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Big fish (and a smallish skate) eat small fish: diet variation and trophic level of *Sympterygia acuta*, a medium-sized skate high in the food web

Santiago A. Barbini[1] & Luis O. Lucifora[2]

1 Laboratorio de Ictiología, Instituto de Investigaciones Marinas y Costeras, Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Universidad Nacional de Mar del Plata, Mar del Plata, Argentina
2 Instituto de Biología Subtropical – Iguazú, Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Universidad Nacional de Misiones, Puerto Iguazú, Misiones, Argentina

Abstract

The bignose fanskate, *Sympterygia acuta*, is a small-to-medium-sized species endemic to shallow coastal waters of the Southwest Atlantic. *Sympterygia acuta* displays a clear seasonal reproductive cycle, characterized by maximum egg-laying activity in spring and hatching in summer. We hypothesized that diet and feeding activity change with maturity stage and season and that, given its smallish size, the trophic level is low. Using a multiple-hypothesis modeling approach, the diet of *S. acuta* in relation to sex, body size, maturity stage, region (*i.e.* north and south) and season was analysed; and a potential relationship between feeding activity and the seasonal reproductive cycle was assessed. *Sympterygia acuta* fed on a broad spectrum of prey, but teleosts were more important (47.97% index of relative importance, %IRI), followed by decapods (39.84%IRI), cumaceans (8.31%IRI) and isopods (1.89%IRI). Maturity stage was a strong determinant of the ontogenetic diet shift of *S. acuta*, and relationships between number of prey consumed with season and region were found.. Feeding activity was higher in the cold season than in the warm season, and was less important in the south region than in the north region. Unexpectedly, the specific trophic level was high (3.87). *Sympterygia acuta* shifts its diet with maturity stage, possibly by a combination of an improved ability to capture prey and a change in energy demand of mature individuals. Despite being a small-to-medium-sized skate, *S. acuta* showed a trophic level similar to that of large-bodied marine predators. It reduces its feeding activity seasonally because in the warm season this species may experience an increased predation risk from large sharks.

Introduction

Body size imposes important constraints on the manner in which predators interact with their prey (Werner & Gilliam 1984), and is one of the most important traits that shape the structure and dynamics of biological communities (Hairston & Hairston 1993; Arim *et al.* 2007). In aquatic communities, energy transfer between trophic levels is predicted to be strongly constrained by body size, given that aquatic predators are generally gape limited (Hairston & Hairston 1993; Jennings *et al.* 2001; Arim *et al.* 2007). This morphological limitation results in a positive correlation between trophic level and body size in many fish species (Romanuk *et al.* 2011).

The feeding behavior of a predator can be affected by many factors, such as prey abundance, sex, body size and reproductive condition (Wetherbee & Cortés 2004). As a result, ontogenetic, regional and/or seasonal changes in

the dietary of a predator can occur. However, feeding behavior can also be influenced by a trade-off between foraging and predation risk and social behavior (Sih *et al.* 2000). In general, elasmobranch species (*i.e.* sharks and skates) that inhabit deep-water environments show year-round reproductive activity, whereas skates that inhabit shallow waters with high variability have seasonal reproductive cycles (Lucifora & García 2004). In the same way, species composition of benthic and demersal coastal communities is variable, as environmental conditions change seasonally (Jaureguizar *et al.* 2006). These changes in prey abundance and distribution affect the foraging ecology of their predators (Muto *et al.* 2001). Therefore, foraging behavior and reproductive strategy should be adapted to seasonal environmental fluctuations in species that dwell in shallow coastal waters.

