA	6.67	2.20	0.50	68.20	25.66	26.30				3.23	0.10	0.08	6.87	6.11	0.78	11.05	9.67	4.54	15.95	24.24	8.39	64.00	55.75	64.26
BIVALVIA				31.82	14.93	6.28							0.69	0.18	<0.01	0.14	0.05	<0.01						
GASTROPODA				13.64	4.41	0.86										0.14	0.01	<0.01						
CEPHALOPODA	6.67	2.20	0.50	4.55	0.45	0.13				3.23	0.10	0.08	6.19	5.93	0.66	8.22	8.95	2.93	16.34	24.24	8.60	64.00	55.75	64.26
Alloteuthis media													0.34	0.57	<0.01									
Eledone spp.													0.34	1.74	0.01									
Heteroteuthis dispar																			0.39	0.70	0.01			
Histioteuthis bonnellii																						4.00	19.67	1.03
Histioteuthis spp.																			0.39	0.05	<0.01			
Illex coindetii																			0.39	1.28	0.01			
Onychoteuthis banksii																			0.39	3.39	0.02			
Sepia spp.				4.55	0.45	0.13																		
Sepiodea																0.28	0.25	<0.01						
Sepiola spp.													0.34	0.07	<0.01	0.14	0.01	<0.01	0.78	0.65	0.01	4.00	2.95	0.21
Sepiolidae													0.69	0.15	<0.01				0.39	1.54	0.01	4.00	2.75	0.20
Theuthoidea										3.23	0.10	0.08	1.72	2.78	0.08	0.57	3.36	0.06	0.39	0.39	<0.01			
Todarodes sagittatus																			13.23	16.24	4.88	52.00	30.38	33.49
Cephalopoda unid.	6.67	2.20	0.50	18.18	5.87	1.72							2.75	0.62	0.05	7.22	5.33	1.71						
Mollusca unid.													0.34	0.14	<0.01	2.55	0.66	0.12						
EUPHAUSIACEA	13.33	1.50	1.10										9.97	0.80	0.66	13.17	5.09	11.48	59.53	18.28	55.89	8.00	5.05	0.90
Meganyctiphanes norvegica													0.69	0.04	<0.01		3.82	3.76	1.69	15.48	14.93	8.00	8.00	5.05
Euphausiacea unid.	13.33	1.50	1.10										9.28	0.75	0.60	9.35	1.34	4.03	33.85	2.80	12.96			
AMPHIPODA							16.67	0.20	2.78	25.81	1.27	3.87	4.47	0.13	0.10	7.93	0.71	0.98	6.23	0.71	0.52			
Phronima sedentaria							16.67	0.20	2.78	25.81	1.27	3.87				0.71	0.40	0.01	4.67	0.60	0.32			
Amphipoda unid.													4.47	0.13	0.10	7.22	0.31	0.76	1.56	0.10	0.03			
ISOPODA	33.33	8.40	7.22				12.50	2.41	1.08	3.23	0.47	0.04	20.27	2.65	2.40	8.92	0.99	1.25	0.78	0.06	0.01	4.00	0.49	0.37
MYSIDACEA	26.67	1.99	6.63				20.83	1.38	2.66	6.45	0.19	0.36	18.90	1.03	2.33	9.07	1.24	1.58	1.56	0.11	0.03			
Lophogaster typicus	13.33	1.73	1.14				20.83	1.38	2.66				16.15	0.64	1.52	5.67	0.54	0.53	1.17	0.07	0.02			
Mysidacea unid.	20.00	0.26	3.26							6.45	0.19	0.31	4.12	0.39	0.12	4.82	0.69	0.39	0.39	0.04	<0.01			

Prey items	R. polystigma			M. aquila			L. naevus			R. miraletus			R. clavata			S. canicula			G. melastomus			E. spinax		
	%F	%V	%IRI	%F	%V	%IRI	%F	%V	%IRI	%F	%V	%IRI	%F	%V	%IRI	%F	%V	%IRI	%F	%V	%IRI	%F	%V	%IRI
REPTANTIA	20.00	5.74	3.35	100.00	60.96	81.94	12.50	0.72	1.32	80.65	36.81	54.88	48.45	26.74	33.93	33.00	19.58	32.65	2.72	0.89	0.11	4.00	0.16	0.08
ANOMURA	6.67	3.29	0.49	90.91	57.96	63.37							13.75	7.51	2.50	20.40	13.60	12.86	0.39	0.02	<0.01			
Dardanus arrosor				50.00	33.39	18.32							0.34	0.24	<0.01	0.99	0.80	0.03						
Galatheidae				4.55	0.05	0.12							2.06	0.08	0.02	1.70	0.08	0.05						
Munida intermedia																0.14	0.07	<0.01						
Munida rutllanti																0.14	0.10	<0.01						
Munida spp.													1.03	0.24	0.02	0.57	0.39	0.01						
Paguridae				36.36	24.51	11.07							6.19	0.78	0.29	13.74	7.34	4.78	0.39	0.02	<0.01			
Pagurus prideauxi	6.67	3.29											3.09	5.38	0.27	2.12	3.36	0.24						
Pagurus spp.													1.03	0.79	0.02	0.99	1.47	0.05						
BRACHYURA	13.33	2.44	1.26	22.73	3.01	2.78	12.50	0.72	1.32	80.65	36.81	54.88	45.70	18.99	22.57	15.72	5.73	5.12	1.17	0.23	0.01	4.00	0.23	0.08
