



Resource partitioning among sympatric elasmobranchs in the central-western Mediterranean continental shelf

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Abstract

Knowledge of the mechanisms that allow coexistence among sympatric species is fundamental to understand ecosystem functioning. Resource partitioning among seven elasmobranchs inhabiting the Sardinian continental shelf (40°07'N, 9°00'E): *Dasyatis pastinaca*; *Raja asterias*; *R. brachyura*; *R. clavata*; *R. miraletus*; *R. polystigma* and *Scyliorhinus canicula*, was investigated through stomach content analysis. Data from 1680 samples collected between 2005 and 2014, in 26–200 m depth, were analysed with respect to population, sex, season (winter and summer) and size groups. Species living in shallower waters (characterized by a narrower bathymetric range) had the most specialized diets. All species appeared to be mesopredators, feeding mainly on Crustacea, Actinopterygii, Mollusca and Polychaeta. Despite shared common morphological features, from the high ecological diversity of prey items, we hypothesized the presence of different predatory behavior among the species studied: some species were able to feed on endobenthic and/or epibenthic organisms, while others had made limited movements in the water column. Non-parametric Multi-Dimensional Scaling analysis highlighted the presence of five predator groups, confirming strong resource partitioning, as also demonstrated by low levels of interspecific niche overlap. The observed variations in feeding habits could be ascribed only to size and not to sex or season. Generally, diet changed from small Crustacean prey, to larger prey, like Actinopterygii and Mollusca. Some species became more generalist during development, others restricted their prey range. Shifts in feeding habits affected species' roles in the food web, with different species occupying different functional trophic groups over the course of their life cycles.

Introduction

Knowledge of marine species' trophic ecology, such as the range of prey consumed, trophic level, ontogenetic changes

in diet, especially at a multispecific level, play an increasing important role in the development of new fisheries management strategies. Unfortunately, most of the literature on trophic interactions, especially in the Mediterranean, usually focuses on the diet comparison of just two or three species (Valls et al. 2011, 2017; Barría et al. 2015, 2018). More complex studies are limited to a few papers, published in recent decades and focusing on the main predator groups, like bony fishes (Cabral et al. 2002; Valls et al. 2014b; Karachle 2017; Park et al. 2017; Paul et al. 2018), elasmobranchs (Orlov 1998; Valls et al. 2011; Barría et al. 2015, 2018; Kousteni et al. 2018), cetaceans (Liu et al. 2015) and cephalopods (Cherel et al. 2009), while studies on between-taxa interactions are even fewer (Valls et al. 2014a, 2017). Concentration on large predator groups is driven by the predators roles in the food chain, i.e. regulating the abundance and dynamics of lower level prey populations, through mechanisms including top-down control (Ferretti et al. 2010; Heithaus et al. 2012). Indeed, decades of ecological research have shown that changes in predator abundance can generate long-term consequences on the functionality and resilience

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of ecosystem structure (Paine 1969; Beddington 1984; Duffy 2002).

In this context, Elasmobranchs are important predators, occupying the highest levels of marine food chains (Cortés 1999; Ebert and Bizzarro 2007; Jacobsen and Bennett 2013; Barría et al. 2015). Their K-selected biological features make them vulnerable to exploitation (Stevens et al. 2000), so their management and preservation is a matter of priority (Dulvy et al. 2014, 2017). Knowledge of their life cycles and the roles they play in marine ecosystems are often fragmented, so predicting the consequences of declining population levels is difficult (Ferretti et al. 2010; Heithaus et al. 2012; Navia et al. 2016). A fundamental aspect of the trophic ecology of all predators is the degree of specialization in their diets. Species with a narrow trophic niche affect only a small number of prey, while generalist feeders can exploit a wider range of prey (Wetherbee et al. 1990; Irschick et al. 2005; Colles et al. 2009; Navarro et al. 2013). Moreover, from an intra-specific perspective, prey type and range can vary among subgroups, e.g. alimentary changes during growth or between sexes among many elasmobranchs (Wetherbee et al. 2012). Such behaviours minimize competition and guarantee higher survival rates during sensitive life stages, e.g. juveniles (Matich et al. 2017). Similarly, at an inter-specific level, more variability of the alimentary spectrum could allow broader coexistence of different species without an associated phenotypic selection for the exploitation of different prey items or in case of a sudden lack of resources that could increase competition (Sánchez-Hernández et al. 2011). Improving the knowledge-base of resource partitioning seems, therefore, crucial, for sympatric species (Valls et al. 2011).

At a global level, the Mediterranean ecoregions are amongst the most impacted by human activities (Katsanevakis et al. 2014). The continental shelf (0–200 m depth) is affected by both sea-based and land-based drivers (Micheli et al. 2013). Because the analysis of the conservation status of Mediterranean elasmobranch species has revealed the area as a hotspot of extinction risk (Dulvy et al. 2014), including some endemic species, like *Leucoraja melitensis*, *Raja polystigma* and *R. radula* (Frodella et al. 2016; Dulvy et al. 2016), the need for more data is clear.

Our work aims to analyse the trophic ecology and the resource partitioning among seven sympatric elasmobranch species inhabiting the Sardinian continental shelf (central-western Mediterranean) (Marongiu et al. 2017). Since these species exploit the same habitats, we hypothesized that strong resource partitioning facilitates coexistence, minimizing trophic niche overlap. Following analysis of stomach content data, we studied the prey range, trophic niche breadth, trophic level and different predatory behaviours of our target populations. We examined how ontogenetic

changes, sex and season may affect intra- and inter-specific interactions, highlighting the roles that these species have in the food webs over the duration of their life cycles, providing a useful tool for the implementation of management measures.

Materials and methods

Data sampling

We analysed a total of 1680 stomachs, belonging to seven elasmobranch species: *Dasyatis pastinaca* (Myliobatiformes, Dasyatidae), *Raja asterias*, *R. brachyura*, *R. clavata*, *R. miraletus*, *R. polystigma* (Rajiformes, Rajidae) and *Scyliorhinus canicula* (Carcharhiniformes, Scyliorhinidae). Samples were collected around Sardinia (central-western Mediterranean) (Fig. 1) at depths between 26 and 200 m, in the period 2005–2014, during the MEDITS (MEDiterranean International Trawl Survey) and GRUND (GRUppo Nazionale risorse Demersali) experimental trawl surveys, carried out, respectively, in summer and winter, and during commercial hauls, conducted in both summer and winter. Specimens were measured (Total Length, TL in mm, Table 1) and sex and maturity stages were determined through the scales provided by the MED.I.T.S. protocol (MEDITS, Handbook 2016).

Stomach content analysis

Stomachs were dissected on board and stored in a 5% formaldehyde solution. Prey items were identified to the lowest taxonomic level possible, counted, dried on tissue paper and weighed. Taxonomic nomenclature followed the most recent World Register of Marine Species (WoRMS Editorial Board 2018), except for the “shrimps group”, for which the traditional subdivision in Decapoda Natantia and Decapoda Reptantia was preferred, as this better expressed the prey’s ecological characteristics.

