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Feeding habits of a large endangered skate from the south-west Atlantic: the spotback skate, *Atlantoraja castelnaui*

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Abstract. Elasmobranch predation has important effects on marine ecosystems. Identifying the main correlates of the feeding habits of skates is of paramount importance for determining their ecological role. We tested the hypotheses that the diet of the spotback skate, *Atlantoraja castelnaui*, off Uruguay and northern Argentina, changes with increasing body size, between seasons and regions and that prey size increased with predator's size using a multiple-hypothesis modelling approach. *A. castelnaui* preyed mainly on teleosts, followed by cephalopods, elasmobranchs and decapods. Small individuals of *A. castelnaui* consumed decapods and large individuals ate elasmobranchs and cephalopods. The consumption of teleosts was constant along the ontogeny but differed between seasons; more demersal-benthic teleosts were consumed in the cold season, whereas more benthic teleosts were eaten in the warm season. Also, *A. castelnaui* consumed more cephalopods in the warm season than in the cold season. Benthic teleosts were consumed more in the south region, whereas decapods were eaten more in the north region. *A. castelnaui* is able to consume larger teleosts as it grows. We conclude that *A. castelnaui* is a versatile, mainly piscivorous, consumer that shifts its diet with increasing body size and in response to seasonal and regional changes in prey abundance or distribution.

Additional keywords: Argentina, diet variation, predation, Rajidae, Uruguay.

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Introduction

Large predators have significant effects on the trophic dynamics of a variety of ecosystems, affecting community structure and energy flow (Estes *et al.* 2011). In marine ecosystems, elasmobranch predation is a major force structuring communities (Heithaus *et al.* 2008, 2010; Ferretti *et al.* 2010). Large sharks prey on smaller sharks and batoids; removing the large sharks results in a cascading effect that changes the structure of the benthic community (Myers *et al.* 2007; Ferretti *et al.* 2010). Large batoids affect the species turnover of benthic communities by disrupting the structure of the bottom and preying on benthic invertebrates (VanBlaricom 1982; Thrush *et al.* 1991).

Skates, by their abundance and species diversity, may play influential roles in marine community dynamics (Ebert and Bizzarro 2007). Therefore, knowing and understanding the feeding habits of skates are very important for determining their ecological role (San Martín *et al.* 2007). The spotback skate *Atlantoraja castelnaui* (Rajidae) is the largest skate of coastal waters and one of the largest benthic batoids in the south-west Atlantic Ocean, attaining 1400 mm in total length. It is endemic to the south-west Atlantic from Rio de Janeiro, Brazil (22°S), to San Jorge Gulf, Argentina (46°39′S) (Menni and Stehmann 2000; Bovcon *et al.* 2011). In Argentinean waters, this species occurs from shallow coastal waters to ~100 m depth (Cousseau *et al.* 2007) and matures at 1089 mm (females) and 980 mm (males) total length (Colonello 2009).

Due to its large body size, *A. castelnaui* has a high commercial value and has been subjected to heavy fishing pressure; as a result, its biomass declined by 75% between 1994 and 1999 (Hozbor *et al.* 2004). For this reason, *A. castelnaui* is categorised as endangered by the International Union for the Conservation of Nature (IUCN), with a decreasing trend in population abundance (Hozbor *et al.* 2004). Its large size makes it ecologically important because other large skate species, such as *Zearaja chilensis* or *Dipturus trachyderma*, do not overlap greatly with *A. castelnaui* in their bathymetric range and occur only in deeper waters (Menni and Stehmann 2000; Cousseau *et al.* 2007). However, the ecology of this species, including its feeding habits, is poorly known. Previous studies of the feeding habits of *A. castelnaui* are limited to descriptions of dietary composition, indicating that the species feeds mainly on teleost fishes (Laureda and Martínez 1981; Soares *et al.* 1992; Paesch 2000).

Variation in the diet of elasmobranchs can be attributed to intrinsic and extrinsic factors (Di Giácomo and Perier 1996; Lucifora 2003). Intrinsic factors are traits of the predator, such as sex, maturity stage and body size; extrinsic factors are characteristics of the prey or the environment that affects the availability of prey. Evaluating the interplay and relative effects of intrinsic and extrinsic factors on the diet will help to identify potential effects of the decline in abundance of predators (Lucifora *et al.* 2009*a*). For example, if skate body size is an important determinant of the consumption of a particular prey, then fishing for the larger skates will affect the predator–prey relationship. However, if geographic region is the main determinant of the consumption of a given prey, then regional differences in fishing effort or coastal development will have a higher impact on the predator–prey relationship than any intrinsic factor.

