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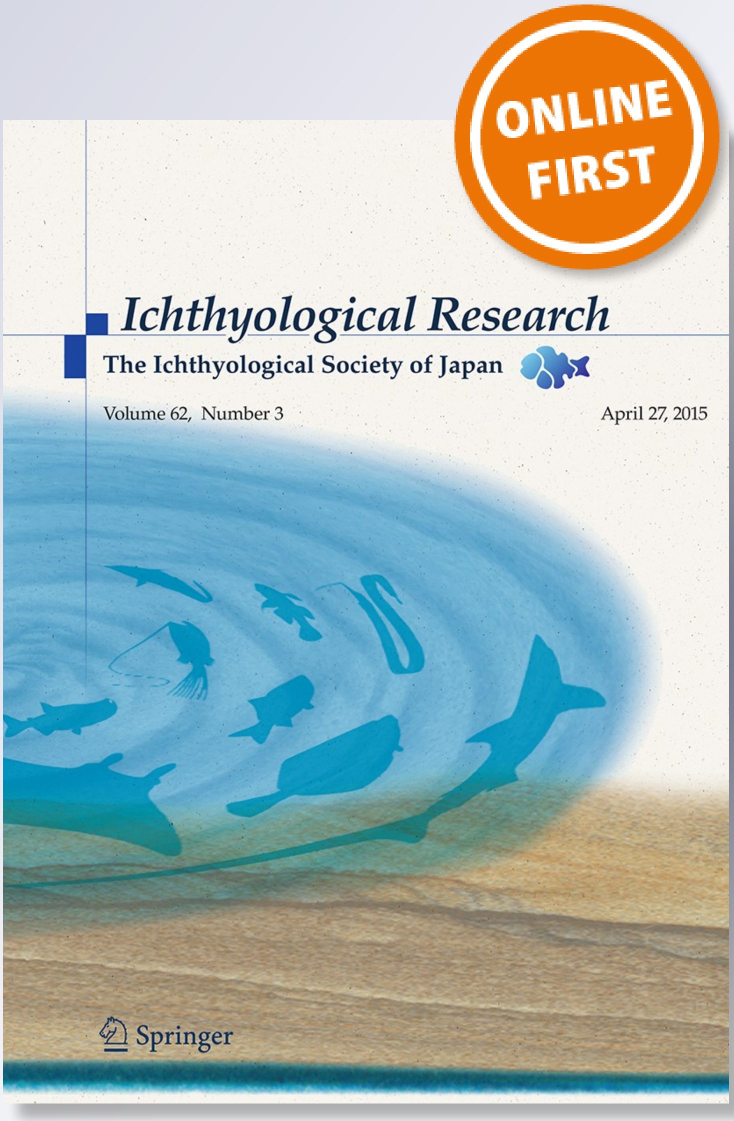

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FULL PAPER

Trophic ecology of the smallnose fanskate *Sympterygia bonapartii* in the San Matías Gulf, northern Patagonia, Argentina

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Abstract This study quantifies and describes the diet composition and variability, and the trophic ecology of *Sympterygia bonapartii* (Batoidea: Arhynchobatidae) in the San Matías Gulf, northern Patagonia, Argentina. A total of 1,047 stomachs were analyzed and 98 % of them contained food. The low proportion of empty stomachs recorded and the presence of prey in different stages of digestion suggested that this skate was a continuous feeder. A total of 81 prey items were identified. However, the diet was mainly composed of crabs. Other important groups in its diet were teleost fishes, shrimps and prawns, bivalves and worms. At the species level, the crab *Peltarion spinosulum* accounted for the highest contribution and the anchovy *Engraulis anchoita* ranked second in importance. By analyzing its diet composition, it was possible to classify *S. bonapartii* as a benthic predator, as are other skates reaching a similar maximum size. In addition, it was placed in the functional group of species that mainly feeds on decapod crustaceans. Trophic level was estimated at 3.61, indicating that the species was a secondary consumer. Significant differences were found in the diet according to sex, size class and season. These differences may be due to extrinsic and intrinsic factors that could be operating together.

Keywords Elasmobranchii · Arhynchobatidae · Southwest Atlantic · Diet composition · Trophic level

Introduction

Chondrichthyes prey on a wide variety of items, ranging from plankton to whales. However, most of the species consume mainly fishes, crustaceans and molluscs (Wetherbee and Cortés 2004).

Skates (Rajiformes: Rajoidei) are the most diverse group of cartilaginous fishes and are important components of the demersal communities and food webs of temperate seas (Ebert and Bizzarro 2007; Ebert and Compagno 2007). Whereas most of them are secondary consumers, the species that reach the largest sizes ($L_T > 100$ cm) are top predators (Wetherbee and Cortés 2004; Ebert and Bizzarro 2007).

Decapods and teleost fishes are the main taxa in a skatés diet. Polychaetes and amphipods are also important. Squids, euphausiids, mysids and small crustaceans make a lower contribution to their diets, while shelled molluscs, octopi, cuttlefishes and chondrichthyan fishes are considered not important items (Ebert and Bizzarro 2007).

At the species level, the diet can vary according to sex, size, reproductive stage, season and geographic region (Wetherbee and Cortés 2004). In particular, the biological and ecological characteristics of the smallnose fanskate *Sympterygia bonapartii* suggest that its diet may be quite variable.

Sympterygia bonapartii inhabits the Southwest Atlantic Ocean from Rio de Janeiro (23° S), Brazil, to Santa Cruz (54° S), Argentina, and it is present in the chondrichthyan assemblage of the San Matías Gulf (SMG: 41°–42° S; 64°–

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65° W) (Figueiredo 1977; Menni and Stehmann 2000; Perier et al. 2011). This species exhibits sexual segregation and a seasonal reproductive cycle (Estalles 2012). These features, together with the particular environment of SMG, may be reflected in its diet, which can differ between sexes, during the ontogeny and throughout the year. The aim of this study is to describe, quantify and investigate the variability in the composition of the diet of this species and to estimate its trophic level in the SMG.