Cumulative prey curves (Ferry and Cailliet 1996) were built using the EstimateS software (Version 8.2, R. K. Colwell 2009, <http://purl.oclc.org/estimates>) to verify the sample size sufficiency. Following Brown et al. (2012), the slope of the linear regression (b) through the last five subsamples was used: $b \leq 0.05$ signified an acceptable levelling off of the prey curve for diet characterization. The Vacuity Coefficient (%CV) was calculated as the percentage number of empty stomachs with respect to the total number of collected stomachs (Hyslop 1980). The percentage Prey Specific Index of Relative Importance (%PSIRI) (Brown et al. 2012), a modification of the classical percentage Index of Relative Importance (%IRI), was adopted to assess the

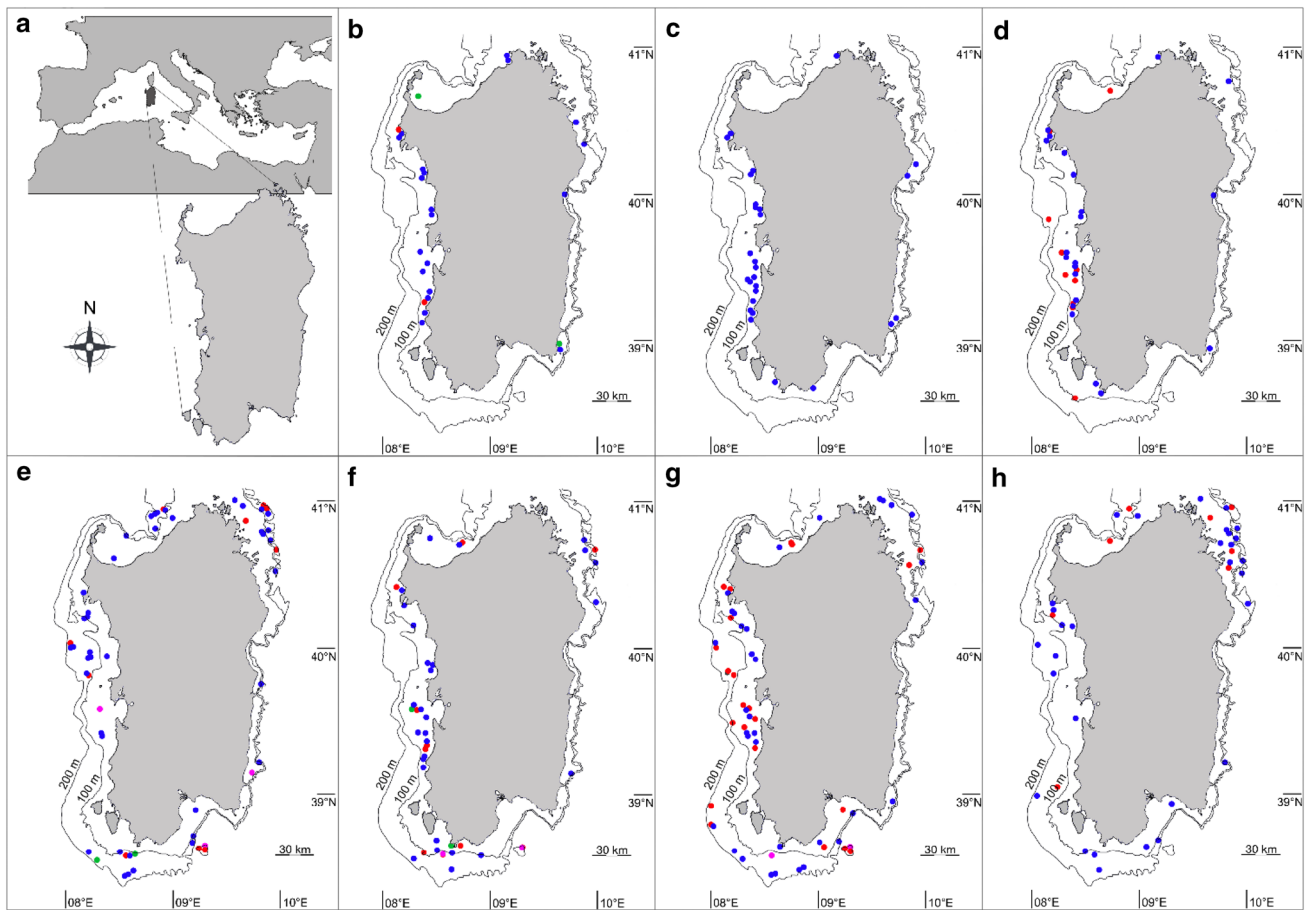


Fig. 1 Investigated area (a) and sampling sites for: **b** *Dasyatis pastinaca*; **c** *Raja asterias*; **d** *Raja brachyura*; **e** *Raja clavata*; **f** *Raja miraletus*; **g** *Raja polystigma*; **h** *Scyliorhinus canicula* (● = samples

collected during MEDITS; ● = samples collected during GRUND; ● = samples collected during summer commercial hauls; ● = samples collected during winter commercial hauls)

contribution of each prey item to the diet according to the formula: $\%PSIRI = \frac{[\%FO_i * (\%PN_i + \%PW_i)]}{2}$, where $\%FO_i$ is the percent Frequency of Occurrence of an item in all samples; $\%PN_i$ and $\%PW_i$ represent the prey specific abundances in terms of number and weight as a modification of IRI's $\%N$ (prey percent number) and $\%W$ (prey percent weight). One of the benefits given by the $\%PSIRI$ is that it is additive with respect to taxonomic levels (Brown et al. 2012).

Diet comparison among size groups, sexes and seasons

To study possible ontogenetic changes in alimentary behaviour, three size groups were identified for each predator species, dependent on the maturity stage: juveniles (immature at stage 1) were the smallest, subadults (maturing at stage 2), were intermediate in size, and adults (mature and resting at stages 3 and 4) were the largest (Table 1). Size groups were labeled with the initial letters of the species' name and a progressive number (1 = juveniles, 2 = subadults, 3 = adults) (Table 1).

Diet was further analysed with respect to sex and season (winter and summer), except for *R. asterias*, which was caught only during summer (Table 1).

Trophic niche breadth and trophic niche overlap

To measure the trophic niche breadth, the Levins' index (B_i) (Levins 1968) was calculated, using the formula: $B_i = \left(\frac{1}{n-1}\right) \times \left(\frac{1}{\sum_j p_{ij}^2}\right)$, where n is the number of prey categories and p_{ij} is the proportion of the prey j in the diet of the species i . The Morisita's index (C_h) (Krebs 1989; Hall et al. 1990) was used to examine the levels of intra- and inter-specific trophic niche overlap, following the equation: $C_h = \frac{2 \sum_k (p_{ik} * p_{jk})}{\sum_k p_{ik}^2 + \sum_k p_{jk}^2}$, where p_{ik} is the proportion of the prey k in the diet of the group i and p_{jk} is the proportion of the prey k in the diet of the group j .

Table 1 Samples characteristics of the seven analysed species: total length (TL, in mm), total number of analysed stomachs (*N*), Coefficient of Vacuity (%CV) and depth range (in m) of the overall populations and subgroups

Species	Group	TL (mm)	<i>N</i>	%CV	Depth range (m)
<i>D. pastinaca</i>	Overall	181–721	229	8.73	28–65
	DP1	<400	89	4.49	
	DP2	400–500	96	10.52	
	DP3	>500	44	13.64	
	Females	181–721	114	8.77	
	Males	286–672	115	8.70	
	Summer	279–685	151	11.26	
	Winter	181–721	78	3.85	
	<i>R. asterias</i>	Overall	195–689	233	14.16
RA1		<450	54	18.52	
RA2		450–550	79	18.99	
RA3		>550	100	8.00	
Females		210–689	134	6.72	
Males		195–622	99	24.24	
Summer		195–689	233	14.16	
Winter		–	–	–	
<i>R. brachyura</i>		Overall	173–1000	250	16.80
	RB1	<400	148	20.33	
	RB2	400–800	60	15.38	
	RB3	>800	42	27.27	
	Females	173–1000	121	19.83	
	Males	176–965	129	16.22	
	Summer	176–1000	145	18.62	
	Winter	173–879	105	14.29	
	<i>R. clavata</i>	Overall	129–900	220	3.64
RC1		<350	43	4.65	
RC2		350–550	93	5.38	
RC3		>550	84	1.19	
Females		185–900	120	4.17	
Males		129–770	100	3.00	
Summer		129–900	128	5.47	
Winter		187–843	92	1.09	
<i>R. miraletus</i>		Overall	94–492	276	3.99
	RM1	<300	111	3.60	
	RM2	300–400	104	3.85	
	RM3	>400	61	4.92	
	Females	115–492	139	3.60	
	Males	94–489	137	4.38	
	Summer	141–492	195	3.59	
	Winter	94–472	81	4.94	

Table 1 (continued)

Species	Group	TL (mm)	<i>N</i>	%CV	Depth range (m)
<i>R. polystigma</i>	Overall	140–785	254	5.12	36–190
	RP1	<300	86	3.49	
	RP2	300–400	96	4.17	
	RP3	>400	72	8.33	
	Females	104–785	127	4.72	
	Males	125–585	127	5.51	
	Summer	179–590	145	2.76	
	Winter	104–785	109	8.26	
	<i>S. canicula</i>	Overall	174–500	218	16.51
SC1		<250	34	2.94	
SC2		250–400	76	11.84	
SC3		>400	108	24.07	
Females		186–500	107	14.95	
Males		174–492	111	18.02	
Summer		174–500	152	20.39	
Winter		184–472	66	7.58	

Trophic level

The trophic level (TROPH) was defined for species and size groups, sexes and seasons, according to the formula proposed by Pauly and Christensen (1995): $1 + \sum_{i=1}^n p_{ij} * TROPH_j$ where $TROPH_j$ (attributed following Pauly et al. 2000) represents the fractional trophic level of the prey *j*.

