Ontogenetic diet shifts and food partitioning between two small sympatric skates (Chondrichthyes, Rajidae) in the Southwestern Atlantic

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Abstract. Knowing how sympatric species partition their resources is very important for understanding the mechanisms that influence marine community structure. We test the hypothesis of resource partitioning between two sympatric, closely related, morphologically similar, small skates, *Psammobatis bergi* and *P. extenta*. The diets of the two species were different. *P. bergi* fed predominantly on crabs, amphipods, isopods and polychaetes. *P. extenta* consumed mainly amphipods and shrimps. Changes in the diet with body size, maturity stage and season varied among species. The consumption of amphipods decreased with increasing size of both species. The consumption of crabs increased with increasing size of *P. bergi*, but decreased with increasing size of *P. extenta*. The consumption of cumaceans increased with size of *P. extenta* and decreased with size of *P. bergi*. Adults preyed on isopods more heavily than juveniles for both species. *P. extenta* preyed on shrimps more heavily in the warm season and, on the contrary *P. bergi* preyed on shrimps more often in the cold season. The dietary breadth was higher in *P. bergi* than in *P. extenta* and was higher in females than in males. Our results showed that these sympatric and closely-related species have clearly different trophic traits.

Additional keywords: dietary breadth, elasmobranch, food partitioning, *Psammobatis bergi*, *Psammobatis extenta*.

Introduction

Competition for limited resources is a major driving force of evolution of related and morphologically similar species (MacArthur and Levins 1967; McDonald 2002). Coexistence could be possible despite high levels of ecological similarity among closely related species if these species partition their resources. Food, space and time are the main resources that can be partitioned (Jaksic 2001). In marine fish assemblages, trophic separation is a more important mode of segregation between co-occurring species than spatial or temporal separation (Ross 1986). Therefore, investigations on food resource utilisation by predators as well as on resource partitioning are important for understanding the mechanisms that influence marine community structure.

The effective conservation of skates, and other elasmobranchs, requires having knowledge on feeding habits and food partitioning among them. Declines of larger skate species by overfishing have been accompanied by increases in the abundance of smaller skate species in the community (Walker and

Hislop 1998; Dulvy *et al.* 2000). The competitive release mechanism has been proposed to explain this pattern: the removal of the larger skates may have driven the increase of smaller species through increased food availability (Dulvy *et al.* 2000; Ruocco *et al.* 2012). Information on food partitioning can assist in predicting both shifts in community structure and the ecological impacts as a result of the decline in the abundance of skates and other elasmobranchs.

Many species of elasmobranchs change their diet with sex, size, maturity stage and season (Wetherbee and Cortés 2004) and food partitioning patterns can be affected by these factors. Then, the competition for food resources among skate species is expected to vary during ontogeny (i.e. intrinsic factors) or seasonally (i.e. extrinsic factors). Therefore, quantifying the relative effects of intrinsic and extrinsic factors in food partitioning is crucial so as to predict the potential effects of removal of a species from an ecosystem.

Two endemic skates of the genus *Psammobatis*, the blotched sand skate *Psammobatis bergi* and the zipper sand skate

P. extenta, co-occur in time and space in coastal waters off northern Argentina and Uruguay (Cousseau *et al.* 2007). The distribution of both species extends from the coast off south-eastern Brazil (22°S), to San Jorge Gulf, Argentina (45°42′S) (Cousseau *et al.* 2007; Bovcon *et al.* 2011). The two species differ in body size, with *P. bergi* maturing between 416–441.6 mm and 443–457.6 mm for females and males, respectively (San Martín *et al.* 2005; Mabragaña 2007), and *P. extenta* maturing between 249–256 mm for females and between 262–263 mm for males (Braccini and Chiaramonte 2002; Mabragaña 2007). The maximal total lengths attained by *P. bergi* and *P. extenta* are 555 and 346 mm, respectively (Cousseau *et al.* 2007). They make part of the by-catch in the multi-species bottom trawl fisheries off north Argentina and are always discarded because of their small body size (Tamini *et al.* 2006). *P. bergi* feeds mainly on decapods, amphipods and isopods (Mabragaña 2007; San Martín *et al.* 2007) and *P. extenta* consumes mainly crustaceans, such as amphipods and decapods (Muto *et al.* 2001; Braccini and Pérez 2005; Mabragaña 2007). For several reasons (i.e. common phylogenetic history, morphological similarities and small body size) an apparent feeding similarity between these two species could occur, although the diet of the two species has never been subjected to any formal comparison.