Atelecyclus rotundatus													2.75	0.58	0.05	0.71	0.13	0.01						
Bathynectes spp.													0.34	0.14	<0.01									
Calappa granulata													1.03	0.40	0.01									
Ethusa mascarone													1.37	0.07	0.01									
Goneplax rhomboides													1.03	0.84	0.02	0.14	0.10	<0.01						
Ilia nucleus																0.14	0.06	<0.01						
Liocarcinus depurator													0.69	0.51	0.01									
Liocarcinus spp.	6.67	1.57	0.24	4.55	0.17	0.07	4.17	0.28	0.07	12.90	6.01	1.35	11.34	2.83	1.14	1.84	0.44	0.08	1.17	0.23	0.01			
Macropipus tuberculatus													6.87	5.67	0.72	0.57	0.24	0.01						
Monodaeus couchii													0.34	0.04	<0.01	0.14	0.16	<0.01						
Parthenope massena																0.14	0.01	<0.01						
Portunidae													0.34	0.11	<0.01	0.14	0.03	<0.01						
Xantidae													1.03	0.20	0.01	0.14	0.06	<0.01						
Brachyura unid.	6.67	0.87	0.39	18.18	2.84	1.96	8.33	0.44	0.73	67.74	30.79	39.02	18.56	7.61	3.68	11.76	4.50	3.05	1.17	0.64	0.03	4.00	0.16	0.08
MACRURA													3.44	0.24	0.08	0.85	0.25	0.01	0.39	0.05	<0.01			
Calocaris macandreae																0.42	0.04	<0.01						
Palinurus mauritanicus													3.09	0.23	0.06									
Polycheles typhlops																			0.78	0.59	0.01			
Scyllaridae																0.14	0.02	<0.01						
Scyllarus spp.													0.34	0.01	<0.01	0.28	0.19	<0.01						
NATANTIA	73.33	37.19	67.97	13.64	0.37	1.10	54.17	24.62	50.88	64.52	22.33	34.78	59.79	11.89	37.52	23.94	4.87	11.64	24.51	12.88	11.25	32.00	7.83	8.54
Alpheidae																0.28	0.07	<0.01						
Alpheus glaber													4.81	0.47	0.17	1.42	0.42	0.04	0.39	0.08	<0.01			
Alpheus spp.													1.03	0.04	0.01	2.27	0.37	0.09						
Chlorotocus crassicornis													9.62	2.11	0.78	0.14	0.19	<0.01						
Crangonidae	13.33	6.00	2.06				4.17	0.11	0.18	6.45	0.20	0.26	2.41	0.18	0.03	0.71	0.06	0.01	0.39	0.15	<0.01			
Pandalina spp.																0.14	<0.01	<0.01						
Pasiphaea multidentata																			2.72	5.27	0.30			
Pasiphaea spp																0.57	0.20	0.01	4.67	2.30	0.35	12.00	2.39	1.17
Pasiphaea sivado																0.28	0.13	<0.01	3.11	0.99	0.16			
Phylocheras spp.																0.14	0.02	<0.01						
Phylocheras trispinosus																0.14	0.17	<0.01						
Plesionika spp.																0.14	0.01	<0.01	0.78	0.09	<0.01			
Pontocaris spp.													1.03	0.26	0.01	0.14	0.10	<0.01						
Procesa spp.	33.33	11.79	11.29	9.09	0.23	0.43	29.17	2.94	5.92	22.58	2.97	2.72	24.74	2.44	4.05	10.20	1.15	1.67	0.39	0.05	<0.01			
Systellaspis debilis																			0.78	0.10	0.01			
Gennadas elegans																			0.39	0.03	<0.01			
Sergestes arcticus																			2.33	0.61	0.06			
Sergestes spp.																			0.39	0.17	<0.01			
Sergia robustus																			2.72	1.87	0.15	4.00	1.97	0.16

Prey items	R. polystigma			M. aquila			L. naevus			R. miraletus			R. clavata			S. canicula			G. melastomus			E. spinax		
	%F	%V	%IRI	%F	%V	%IRI	%F	%V	%IRI	%F	%V	%IRI	%F	%V	%IRI	%F	%V	%IRI	%F	%V	%IRI	%F	%V	%IRI
Solenocera membranacea	13.33	14.30	3.01				33.33	18.16	14.80	22.58	14.30	4.71	13.75	3.27	1.58	1.27	0.60	0.04						
Solenocera spp.													4.47	0.91	0.13	0.71	0.23	0.01						
Natantia unid.	26.67	5.11	5.53	4.55	0.14	0.15	16.67	3.41	4.17	25.81	4.87	4.38	21.99	2.21	3.82	8.50	1.15	1.32	7.78	1.16	0.75	16.00	3.47	2.05
OTHER CRUSTACEA																								
Rissoides desmaresti							4.17	2.27	0.14				1.03	0.29	0.01	0.71	0.51	0.02				4.00	0.83	0.22
Crustacea unid.										3.23	0.77	0.06	5.50	0.27	0.16	6.80	1.35	0.82	3.89	1.33	0.22	32.00	29.63	25.25