Materials and methods

Study area. San Matías Gulf is the largest gulf in northern Patagonia and constitutes a unique ecosystem in the Argentine Sea (Fig. 1). Its central region is approximately 200 m deep, with maximum depressions of 219 m. The gulf is separated from the adjacent continental shelf by an 80 m-deep sill. This area is the mouth of the gulf, which is approximately 120 km wide. The mouth geometry restricts the water exchange between the SMG and the adjacent continental shelf, turning it into a semi-closed basin (Perier and Di Giácomo 2002).

Sampling. Samples of *Sympterygia bonapartii* (Fig. 2) came from three sources: bottom trawl research surveys, an onboard observer program and local fish-processing plants. Research surveys were conducted during spring (October to December) from 2004 to 2007. They were carried out along the area of the SMG at a depth range of 40 to 175 m. An onboard observer program provided samples of juveniles which, due to their size, would have been discarded by commercial vessels during 2007 and 2008. In addition, a monthly sampling of skates coming from commercial landings was performed at local fish-processing plants from April 2007 to December 2009.

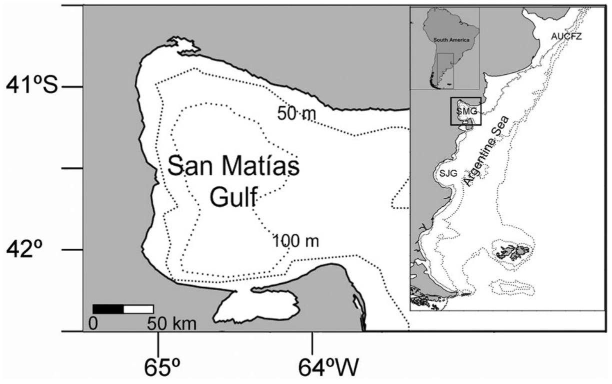

Fig. 1 Spatial location of the study area, the San Matías Gulf and other important references. *AUCFZ* the Argentine–Uruguayan Common Fishing Zone (34° 30′-39° 30′ S); *SMG* San Matías Gulf (41°-42° S; 64°-65° W); *SJG* San Jorge Gulf (44° 55′S 65° 31′W-47° 06′S 65° 51′W)

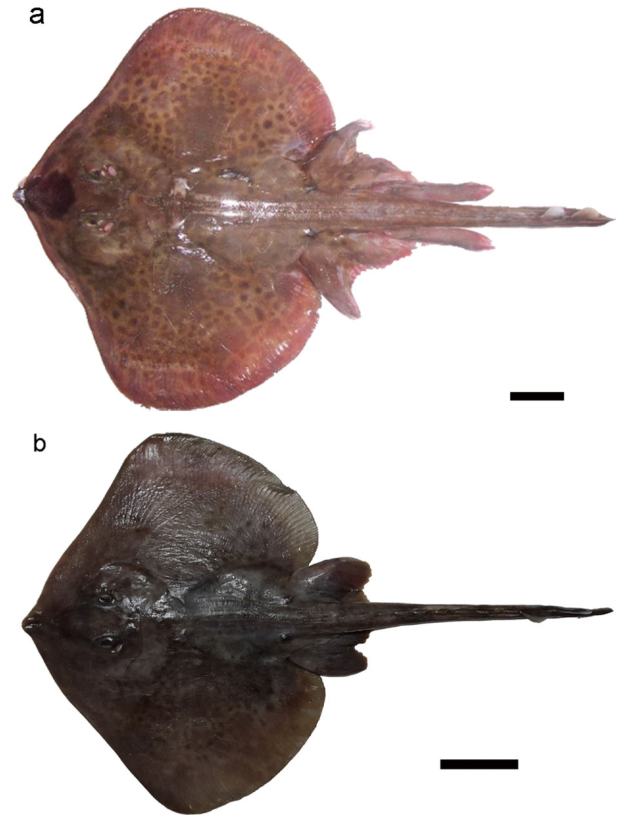

Fig. 2 Dorsal view of *Sympterygia bonapartii*. **a** Male of 585 mm of total length and **b** female of 412 mm of total length. *Scale bar* represents 50 mm

Minimum sample size. The minimum number of stomachs required to describe and analyse the diet was determined by plotting the number of samples analysed against the mean cumulative value of the Shannon–Wiener diversity index (*H*). One hundred randomizations of the original matrices were performed to prevent bias in the index value. The final curves were constructed with the mean values of *H* and their standard deviation (SD) (Barbini and Lucifora 2011). The number of samples was considered sufficient when the SD was <0.05 (Koen Alonso et al. 2001). A curve was estimated for the entire sample and for each of the factors assessed using the Vegan Community Ecology Package (Oksanen 2011) and the R software version 2.11.1 (R Development Core Team 2010).

Diet composition, trophic level and feeding strategy. Prior to the analysis, stomachs were dissected and preserved in 70 % alcohol. Then, their contents were washed and drained in an 800 µm sieve.

Prey items were identified to the lowest taxonomic level possible. They were counted, weighed and measured, whenever possible, as well. Measurements were: standard length for fishes (L_S), carapace length for crabs (L_C), cephalothorax length for shrimps (CP), mantle length for cephalopods (L_M) and total length for bivalves (L_T).

Contribution by number (%N), frequency of occurrence (%FO), weight (%W) and compound index of relative importance (%IRI) were estimated for each prey item. All the parameters were expressed as percentage (Hyslop 1980; Cortés 1997).