According to Stergiou and Karpouzi (2002) TROPH values were used to assess the functional trophic groups of each species and sub-group as follows:

- $2.0 < TROPH < 2.1$ (H) pure herbivores.
- $2.1 < TROPH < 2.9$ (OV) omnivores with a preference for plants.
- $2.9 < TROPH < 3.7$ (OA) omnivores with a preference for animals.
- $3.7 < TROPH < 4.0$ (CD) carnivores with a preference for crustacean decapods/fish.
- $4.0 < TROPH < 4.5$ (CC) carnivores with a preference for fish/cephalopods.

Statistical analysis

The Primer v.7 software (Clarke and Gorley 2015) was used to perform ANOSIM (ANalysis Of SIMilarities) tests, for possible statistical differences among groups' diets. The SIMPER (SIMilarity PERcentages) test was used to determine which items were primarily responsible

for dietary differentiation and the nMDS (non-parametric Multi-Dimensional Scaling) analysis, to highlight the presence of major predator groups. The results obtained by the Morisita's index were tested through the null model analysis using the software EcoSim v.7.72 (Goetelli and Entsminger 2005). Null model analysis compares the observed dietary overlap values to a distribution of expected overlaps values constructed with a null model simulation (Bizzarro et al. 2007).

Results

Our sample sizes were sufficient to describe the species-specific diets for our sampled populations, size groups, sexes and seasons, as the cumulative prey curves always reached the asymptote (b values ≤ 0.05 ; Tables 2, 3).

Table 2 Sampling adequacy, trophic niche breadth and trophic level of the overall populations and size groups (1=juveniles; 2=sub-adults; 3=adults) of the analysed species: cumulative prey curves b values, Levins' index (B_i) and trophic level (TROPH \pm SE)

Species	Group	b value	B_i	TROPH \pm SE
<i>D. pastinaca</i>	Overall	0.000	0.27	3.44 \pm 0.51
	DP1	0.023	0.13	3.27 \pm 0.44
	DP2	0.036	0.32	3.61 \pm 0.58
	DP3	0.030	0.43	3.71 \pm 0.63
<i>R. asterias</i>	Overall	0.000	0.23	3.81 \pm 0.65
	RA1	0.047	0.16	3.54 \pm 0.58
	RA2	0.017	0.22	3.78 \pm 0.64
	RA3	0.010	0.25	3.96 \pm 0.68
<i>R. brachyura</i>	Overall	0.005	0.31	3.83 \pm 0.65
	RB1	0.000	0.58	3.46 \pm 0.53
	RB2	0.020	0.07	4.33 \pm 0.77
	RB3	0.003	0.17	4.42 \pm 0.76
<i>R. clavata</i>	Overall	0.005	0.44	3.81 \pm 0.65
	RC1	0.005	0.55	3.37 \pm 0.50
	RC2	0.000	0.44	3.75 \pm 0.63
	RC3	0.013	0.24	4.10 \pm 0.71
<i>R. miraleetus</i>	Overall	0.005	0.37	3.49 \pm 0.54
	RM1	0.000	0.41	3.37 \pm 0.49
	RM2	0.020	0.31	3.52 \pm 0.57
	RM3	0.000	0.23	3.65 \pm 0.56
<i>R. polystigma</i>	Overall	0.000	0.45	3.55 \pm 0.54
	RP1	0.013	0.33	3.31 \pm 0.46
	RP2	0.010	0.48	3.53 \pm 0.53
	RP3	0.015	0.40	3.88 \pm 0.65
<i>S. canicula</i>	Overall	0.005	0.44	3.72 \pm 0.56
	SC1	0.000	0.85	3.59 \pm 0.51
	SC2	0.015	0.51	3.69 \pm 0.56
	SC3	0.000	0.40	3.79 \pm 0.58

General diet description

Population dietary characteristics of the seven analysed species are reported in Table 1. During the study, a total of 1680 stomachs was collected. Vacuity coefficient (%CV) was quite variable (Table 1), ranging from 3.6 in *Raja clavata* and 16.8 in *R. brachyura*. Prey belonged to nine major taxonomic groups: Crustacea, Actinopterygii, Mollusca and Polychaeta were the most important, while Cephalochordata, Elasmobranchii, Cnidaria, Sipuncula and Tunicata could be considered as occasional or accidental in most of the predators' diets (Table S1). Crustacea represented the first trophic resource in almost all the examined species, reaching the highest %PSIRI values in *R. miraleetus* (89.12). Actinopterygii were the second most consumed items (Table S1) except for *R. brachyura*, which fed to a larger extent on these prey (%PSIRI = 46.12). Mysida, Lophogastrida, Decapoda and Amphipoda were the most frequently consumed Crustacea. Mysida represented 48.11% (%PSIRI) of the diet of *Dasyatis pastinaca*, and 18.13% (%PSIRI) of that of *R. brachyura*, while Lophogastrida characterized the feeding of *R. polystigma* (%PSIRI = 32.51) (Table S1). Among Decapoda, Brachyura were the most important in *R. asterias*' diet (%PSIRI = 36.17), as well as Natantia in that of *R. miraleetus*, *Scyliorhinus canicula* and *R. clavata* (%PSIRI = 38.92, 15.73 and 11.01, respectively). Anomura consumption was considerable in *S. canicula* and *R. clavata* (%PSIRI = 14.0 and 8.37, respectively). The highest Amphipoda %PSIRI values were observed in *R. miraleetus* (15.98), *R. polystigma* (14.02), *R. brachyura* (12.78) and *D. pastinaca* (11.60) (Table S1).

All studied species preyed upon Polychaeta and Cephalopoda (Table S1). Polychaeta reached maximum values of %PSIRI in *S. canicula* (15.19) and *R. brachyura* (13.80), while Cephalopoda were more important in the diet of *S. canicula* (%PSIRI = 11.10) (Table S1).

Resource partitioning

An nMDS analysis (Fig. 2) highlighted the presence of five major predator groups, divided primarily on the basis of differential consumption of Crustacea (Table S1):

1. *Dasyatis pastinaca* and *R. miraleetus* (high percentage of Mysida, Amphipoda and Decapoda Natantia in the diet).
2. *Raja asterias* (Decapoda Brachyura and Sipuncula).
3. *Raja polystigma* (Lophogastrida).
4. *Raja clavata* and *S. canicula* (significant presence of Decapoda Anomura, Euphausiacea and Mollusca Cephalopoda).
5. *Raja brachyura* (most piscivorous diet, with a particular preference for *Gymnammodytes cicereus*).