TELEOSTEA																								
Anguilliformes	20.00	38.81	13.51				37.50	68.23	40.80	12.90	37.99	5.88	31.62	48.92	30.71	20.40	33.04	24.92	24.51	39.67	23.17			
Aphia minuta													1.03	0.23	0.01	0.28	0.26	<0.01						
Argentina sphyraena													0.69	0.02	0.01									
Callionymus spp.													0.34	0.06	<0.01	0.14	0.05	<0.01						
Capros aper													0.34	0.12	<0.01	0.14	0.04	<0.01						
Cepola macrophthalma													0.34	0.07	<0.01	0.42	1.50	0.02						
Chauliodus sloani																			1.17	3.92	0.09			
Chelidonichthys cuculus													0.34	1.62	0.01									
Citharus linguatula													0.34	0.48	<0.01									
Diplodus spp.																0.14	0.27	<0.01						
Gadiculus argenteus													0.69	1.26	0.01	0.28	1.03	0.01						
Glossanodon leioglossus													5.84	10.63	1.30									
Gobiidae	6.67	10.81	1.00										2.75	0.35	0.12	0.42	0.03	<0.01				4.00	0.15	0.21
Gymnammodites cicerelus										3.23	14.02	0.52												
Helicolenus dactylopterus													0.34	0.03	<0.01									
Lampanyctus crocodilus																			1.56	14.93	0.38			
Lepidorhombus spp.																0.14	0.38	<0.01						
Maurolicus muelleri																			1.17	0.77	0.02			
Merluccius merluccius													1.03	0.37	0.01									
Micromesistius poutassou													1.03	1.11	0.02	0.14	0.01	<0.01						
Myctophidae																			3.11	1.25	0.18	12.00	4.90	1.95
Myctophum punctatum																			0.39	0.26	<0.01			
Nemichthys scolopaceus																			0.39	0.18	<0.01			
Nezumia aequalis																			0.39	1.16	0.01			
Notoscopelus spp.																						4.00	17.21	1.04
Ophichthus rufus													0.34	0.02	<0.01	0.42	1.33	0.02						
Phycis blennoides													0.34	1.43	0.01				0.78	0.28	0.01			
Pleuronectidae													1.03	0.24	0.01	0.85	0.63	0.02						
Regalecus glesne							4.17	29.83	1.69															
Sardina pilchardus													1.03	1.70	0.03									
Serranus hepatus													1.03	3.12	0.05									
Spicara smaris										3.23	23.39	0.76	2.06	10.23	0.32	0.14	0.54	<0.01						
Stomias boa boa																0.14	0.19	<0.01	1.17	7.72	0.15			
Syngnathidae																0.14	0.16	<0.01						
Symphurus ligulatus																0.14	0.02	<0.01						
Symphurus nigrescens																0.14	0.22	<0.01						
Symphurus spp.													0.34	0.07	<0.01									
Trachinus draco													0.69	1.62	0.01									
Trachurus spp.																								
Teleost unid.	13.33	28.00	7.00				33.33	38.40	22.75	6.45	0.58	0.38	16.84	14.16	4.97	16.86	25.56	16.01	17.51	9.21	6.03	24.00	7.37	7.05
THALIACEA																								
Doliolid																0.42	0.12	<0.01	2.33 / 0.39	0.70 / 0.08	0.10 / <0.01			

Prey items	R. polystigma			M. aquila			L. naevus			R. miraletus			R. clavata			S. canicula			G. melastomus			E. spinax		
	%F	%V	%IRI	%F	%V	%IRI	%F	%V	%IRI	%F	%V	%IRI	%F	%V	%IRI	%F	%V	%IRI	%F	%V	%IRI	%F	%V	%IRI
Pyrosoma atlanticum																			0.78	0.38	0.01			
Salpidae unid.																0.42	0.12	<0.01	1.17	0.24	0.03			
OTHERS																								
Cnidaria				4.55	0.08	0.21							2.06	0.80	0.05	5.81	3.73	1.03	4.28	1.00	0.29	4.00	0.10	0.07
Echinoidea																0.57	0.19	0.01						
Ostracoda													1.03	0.55	0.01	0.28	0.28	<0.01						
Eggs unid.																0.14	0.01	<0.01	0.39	0.21	<0.01			
Ascidiacea																0.28	1.02	0.01	0.78	0.31	0.01			
																1.56	0.63	0.07						
Unid. remains				4.55	0.08	0.21							1.03	0.26	0.01	2.97	1.61	0.30	3.11	0.49	0.15	4.00	0.10	0.07