Sympterygia bonapartii trophic level (TL) was estimated as

$$TL = 1 + \left(\sum_{j=1}^{n} Pj \times TLj \right),$$

where TL is the trophic level, Pj the proportion of prey category j in the diet, n the total number of prey categories, and TLj the trophic level of prey category j. Trophic levels of prey items are shown in Table 1 (Cortés 1999; Ebert and Bizzarro 2007).

The feeding strategy of this skate and the relative importance of prey items in its diet were analysed using the graphic method of Amundsen et al. (1996). To perform the analysis, prey items were grouped into discrete categories (Table 2). The frequency of occurrence of each group was then plotted against its specific abundance (Amundsen et al. 1996). According to this graphic method, a species is considered a generalist when groups of prey occur at a frequency of occurrence <0.5 and at a specific abundance <50 %. In contrast, specialists feed on one or a few groups of prey with frequencies of occurrence close to one and specific abundances close to 100 % (Amundsen et al. 1996).

Predator–prey size relationships. These relationships were assessed using the Spearman correlation test (r) because the variables did not follow a normal distribution (Zar 1984). Correlated variables were skate $L_{T,}$ and L_S of teleost fishes; L_C of crabs; CP of shrimps; L_M of octopi and L_T of bivalves. Data were considered insufficient to perform a correlation test if $n < 20$.

Changes in diet. First, a qualitative analysis was performed to assess differences in diet composition. Skates were divided into length-class intervals of 20 mm L_T by sex. For each interval, the contribution (%N) of each group of prey was plotted. The groups used are shown in Table 2.

Then, a quantitative analysis was performed. Differences in diet composition were assessed according to sex, size class and season. The variable analysed was the number of items in each prey group. Differences were analysed with a non-parametric multivariate analysis of variance (PERMANOVA) using Bray–Curtis distances on fourth root-transformed data (Anderson 2001, 2005). They were considered significant when $P < 0.05$.

Ontogenetic differences were analysed for each sex, and skates were divided into two groups. Groups were made taking into account the differences observed in the qualitative analysis performed previously. Although three groups were visually identified for each sex in the qualitative analysis, skates were divided into only two groups to comply with the sample size required for the statistical analysis. For males, “small” skates were ≤540 mm L_T and “large” skates were >540 mm L_T. For females, “small” skates were ≤580 mm L_T and “large” skates were >580 mm L_T.

Seasonal variations in diet composition could only be assessed in large females. For these analyses, samples were divided into three periods. Period I extended from March to June; period II from July to October; and period III from November to February. When significant differences were found, multiple comparison tests were conducted.

Results

Diet composition, trophic level and feeding strategy. A total of 1,047 stomachs were analysed and 98 % of them ($n = 1{,}024$) contained prey items. The minimum number of samples required to describe *Sympterygia bonapartii* diet composition was estimated at 301 stomachs; hence the sample size used in this study was enough (Fig. 3).

Table 1 Prey categories and trophic levels used to estimate the trophic level of *Sympterygia bonapartii*. Trophic level followed Cortés (1999) and Ebert and Bizzarro (2007)

Group code	Taxa included	Trophic level
FISH	Class Actinopterygii	3.24
CEPH	Class Cephalopoda	3.20
ISOP	Order Isopoda	3.18
AMPH	Order Amphipoda	3.18
POLY	Class Polychaeta	2.60
CRAB	Suborder Pleocyemata: Infraorder Anomura and Brachyura	2.52
OINV	Phyla Echinodermata and Echiura	2.50
SHRI	Suborder Dendrobranchiata and Pleocyemata: Infraorder Caridea	2.40
STOM	Order Stomatopoda	2.40
CUMA	Order Cumacea	2.40
SCRU	Order Mysida, Lophogastrida and Euphausiacea	2.25
BIVA	Class Bivalvia	2.10

Table 2 Prey categories used to analyze the feeding strategy and diet variations of *Sympterygia bonapartii*

Group code	Common denomination	Taxa included
FISH	Teleosts	Class Actinopterygii
CEPH	Cephalopods	Class Cephalopoda
POLY	Worms	Class Polychaeta
BRAC	Crabs	Suborder Pleocyemata: Infraorder Anomura and Brachyura
SHRI	Shrimps and prawns	Suborder Dendrobranchiata and Pleocyemata: Infraorder Caridea
STOM	Stomatopods	Order Stomatopoda
SCRU	Small crustaceans	Order Cumacea, Amphipoda, Isopoda, Mysida, Lophogastrida and Euphausiacea
BIVA	Bivalves	Class Bivalvia

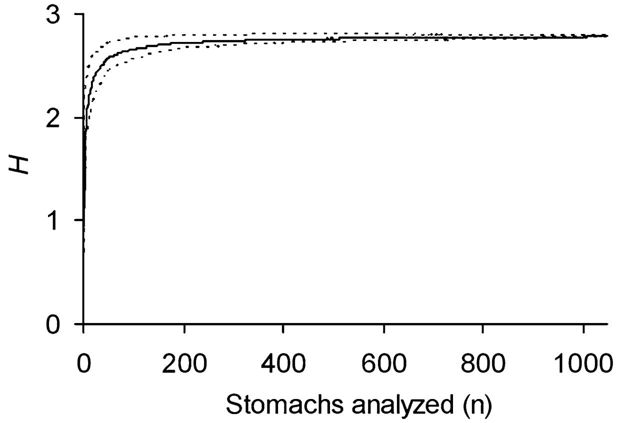

Fig. 3 Randomized cumulative prey curve in the dietary analysis of *Sympterygia bonapartii*. Shannon–Wiener diversity index (*H*), mean value (*continuous line*) and standard deviation (*dashed lines*), as a function of the number of stomachs analyzed

A total of 81 prey items were identified (Table 3). The number of different items found in each stomach varied from 0 to 11, with three being the most frequent value (Fig. 4).