The aim of the present study was to analyse the inter-specific relationship of the diet between two closely related, morphologically similar and small skates, *P. bergi* and *P. extenta*, off Uruguay and northern Argentina, to test the following hypotheses: (1) both species partition its trophic niche in sympatry, (2) the food partitioning changes along ontogeny and seasonally, responding to both intrinsic and extrinsic factors, and (3) the diet breadth between both species is significantly different.

Material and methods

Study area and sampling

The study area, off Uruguay and northern Argentina (between 34°S and 38°S) (Fig. 1), is a stratified coastal zone influenced by the discharge of the continental waters of the Río de la Plata, the second largest South American basin. This system is characterised by strong vertical salinity stratification: freshwater flows on the surface, whereas denser shelf waters intrude at the bottom, taking the shape of a salt wedge. The dynamics of the upper layer is driven by wind stress, whereas the bottom layer is controlled by the bathymetry. The salinity stratification is disrupted by moderate to strong onshore winds (Guerrero *et al.* 1997).

Individuals of *P. bergi* and *P. extenta* were obtained from four research cruises conducted by the Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP, Argentina) during 2005 (December), 2006 (February and June) and 2008 (November). Also, samples were obtained from commercial landings of the coastal fleet of Mar del Plata harbour (38°S 57°33′W) during 2007 (May, August and December) and 2008 (May and July) (Fig. 1). Each skate was sexed and total length (TL) was measured (mm). The stomachs were excised and stored at −20°C. In the laboratory, the stomach contents of each skate were sorted, identified to the lowest taxonomic level, counted and weighed.
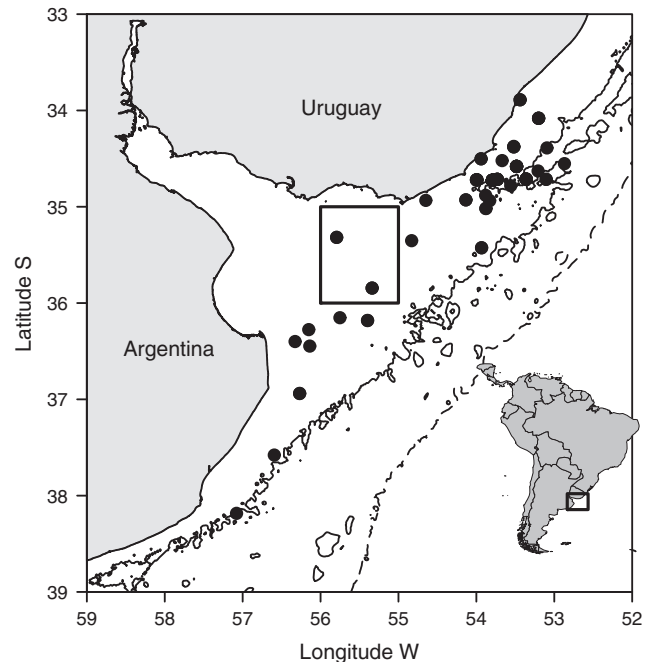
Fig. 1. Map of the coastal ecosystem off Uruguay and northern Argentina showing position of trawl stations (black circles) and cell of the fishing grid (black rectangle) where specimens were collected. Continuous and dashed lines represent 50 m and 200 m isobaths, respectively. The rectangle in the inset depicts the study area off South America.

Data analysis

To quantify the diet composition of the two species and to allow for comparison with other studies the following indices were used: percentage by number (%N), percentage by mass (%M), percentage frequency of occurrence (%F), index of relative importance (IRI) (Pinkas *et al.* 1971) and IRI expressed as a percentage (%IRI) (Cortés 1997).

The cumulative number of stomachs sampled was randomised 100 times and the mean cumulative Shannon–Wiener diversity index was plotted as a function of sample size to determine whether a sufficient number of skates were sampled (Magurran 2004). Sample size was considered sufficient if the diversity index reached an asymptote. Diversity curves were calculated for each combination of variables considered.

To test the hypothesis of differences in diet composition between both species and the effect of ontogeny and season in food partitioning, we grouped prey into shrimps, crabs, amphipods, cumaceans, isopods and polychaetes. These categories were chosen because they included prey with %F > 5 and they reflected the zoological variability of the diet of both species of skates. For each prey category, we built a generalised linear model (GLM) (McCullagh and Nelder 1989), where the response variable was the number of prey consumed and the independent variables were predator size (TL), sex, maturity stage (juvenile or adult) season (cold or warm) and species of skates. By using GLMs, we were able to incorporate species (i.e. *P. bergi* and *P. extenta*) as a categorical independent variable. Therefore, models with the combination sex + species, maturity stage + species, TL + species and season + species

were fitted. Interactions between the two species of skates (species variable) and the other independent variables were also evaluated by building the following models: sex × species, maturity stage × species, TL × species and season × species. We also fitted a null model (i.e. a model without any of the independent variables) to test the hypothesis that none of the variables tested had an effect on the consumption of any prey (Lucifora *et al.* 2009). The response variable of models with number of prey had a large variance because of the large number of zero values in the samples; therefore a negative binomial error distribution was specified (Crawley 2005). A log link was used in the models because response variables could only take zero or positive values (Crawley 2005).