In this paper, we explored the importance of several intrinsic and extrinsic factors in determining the diet of a large skate, the spotback skate, *A. castelnaui*. Specifically, we tested the following hypotheses: (1) the diet of *A. castelnaui* changes with increasing body size; (2) the diet composition changes between seasons; (3) there are differences in the diet between regions; and (4) prey size increases with increasing body size of *A. castelnaui*.

Materials and methods

Study site and sampling

The coastal region off Uruguay and northern Argentina (between 34°S and 41°S) consists of two large ecosystems. The first, the northern region (34–38°S), is a stratified coastal zone influenced by the very large discharge of continental waters of the Río de la Plata. The second, the southern region (38–41°S), is a homogeneous coastal zone, called El Rincón, influenced by the smaller discharges of the Negro and Colorado rivers and by high-salinity waters of the San Matías Gulf (Guerrero and Piola 1997; Lucas *et al.* 2005).

Samples (390 individuals, 255 with stomach contents) were obtained from scientific trawl surveys conducted by the Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP, Argentina) during December 2005, February and June 2006 and from commercial landings of the coastal fleet of Mar del Plata harbour (Fig. 1) during May, September, October and November 2006 and April, May, June, July, August, October, November and December 2007 (Fig. 1). Each specimen captured was measured (total length (TL), mm) and sexed. Also, the maturity stage (juvenile or adult) was determined according to the degree of calcification of the claspers and the development of testes and reproductive ducts in males and to the presence of eggs and observation of the uteri, oviducal glands and ovarian follicles in females (Stehmann 2002; Colonello 2009). The stomachs were removed and stored at −20°C. In the laboratory, prey were sorted, identified to the lowest possible taxonomic level using published catalogues, counted and wet weight was recorded (±0.01 g).

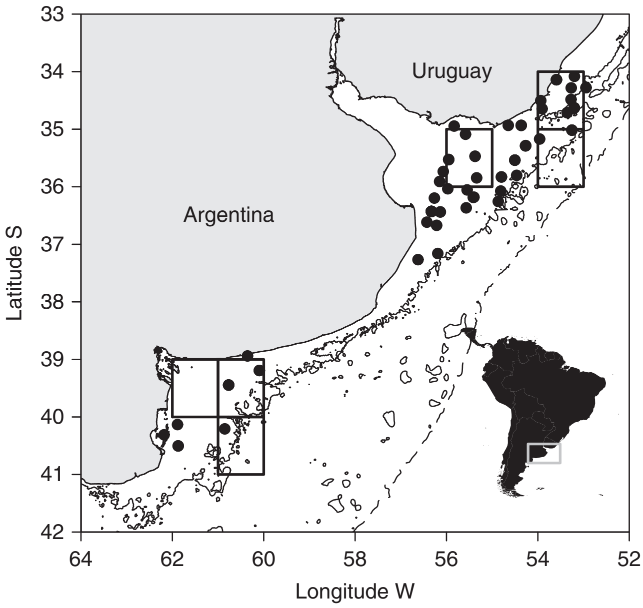

Fig. 1. Map of the sampling area from off Uruguay and north Argentina, showing positions of trawls stations (black circles) and cells of the fishing grid (black rectangles) where individuals of *Atlantoraja castelnaui* were captured. The 50-m and 200-m isobaths are shown as solid and dashed lines respectively. The rectangle in the inset shows the location of the study area in South America.

Feeding habits

The importance of each prey was evaluated using percentage by number (%N), mass (%M), frequency of occurrence (%F) and index of relative importance (%IRI; Pinkas *et al.* 1971; Cortés 1997).

For statistical analyses, we grouped prey into six categories: benthic teleosts, demersal-benthic teleosts, pelagic teleosts, elasmobranchs, cephalopods and decapods. The number of sampled *A. castelnaui* with prey was tested to evaluate whether sample size by sex, maturity stage, region and season was sufficient for the statistical analyses. The sampling order of stomachs was randomised 100 times and the mean cumulative Shannon–Wiener diversity index was plotted as a function of sample size. Sample size was considered sufficient to describe diet if the cumulative prey curve reached an asymptote (Magurran 2004).