Sympterygia bonapartii diet was mainly composed of crabs (Crustacea: Infraorder Brachyura). Fishes in the Class Actinopterygii ranked second in importance. Other important prey items, considering the values of %IRI, were shrimps and prawns (Crustacea: Suborder Dendrobranchiata), bivalves, worms (Class Polychaeta), amphipods, and cephalopods (Table 3).

The predominance of crabs in the diet was also shown in the graphical analysis. According to this analysis, the contribution of the other groups of prey items was considerably lower (Fig. 5).

At the species level, the diet consisted mainly of the crab *Peltarion spinosulum*, followed by the anchovy *Engraulis anchoita*. Other important species were the shrimp *Pleoticus muelleri*, the common hake *Merluccius hubbsi*, the crab *Libidoclea granaria*, the bivalves *Malletia* sp. and *Solemya* sp. and the octopus *Eledone massyae* (Table 3).

The trophic level of *S. bonapartii* was estimated at 3.61, indicating that the species was a secondary consumer.

Predator–prey size relationship. A positive correlation between skate size and prey size was detected for *P. spinosulum*, *L. granaria* and *E. massyae*. No significant correlations were found for other species (Table 4).

Changes in diet. Changes in diet composition were observed in both sexes. Crabs were an important component throughout the ontogeny. The contribution made by teleost fishes increased with skate size. Conversely, the larger the size of the skates, the smaller was the contribution small crustaceans made to their diet (Fig. 6).

Three dietary groups were distinguished in both sexes (Fig. 6). Group 1 was composed of skates up to 480 mm L_T. For both sexes, small crustaceans predominated in their diet, while crabs ranked second in importance. Group 2, comprised males from 481 to 540 mm L_T and presented a diet of transition. Its diet was mainly composed of crabs and shrimps, with a high contribution of small crustaceans. For females, group 2 was composed of skates from 481 to 580 mm L_T. Its diet consisted mainly of crabs, the presence of small crustaceans remained high and teleost contribution started to increase. Group 3 was composed of males ≥541 mm L_T and females ≥581 mm $L_{T.}$ For males, crabs and shrimps were the most important items. The contribution of teleost fishes and cephalopods became more important and the presence of small crustaceans decreased markedly. For females, crabs were the dominant group, and teleost fishes and cephalopods increased contribution. The presence of small crustaceans decreased sharply and completely disappeared from the diet of skates larger than 700 mm L_T (Fig. 6).

Quantitative analysis. The diet of males and females differed significantly ($F = 7.81$; $d.f. = 1$; $d.f. = 654$; $P < 0.01$). Females had a more diverse diet and a lower record of empty stomachs (Table 5). The diet of males had a higher contribution of shrimp and small crustaceans, and a lower contribution of teleost fishes and cephalopods. In addition, the percentage of stomatopods was nearly zero in males, while it reached approximately 4 % in females. The

Table 3 Diet composition of *Sympterygia bonapartii* expressed as percentage by number (*% N*), percentage by mass (*% M*), percentage frequency of occurrence (*% FO*) and the index of relative importance (*IRI*) and its expression in percentage (*% IRI*)

Prey		%N	%P	%F	IRI	%IRI
Phylum Annelida						
Polychaeta		**5.26**	**4.11**	**36.61**	**343.04**	**3.43**
	Unidentified Polychaeta	2.46	1.31	17.43	65.70	1.08
Aphroditidae	*Aphroditella alta*	0.47	1.39	4.18	7.77	0.13
Glyceridae	Unidentified Glyceridae	0.08	0.09	0.68	0.12	0.002
	Glycera americana	0.05	0.07	0.49	0.06	0.001
	Glycera capitata	0.38	0.26	3.51	2.25	0.043
	Glycera magellanica	0.01	0.003	0.10	0.001	0.0002
Goniadidae	*Goniada gigantea*	0.01	0.01	0.10	0.002	0.0003
Sigalionidae	*Leanira quatrefagesi*	0.03	0.01	0.29	0.01	0.0002
Flabelligeridae		0.50	0.22	4.67	3.36	0.06
Maldanidae		1.26	0.73	11.49	22.87	0.38
Terebellidae	*Artacama proboscidea*	0.01	0.01	0.10	0.002	0.00003
Phylum Arthropoda						
Order Stomatopoda		**2.74**	**0.94**	**11.98**	**44.09**	**0.44**
Squillidae	*Pterygosquilla armata armata*	2.74	0.94	11.98	44.09	0.72
Order Mysida		**4.26**	**0.03**	**2.63**	**11.28**	**0.11**
	Unidentified Mysida	4.26	0.03	2.63	11.28	0.19
Order Amphipoda		**7.22**	**0.14**	**16.16**	**118.94**	**1.19**
	U/I Amphipoda	6.26	0.12	14.11	90.02	1.48
Gammaridae		0.96	0.02	2.04	2.00	0.03
Order Isopoda		**3.68**	**0.35**	**17.04**	**68.67**	**0.68**
	U/I Isopoda	0.26	0.02	1.85	0.52	0.01
Serolidae		0.38	0.05	2.24	0.96	0.016
	Acanthoserolis schythei	0.05	0.003	0.39	0.02	0.0003
	Neoserolis exigua	0.01	0.006	0.10	0.002	0.0003
Anth uridae		0.01	0.0003	0.10	0.001	0.0002
Cirolanidae	Unidentified Cirolanidae	2.62	0.24	11.30	32.32	0.53
	Natatolana pastorei	0.28	0.03	1.85	0.57	0.01
Idoteidae		0.03	0.001	0.19	0.006	0.0001
Chaetiliidae	*Macrochiridothea sp.*	0.04	0.001	0.19	0.008	0.0001
Order Cumacea		**10.29**	**0.34**	**3.99**	**42.41**	**0.70**
	Unidentified Cumacea	10.29	0.34	3.99	42.41	0.42
Order Lophogastrida		**2.51**	**0.15**	**9.54**	**25.38**	**0.23**
Eucopiidae	*Eucopia sp.*	2.51	0.15	9.54	25.38	0.42
Order Euphausiacea		**0.97**	**0.02**	**3.02**	**2.99**	**0.03**
	Unidentified Euphausiacea	0.97	0.02	3.02	2.99	0.05
Order Decapoda						
Suborder Dendrobranchiata		**8.72**	**19.36**	**6.57**	**17.53**	**28.14**
	Unidentified Dendrobranchiata	0.06	0.01	0.19	0.01	0.0002
Penaeidae	*Artemisa longinaris*	0.07	0.02	0.19	0.02	0.0003
Solenoceridae	*Pleoticus muelleri*	9.05	3.53	28.04	352.74	5.79
Sergestidae	*Peisos petrunkevitchi*	0.01	0.001	0.10	0.001	0.00002
Suborder Pleocyemata						
Infraorder Caridea		**2.26**	**0.83**	**14.70**	**45.42**	**0.45**
Alpheidae	*Alpheus puapeba*	1.07	0.44	9.83	14.84	0.24
	Betaeus lilianae	0.01	0.005	0.10	0.002	0.00003
Hippolytidae	*Nauticaris magellanica*	0.14	0.02	1.07	0.17	0.003