The significance of TL, sex, maturity stage, season and species as independent variables in the consumption of a particular prey were assessed by using information theory (Franklin *et al.* 2001; Johnson and Omland 2004). Each model was considered as a hypothesis explaining the consumption of a given prey. We calculated the Akaike Information Criterion (AIC) and Akaike weights (w) for all hypotheses considered. AIC measures the amount of information lost when fitting a model and w can be considered as the likelihood of each model fitted given the data (Akaike 1973). The models were ranked by AIC, with the best model being the one with lowest AIC value (Crawley 2005). If w did not provide strong support for any hypotheses (i.e. the best AIC model is not strongly supported), we computed model averaging (Symonds and Moussalli 2011). We expected a significant difference in the consumption of most prey between both skate species if food partitioning was present.

To test the hypothesis of differential diet breadth between the two species, we built a GLM with number of prey species consumed ($N_{species}$, i.e. richness of prey by individual) as the dependent variable and TL, sex, maturity stage and season as independent variables. Models with combinations and interactions of independent variables were fitted. The log of the total number of prey consumed (N_{prey}) by individual was included as an independent variable in the models to account for the different number of prey in each sample. The models had a Poisson error distribution and a log link because the dependent variable consists of count data that take only positive or zero values (Crawley 2005). As in previous analyses, the best model was assessed by using information theory.

Results

In total, 90 individuals (5 empty) of *P. bergi* and 123 (7 empty) of *P. extenta* were examined. The size ranges of the individuals sampled for this study were 110–508 mm TL and 96–346 TL for *P. bergi* and *P. extenta*, respectively (Fig. 2). For all combinations, the cumulative curves of diversity reached an asymptote, therefore, the sample sizes were sufficient (see Fig. S1, available as Supplementary Material to this paper).

The diet composition of *P. bergi* was composed of 49 taxonomic categories of prey: 18 brachyuran crabs, eight isopods, five polychaetes, three shrimps, two amphipods, three anomuran crabs, two cumaceans, three mollusks, two teleost fishes, and one cephalochordate (Table 1). The most important prey, in terms of %IRI, were brachyuran crabs, followed by amphipods, polychaetes and isopods. Cumaceans and shrimps
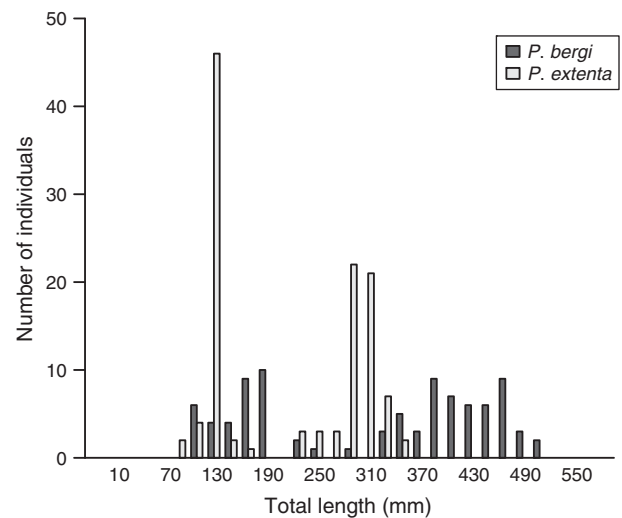

Fig. 2. Length–frequency distributions of *Psammobatis bergi* and *P. extenta* caught off Uruguay and northern Argentina.

were less important (less than 1%IRI). The most important prey by number were amphipods. The diet of *P. bergi* was dominated in %M by brachyuran crabs. Brachyuran crabs and polychaetes were the prey most frequently found (%F), followed by isopods and amphipods.

Prey consumed by *P. extenta* were from 30 taxonomic categories: seven brachyuran crabs, five polychaetes, four shrimps and amphipods, three cumaceans and isopods, two mollusks, one anomuran crab and one misidacean (Table 1). In terms of %IRI, amphipods dominated the diet of this species, followed by shrimps, brachyuran crabs and polychaetes. Cumaceans and isopods showed a %IRI < 1. Amphipods were the dominant prey in %N, %M and %F. The second most important prey by number, mass and frequency of occurrence were shrimps.