The bignose fanskate, *Symperygia acuta* Garman 1877 (Chondrichthyes, Rajidae), is endemic to the Southwest Atlantic and is distributed from Rio de Janeiro, Brazil (22°S) to the San Jorge Gulf, Argentina (45°43′ S) (Cousseau *et al.* 2007; Bovcon *et al.* 2011). This species occurs in shallow coastal waters (up to 50 m depth) and has a small-to-medium body size (Cousseau *et al.* 2007). Males mature at 475 mm total length (TL), whereas females mature at 478 mm TL (Mabragaña *et al.* 2014). Off Uruguay and North Argentina, *S. acuta* displays a clear seasonal reproductive cycle, characterized by maximum egg-laying activity in spring and hatching in summer (Mabragaña *et al.* 2014). Although *S. acuta* is common in this region, there has been no detailed study of the feeding ecology of this species. As *S. acuta* lives in shallow coastal waters with great environmental variability and shows a seasonal reproductive cycle, our hypothesis was that diet changes with maturity stage and season. Furthermore, given the rather small body size of *S. acuta* and the positive association between body size and trophic level observed in skates (Ebert & Bizzarro 2007), we also hypothesized that the trophic level of *S. acuta* is low.

The purposes of this study were to determine the feeding habits and the feeding activity of *S. acuta* off Uruguay and North Argentina. Our specific aims were to (i) quantify the diet; (ii) assess whether there are sexual, ontogenetic, regional and/or seasonal shifts in the diet composition; (iii) evaluate a potential relationship between feeding activity and the seasonal reproductive cycle; and (iv) estimate the trophic level of *S. acuta*.

Material and Methods

Study area

The study area was located in the coastal region off Uruguay and North Argentina between 34° and 41°S, from 5

to 50 m depth. This region consists of two large ecosystems: a northern (between 34° and 38°S) stratified coastal zone influenced by the very large discharge of continental waters of the Río de la Plata; and a southern (38°–41°S), more 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 & Piola 1997; Lucas *et al.* 2005).

Sampling

Individuals of *Symperygia acuta* were collected during November and December 2005, February 2006 and June 2007 from scientific trawl surveys conducted by the Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP, Argentina; Fig. 1). Additional samples were obtained from commercial landings of the coastal fleet based in Mar del Plata harbor during October and November 2006 and February, June, July, August, October, November and December 2007 (Fig. 1).

All specimens used in this study were obtained already dead and frozen from both the scientific surveys and commercial fisheries. This ensured that our study did not impose any additional mortality upon the studied population.

For each captured individual, sex, maturity stage and TL (mm) were recorded. Maturity stage (immature or mature) was determined according to the condition of
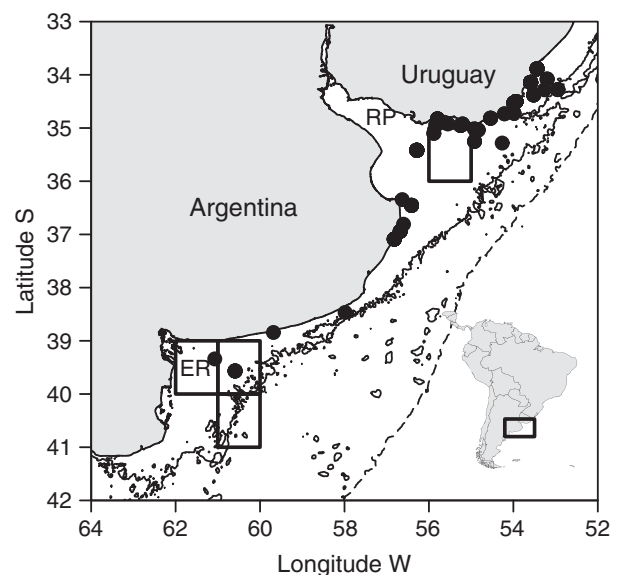

Fig. 1. Map of study area where individuals of *Symperygia acuta* were collected off Uruguay and North Argentina. Black circles: trawl stations; black rectangles: cells of the fishing grid. The 50-m and 200-m isobaths are shown as solid and dashed lines, respectively. The rectangle in the inset shows the location of the study area in South America. ER = El Rincón; RP = Río de la Plata.

uteri, oviducal glands and ovarian follicles in females, and the development of sperm ducts and testes and the degree of clasper calcification in males (Stehmann 2002; Colonello *et al.* 2011). The stomachs were dissected from each individual and stored at −20 °C. In the laboratory, prey found in the stomachs were sorted, identified to the lowest possible taxonomic level using published catalogues (Boschi *et al.* 1992; Cousseau & Perrotta 2000), counted and weighed (±0.01 g).