To test the hypothesis of change in the diet of *A. castelnaui* with increasing body size and of differences in the diet composition between seasons and regions, we adopted a multiple-hypothesis modelling approach (Franklin *et al.* 2001; Johnson and Omland 2004; Symonds and Moussalli 2011). We assessed whether the consumption of the prey categories varied with sex, maturity stage (juvenile and adult), total length, season (warm = October–March; cold = April–September) and region (north = 34°–38°S; south = 38°–41°S) using generalised linear models (GLM) (Venables and Ripley 2002). For each prey category, we built GLMs in which the response variable was the number of the prey consumed and the independent variables were sex, maturity stage, TL, season and region (Lucifora *et al.* 2009*a*). Further, models with combinations between two independent variables were fitted: sex + season, sex + region, maturity stage + season, maturity stage + region, TL + season, TL + region and season + region. Models without any of the independent variables (i.e. null models) were fitted to test the hypothesis that none of the variables tested had an effect on the consumption of a prey category (Lucifora *et al.* 2009*b*). All models had a negative binomial error distribution (i.e. a high number of zero-values and variance much greater than the mean) and a log link (Crawley 2005).

For each model fitted within a prey category, we calculated the Akaike information criterion (AIC) and the model with the lowest AIC was selected as the best model. AIC measures the amount of information lost when fitting a model, so the model with the lowest AIC is the best one explaining the observed data (Crawley 2005). To obtain the likelihood of each model fitted, Akaike's weight (w) was calculated (Franklin *et al.* 2001; Johnson and Omland 2004). If w did not provide strong support for any model fitted, we used model averaging to measure the effects of the variable explaining most of the variation (Johnson and Omland 2004; Symonds and Moussalli 2011).

The hypothesis that prey size increased with increasing body size of the predator was assessed using the TL of *A. castelnaui* and the TL of prey teleosts. Regressions on the 5, 50 and 95% quantiles were fitted to test an increase in minimum, medium and maximum prey size consumed with increasing TL of *A. castelnaui* respectively (Scharf *et al.* 1998).

Results

Of the individuals with food in the stomachs ($n = 255$), 121 were female (243–1365 mm TL) and 134 were male (332–1400 mm TL). The cumulative diversity curves reached an asymptote, indicating that sample size was sufficient for all groups considered (see Fig. S1, available as Supplementary Material to this paper).

Forty-five prey were identified to the lowest taxonomic level: 27 teleosts, eight decapods, six elasmobranchs, three molluscs and one cephalochordate (Table 1). Teleosts were the dominant prey consumed by *A. castelnaui*. Decapods, cephalopods and elasmobranchs were less important components of the diet. The most important teleost by number was *Dules auriga*, followed by *Raneya brasiliensis*, *Porichthys porosissimus* and *Trachurus lathami*. In terms of weight, *Cynoscion guatucupa* was the most important prey, followed by *P. porosissimus* and *Prionotus nudigula*. *D. auriga* and *R. brasiliensis* were the most important prey by frequency of occurrence. The decapods, cephalopods and elasmobranchs consumed were predominantly shrimps, octopi and skates respectively.

Relationships between number of prey consumed with TL, season and region were found (Table 2). The effect of each of these variables was dependent on the prey group; therefore, below we present the results for each prey group. In all models, the residual deviance was less than the residual degrees of freedom, indicating that the models had a good fit to the data (see Table S1, available as Supplementary Material to this paper).

The consumption of benthic teleosts was affected by season and region. Benthic teleosts were consumed more in the warm season than in the cold season (Fig. 2). In the warm season, the most important benthic teleosts in the diet were *P. porosissimus*, *Etropus longimanus* and *Percophis brasiliensis* (Fig. 3). The number of the benthic teleosts consumed was higher in the south region than in the north region (Fig. 2).

Season was the only factor affecting the consumption of demersal-benthic teleosts. More demersal-benthic teleosts were consumed in the cold season than in the warm season (estimated number of demersal-benthic teleosts by GLM: warm = 0.388; cold = 0.747). *D. auriga* was the most consumed demersal-benthic teleost by *A. castelnaui* in the cold season (Fig. 3). The model of consumption of demersal-benthic teleosts had a low w, so we computed model averaging. The averaged coefficient was 0.642 (s.e. = 0.195) for the cold season, with a combined w of 0.981. The consumption of pelagic teleosts was independent of sex, maturity stage, TL, season or region.

Body size was the only variable with a significant effect on the consumption of elasmobranchs by *A. castelnaui*; consumption of elasmobranchs increased with increasing TL of *A. castelnaui* (Fig. 4). Body size and season significantly affected the consumption of cephalopods by *A. castelnaui*. The number of cephalopods consumed increased with the size of *A. castelnaui* and was higher in the warm season than in the cold season (Fig. 4). The main cephalopod consumed in the warm season was the octopus *Octopus tehuelchus*.

A combination of body size and region was the most plausible explanation for the pattern of consumption of decapods. Contrary to the pattern found for elasmobranchs and cephalopods, the consumption of decapods decreased with increasing TL of *A. castelnaui* (Fig. 4). Decapods were consumed more in the northern region than in the southern region (Fig. 4).