The diets of the two species of skates were significantly different. For each prey category, the best models showed different patterns between the two species (Table 2). *P. bergi* consumed more polychaetes than *P. extenta* (estimated mean number of polychaetes consumed by GLM: *P. bergi* = 1.400; *P. extenta* = 0.517). Shrimps were more consumed by *P. extenta* than by *P. bergi* (Fig. 3). Seasonally, *P. extenta* preyed on shrimps more heavily in the warm season than in the cold season and, on the contrary *P. bergi* preyed on shrimps more often in the cold season than in the warm season (Fig. 3).

The consumption of crabs increased with increasing TL of *P. bergi*, but this consumption decreased with increasing TL of *P. extenta* (Fig. 4). On the contrary, the consumption of cumaceans increased slightly with size of *P. extenta* and decreased with size of *P. bergi* (Fig. 4). For both species of skates, the consumption of amphipods decreased with increasing TL, but this prey was consumed more often by *P. extenta* than by *P. bergi* (Fig. 4). Adults preyed on isopods more heavily than juveniles for both *P. extenta* and *P. bergi*, and the latter skate preyed more heavily on isopods than *P. extenta* (Fig. 5). The consumption of the main prey categories was independent from sex.

Table 1.   Diet composition of *Psammobatis bergi* and *P. extenta* expressed as percentage by number (%N), mass (%M), frequency of occurrence (%F), index of relative importance (IRI) and percentage of IRI (%IRI)
Unident.: unidentified

Prey	*Psammobatis bergi*					*Psammobatis extenta*				
	%N	%M	%F	IRI	%IRI	%N	%M	%F	IRI	%IRI
Crustaceans										
Shrimps	1.07	2.36	11.75	40.41	0.39	11.12	38.48	54.70	2712.9	21.06
Unident. shrimps	0.50	0.63	7.06	7.98		1.80	6.36	17.95	146.60	
Artemesia longinaris	0.43	0.30	2.35	1.72		7.16	20.16	20.51	560.37	
Pontocaris boschii						0.44	3.22	5.98	21.92	
Pleoticus muellerii	0.14	1.43	2.35	3.70		1.71	8.73	14.53	151.78	
Anomuran crabs	0.35	0.18	5.88	3.17	0.03	0.09	0.30	0.85	0.33	<0.01
Unident. anomuran	0.14	0.10	2.35	0.57						
Pagurus exilis	0.07	0.02	1.18	0.10						
Loxopagurus loxochelis						0.09	0.30	0.85	0.33	
Porcellana spp.	0.14	0.07	2.35	0.50						
Brachyuran crabs	16.90	49.12	68.23	4504.4	43.86	2.55	9.53	37.61	454.39	3.53
Unident. brachyuran	5.20	12.17	36.47	633.89		1.71	6.65	30.77	257.40	
Eurypodius latrellei	0.07	1.23	1.18	1.53		0.57	1.58	5.98	12.89	
Leurocyclus tuberculosus	1.21	15.41	10.58	175.95						
Libinia spinosa	0.43	7.92	5.88	49.10						
Libidoclea granaria	0.07	0.13	1.18	0.24						
Rochinia gracilipes	0.14	0.28	2.35	0.99						
Leucippa pentagona	7.13	5.39	23.53	294.47		0.09	0.07	0.85	0.13	
Peltarium spinosulum	0.21	1.87	3.53	7.37						
Callinectes sapidus	0.07	0.23	1.18	0.35		0.04	0.73	0.85	0.66	
Ovalipes trimaculatus	0.07	0.72	1.18	0.93						
Xanthidae	0.07	1.01	1.18	1.27						
Pilumnus reticulatus	0.07	0.17	1.18	0.28		0.04	0.03	0.85	0.06	
Panopeus margentus	0.43	0.59	1.18	1.20						
Panopeus meridionalis	0.57	0.36	4.70	4.37						
Corystoides abbreviatus	0.14	0.64	2.35	1.85						
Cyrtograpsus affinis	0.43	0.21	4.71	2.98		0.04	0.03	0.85	0.06	
Pinnixa brevipolex	0.36	0.59	4.71	4.45		0.04	0.44	0.85	0.41	
Dissodactylus criniticholis	0.21	0.19	1.18	0.48						
Amphipods	52.17	8.26	37.65	2275.2	22.16	81.06	43.06	74.36	9229.80	71.64
Unident. amphipods	44.26	6.44	32.94	1670.3		53.78	29.57	53.84	4487.82	
Ampelisca spp.	3.85	0.96	2.35	11.33		26.93	13.26	18.80	755.88	
Hyalidae	4.06	0.85	3.53	17.33		0.35	0.23	2.56	1.48	
Cumaceans	3.06	0.41	18.82	65.35	0.64	1.45	0.69	11.96	25.57	0.20
Unident. cumaceans	0.93	0.08	5.88	5.95		0.57	0.26	5.13	4.25	
Bodotriidae	0.36	0.05	5.88	2.36		0.57	0.26	5.98	4.96	
Diastylidae	1.78	0.28	7.06	14.53		0.31	0.17	3.41	1.64	
Isopods	16.46	17.48	48.23	1637.6	15.95	0.88	0.38	7.70	9.70	0.07
Unident. isopods	0.21	0.12	3.53	1.17						
Exocirolana armata	0.21	0.07	2.35	0.66						
Unident. *Serolis*	1.85	2.48	15.30	66.33		0.48	0.24	5.13	3.70	
Serolis polaris	6.13	5.35	8.23	94.54						
Serolis marplatensis	0.85	0.42	4.70	5.99						
Serolis schytei	4.49	8.01	14.12	176.54						
Cirolana spp.						0.04	0.06	0.85	0.09	
Macrochiridothea spp.						0.35	0.09	2.56	1.12	
Anthuridae	2.71	1.03	8.23	30.81						
Misidaceans						0.04	0.03	0.85	0.06	<0.01
Lancelets	0.14	0.01	1.18	0.18	<0.01					
Polychaetes	8.98	19.84	60	1729.2	16.84	2.63	7.50	44.44	450.56	3.50
Unident. polychaetes	5.06	9.88	48.23	720.61		2.15	6.23	35.90	301	
Flabelligeridae	2.85	7.95	23.53	254.15						
Maldanidae	0.28	1.11	4.71	6.57		0.31	1.19	5.99	8.98	
Nereidae	0.07	0.15	1.18	0.26						