Data analyses

The importance of each prey in the diet was calculated using percentage by number (%N), percentage by mass (%M), percentage frequency of occurrence (%FO) and index of relative importance (IRI) (Pinkas *et al.* 1971). IRI was expressed as percentage (%IRI; Cortés 1997).

Mean cumulative Shannon diversity index was plotted as a function of sample size by sex, maturity stage, season and region, randomized 100 times (Magurran 2004), to assess whether the number of stomachs analysed was sufficient to conduct statistical analyses. Sample size was considered sufficient to describe diet if the cumulative diversity reached an asymptote.

For statistical purposes, the prey were grouped separately in seven zoological categories (teleosts, shrimps, crabs, amphipods, cumaceans, isopods and polychaetes). To identify changes in the diet composition of *Sympterygia acuta* with sex, ontogeny, region and season, we adopted a multiple-hypothesis modeling approach (Franklin *et al.* 2001; Johnson & Omland 2004; Symonds & Moussalli 2011). Ontogenetic changes in the diet were assessed for body size (TL) and for maturity stage between immature and mature individuals. Regional dietary changes were assessed between north (between 34 and 38°S) and south regions (between 38 and 41°S). Seasonal differences in the diet were evaluated between warm (October to March) and cold seasons (April to September). For each prey category, we built generalized linear models (GLMs; Venables & Ripley 2002) where the response variable was the number of prey consumed and independent variables were sex, maturity stage, TL, region and season. Further, models with containing up to two independent variables in different cominations were fitted. We also fitted a model without any of the independent variables (*i.e.* a null model) to test the hypothesis that none of the variables considered had an effect on the consumption of a particular prey. The models with number of prey as response variable had large variances because of the large number of zero-values in the samples; therefore, a negative binomial error distribution and a log link were used (Crawley 2005).

For each model fitted, we calculated the Akaike information criterion (AIC) and Akaike weights (w). AIC measures the amount of information lost when fitting a model; hence, the model with the lowest AIC was selected as the best model (Crawley 2005). To obtain the likelihood of each model fitted given the data, w was calculated (Franklin *et al.* 2001). If the best model was not clearly superior to some of the others in the set, we used model averaging to estimate the parameters of the variables included in the best model (Johnson & Omland 2004; Symonds & Moussalli 2011).

To test the hypothesis that feeding activity changes with maturity stage and season, we built a GLM with diet breadth (*i.e.* number of prey species consumed, $N_{species}$), number of prey consumed (N_{prey}) and proportion of empty stomachs as response variables, and sex, maturity stage, TL, region and season as independent variables. As explained above, models containing multiple independent variables were fitted and the best model was selected by using a multiple-hypothesis modeling approach. To account for the different number of prey in each sample in the models having $N_{species}$ as response variable, the log of the total number of prey consumed (log N_{prey}) by individual was included as an independent variable (Barbini & Lucifora 2012a). Models with $N_{species}$ as the response variable had a Poisson error distribution and a log link because this variable consists of count data, which take only positive or zero values (Crawley 2005). Models with N_{prey} as the response variable had a negative binomial error distribution and a log link because the variance was much greater than the mean (Crawley 2005). Models with proportion of empty stomachs as the response variable had a binomial error distribution and a logit link due to their binary nature (*i.e.* containing food or empty; Crawley 2005). We interpreted the changes in the type and amount of prey consumed as a reflection of the feeding activity of *S. acuta*, *i.e.* a broad diet breadth and a higher number of prey consumed and a proportion of stomachs with food, indicate high feeding activity and *vice versa*. All statistical analyses were performed using the R statistical software, version 3.1.0. (R Development Core Team, 2014). The trophic level of *S. acuta* was calculated using the trophic index (TL_k) proposed by Cortés (1999) as:

$$TL_k = 1 + \left(\sum_{j=1}^{n} P_j \times TL_j \right) \tag{1}$$

where P_j is the proportion of each prey category based on %IRI, TL_j is the trophic level of each prey category j, and n is the total number of prey categories. Trophic level of each prey category was obtained from Ebert & Bizzarro (2007). The trophic dynamics of a species may vary

substantially along its life history (Garrison & Link 2000; Ebert & Bizzarro 2007), then the relationship between maturity stage and TLk was analysed. For that purpose, the observations were randomly sampled 100 times with replacement in order to obtain the frequency distribution of TL_k. A GLM was then used to model TL_k as a function of maturity stage of *S. acuta*. We fitted a null model to judge whether or not maturity stage had an effect on TL_k.

Results

A total of 417 individuals of *Sympterygia acuta* was examined, with 301 (72.18%) containing food in their stomachs. The sample was composed of 85 immature females (253–512 mm TL), 57 mature females (435–620 mm TL), 80 immature males (260–516 mm TL) and 79 mature males (448–570 mm TL). The cumulative diversity curves reached an asymptote in all subgroups, indicating that the sample size was large enough (Fig. 2).

Overall, 2556 prey with a total weight of 1458.3 g were found in the stomachs. In total, 68 different prey taxa were identified within stomachs: 21 decapods, 16 teleosts, 10 isopods, seven polychaetes, three amphipods, cumaceans and mollusks, two chondrichthyans and one mysidacean and lancelet. In terms of %IRI, the dominant prey were teleosts and decapods, followed by cumaceans and isopods. Amphipods, mysidaceans and polychaetes had minor importance (%IRI <1; Table 1). The most important prey by weight were teleosts. Decapods were the most important prey by number and frequency of occurrence. Among the teleosts, *Dules auriga* was the most important in number, weight and frequency of occurrence, followed by *Engraulis anchoita*. The most common decapod prey by number, weight and frequency of occurrence was *Artemesia longinaris*, the second by number and frequency of occurrence was *Cyrtograpsus affinis*, and *Libinia spinosa* was the second by weight.

Ontogenetic, regional and seasonal patterns in the diet composition of *S. acuta* were found (Table 2 and Fig. 3). The consumption of all prey categories was independent of sex. Immature individuals preyed on shrimps, crabs, cumaceans, isopods and polychaetes more heavily than mature individuals. By contrast, teleosts were consumed more by mature than by immature individuals. The consumption of amphipods decreased with increasing TL of *S. acuta* (Table 3). The consumption of teleosts, shrimps and crabs was affected by the region. *Sympterygia acuta* preyed more heavily on teleosts in the south region than in the north region, whereas shrimps and crabs were consumed more in the north region than in the south region. Seasonally, *S. acuta* preyed more heavily on cumaceans, isopods and polychaetes in the cold season than in the warm season.

For shrimp, amphipod and polychaete prey, there were no single models that prevailed over the others, since all models had a low *w*; therefore, an average of all models was computed (i.e. model averaging). For amphipods, the model averaging slope was −0.045 for TL (w = 0.812). The averaged coefficients for polychaetes were 0.821 for immature individuals (w = 0.515) and 1.307 for the cold season (w = 0.901).

The best models explaining $N_{species}$, N_{prey} and the proportion of empty stomachs included season and region (Table 3). These response variables were not affected by sex, maturity stage or TL. For both $N_{species}$ and N_{prey}, consumption was higher in the cold season than in the warm season, and less important in the south region than in the north region. Seasonally, the proportion of *S. acuta* with empty stomachs was lower in the cold season than in the warm season, and regionally the proportion of empty stomachs was higher in the south region than in the north region. The best model for $N_{species}$ had a low *w*; therefore, we computed model averaging: coefficients were 0.172 for the cold season (relative to the warm season, w = 0.794) and 0.079 for the south region (relative to the north region, w = 0.344).