For elasmobranchs, cephalopods and decapods, model averaging was computed. For elasmobranchs, the model averaged slope for TL was 0.002 (s.e. = 0.0007) with a combined w of 0.636. The estimated averaged coefficients for cephalopods were 0.004 (s.e. = 0.002) for TL and −0.740 (s.e. = 0.630) for the cold season with a combined w of 0.90. The averaged coefficients for decapods were −0.004 (s.e. = 0.001) for TL and −0.259 (s.e. = 0.252) for the south region with a combined w of 0.778.

Significant relationships between predator and prey body size were found. As TL of *A. castelnaui* increased, minimum, medium and maximum TL of teleosts increased (slope and intercepts of 5, 50 and 95% quantile regressions = 0.081 and 15.673; 0.131 and 32.817; 0.366 and −39.170, respectively, $P < 0.05$) (Fig. 5).

Discussion

Dietary composition

Corroborating our results, a previous study conducted off Mar del Plata (38°S) found that teleosts were the main prey consumed by *A. castelnaui*, followed by molluscs, crustaceans and other invertebrates (Laureda and Martínez 1981). However, the main species of teleosts consumed were different between studies. The most important species of teleosts observed by Laureda and Martínez (1981) were flatfishes, *Symphurus* spp. and *R. brasiliensis*. In our study, *D. auriga*, *R. brasiliensis*,

Table 1. Diet composition of *Atlantoraja castelnaui* off Uruguay and northern Argentina
%N, percentage by number; %M, percentage by mass; %F, percentage frequency of occurrence; %IRI, percentage index of relative importance

Group	Prey	%N	%M	%F	%IRI
Teleosts[A]		74.40	92.52	89.41	97.81
Unidentified teleosts		19.40	14.54	30.20	
Congridae	*Conger orbignyanus*	0.22	1.70	0.39	
Engraulidae	*Engraulis anchoita*	0.22	0.03	0.39	
Ophidiidae	*Raneya brasiliensis*	6.13	4.77	10.59	
Batrachoididae	*Porichthys porosissimus*	5.47	7.60	9.02	
	Triathalassothia argentina	2.19	1.54	3.14	
Triglidae	*Prionotus nudigula*	3.50	7.32	5.88	
Serranidae	*Dules auriga*	11.82	3.84	12.55	
Carangidae	*Trachurus lathami*	5.47	4.37	5.88	
	Parona signata	0.22	0.62	0.39	
Sparidae	*Pagrus pagrus*	0.44	2.07	0.78	
Sciaenidae	*Cynoscion guatucupa*	2.62	16.10	4.31	
	Umbrina canosai	0.87	2.04	1.57	
	Paralonchurus brasiliensis	0.22	0.14	0.39	
Mullidae	*Mullus argentinae*	2.62	2.72	2.74	
Cheilodactylidae	*Nemadactylus bergi*	0.44	2.10	0.78	
Percophidae	*Percophis brasiliensis*	2.84	6.17	4.31	
Pinguipedidae	*Pinguipes brasiliensis*	1.31	5.41	1.96	
Gobiidae	*Gobiosoma parri*	0.87	<0.01	0.39	
Stromateidae	*Stromateus brasiliensis*	0.22	0.46	0.39	
Paralichthyidae	*Paralichthys orbignyanus*	0.22	5.25	0.39	
	Paralichthys patagonicus	0.66	1.53	1.17	
	Xystreurys rasile	0.22	0.29	0.39	
	Achiropsetta tricolepis	0.66	0.07	0.78	
	Etropus longimanus	3.72	0.55	4.70	
	Unidentified Paralichthyidae	0.66	1.15	1.18	
Cynoglossidae	*Symphurus* spp.	0.87	0.10	1.59	
Elasmobranchs[A]		4.16	2.63	5.49	0.24
Triakidae	*Mustelus schmitti*	0.22	0.55	0.39	
Rajidae	*Atlantoraja castelnaui*	0.22	0.05	0.39	
	Psammobatis extenta	0.22	0.43	0.39	
	Psammobatis spp.	0.22	0.52	0.39	
	Sympterygia bonapartii	0.22	0.07	0.39	
	Unidentified Rajidae	3.06	1.00	3.53	
Cephalochordates[A]	*Branchiostoma platae*	0.22	<0.01	0.39	<0.01
Molluscs[A]					
Cephalopods[A]		3.50	4.09	5.10	0.25
Unidentified squid		0.44	0.18	0.78	
Octopodidae	*Octopus tehuelchus*	3.06	3.90	4.31	
Gastropods	Unidentified Fissurellidae	0.22	0.03	0.39	
Crustaceans[A]					
Decapods[A]		17.50	0.73	14.12	1.69
Penaeidae	*Artemesia longinaris*	1.31	0.07	1.96	
Solenoceridae	*Pleoticus muelleri*	3.28	0.02	0.78	
	Unidentified shrimps	8.31	0.04	5.10	
Majidae	*Collodes rostratus*	0.22	<0.01	0.39	
	Libinia spinosa	0.44	<0.01	0.39	
	Libidoclaea granaria	0.44	0.01	0.39	
Portunidae	*Ovalipes trimaculatus*	0.66	0.47	1.18	
	Unidentified crabs	2.84	0.12	4.31	
Total number of prey		457			
Total mass (g)		17 813			