(*Continued*)

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Table 1.   (Continued)

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Prey	*Psammobatis bergi*					*Psammobatis extenta*				
	%N	%M	%F	IRI	%IRI	%N	%M	%F	IRI	%IRI
Orbinidae	0.71	0.74	4.71	6.85		0.04	0.03	0.85	0.06	
Armandia loboi						0.13	0.05	1.71	0.31	
Mollusks	0.57	0.76	4.71	6.28	0.06	0.17	0.03	1.71	0.35	<0.01
Unident. cephalopods						0.04	0.01	0.85	0.05	
Loligo sampaulensis	0.07	0.58	1.18	0.76						
Unident. gasteropods	0.14	<0.01	1.18	0.17						
Unident. bivalves	0.36	0.18	3.53	1.90		0.13	0.02	0.85	0.13	
Teleosts	0.21	1.50	3.53	6.04	0.06					
Unident. teleosts	0.14	1.24	2.35	3.25						
Trachurus lathami	0.07	0.26	1.18	0.39						

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Table 2.   Best models explaining the consumption in number of the main prey category of *Psammobatis bergi* and *P. extenta*

Akaike Information criterion (AIC) and Akaike weights (*w*) for each model are shown. The coefficients of the models are relative to *P. bergi*, juvenile and warm season

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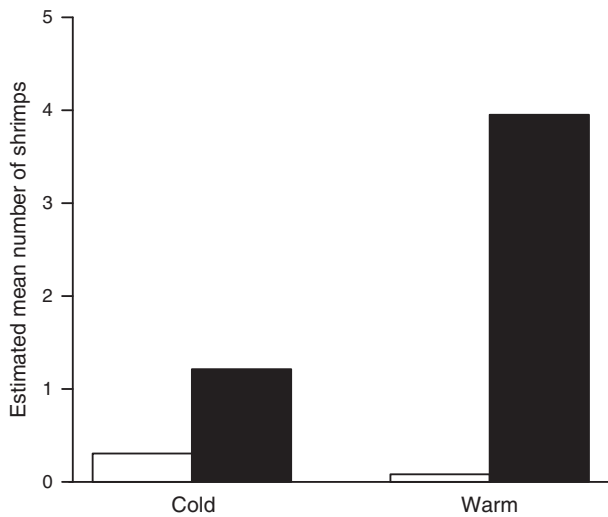| Prey	Intercept	Coefficients	AIC	*w*
Shrimps	−2.505	1.319 cold + 3.879 *P. extenta* − 2.500 (cold × *P. extenta*)	530.3	0.76
Crabs	−0.525	0.004 TL + 1.146 *P. extenta* − 0.011 (TL × *P. extenta*)	586.6	0.99
Amphipods	3.491	−0.004 TL + 0.271 *P. extenta*	1247.2	0.71
Cumaceans	1.300	−0.008 TL − 3.299 *P. extenta* + 0.011 (TL × *P. extenta*)	269.2	0.34
Isopods	1.930	−1.409 juvenile − 3.183 *P. extenta*	431.5	0.48
Polychaetes	0.393	−1.052 *P. extenta*	512.7	0.26