Table 3 continued

Prey		%N	%P	%F	IRI	%IRI
Pandalidae	*Austropandolus grayi*	0.22	0.07	0.58	0.17	0.003
Crangonidae	*Pontoscaris boschii*	0.76	0.27	4.09	4.21	0.07
Infraorder Anomura		**0.53**	**0.21**	**3.41**	**2.52**	**0.03**
Galatheidae	*Munida sp.*	0.37	0.18	2.43	1.33	0.02
	Munida gregaria	0.16	0.03	0.97	0.18	0.002
Infraorder Brachyura		**36.90**	**43.23**	**84.71**	**6787.81**	**66.82**
	Unidentified Brachyura	0.36	0.59	3.41	3.24	0.05
Majidae	Unidentified Majidae	0.03	0.004	0.10	0.003	0.0005
	Collodes rostratus	0.02	0.001	0.19	0.004	0.00007
	Leurocyclus tuberculosus	1.25	0.75	9.06	18.12	0.30
	Libinia spinosa	0.01	0.07	0.10	0.01	0.00001
Majidae	*Libidoclea granaria*	3.04	7.82	19.96	216.77	3.56
	Rochinia gracilipes	0.1	0.21	0.49	0.15	0.002
	Lucippa pentagona	0.01	0.01	0.10	0.002	0.00003
Atelecyclidae	*Peltarion spinosulum*	29.68	28.42	68.84	3999.60	65.62
Portunidae	*Coenophthalmus tridentatus*	1.00	0.98	5.94	11.76	0.19
Platyxanthidae	*Platyxanthus patagonicus*	0.72	4.25	6.43	31.96	0.52
Xanthidae	*Pilumnoides hassleri*	0.01	0.003	0.10	0.001	0.0002
	Pilmnus reticulatus	0.01	0.003	0.10	0.001	0.0002
Pinnotheridae	*Pinnixa sp.*	0.61	0.13	5.16	3.82	0.06
	Pinnixa brevipollex	0.04	0.04	0.39	0.03	0.0005
	Pinnotheres garthi	0.01	0.001	0.10	0.001	0.00002
Phylum Mollusca						
Class Bivalvia		**5.18**	**5.83**	**32.13**	**353.75**	**3.48**
	Unidentified Bivalvia	0.06	0.004	0.58	0.04	0.001
Solemyidae	*Solemya sp*	1.99	2.36	11.68	50.81	0.83
Nuculidae	*Ennucula puelcha*	0.04	0.001	0.29	0.01	0.0002
Malletidae	*Malletia sp.*	3.06	3.46	23.27	151.72	2.49
Cuspidariidae	*Cuspidaria patagonica*	0.02	0.06	0.19	0.02	0.0003
	Cardiomya cleryana	0.01	0.003	0.10	0.001	0.00001
Pectinidae	*Aequipecten tehuelchus*	0.04	0.001	0.39	0.02	0.0003
	Zygochlamys patagonica	0.01	0.001	0.10	0.001	0.00002
Class Cephalopoda		**1.10**	**8.83**	**8.96**	**88.97**	**0.88**
	Unidentified Cephalopoda	0.31	1.17	2.24	3.32	0.05
Ommastrephidae	*Illex argentinus*	0.13	0.80	1.07	1.00	0.02
Loliginidae	*Loligo sp.*	0.14	0.20	1.07	0.36	0.006
Octopodidae	*Eledone massyae*	0.53	6.66	4.67	33.58	0.55
Phylum Echinodermata		**0.04**	**0.001**	**0.39**	**0.02**	**0.0002**
Class Ophiuroidea	Unidentified Ophiurida	0.01	0.0002	0.10	0.001	0.00002
Class Echinoidea	Unidentified Echinoidea	0.02	0.0004	0.19	0.004	0.0001
	Sterechinus agassizii	0.01	0.0002	0.10	0.001	0.00002
Phylum Echiura		**0.01**	**0.04**	**0.10**	**0.005**	**0.0002**
Urechidae	*Urechis chilensis*	0.01	0.04	0.10	0.005	0.0001
Phylum Chordata						
Class Actinopterygii		**7.75**	**32.91**	**44.21**	**1797.58**	**17.70**
	Unidentified Actinopterygii	0.21	0.39	1.95	1.17	0.02
Batrachoididae	*Triathalassothia argentina*	0.01	0.16	0.10	0.017	0.0003
Engraulidae	*Engraulis anchoita*	6.23	10.53	36.32	608.72	9.99