The mean TL_k of *S. acuta* was 3.87 (SD = 0.022). The TL_k was significantly different between maturity stages (TL immature = 3.56; TL mature individuals = 4.15). The parameters of the model were: intercept = 4.15, maturity stage = 3.56 immature (relative to mature); AIC = −1120.1; w = 0.99.

Discussion

The typical pattern found in the diet composition of skate species is as follows: small-bodied skates are benthophagic, consuming worms and small crustaceans; mid-sized skates are predators of small and large crustaceans and, occasionally, cephalopods and fishes; and large-bodied skates consume mainly fishes (Orlov 1998). Our results indicate that *Sympterygia acuta* consumed mainly teleosts. As *S. acuta* is a small-to-medium-sized species, this pattern does not follow the general pattern of diet composition in skates. Food partitioning among sympatric skate species is mainly associated with body size (Ebert *et al.* 1991; Bizzarro *et al.* 2007; Treloar *et al.* 2007). *Sympterygia acuta* uses a trophic resource (i.e. teleosts) that is not available to other skates of small and medium sizes. This competitive advantage may be associated with morphologic traits (i.e. large snout size). A diet based on teleosts is a phenomenon widely observed in skates that have an elongated snout and occur in deep water, as for example in some species of the genera *Dipturus* (Kyne *et al.* 2008), *Zearaja* (Lucifora *et al.* 2000; Koen Alonso *et al.* 2001) and *Raja* (Robinson *et al.*
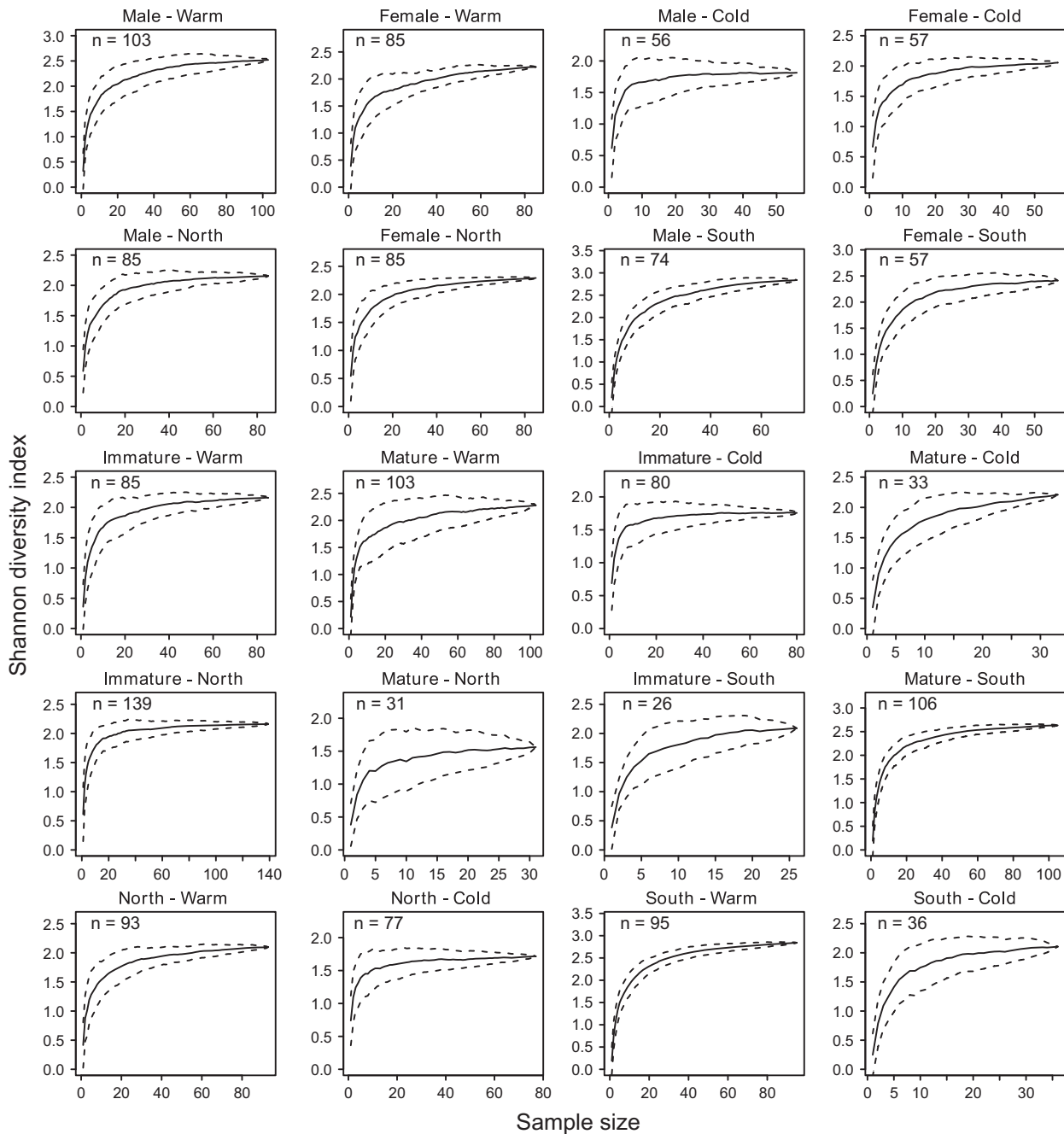
Fig. 2. Cumulative mean Shannon diversity index (continuous lines) and SD (dashed lines) as a function of sample size for *Sympterygia acuta* from off Uruguay and North Argentina.