Fig. 3.   Seasonal change in consumption of shrimps by *Psammobatis bergi* and *P. extenta* from off Uruguay and northern Argentina estimated by generalised linear models. The models had a log link and a negative binomial error distribution. White, *P. bergi*; black, *P. extenta*.

The best models of the consumption of cumaceans, isopods and polychaetes were not strongly better than the alternatives, therefore we used model averaging for these models. For cumaceans, the model averaging slope was −0.003 (s.e. = 0.001) for TL, −1.447 (s.e. = 3.270) for *P. extenta* and −0.004 (s.e. = 0.001) for TL × *P. extenta* with a combined *w* of 0.96. The estimated model averaged coefficients for isopods was −0.899 (s.e. = 0.475) for juveniles of both species of skates and −2.752 (s.e. = 0.566) for *P. extenta* with a *w* of 0.95. The averaged coefficient for polychaetes was −1.063 (s.e. = 0.239) for *P. extenta* with a combined *w* of 0.99.

There was a significant difference in the dietary breadth between species and sexes. The coefficients of the best model were the following:

$$N_{species} = 0.852 - 0.367 \, P. \, extenta - 0.143 \, male + 0.183 \log(N_{prey})$$
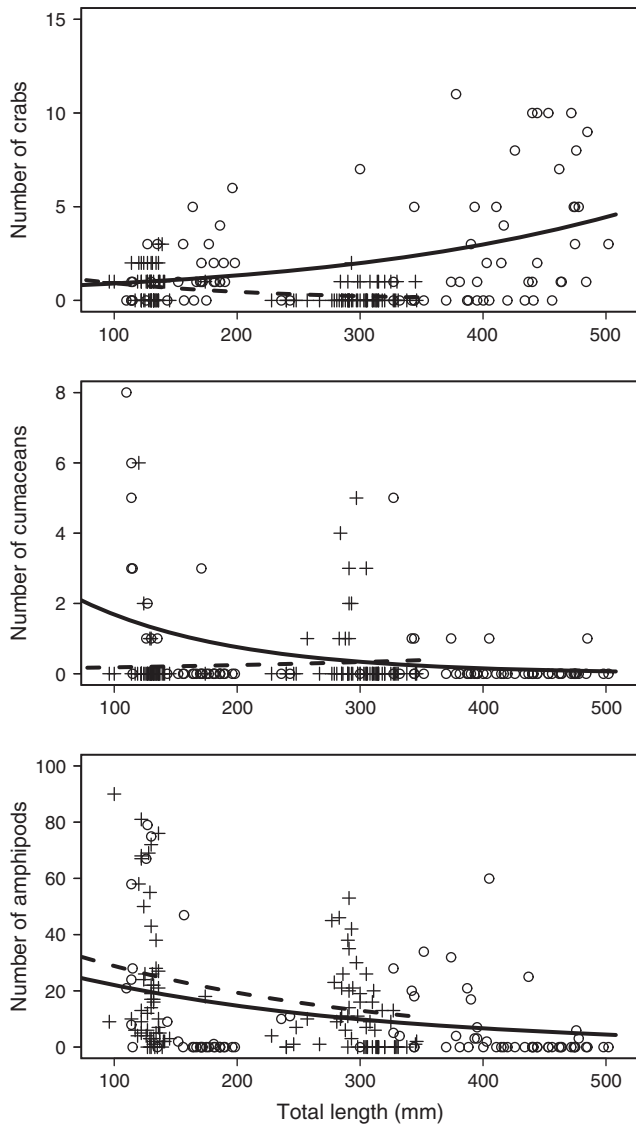
with AIC = 696.5 and *w* = 0.261. The coefficients of the model are relative to *P. bergi* and females of both species of skates. This model implies that the $N_{species}$ consumed was higher in *P. bergi* than in *P. extenta*, and in females than in males for both species. The $N_{species}$ consumed was independent from TL, maturity stage and season. The best model had a low *w*, therefore we computed model averaging. The estimated model-averaged coefficients were −0.047 (s.e. = 0.042) for males and −0.297 (s.e. = 0.128) for species with a combined *w* of 0.99.
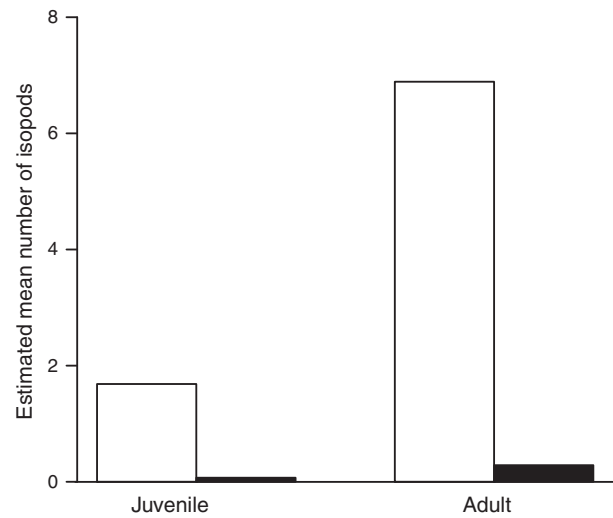
Discussion