Table 3 continued

Prey		%N	%P	%F	IRI	%IRI
Merlucciidae	*Merluccius hubbsi*	1.30	21.88	9.93	230.18	3.78
Serranidae	*Serranus auriga*	0.01	0.20	0.10	0.02	0.0003
Paralichthyidae	*Paralichthys sp.*	0.01	0.0002	0.10	0.001	0.0001
Moridae	*Salilota australis*	0.01	0.04	0.10	0.005	0.0001
Digested material		0.07	0.13	0.68	0.14	0.002
Unidentified material		0.02	0.06	0.19	0.02	0.002
Number of samples	**1,047**					
Empty stomachs (*n*)	**23**					

The contribution of the main groups is in *bold*

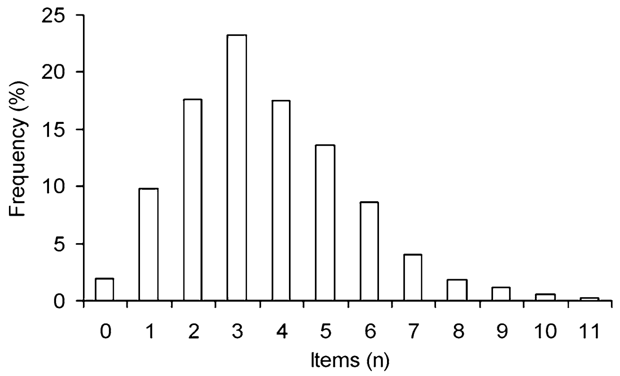

Fig. 4 Frequency distribution of the number of prey items recorded per stomach

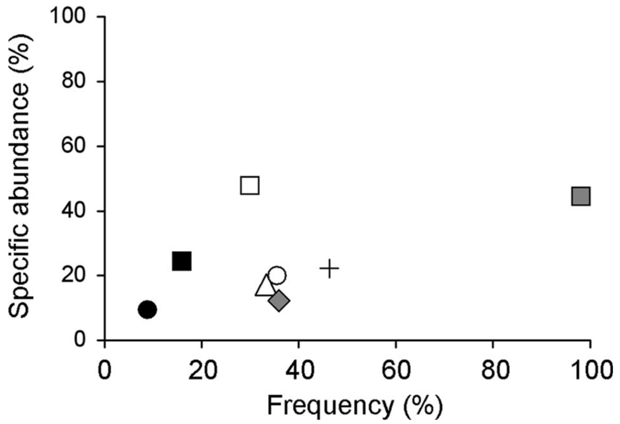

Fig. 5 Graphical representation of the feeding strategy of *Sympterygia bonapartii*. Specific abundance of groups of prey plotted against its frequency of occurrence. Crabs (*gray closed square*), teleost fishes (*crossed bars*), shrimps and prawns (*open triangle*), bivalves (*open circle*), small crustaceans (*open square*), worms (*gray diamond*), cephalopods (*closed circle*), stomatopods (*closed square*)

trophic level of females was only slightly higher than that of males (Fig. 6; Table 5).

For males, the diet composition of small and large skates was significantly different ($F = 15.23$; *d.f.* $= 1$; *d.f.* $= 296$; $P < 0.001$). Large males had a less diverse diet and a higher proportion of empty stomachs. The main differences in the diets of these groups were small crustaceans, crabs, shrimps and teleost fishes. However, despite these differences, their trophic levels were similar (Table 5).

The diet composition of small and large females also differed significantly ($F = 20.21$; *d.f.* $= 1$; *d.f.* $= 634$; $P < 0.001$). Large females had a less diverse diet and a higher proportion of empty stomachs than small females as well as a slight increment in their trophic level. The main differences were in the contribution of small crustaceans, teleost fishes and cephalopods (Table 5).

In the group of large females, the samples were sufficient to assess the probability of differences in diet composition throughout the year. Significant differences were detected among the periods analysed ($F = 7.94$, *d.f.* $= 2$, *d.f.* $= 294$, $P < 0.001$). The multiple comparison tests indicated significant differences among the three periods (period I vs II: $t = 2.56$; *d.f.* $= 196$; $P < 0.001$; period I vs III: $t = 3.03$; *d.f.* $= 196$; $P < 0.001$; period II vs III: $t = 2.81$; *d.f.* $= 196$; $P < 0.001$). From period I to III, there was an increase in the contribution of crabs and cephalopods and a decrease in the contribution of shrimps, bivalves and small crustaceans (Table 5).

Discussion

This is the first study to describe and quantify the diet of *Sympterygia bonapartii* in the SMG, northern Patagonia. Several methodologies have been applied to estimate the measurements for diet description (%W; %N; %FO and %IRI), particularly the new ones proposed by Brown et al. (2012). However, and perhaps due to high predominance of brachyurans in the diet of this skate, no marked changes were found among measurements. For that reason, this study presents the parameters most commonly used to facilitate comparisons among studies.