[A]Major taxonomic group.

P. porosissimus and *T. lathami* were the most consumed teleosts. This difference in consumption of teleosts may be associated with local differences in prey availability, because the results from Laureda and Martínez (1981) reflected the diet of samples taken from off Mar del Plata whereas the samples in our study covered a much larger area.

Off the Río de la Plata, between 50 and 100 m depth, the diet composition of *A. castelnaui* is also dominated by teleosts

Table 2. Best models explaining the consumption in number of the main prey categories of *Atlantoraja castelnaui*
TL, total length; AIC, Akaike information criterion; *w*, Akaike's weigths; standard errors are in parentheses. South and cold are levels of factors region and season respectively

Prey categories	Intercept	Coefficient	AIC	*w*
Benthic teleosts	−1.357 (0.262)	0.706 (0.293) south − 0.346 (0.250) cold	372.4	0.559
Demersal-benthic teleosts	−0.944 (0.148)	0.653 (0.197) cold	500.9	0.325
Elasmobranchs	−5.981 (1.136)	0.003 (0.001) TL	128.4	0.244
Cephalopods	−6.831 (1.463)	−1.443 (0.680) cold + 0.004 (0.001) TL	109.5	0.421
Decapods	1.700 (0.674)	−0.881 (0.449) south − 0.004 (0.001) TL	286.6	0.279

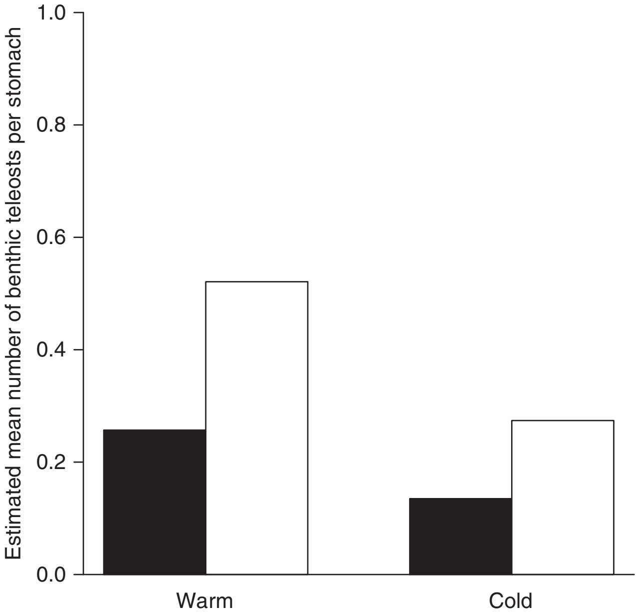

Fig. 2. Changes in consumption of benthic teleosts (in number) with season and region of *Atlantoraja castelnaui* estimated by generalised linear models. The models had a log link and a negative binomial error distribution. Black, north region; white, south region.

(Paesch 2000). In contrast, in Ubatuba Bay (24°S, Brazil), the diet composition consisted of two main prey items: teleosts and decapods (Soares *et al.* 1992). The high consumption of decapods may be due to a bias in the frequency distribution of samples towards small skates (range of TL: 217–865 mm), since our results indicate a negative relationship between skate size and decapod consumption. The pattern found in Ubatuba Bay could also be a result of lower sample size ($n = 24$).