2007). Among skates, *S. acuta* is the only species with a relatively small body size and a very elongated snout that occurs in shallow waters. The large snout of *S. acuta* may improve its sensory capacity to catch teleosts, in a similar way as the cephalofoil increases the sensory capabilities in prey searching of hammerhead sharks (Kajiura 2001). Further studies are needed to test this hypothesis.

Body size influences trophic hierarchies in aquatic communities (Hairston & Hairston 1993); therefore, small species such as *S. acuta* would be expected to feed at lower trophic levels. This prediction has been confirmed in elasmobranch fishes, such as some shark (Cortés 1999) and skate species (Ebert & Bizzarro 2007), and in many other fish species (Romanuk *et al.* 2011).

Table 1. Diet composition of *Sympterygia acuta* expressed as percentage by number (%N), mass (%M), frequency of occurrence (%FO), index of importance relative (IRI) and percentage of IRI (%IRI).

prey	%N	%M	%FO	IRI	%IRI
Teleostei	6.69	75.45	45.18	3711	47.97
Unidentified teleosts	3.32	17.37	25.25	522.7	
Engraulidae					
Anchoa marinii	0.04	0.07	0.33	0.03	
Engraulis anchoita	0.58	13.08	4.65	63.6	
Phycidae					
Urophycis brasiliensis	0.04	0.02	0.33	0.02	
Ophidiidae					
Raneya brasiliensis	0.08	1.28	0.66	0.90	
Batrachoididae					
Porichthys porosissimus	0.31	4.79	2.32	11.87	
Triglidae					
Prionotus nudigula	0.04	0.57	0.33	0.20	
Serranidae					
Dules auriga	0.82	20.81	5.31	115	
Carangidae					
Trachurus lathami	0.12	2.64	0.66	1.84	
Sciaenidae					
Cynoscion guatucupa	0.12	2.53	0.99	2.64	
Micropogonias furnieri	0.04	0.64	0.33	0.22	
Paralonchurus brasiliensis	0.12	0.82	0.99	0.93	
Achiropsettidae					
Achiropsetta tricholepis	0.12	0.57	0.66	0.45	
Paralichthyidae					
Etropus longimanus	0.39	3.98	2.66	11.61	
Cynoglossidae					
Unidentified Cynoglossidae	0.12	0.61	0.99	0.73	
Symphurus spp.	0.43	5.65	2.32	14.14	
Chondrichthyes	0.23	1.10	1.33	1.77	0.02
Rajidae					
Unidentified skates	0.19	0.68	0.99	0.87	