Table 4 Results of the correlation tests

Species	Mean size (mm)	SD	*n*	*r*	$CI_{95\%}$	*P*
Eledone massyae	40.36	18.11	22	0.77	0.52–0.90	0.0001*
Engraulis anchoita	81.26	20.00	109	0.14	-0.05–0.33	0.14
Libidoclea granaria	19.46	11.15	49	0.66	0.45–0.80	0.0001*
Peltarion spinosulum	15.05	8.74	429	0.47	0.39–0.54	0.0001*
Pleoticus muelleri	9.80	5.92	174	0.01	-0.14–0.16	0.89
Solemya sp.	23.99	8.37	27	0.18	-0.23–0.53	0.37

n Pairs of data analyzed, *r* Spearman correlation coefficient, $CI_{95\%}$ confidence interval of the coefficient of correlation

* significant differences

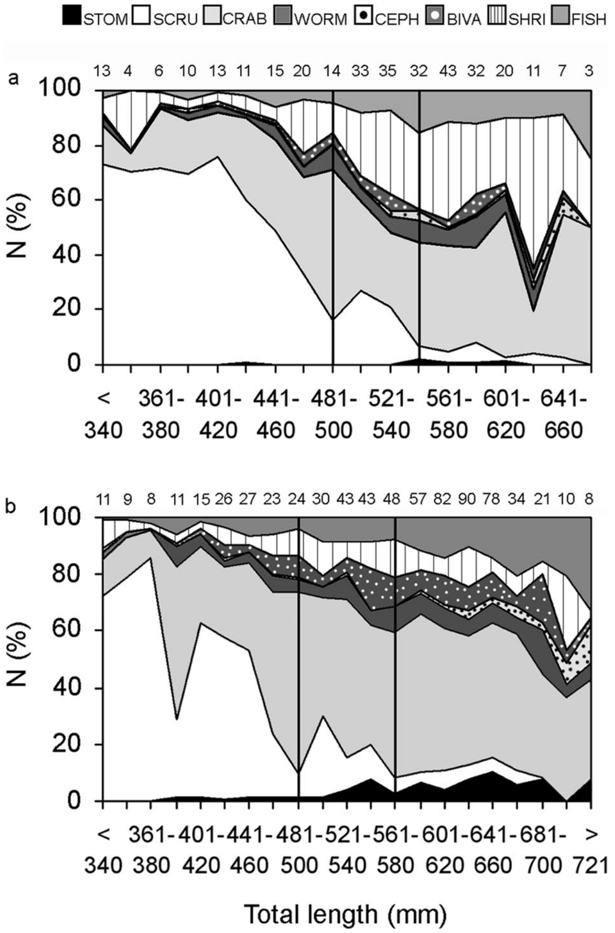

Fig. 6 Contribution by number (%) of groups of prey to the diet of *Sympterygia bonapartii* by length-class intervals of 20 mm L_T. Sample size of each interval is given at the upper section of the plot. Males (**a**) $n = 324$ and females (**b**) $n = 698$. *Vertical black lines* delimitate size groups

The diet of *S. bonapartii* diet was composed of more than 80 prey items from different groups of marine invertebrates and fishes. A low proportion of empty stomachs were recorded and the prey was usually found in different stages of digestion, which suggested that the species was a continuous feeder.

The diet consisted primarily of brachyuran crabs, while teleost fishes ranked second in importance. A similar pattern was also reported in the diet of *S. bonapartii* in the Argentine–Uruguayan Common Fishing Zone (AUCFZ) and the Buenos Aires coastal area (Barrera Oro and Maranta 1996; Paesch 2000; Barbini 2010). However, in the San Jorge Gulf, galatheid crabs and stomatopods were the most important items and teleost fishes were only found in the diet of larger skates (Sánchez and Prenski 1996). This suggests that even though crabs are the main items, the diet of *S. bonapartii* may vary between areas, probably due to prey availability in each environment.

Bivalves, in particular those with soft shells, were the other important items in the diet of *S. bonapartii* in the SMG. Other skates also have a high incidence of bivalves in their diet (McEachran et al. 1976). *Raja ocellata*, like *S. bonapartii*, feeds on *Solemya* spp. and the frequency of occurrence of bivalves in its diet is also high, reaching 40 % (McEachran et al. 1976). Nonetheless, a study analysing the diet of 14 skate species in the Benguela ecosystem revealed that bivalves were not present among the prey of these skates, while they did appear in the diet of other chondrichthyans (Ebert et al. 1991). This indicates that although bivalves are not considered an important prey item for the group of skates (Bizzarro et al. 2007; Ebert and Bizzarro 2007), there are specific cases in which their contributions are significant, particularly for those bivalves that could be easily digested.

Trophic ecology. Due to the predominance of brachyurans in its diet, *S. bonapartii* fell within the functional group that mainly feeds upon decapod crustaceans, according to the classification proposed by Ebert and Bizzarro (2007). However, this classification fails to highlight the ecological differences between sympatric skates in the SMG. It is proposed then that this functional group should be further split into species that feed mainly upon shrimp and prawns, such as *Atlantoraja platana* (see