Relationships between diet and body size, season and region

The diet of *A. castelnaui* was affected by ontogeny, season and geographic area. Body size (i.e. total length) has an important effect on the diet composition of *A. castelnaui*; small individuals consume decapods and large individuals consume elasmobranchs and cephalopods. An increase in the consumption of elasmobranchs with body size has been reported for sharks (Smale 1991; Lowe *et al.* 1996; Lucifora *et al.* 2005, 2009*a*). However, elasmobranchs are not important prey in the diet of skates and this pattern has not been documented before in any skate. In other studies on the diet of *A. castelnaui*, elasmobranchs such as angel sharks, *Squatina* spp. and skates (Laureda and Martínez 1981; Paesch 2000) were also found. Skates were the main elasmobranchs consumed by *A. castelnaui* and there was even one case of cannibalism by an adult male (TL = 1063 mm) that consumed a juvenile individual. As the morphology of skates as prey (i.e. dorsoventrally flattened) complicates the handling and suction by small individuals of *A. castelnaui*, large individuals may be more able to capture this prey. The importance of body size in determining the consumption of elasmobranchs indicates that shifting size distributions towards smaller individuals, a common result of overfishing (Bianchi *et al.* 2000), would relax the predation pressure on these prey by *A. castelnaui*. Body size has been identified as the main determinant of elasmobranch predation by the copper shark *Carcharhinus brachyurus* (Lucifora *et al.* 2009*a*) and the sand tiger shark *Carcharias taurus* (Lucifora *et al.* 2009*b*), which indicates that body size may be a general determinant of elasmobranch consumption regardless of the taxonomic identity of the predator. A decrease in the consumption of decapods with increasing body size has been described for other skates (Koen Alonso *et al.* 2001; Treloar *et al.* 2007). In *A. castelnaui*, this pattern may be associated with an increase in the quality of the diet, where decapods are replaced by more energetically profitable prey such aselasmobranchs and cephalopods. The most important cephalopod in the diet of *A. castelnaui* is the octopus *O. tehuelchus* and its higher consumption in the warm season may be related to the behaviour of this prey. The warm season is a period of intense reproductive (mating) and feeding activity by *O. tehuelchus*, potentially increasing its exposure and vulnerability to predation (Iribarne 1991; Ré and Gómez Simes 1992). Season was also the main factor affecting the consumption of teleosts by *A. castelnaui*. The higher consumption of demersal-benthic teleosts in the cold season and the higher consumption of benthic teleosts in the warm season may be related to seasonal shifts in the distribution and abundance of teleosts. In the same study area, other coastal skates, such as *Psammobatis extenta* (Braccini and Perez 2005), *Psammobatis bergi* (San Martín *et al.* 2007) and *Rioraja agassizi* (Barbini and Lucifora 2011), also have seasonal shifts in diet composition. These skates have evolved strategies to cope with temporal variability in prey abundance (Caddy and Sharp 1986; Braccini and Perez 2005).

The dominant benthic teleosts in the diet during the warm season were *P. porosissimus*, *E. longimanus* and *P. brasiliensis*, while *D. auriga* was the most important in the cold season. In the