Overall diet

The diet composition observed for both skates were in part in agreement with published information on these species. For *P. extenta*, our results are consistent with observations in the

Fig. 4. Change in consumption of crabs, cumaceans and amphipods, with body size of *Psammobatis bergi* and *P. extenta* from off Uruguay and northern Argentina estimated by generalised linear models. The models had a log link and a negative binomial error distribution. *P. bergi*: solid lines and open circles; *P. extenta*: dashed lines and crosses.

Fig. 5. Change in consumption of isopods with the maturity stage of *Psammobatis bergi* and *P. extenta* from off Uruguay and northern Argentina estimated by generalised linear models. The models had a log link and a negative binomial error distribution. White, *P. bergi*; black, *P. extenta*.

whatsoever. These differences in diet composition may arise from differences in sampling areas. In this study, the distribution range of the sampled individuals of *P. bergi* was between 34° and 38°S, in Mabragaña's (2007) study it was between 34° and 42°S and in San Martín *et al.*'s (2007) study was in adjacent waters to Puerto Quequén (38°37′S, 58°50′W).

Ontogenetic shifts and food partitioning

The fact that both species of skates are closely related and occur sympatrically could suggest that their feeding habits are very similar. The foraging lifestyles of both *P. bergi* and *P. extenta* are clearly benthophagous and their diets are dominated by invertebrates. However, the results of this study showed that their dietary compositions were significantly different. The most important prey for *P. bergi* were crabs, isopods and polychaetes, whereas *P. extenta* preyed predominantly on amphipods and shrimps. This partitioning of food resources may be, in part, a strategy to avoid direct competition between these two closely-related species (Schoener 1974). In another study conducted on sympatric skates in the south-west Atlantic, the dietary compositions of *Psammobatis normani* and *P. rudis* were not significantly different statistically, although there was still evidence of some food partitioning among these two species (Mabragaña and Giberto 2007). Differences in diet composition were observed between other closely-related chondrichthyans in sympatry, like skates (e.g. *Dipturus* spp., Treloar *et al.* 2007; *Raja* spp., McEachran *et al.* 1976; Bizzarro *et al.* 2007), urolophids (*Urolophus* spp., Platell *et al.* 1998; Platell and Potter 2001; Marshall *et al.* 2008), dasyatids (*Neotrygon* spp., Jacobsen and Bennett 2012) and chimaeroids (Mauchline and Gordon 1983). Thus, the studies of trophic ecology of closely-related species have shown that they have clearly different ecological traits.

Chondrichthyans that feed on hard prey, such as crustaceans and mollusks, have crushing and grinding teeth (Wilga and

same region (Braccini and Pérez 2005; Mabragaña 2007) and in Ubatuba Bay, Brazil (Muto *et al.* 2001). Amphipods are its main prey, followed by shrimps and, to a lesser extent by crabs and polychaetes (Muto *et al.* 2001; Braccini and Pérez 2005; Mabragaña 2007). Crabs were the main prey of *P. bergi*. This is consistent with observations in waters from off north Argentina (San Martín *et al.* 2007; Mabragaña 2007). However, the consumption of amphipods, cumaceans and isopods by *P. bergi* is clearly different between our results and other studies. The importance of amphipods, cumaceans and isopods as prey of *P. bergi* is very low according to Mabragaña (2007). San Martín *et al.* (2007) observed that isopods are a minor prey and that both amphipods and cumaceans are not present in the diet of *P. bergi*