Table 3 Sampling adequacy, trophic niche breadth, trophic niche overlap and trophic level of the sexes and seasons of the analysed species: Cumulative prey curves b values, Levins' index (B_i), trophic level (TROPH \pm SE), Morisita's index (C_h) and null model analysis p values

Species	Group	b value	B_i	TROPH \pm SE	C_h	Null model analysis (p value)
<i>D. pastinaca</i>	Females	0.020	0.34	3.47 \pm 0.53	1	0.000
	Males	0.010	0.24	3.42 \pm 0.50		
	Summer	0.015	0.29	3.48 \pm 0.54	0.97	0.000
	Winter	0.015	0.23	3.35 \pm 0.48		
<i>R. asterias</i>	Females	0.000	0.24	3.87 \pm 0.66	0.89	0.050
	Males	0.027	0.23	3.71 \pm 0.64		
	Summer	0.000	0.23	3.81 \pm 0.65	–	–
	Winter	–	–	–		
<i>R. brachyura</i>	Females	0.010	0.33	3.81 \pm 0.63	0.98	0.000
	Males	0.000	0.33	3.84 \pm 0.65		
	Summer	0.017	0.17	4.06 \pm 0.72	0.79	0.002
	Winter	0.013	0.52	3.52 \pm 0.53		
<i>R. clavata</i>	Females	0.017	0.38	3.84 \pm 0.65	0.9	0.002
	Males	0.010	0.52	3.78 \pm 0.64		
	Summer	0.007	0.37	3.88 \pm 0.65	0.77	0.017
	Winter	0.023	0.46	3.73 \pm 0.62		
<i>R. miraletus</i>	Females	0.015	0.34	3.48 \pm 0.54	0.98	0.000
	Males	0.000	0.45	3.49 \pm 0.54		
	Summer	0.000	0.42	3.50 \pm 0.55	0.59	0.064
	Winter	0.013	0.39	3.46 \pm 0.52		
<i>R. polystigma</i>	Females	0.007	0.49	3.55 \pm 0.55	1	0.000
	Males	0.007	0.47	3.55 \pm 0.54		
	Summer	0.007	0.36	3.55 \pm 0.54	0.64	0.005
	Winter	0.000	0.23	3.55 \pm 0.55		
<i>S. canicula</i>	Females	0.000	0.49	3.76 \pm 0.58	0.92	0.000
	Males	0.010	0.48	3.67 \pm 0.54		
	Summer	0.007	0.45	3.73 \pm 0.57	0.87	0.000
	Winter	0.000	0.61	3.69 \pm 0.53		

Trophic niche breadth and trophic level

The width of the trophic spectrum showed modest differences among the seven species. The Levins' index (B_i) values ranged between 0.23 in *D. pastinaca*, that could be considered as a moderately specialist species and 0.45 in *R. polystigma*, a moderately generalist species (Table 2).

The trophic level (TROPH \pm SE) comprised a range between 3.44 \pm 0.51 (in *D. pastinaca*) and 3.83 \pm 0.65 (in *R. brachyura*) (Table 2) with species belonging to two functional trophic groups:

- (1) OA: *D. pastinaca*, *R. miraletus*, *R. polystigma*.
- (2) CD: *R. asterias*, *R. brachyura*, *R. clavata*, *S. canicula*.

Diet comparison among sexes and seasons

No significant differences were found in the diets between sexes and seasons, a finding also reflected in the values of the

Morisita's index, which displayed a high degree of trophic niche overlap, confirmed by statistical analysis (Table 3). In the same way, neither sex nor season influenced trophic level (Table 3).

Ontogenetic changes in the diet

Vacuity coefficient per size group was very variable. The number of empty stomachs generally increased with predator size, except for *R. asterias* and *R. clavata*, which showed the opposite tendency (Table 1). *Scylliorhinus canicula* exhibited the widest range with a %CV of 2.94 in juveniles, 11.84 in subadults and 24.07 in adults.

Amphipoda, Mysida and Lophogastrida represented the main food source for the juveniles of almost all species (Fig. 4; Table S2). Amphipoda (%PSIRI = 30.49) (particularly Gammaridea) represented the main prey for *R. miraletus* juveniles (Fig. 4; Table S2). *Dasyatis pastinaca* and *R. brachyura* juveniles fed on Mysida (%PSIRI = 70.03 and 26.94, respectively) belonging mainly to the genus

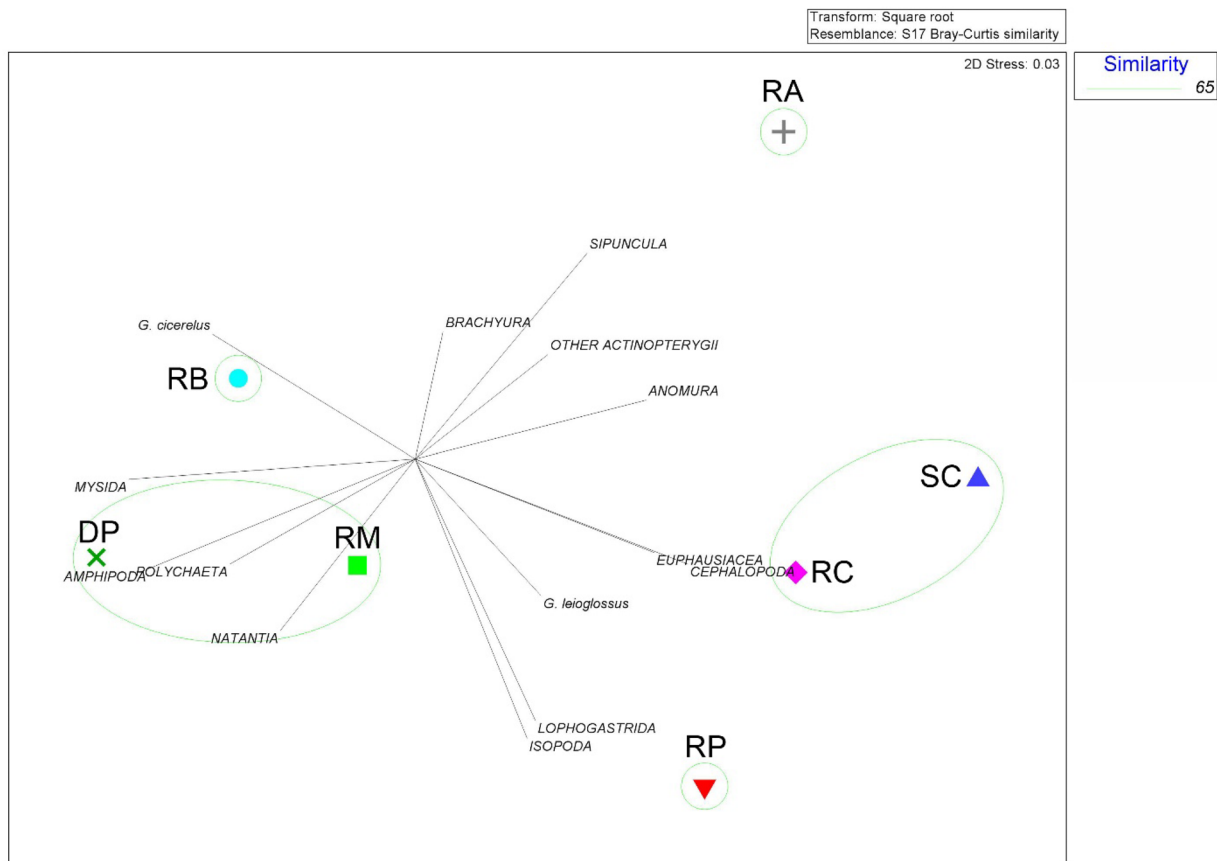


Fig. 2 Resource partitioning among the populations sampled as highlighted by the non-parametric Multi-Dimensional Scaling (nMDS) analysis for: DP *Dasyatis pastinaca*; RA *Raja asterias*; RB *Raja*

brachyura; RC *Raja clavata*; RM *Raja miraletus*; RP *Raja polystigma*; SC *Scyliorhinus canicula*

Gastrosaccus spp. and particularly to the species *G. sanctus* (Table S1). *Raja polystigma* and *R. clavata* juveniles showed a clear preference for the Lophogastrida *Lophogaster typicus* (%PSIRI = 47.22 and 26.6, respectively) (Table S2). *Raja asterias* juveniles main prey were Decapoda Brachyura (%PSIRI = 52.30) (particularly *Liocarcinus* spp.: %PSIRI = 36.32), while *S. canicula* juveniles had a more varied diet, composed mainly of Decapoda Natantia (%PSIRI = 19.55), Decapoda Anomura (%PSIRI = 17.40) and Euphausiida (%PSIRI = 16.88) (Fig. 4; Table S2).

Juveniles of only some species preyed consistently on items other than Crustacea. These included Polychaeta and Actinopterygii (particularly *G. cicerelus*) in *R. brachyura*, Cephalopoda in *S. canicula*, and Sipuncula (mainly *Sipunculus nudus*) in *R. asterias* (Fig. 3; Table S2).