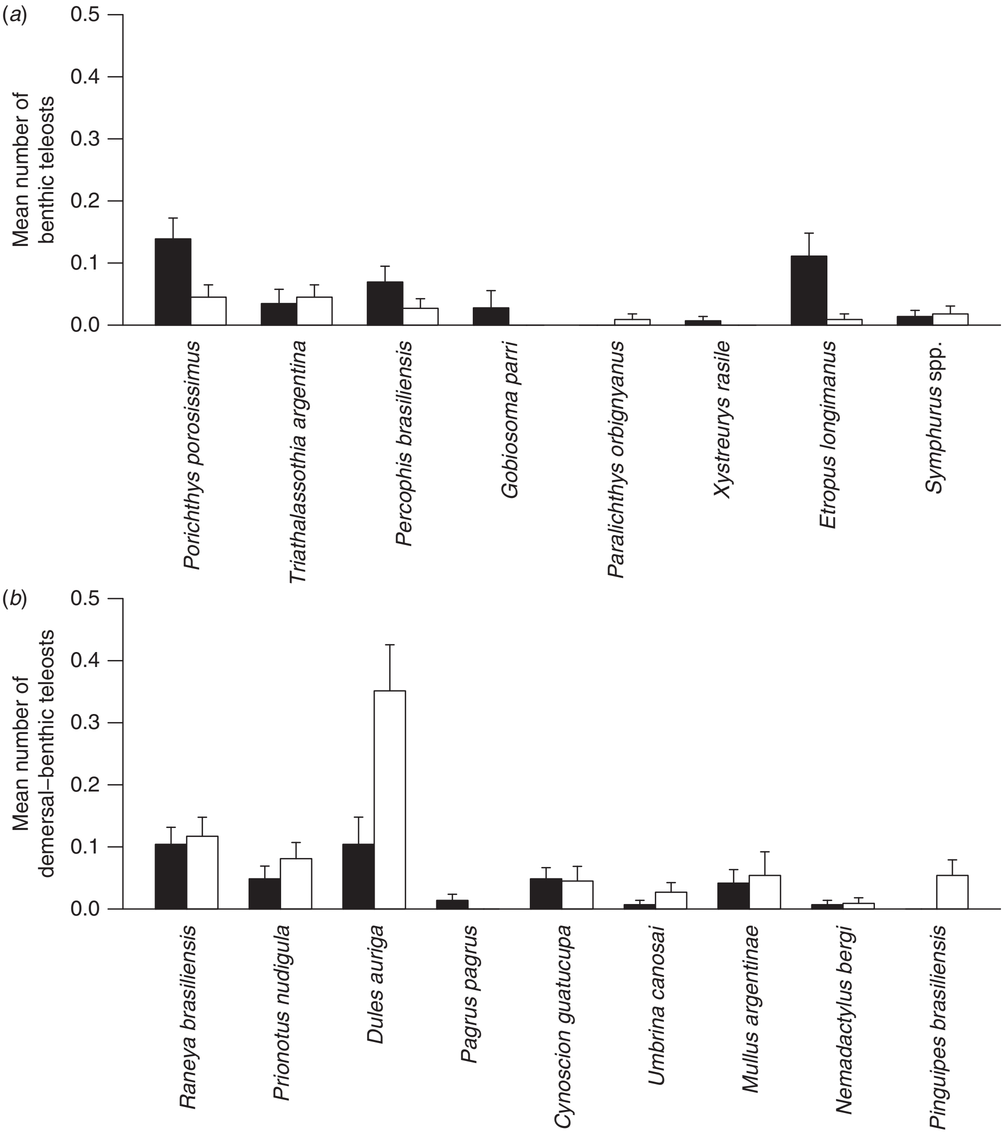

Fig. 3. Mean number and standard error of (*a*) benthic and (*b*) demersal-benthic teleosts consumed for *Atlantoraja castelnaui* with season. Black, warm season; white, cold season.

warm season, male *P. porosissimus* migrate to rocky habitats where they establish and maintain a territory, emitting low frequency sounds (Brantley and Bass 1994) and producing a bioluminescent display to attract females (Crane 1965). This reproductive behaviour may increase the vulnerability and availability of this prey to elasmobranch predators in the warm season, due to the increased visual exposure or audible detection related to the breeding activity (Lucifora *et al.* 2006). *P. brasiliensis* has a constant spatial distribution in this area (Barreto 2007), but higher abundances were observed during spring, possibly associated with reproductive movements of adult individuals from deep areas towards shallower spawning areas (Perrotta and Fernández Giménez 1996; Barreto 2007). These seasonal patterns indicate that *A. castelnaui* is a versatile consumer of teleosts and can shift its diet in response to seasonal changes in the abundance or distribution of these prey.

The consumption of pelagic teleosts was not related to any of the variables tested in our study. In *Carcharhinus brachyurus*, the consumption of pelagic teleosts is a bell-shaped function of predator age (Lucifora *et al.* 2009*a*). We did not test age as a potential variable explaining consumption of any prey in *A. castelnaui*. It remains a question for future studies to test whether the consumption of pelagic teleosts in skates is also affected mostly by age or some other variable.

Relationships between prey size and predator size

The consumption of teleosts is homogeneous throughout the ontogeny of *A. castelnaui*, but this species is able to consume larger teleosts as it grows. The same pattern has been observed in other piscivorous skates, such as *Zearaja chilensis* in the south-west Atlantic (Lucifora *et al.* 2000) and *Dipturus gudgeri* and