Motta 2000). The number of tooth rows, and the shape and arrangement of teeth may be related to the feeding habits of skates (McEachran *et al.* 1976). Both *P. bergi* and *P. extenta* have sexually-dimorphic heterodonty (Barbini 2011), but these sexual dimorphism is probably related to reproductive behaviour rather than to feeding (McEachran 1977), because our analysis did not find any sexual difference in diet composition. The teeth of both skate species have a different morphology and arrangement. The teeth of *P. bergi* are hexagonal in shape and are arranged in pavement (Barbini 2011), morphological characteristics associated to feeding on hard prey, like crabs. On the other hand, the teeth of *P. extenta* have rounded crowns and are arranged in parallel rows (Barbini 2011), and this species consumes mainly small crustaceans. Tooth morphology could allow *P. bergi* to take advantage of a resource that is not easily available to *P. extenta*.

Our results showed that body size and maturity stage have an important effect on the feeding habits of both skate species. In *P. bergi* small individuals preyed on cumaceans and amphipods, whereas large individuals consumed crabs and isopods. In *P. extenta*, small individuals consumed amphipods and small crabs, such as *Eurypodius latreille*, and large individuals consumed cumaceans and isopods. Food partitioning between sympatric predators may change at particular times in the life history (Piet *et al.* 1998). These ontogenetic patterns of both skate species may be associated with combined effects of competition and individual intrinsic factors (i.e. body size or maturity stage) of each species: large individuals may have a different ability to capture larger or harder prey than small individuals.

Interspecific differences in diet are not only expected to be governed by morphological constraints between species; habitat use and extrinsic factors may also play an important role in food partitioning, as noted in other elasmobranch communities (Sommerville *et al.* 2011). A seasonal interaction was found in the consumption of shrimps between both skate species: *P. extenta* preyed heavily on shrimps in the warm season, whereas the consumption of this prey by *P. bergi* increased in the cold season. There is very little information on seasonal abundance of invertebrates in this region and the causes of this pattern are not clear. But possible seasonal change in the abundance of shrimps and different uses of habitat between skate species could be the explanation.

Dietary breadth

We found differences in the dietary breadth between both species and sexes. *P. bergi* has a wider dietary breadth than *P. extenta*. This pattern could be related to several causes: differences in tooth morphology (see before), differential use of microhabitats between species, with *P. bergi* favouring microhabitats with a richer prey diversity; or differences in foraging tactics between species, with, for example, *P. bergi* having a longer prey searching time than *P. extenta*. This could affect the foraging capabilities of *P. bergi* (i.e. increased capacity to capture higher number of prey species) with regard to *P. extenta*.

Females of both species have a higher dietary breadth than males. This sexual difference could be related to the high energy demand of females for reproduction. Since oocyte and egg case production are energetically demanding, females may be required to eat more often than males (e.g. Horppila *et al.* 2011), which could result in a higher prey diversity for females. Thus, Braccini and Chiaramonte (2002) found that in *P. extenta* the mass-length relationship was different between sexes, with females attaining a greater mass than males of the same size. The positive allometric growth of females in *P. extenta* (i.e. higher growth in mass than in length) would allow them to achieve a greater reproductive success (Braccini and Chiaramonte 2002). Therefore, the higher number of prey consumed by females could likely represent an advantage in maintaining the energy demand required for the reproductive process.

Finally, fishery overexploitation threatens elasmobranch species almost worldwide (Ferretti *et al.* 2010). Given that batoids can affect the benthic communities by disrupting the structure of the bottom (O'Shea *et al.* 2012), their removal can influence community structure. *P. bergi* and *P. extenta* are commonly caught and discarded by the coastal bottom trawlers operating off north Argentina (Tamini *et al.* 2006), the area with the country's highest catch and diversity of elasmobranchs (Lucifora *et al.* 2012). The genus *Psammobatis* has been historically of low priority in fishery statistics and research in Argentinean waters. This lack of information precludes an assessment of the impact of fisheries on these skate species. Therefore, knowing the population trends and ecology of the genus *Psammobatis* is very important for determining their conservation status and ecological role in the community, respectively. Further, the destruction and loss of the benthic habitat caused by the coastal fleets of bottom trawlers (Brazeiro *et al.* 2003) affects the benthic community structure, generating indirect effects on benthic feeders, like *P. bergi*, *P. extenta* and other benthic predators.

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