Table 5 Diet variations among factors. Group codes are shown in Table 1

Groups	Males		Females		Males				Females				Females > 580 mm LT					
	%N	%FO	%N	%FO	Small		Large		Small		Large		Period I		Period II		Period III	
					< or = 540 mm LT		>540 mm LT		< or = 580 mm LT		>580 mm LT							
					%N	%FO	%N	%FO	%N	%FO	%N	%FO	%N	%FO	%N	%FO	%N	%FO
SHRI	17.8	43.8	8.7	35.8	12.8	43.8	30.5	43.9	8.0	43.2	9.8	29.8	13.9	37.2	9.6	27.7	4.62	22.8
CRAB	29.8	79.8	41.0	84.8	26.2	85.8	39.0	72.9	37.0	88.2	46.6	82.4	33.0	78.8	42.9	84.5	69.8	84.2
POLY	4.7	37.5	5.6	35.2	3.6	39.2	7.6	35.5	4.7	41.6	6.9	30.0	7.4	35.8	8.5	29.7	3.9	22.8
CEPH	1.0	9.1	1.2	8.7	0.7	8.5	1.9	9.7	0.4	4.7	2.2	12.0	1.4	7.8	2.7	12.9	2.7	14.9
BIVA	2.7	23.9	6.6	35.1	2.5	28.4	3.4	18.7	5.2	36.0	8.7	34.4	10.3	41.6	10.1	38.1	4.6	18.8
FISH	6.1	39.0	8.8	45.4	3.7	35.2	12.2	43.2	5.3	40.4	13.8	49.6	11.0	46.0	20.7	61.9	7.7	35.6
STOM	0.4	3.3	4.1	15.6	0.2	1.7	0.9	5.16	2.0	12.1	7.1	18.6	14.9	29.9	1.9	11.0	3.9	14.9
SCRU	37.6	39.3	24.1	29.5	50.5	55.1	4.5	21.3	37.6	45.7	5.0	16.3	8.1	26.3	3.5	11.6	2.8	9.9
N items	3572		6420		2572		1000		3774		2646		942		989		715	
N samples	331		716		177		154		322		393		137		155		101	
Minimum sample size	131		223		116		109		182		203		89		98		86	
Empty stomachs (%)	2.4		1.7		1.1		3.2		1.1		2.3		1.5		2.6		3.0	
H ± *SD*	2.67 ± 0.05		2.75 ± 0.05		2.54 ± 0.05		2.37 ± 0.05		2.64 ± 0.05		2.58 ± 0.05		2.81 ± 0.05		2.43 ± 0.05		1.96 ± 0.05	
Trophic level	3.58		3.61		3.59		3.60		3.58		3.60							

%N Contribution in number, *%FO* frequency of occurrence of the main groups of prey items, *Minimum sample size* minimum number of stomachs required to perform the statistical analysis, *H* ± *SD* mean value ± standard deviation of the Shannon–Wiener diversity index

Coller 2012), and species which feed mainly upon crabs, such as *S. bonapartii*.

In addition, *S. bonapartii* appeared to a benthic predator as other skates reaching a similar maximum size. Most of the items in its diet were epifaunal benthonic species (crabs, amphipods, cumaceans, isopods, stomatopods and octopi) and the presence of demersal and pelagic prey, such as *M. hubbsi* and *E. anchoita*, could be explained by the daily vertical migrations that these species performed. These migrations may allow *S. bonapartii* to capture them when they are close to the bottom, as postulated for other skates (Orlov 2003; Bizzarro et al. 2007; Treolar et al. 2007).

According to its trophic level, *S. bonapartii* is a secondary consumer. Given that the determination of prey categories and the values assigned to each group can have an impact on estimations, it was difficult to compare punctual values among studies. Furthermore, in this study, trophic levels did not reflect the significant differences among groups recorded by statistical analyses. However, it did agree with the estimations made for other skates reaching similar maximum size that are also considered secondary consumers (Ebert and Bizzarro 2007).

Changes in diet. The diet varied according to sex, size class and throughout the year. The variations could be due to extrinsic and intrinsic factors that could be working together (Di Giácomo and Perier 1996). The extrinsic factors include changes in the abundance and availability of prey. Intrinsic factors are associated with predators and include morphological changes, behavioural differences and differences in energy requirements linked to reproduction (Di Giácomo and Perier 1996).

Differences in the diet of males and females could be due to the availability of prey and/or the energy requirements of reproduction. *Sympterygia bonapartii* exhibits sexual segregation (Estalles et al. 2011) and thus its diet may be reflecting differences in the distribution of prey in the environment. In addition, the higher energy requirements of female reproduction could also be reflected in their diet. This statement is supported by the fact that major differences were observed among individuals of larger sizes, most of them mature.

Changes in diet composition during ontogeny were also recorded. Numerous studies on skates reported an increase in fish consumption and the incorporation of prey of larger size as skate size increases (e.g. Holden and Tucker 1974; Ellis et al. 1996; Orlov 2003). In the present study, a decrease in the consumption of small crustaceans and an increase in the contribution of crustaceans of larger sizes, teleost fishes and cephalopods were detected. This pattern is consistent with previous studies on other rajoids and with previous studies on *S. bonapartii* (see Barrera Oro and Maranta 1996; Sánchez and Prenski 1996; Paesch 2000; Barbini 2010). An explanation is that as predators reach larger sizes, they improve their swimming capacity, which allows them to expand their niche and/or to optimize their ability to capture prey (Holden and Tucker 1974; Ellis et al. 1996). Furthermore, the increase in body size is generally correlated with an increase in mouth opening, which allows for the incorporation of larger prey (Ellis et al. 1996; Treolar et al. 2007).

In addition, ontogenetic changes could also be linked to reproduction. In both sexes, the L_T that defined size groups with significant differences was close to the $L_{T50\%}$ estimated for *S. bonapartii* in the SMG ($L_{T50\%} = 545$ mm for males and $L_{T50\%} = 594$ mm for females; Estalles 2012). This suggests a relationship between the energy expenditure of reproduction and the increase in the consumption of prey with higher energy contributions such as teleost fishes and cephalopods.

Temporal changes were also observed in the diet of *S. bonapartii* and they could be related to at least three factors. The first one is bias due to the origin of the samples which, in most cases, came from commercial fishing vessels. Fishing sites vary throughout the year according to the distribution of the target species of fishery, the common hake *M. hubbsi* or the savorin *Seriolella porosa*, and the establishment of seasonal closure (Di Giácomo and Perier 1992; Perier and Di Giácomo 2002; Di Giácomo et al. 2005). The second factor is the variation over the year in the abundance and availability of prey. The third factor may be differences in the energy requirements during the reproductive cycle of *S. bonapartii*. The only group in which temporal changes were evaluated was the one of female with an $L_T > 580$ mm. This group was composed mainly of mature females. The increase in the consumption of teleost fishes and cephalopods was detected during the mating and the egg-laying season (July to February: Estalles 2012). This could be related to an increase in energy requirements during the maturation of yolk oocytes and the formation of the egg capsules.

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