During development, Decapod Crustacean consumption became more important in almost all predator's diets (Fig. 4; Table S2) and only *D. pastinaca* and *R. polystigma* subadults and adults continued to prey consistently on *Gastrosaccus* spp. and *Lophogaster typicus*, respectively (Table S2). In *R.*

miraletus subadults and adults, Decapoda consisted mainly of Natantia (particularly *Solenocera membranacea*) while in *S. canicula* and *R. clavata*, of Natantia, Brachyura and Anomura (Fig. 4; Table S2). *Raja asterias* preyed almost exclusively on Brachyura (in particular *Liocarcinus* spp.) throughout its life cycle (Fig. 4; Table S2).

Raja brachyura showed the clearest shift from a crustacean-based diet typical of juveniles to a piscivorous one, in subadults and adults (Actinopterygii %PSIRI = 81.80 and 85.51 in RB2 and RB3, respectively) (Fig. 3; Tab S2). Although Actinopterygii consumption increased in other species including *R. clavata* and *R. asterias*, this was limited to adults and comprised lower percentages (Actinopterygii %PSIRI = 52.57 and 44.13, in RC3 and RA3 respectively) (Fig. 3; Table S2).

The most preyed on Actinopterygii were *G. cicerelus* and *Glossanodon leioglossus*. *Gymnamodytes cicerelus* reached the highest %PSIRI values in *R. brachyura* subadults and adults (%PSIRI = 43.68 and 54.90, in RB2 and RB3 respectively), but was also consumed by *D. pastinaca* (%PSIRI = 7.43 and 28.74, in DP2 and DP3, respectively).

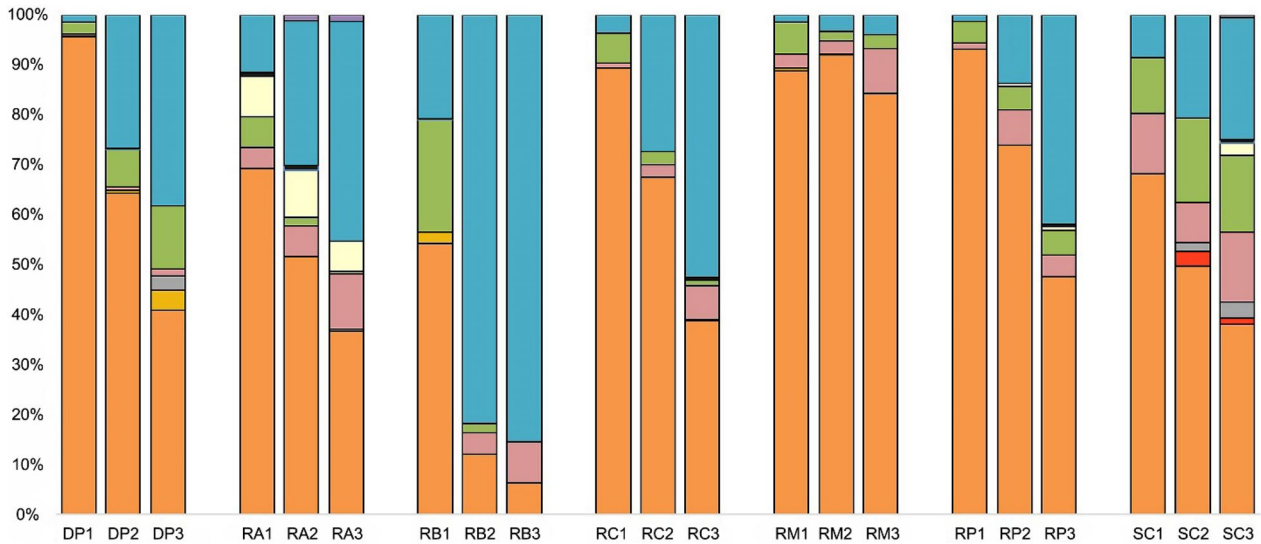


Fig. 3 Changes in the %PSIRI (percentage Prey Specific Index of Relative Importance) of the main taxa in the diet of the size groups. Taxa with %PSIRI < 1 are not displayed (■ = Actinopterygii; ■ = Cephalochordata; ■ = Cnidaria; ■ = Crustacea; ■ = Echinodermata; ■ = Elasmobranchii; ■ = Mollusca; ■ = Poly-

chaeta; ■ = Sipuncula; ■ = Tunicata). *DP* *Dasyatis pastinaca*; *RA* *Raja asterias*; *RB* *Raja brachyura*; *RC* *Raja clavata*; *RM* *Raja miraletus*; *RP* *Raja polystigma*; *SC* *Scyliorhinus canicula*. 1 = juveniles; 2 = subadults; 3 = adults

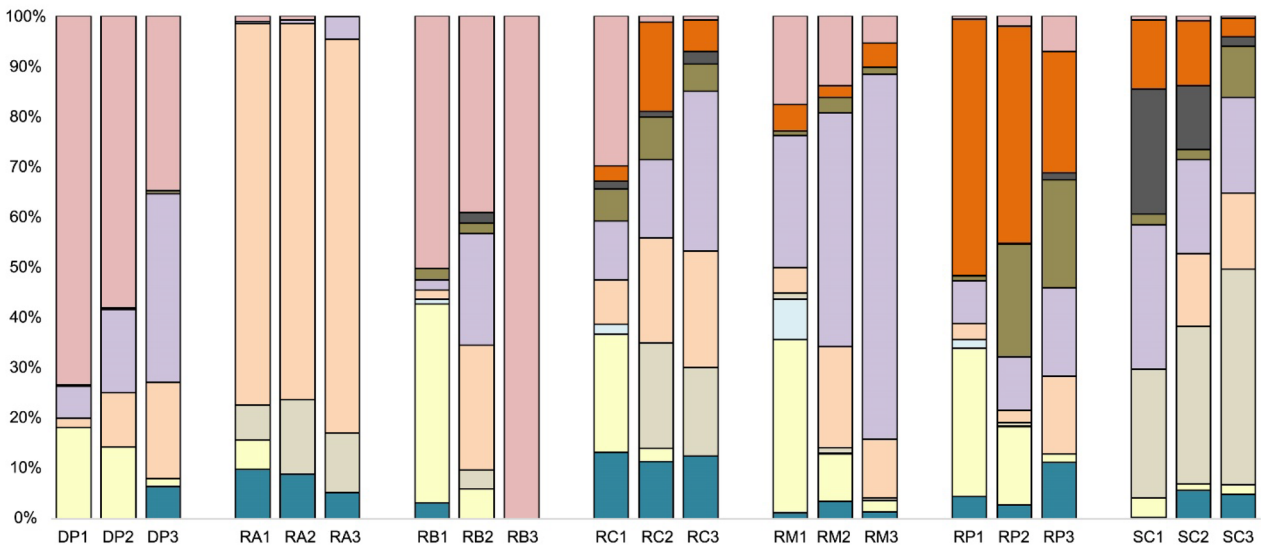


Fig. 4 Changes in the %PSIRI (percentage Prey Specific Index of Relative Importance) of the Crustacean taxa in the diet of the size groups. Taxa with %PSIRI < 1 are not displayed (■ = Amphipoda; ■ = Decapoda Anomura; ■ = Decapoda Brachyura; ■ = Copepoda; ■ = not identified Crustacea; ■ = Euphausiacea; ■ = Isop-

oda; ■ = Lophogastrida; ■ = Mysida; ■ = Decapoda Natantia). *DP* *Dasyatis pastinaca*; *RA* *Raja asterias*; *RB* *Raja brachyura*; *RC* *Raja clavata*; *RM* *Raja miraletus*; *RP* *Raja polystigma*; *SC* *Scyliorhinus canicula*. 1 = juveniles; 2 = subadults; 3 = adults

Glossanodon leioglossus was most important for *R. clavata* (%PSIRI = 10.80 and 13.93, in RC2 and RC3, respectively) (Table S2).

Among the secondary prey, Polychaeta were found mainly in the diet of *D. pastinaca* (%PSIRI = 7.61 and

12.68 for DP2 and DP3, respectively) and in that of *S. canicula* (%PSIRI = 17.01 and 15.30 for SC2 and SC3, respectively), together with Mollusca (%PSIRI = 8.04 and 14.03 for SC2 and SC3, respectively) (Fig. 3; Table S2). Mollusca was also important for *R. asterias* subadults

and adults (%PSIRI = 6.19 and 10.99 for RA2 and RA3, respectively), together with Sipuncula (%PSIRI = 9.53 and 6.02 for RA2 and RA3, respectively) (Fig. 4; Table S2).