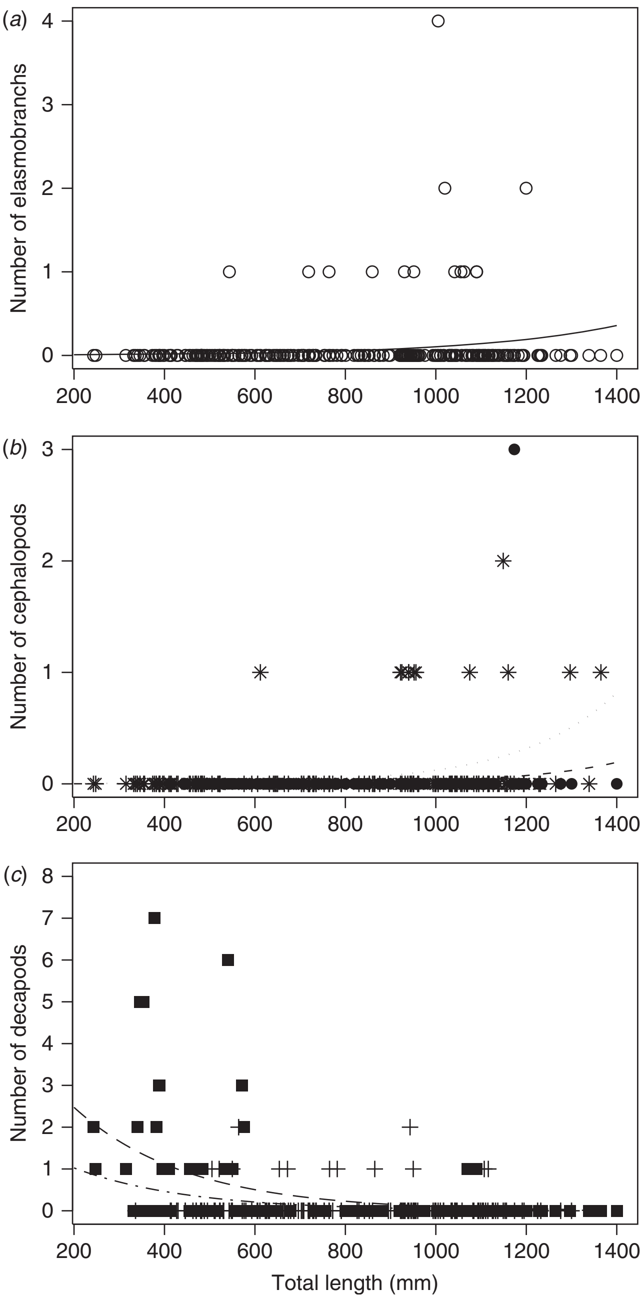

Fig. 4. Shifts with total length, season and region of *Atlantoraja castelnaui* estimated by generalised linear models for number of (*a*) elasmobranchs, (*b*) cephalopods and (*c*) decapods. Cold season, dashed lines and asterisk; warm season, dotted line and solid circle; north region, long-dash line and solid square; south region, two-dash line and cross.

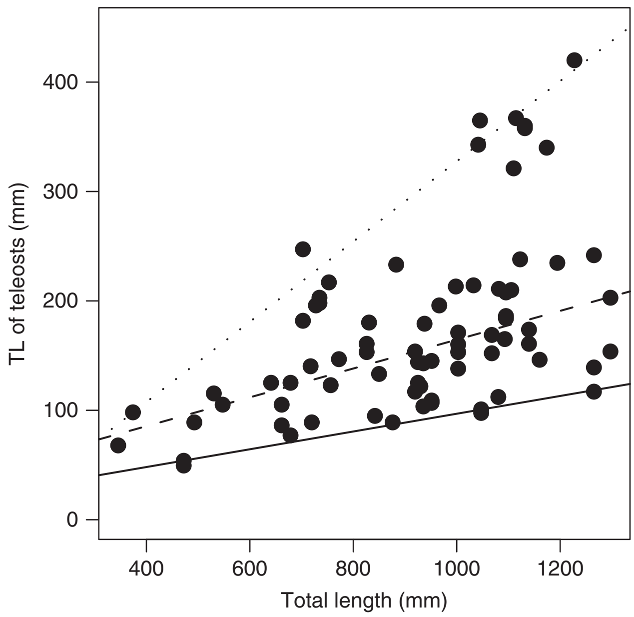

Fig. 5. Relationship between teleost total length (TL) and predator total length of *Atlantoraja castelnaui*. The dotted, dashed and solid lines are 5, 50 and 95% quantile regressions respectively.

Dipturus whitleyi in south-eastern Australian waters (Treloar *et al.* 2007). Skates are suction feeders that ingest their prey whole by creating a hydrodynamic flow (Dean *et al.* 2005). Then, gape size imposes a limit on the size and type of prey consumed (Scharf *et al.* 2000). Some elasmobranchs, such as sharks, evade gape limitation by cutting prey with their teeth (Frazzetta 1988; Lucifora *et al.* 2006; Braccini 2008), but skate teeth are not able to cut. Therefore, the only way to increase prey size in skates is by increasing body size.

Our results identified a heterogeneous array of factors affecting the consumption of different prey groups in a large endangered skate, suggesting a complex situation for managers attempting to maintain the ecological function of this predator. This array includes both extrinsic factors (e.g. season and region) and intrinsic factors such as body size. Piscivorous fish generally achieve the largest body size within their community and have potentially large impacts on their communities through predation (Juanes *et al.* 2002). Overfishing alters the size structure of the populations because larger fishes are selectively removed from the marine community (Bianchi *et al.* 2000). The removal of large predators has indirect effects that involve trophic interactions at the community level (e.g. trophic cascades and non-lethal risk effects, indirect effects such as apparent competition, Heithaus *et al.* 2008, 2010). Thus, the decline and removal of large elasmobranchs, such as *A. castelnaui*, may have marked ecological consequences in marine ecosystems.

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