Trophic niche breadth and trophic niche overlap among size groups

With regard to trophic niche breadth (Levins' index, B_i), species showed two different strategies: *R. brachyura*, *R. clavata*, *R. miraletus* and *S. canicula* contracted their trophic niche with growth, while *D. pastinaca*, *R. asterias* and *R. polystigma* had a much wider food range (Table 2).

Table 4 reports the Morisita's index (C_h), SIMPER test and null model analysis values related to the groups displaying high trophic niche overlap. Generally, C_h analysis revealed low levels of overlap; slightly higher values were found only at intraspecific level. These results were also confirmed by statistical analysis (ANOSIM), the null-hypothesis of no differences among the trophic niches being rejected (global R statistic 0.38, $P < 0.001$).

At the intra-specific level, the SIMPER test showed how high consumption of *Gastrosaccus* spp. was responsible for the strong trophic niche overlap among all *D. pastinaca* groups (Table 4). Similarly, *L. typicus* determined the overlap among the trophic niches in *R. polystigma* (Table 4). Decapoda Brachyura caused the niche overlap between *R. asterias* size groups, while the common consumption of Decapoda Natantia determined the high C_h values found among immature *S. canicula* and subadults, and between subadults and adults of *R. miraletus* (Table 4). Actinopterygii and Decapoda Anomura were responsible for the niche overlap between subadult and adult individuals both in *S. canicula* and *R. clavata*, while *G. cicereus* gave the main contribution to the overlap between the same groups in *R. brachyura* (Table 4).

At the inter-specific level, the high consumption of *G. sanctus* led to a strong trophic niche overlap among all groups of *D. pastinaca*, *R. brachyura* juveniles and *R. miraletus* subadults (Table 4). For the same reason, a high niche overlap was also observed between *R. brachyura* juveniles and *R. miraletus* subadults, as well as between *R. brachyura* and *R. clavata* juveniles (Table 4). Amphipoda were responsible for the niche overlap among *R. miraletus* juveniles and *R. asterias* and *R. clavata* juveniles. *Lophogaster typicus* was a common feeding resource of *R. clavata* juveniles and subadults, *S. canicula* subadults and all *R. polystigma* size groups and led to the niche overlap among these groups. Actinopterygii were primarily responsible for the trophic niche overlap between *R. clavata* adults and subadults and *S. canicula* adults (Table 4).

Table 4 SIMPER test and null model analysis for the size groups with significant Morisita's index (C_h) values

Groups	C_h	SIMPER		Null model analysis p value
		Prey Items	Contribute (%)	
DP1-DP2	0.99	<i>Gastrosaccus</i> spp.	44.59	0
DP1-DP3	0.72	<i>Gastrosaccus</i> spp.	42.06	0.009
DP2-DP3	0.75	<i>Gastrosaccus</i> spp.	33.37	0.005
RA1-RA2	0.64	Decapoda Brachyura	30.14	0.089
RA2-RA3	0.87	Decapoda Brachyura	28.52	0.001
RB2-RB3	0.89	<i>Gymnammodytes cicereus</i>	47.11	0.003
RC2-RC3	0.69	Actinopterygii	15.24	0.044
		Decapoda Anomura	13.54	
RM2-RM3	0.69	Decapoda Natantia	22.98	0.05
RP1-RP2	0.98	<i>Lophogaster typicus</i>	29.08	0
RP1-RP3	0.71	<i>Lophogaster typicus</i>	24.94	0.035
RP2-RP3	0.83	<i>Lophogaster typicus</i>	22.31	0.007
SC1-SC2	0.82	Decapoda Natantia	14.89	0
SC2-SC3	0.77	Actinopterygii	15.30	0.014
		Decapoda Anomura	15.05	
RB1-DP1	0.92	<i>Gastrosaccus sanctus</i>	47.28	0.001
RB1-DP2	0.92	<i>Gastrosaccus sanctus</i>	37.19	0.001
RB1-DP3	0.79	<i>Gastrosaccus sanctus</i>	26.21	0.003
RC1-RA1	0.68	Decapoda Brachyura	21.21	0.007
		Amphipoda	19.12	
RC1-RB1	0.66	<i>Gastrosaccus sanctus</i>	23.97	0.005
RM1-RA1	0.68	Amphipoda	26.81	0.007
RM1-RC1	0.76	Amphipoda	26.43	0.003
RM2-DP1	0.82	<i>Gastrosaccus</i> spp.	45.80	0.001
RM2-DP2	0.84	<i>Gastrosaccus</i> spp.	34.73	0
RM2-DP3	0.83	<i>Gastrosaccus</i> spp.	19.79	0.003
RM2-RB1	0.91	<i>Gastrosaccus sanctus</i>	25.42	0
RM2-RC1	0.72	Amphipoda	18.90	0.006
RP1-RC1	0.63	<i>Lophogaster typicus</i>	23.61	0.004
		Amphipoda	21.85	
RP2-RC1	0.61	<i>Lophogaster typicus</i>	20.67	0.032
		Amphipoda	18.95	
RP3-RC2	0.71	<i>Lophogaster typicus</i>	16.24	0.003
SC2-RC2	0.74	<i>Lophogaster typicus</i>	14.53	0.005
		Decapoda Anomura	14.45	
SC2-RC3	0.63	Actinopterygii	17.51	0.006
		Decapoda Natantia	12.56	
		Decapoda Anomura	12.14	
SC3-RC2	0.72	Decapoda Anomura	14.83	0.004
		<i>Lophogaster typicus</i>	13.07	
SC3-RC3	0.67	Actinopterygii	18.61	0.003
		Decapoda Anomura	12.84	
		Decapoda Natantia	12.14	

DP *Dasyatis pastinaca*; RA *Raja asterias*; RB *Raja brachyura*; RC *Raja clavata*; RM *Raja miraletus*; RP *Raja polystigma*; SC *Scyliorhinus canicula*. 1 = juveniles; 2 = subadults; 3 = adults

Ontogenetic changes in the trophic level

The trophic level increased with size (Table 2). With the exception of *R. brachyura* and *R. clavata*, TROPH values were always between 3 and 4 (Table 2). *Raja brachyura* subadults and adults, and *R. clavata* adults represented the only size groups with TROPH values higher than 4 (TROPH \pm SE = 4.33 ± 0.77 , 4.42 ± 0.76 , 4.10 ± 0.41 for RB2, RB3 and RC3, respectively) (Table 2). Moreover, *R. brachyura* showed the widest gap between juveniles and the other size groups (TROPH \pm SE = 3.46 ± 0.53 for RB1) (Table 2). *Dasyatis pastinaca* juveniles fed on the lowest trophic level (TROPH \pm SE = 3.27 ± 0.44) (Table 2). Based on size groups, species belonged to three functional trophic groups (Fig. 5): OA, CD, CC.

Discussion

General diet description

In this work, we analysed the feeding habits and the resource partitioning of seven elasmobranch species living on the central-western Mediterranean continental shelf. As previously reported by other authors worldwide (e.g.

Farias et al. 2006; Valls et al. 2011; Martinho et al., 2012; Šantić et al. 2012b; Barría et al. 2015, 2018), these species exhibited a high degree of full stomachs. This could be indicative of these fishes' "continuous feeder" alimentary patterns (Wetherbee et al. 2012) typical of most skates and stingrays (Jacobsen and Bennett 2013) which can also be extended to *Scyliorhinus canicula*. All of these elasmobranchs feed at regular intervals, resulting in a high number of prey at various stages of digestion and in a low number of empty stomachs (Wetherbee et al. 2012).

The occurrence of prey of demersal, epi- and endobenthic origin suggests that several different predatory strategies could have facilitated the strong resource partitioning observed. The batoids studied can identify food both on and in the substrate, probably moving sediments with their pectoral fins, as also stated by Gray et al. (1997). In some cases they can move up into the water column (e.g. Morato et al. 2003). The peculiar batoid morphology (ventrally located mouth, with a close connection with the seabed) should notionally restrict food gathering to the sea-bed, suggesting that these fish would take advantage of dead prey e.g. fish, cephalopods etc. stunned by trawling (Berestovskiy 1989). While not excluding batoids (as well as *S. canicula*) from being able to take advantage of fishing discards, as demonstrated by Olaso et al. (2002),

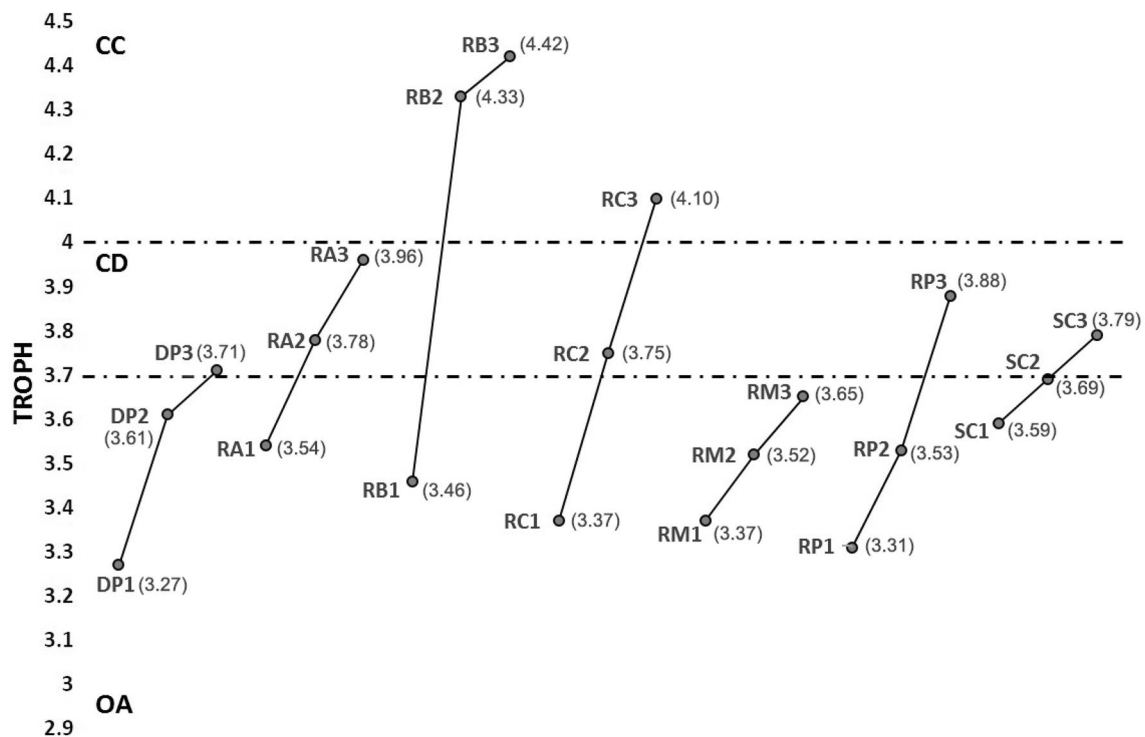


Fig. 5 Variations in the functional trophic groups during the ontogenetic development (CC carnivores with a preference for fish/cephalopods; CD carnivores with a preference for crustacean decapods/fish; OA omnivores with a preference for animals; in brackets the TROPH

values). *DP* *Dasyatis pastinaca*; *RA* *Raja asterias*; *RB* *Raja brachyura*; *RC* *Raja clavata*; *RM* *Raja miraletus*; *RP* *Raja polystigma*; *SC* *Scyliorhinus canicula*. 1 = juveniles; 2 = subadults; 3 = adults

our results seem to confirm that batoids can actively prey in the water column. This should not be surprising, given the highly active behaviour that these predators can display (e.g. swimming activity, migration movements etc.) (Hunter et al. 2005a, b). Moreover, if these batoids were only scavengers, the range of demersal by-catch prey would be wider, and their trophic niche less specialized.

Although there are some difficulties in comparing our results with existing literature mainly due to the use of heterogeneous methods over time, it emerged that feeding habits may vary markedly in relation to geographic area (Wetherbee et al. 2012), and for the most part our results agreed only partially with what has previously been reported in literature. Except for *Raja brachyura*, the batoid species fed mainly on Crustacea, confirming previous observations by other authors for Rajiformes and Myliobatiformes (Ebert and Bizzarro 2007, Jacobsen and Bennet 2013; Barría et al. 2015). *Dasyatis pastinaca* and smaller skates, like *R. polystigma* and *R. miraletus*, showed the highest levels of Crustacea in their diets. All these species had a preference for endobenthic prey, which contrasts with observations from previous studies (Smale and Cowley 1992; Ismen 2003; Yeldan et al. 2009; Saglam et al. 2010; Šantić et al. 2011; Valls et al. 2011; Kadri et al. 2014b; Barría et al. 2015; Saadaoui et al. 2015). To our knowledge, the importance of Mysida (*Gastrosaccus* spp.), has not previously been observed in the diet of *D. pastinaca*. Moreover, in a comparative analysis of the feeding and trophic levels of batoids, Jacobsen and Bennet (2013) stated that Mysida are generally prey of low importance for Dasyatidae. *Raja asterias* fed mainly on epibenthic Crustacea and, secondly, on demersal Actinopterygii, as described by other authors (Romanelli et al. 2007; Coll et al. 2013; Navarro et al. 2013; Barría et al. 2015). However, in Sardinian waters *R. asterias* also preyed consistently on endobenthic items, such as Sipuncula. *Raja clavata* has previously been reported to display a Crustacean based (Smale and Cowley 1992; Saglam and Bascinar 2008; Valls et al. 2011; Šantić et al. 2012b) or piscivorous diet (Demirhan et al. 2005; Kadri et al. 2014a). Even if *R. clavata* fed mainly on Crustacea in Sardinian waters, the consumption of burrowing prey (e.g. *Lophogaster typicus*) distinguished its feeding habits in this zone from previous reports by the above-mentioned authors, highlighting closer analogies with studies carried out in the Portuguese waters by Farias et al. (2006). *Raja brachyura* fed mainly on Actinopterygii and secondly on Crustacea, with a clear preference for burrowing prey, such as *Gymnammodytes cicereus* and *Gastrosaccus* spp. (Catalano et al. 2007; Follesa et al. 2010). Outside the Mediterranean basin, the importance of Ammoditidae and *Gastrosaccus* spp. in the diet of *R. brachyura* was previously reported by Quiniou and Rabarison-Andriamirado (1979) and Farias et al. (2006). *Scyliorhinus canicula* had a more varied diet (Patokina and

Litvinov 2004; Olaso et al. 2005; Valls et al. 2011; Martinho et al. 2012; Barría et al. 2018), preying with similar intensity on demersal, epibenthic and endobenthic items. Our results for *S. canicula* align with results reported by Valls et al. (2011) in the Balearic continental shelf and by Martinho et al. (2012) in Portuguese waters.

Trophic niche breadth and resource partitioning

The feeding strategies observed ranged from moderate stenophagy (specialist feeders, with a narrow trophic niche breadth), as in *R. asterias* and *D. pastinaca*, to moderate euriphagy (generalist feeders, with a broad trophic niche breadth), as in *R. polystigma*, *R. clavata* and *S. canicula*. In general, these species with a narrower bathymetric distribution, and occupying shallower waters, showed a more specialized trophic niche with respect to those distributed in a wider depth range. Barbini et al. (2018) underlined a positive correlation between trophic and habitat niche range in batoid species, maybe due to the higher prey availability to those species that can exploit different habitats. Moreover, the levels of specialization found on the Sardinian continental shelf were higher than those reported for the same species in other areas worldwide (e.g. Patokina and Litvinov 2004; Farias et al. 2006; Martinho et al. 2012; Mnasri et al. 2012; Šantić et al. 2012a, b, 2013; Kadri et al. 2014a, b; Yemişken et al. 2018). Interestingly Valls et al. (2011) reported similar Levins' index values for *R. clavata*, *R. miraletus* and *R. polystigma* from the Balearic continental shelf.

Even if the main prey taxa were common to all predators, at lower taxonomic levels, resource partitioning was clear, and was emphasized by the multivariate analysis. This could be due to the fact that, when species coexist in the same restricted area, they modify their feeding habits to share resources and minimize competition (Heithaus 2001; Motta and Wilga 2001; Carrassón and Cartes 2002; Barría et al. 2015).

Trophic level

From a functional point of view, our study species belonged to two trophic groups: smaller skates and *D. pastinaca* were omnivores with a preference for animals, while the larger skates and *S. canicula* were carnivores with a preference for crustacean decapods and fish (sensu Stergiou and Karpouzi 2002). Sardinian specimens fed at lower trophic levels and can be considered as mesopredators (Karachle and Stergiou 2006; Navarro et al. 2013). Our TROPH values were generally close to the standardized values reported by Ebert and Bizzarro for skates (2007) and Jacobsen and Bennett (2013) for stingrays, and consistent to those values reported in other Mediterranean areas (Karachle and Stergiou 2006; Mnasri et al. 2012; Navarro et al. 2013; Barría et al. 2015,

2018; Valls et al. 2014a, 2017). Outside the Mediterranean, these values are similar to those observed for other batoids in tropical coastal habitats (Navia et al. 2016). These results confirm batoids roles as mesopredators in marine ecosystems worldwide (Karachle and Stergiou 2006; Navarro et al. 2013). Our species trophic levels can be also compared with those of some mesopredator Actinopterygii (e.g. *Lepidorhombus boscii*, *L. whiffiagonis*, *Lophius budegassa*, *Merluccius merluccius*) and Cephalopoda (e.g. *Todarodes sagittatus*, *Loligo forbesi*), also abundant in the Mediterranean Sea (Valls et al. 2014a).

Ontogenetic changes in the diet

Shifts in the feeding habits associated with ontogenetic development are well documented in elasmobranchs (Wetherbee et al. 2012; Barbini et al. 2018). However, comprehension of the consequences of changing dietary preferences with ontogeny on resource partitioning, species interactions, trophic level and, more generally, on the ecological role of these species in marine ecosystems is still lacking (Navia et al. 2016). Our results suggest that younger individuals, with smaller mouths and fewer predatory skills, fed mainly on small benthic prey, while adults focused on larger, more mobile organisms that guarantee a higher energetic income. This change in preference could explain the increasing vacuity coefficient generally observed in the larger individuals. Bigger prey (like Actinopterygii) would ensure a higher energy intake and, consequently, would reduce the feeding frequency (Ellis et al. 1996).

Raja brachyura exhibited the clearest shift in diet, changing its alimentary spectrum from small Crustacea and Polychaeta in juveniles, to an almost entirely piscivorous diet in subadults and adults. This skate appeared to have more benthic feeding habits during ontogenetic development in Sardinian waters, than those observed by Farias et al. (2006) in Portugal. The transition to a piscivorous diet was less marked in the other species observed. Like *R. brachyura*, *D. pastinaca* was able to excavate the sea-bed in search of prey from its early life stages. Although with less intensity, subadults and adults of *D. pastinaca* continued to prey on endobenthic items. For this species, Ismen (2003) confirmed a shift to bony fish consumption amongst adults along the Turkish coast. *Raja asterias*, *R. clavata* and *R. polystigma* preyed on endo- and epibenthic prey during their initial life stages. Then as subadults and adults they added demersal items to their diets. Romanelli et al. (2007) described a similar trend in *R. asterias* diet, while Navarro et al. (2013) and Coll et al. (2013) observed no difference between the diets of the different size groups of this skate. A similar behaviour was also observed for *R. clavata* (e.g. Quiniou and Rabarison-Andriamirado 1979; Smale and Cowley 1992; Farias et al. 2006; Saglam and Bascinar

2008; Valls et al. 2011; Šantić et al. 2012b). Notably, Quiniou and Rabarison-Andriamirado (1979) stated that, in *R. clavata*, the shift to more important prey occurred at 35 cm TL, while Farias et al. (2006) observed a change in the diet from benthic shrimps to crabs at 45–55 cm TL. These measures correspond to the size range of *R. clavata* subadults in this study. *Raja miraletus* differed from the other batoids, feeding mainly on Crustacea during ontogenetic development. The consumption of Decapoda by *R. miraletus* increased during growth, as did that of Cephalopoda. *Scyliorhinus canicula* preyed on demersal, epi- and endobenthic items during its entire life cycle, increasing prey size during ontogenetic development. Olaso et al. (2005) and Valls et al. (2011) also reported similar changes in the alimentary spectrum of *S. canicula* with ontogenetic development. The first authors reported cannibalism in individuals larger than 50 cm TL, a behaviour not observed among Sardinian specimens.

Trophic niche breadth and trophic niche overlap among size groups

The changes in feeding strategy during ontogenetic development also influenced the trophic niche breadth of the species studied. Some species (*D. pastinaca*, *R. asterias* and *R. polystigma*) became more generalist, with others (*R. brachyura*, *R. clavata*, *R. miraletus*, *S. canicula*) becoming more specialist. The species with a narrower bathymetric distribution belonged to the first group. Barbini et al. (2018) observed a positive correlation between trophic niche breadth and size in skates ≤ 100 cm TL, suggesting that the increase in size could benefit individuals by allowing them to expand their prey range. Over 100 cm TL, the correlation became negative, maybe because larger individuals selected more energy-rich prey. None of the species analysed here exceeded 100 cm TL. It is probable that the processes resulting in the observed contraction of niche breadth in those species that become more specialist during ontogenetic development are not size-related. Similarly, Barría et al. (2015) observed no positive correlation between trophic niche breadth and size in Rajiformes from the Western Mediterranean sea. In coexisting species, various mechanisms useful to minimize competition for food resources, e.g. habitat separation, prey size, predator size and morphology, species segregation, differentiation in foraging tactics, have been reported (MacPherson 1979; Karachle 2017). Among these mechanisms, a differentiation in foraging tactics could partially explain the results obtained in this study and in Barría et al. (2015).

Interspecific trophic niche overlap was limited only to a few species, especially among the smaller groups. This was due to the common consumption of recurring prey such as *Gastrosaccus* spp., *G. cicereus*, *L. typicus*, and consequently

intraspecific levels of trophic niche overlap appeared slightly higher, as also reported by Valls et al. (2011). Real competition should arise only in the event of a particular paucity of these peculiar prey items (Cartes 1998). Predation focused on particularly abundant prey during vulnerable phases of the life cycle, notably juveniles, could represent another useful adaptation to ensure higher survival rates.

Ontogenetic changes in the trophic level

Ontogenetic changes have also been found to influence the trophic level, and consequently, the predators ultimate roles in marine ecosystems (Navia et al. 2016). During their life cycles, Sardinian species occupied intermediate trophic levels typical of mesopredators. However, a more in-depth analysis showed that during ontogenetic development these species belonged to different functional trophic groups, as also stated by other authors (e.g. Navia et al. 2016; Valls et al. 2017). For those species attaining larger sizes, notably *R. brachyura* and *R. clavata*, predation on a higher number of trophic functional groups was more prevalent than in smaller species, such as *R. miraletus* or *R. polystigma*. Subadult and adult *R. brachyura* and adult *R. clavata* were, in fact, the only predators studied here that displayed trophic levels > 4 (carnivores with a preference for fish and cephalopods), while juveniles occupied lower trophic levels, similar to those of smaller species. In particular, *R. brachyura* subadult and adult trophic levels are comparable to those of large sharks in tropical marine habitats (Navia et al. 2016). This highlights their potential role as top-predators in coastal habitats of temperate areas.

Ultimately, our study highlights the diversity of trophic roles that elasmobranchs can play during their life cycles, providing new information that can be applied to better understand the structure and the functioning of marine coastal ecosystems. Considering the vulnerability of the poorly-studied Mediterranean Ecoregion (Micheli et al. 2013) the reduction of predators over time may negatively affect the food web structure, resulting in the establishment of new interactions among species and marine ecosystem degradation (Britten et al. 2014). We anticipate that the results presented here may be applied to the development of effective management plans for these and other species.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval Samples were collected from monitoring programs. All applicable international, national, and/or institutional guidelines for the care and use of organisms for the study were followed.

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