Atlantoraja cyclophora	0.04	0.42	0.33	0.15	
Crustacea					
Decapoda	31.73	18.42	61.46	3082	39.84
Unidentified shrimps	5.05	1.46	12.96	84.27	
Penaeidae					
Artemesia longinaris	14.75	5.67	24.25	495.2	
Solenoceridae					
Pleoticus muelleri	0.51	2.18	2.66	7.16	
Sergestidae					
Sergia mirin	0.12	0.07	0.33	0.06	
Peisos spp.	0.31	0.02	0.66	0.22	
Anomura					
Unidentified anomurans	0.12	0.07	0.66	0.13	
Diogenidae					
Loxopagurus loxochelis	0.31	0.36	1.66	1.11	
Paguridae					
Pagurus exilis	0.31	0.52	1.99	1.67	
Albuneidae					
Blepharipoda doelloi	0.39	1.15	2.66	4.1	

Table 1. Continued

prey	%N	%M	%FO	IRI	%IRI
Brachyura					
Unidentified brachyurans	1.88	1.95	11.29	43.24	
Majidae					
Collodes rostratus	0.12	0.10	0.33	0.07	
Leurocyclus tuberculosus	0.04	0.05	0.33	0.03	
Libinia spinosa	0.16	1.93	1.33	2.77	
Pelia rotunda	0.09	0.04	0.33	0.04	
Atelecyclidae					
Peltarion spinosulum	0.39	0.49	0.66	0.59	
Portunidae					
Ovalipes trimaculatus	0.59	0.57	1.33	1.54	
Xanthidae					
Pilimnus reticulatus	0.04	0.02	0.33	0.02	
Belliidae					
Corystoides abbreviatus	0.62	0.21	1.33	1.12	
Grapsidae					
Cyrtograpsus affinis	4.26	1.09	7.97	42.72	
Pinnotheridae					
Pinnixa patagoniensis	0.39	0.10	2.66	1.31	
Pinnixa brevipollex	1.25	0.33	6.64	10.50	
Dissodactylus crinitichelis	0.04	<0.01	0.33	0.01	
Amphipoda	8.99	0.55	7.97	76.13	0.98
Unidentified amphipods	8.53	0.54	6.31	57.23	
Ampeliscidae	0.43	0.01	1.33	0.58	
Caprellidae	0.04	<0.01	0.33	0.01	
Cumacea	34.54	1.98	17.61	643.2	8.31
Unidentified cumaceans	0.27	0.01	0.33	0.09	
Bodotriidae	2.23	0.14	5.98	14.20	
Diastylidae	32.04	1.83	15.61	528.9	
Isopoda	5.98	0.81	21.59	146.8	1.89
Unidentified isopods	0.43	0.09	3.65	1.89	
Sphaeromatidae					
Sphaeroma serratum	0.16	<0.01	0.99	0.16	
Cirolanidae					
Excirolana armata	0.12	<0.01	0.99	0.12	
Cirolana spp.	0.04	0.01	0.33	0.02	
Serolidae					
Serolis spp.	0.39	0.04	3.32	1.45	
Serolis gaudichaudii	0.08	0.02	0.66	0.06	
Serolis marplatensis	2.46	0.42	9.30	26.84	
Serolis polaris	0.09	0.06	0.66	0.09	
Idoteidae					
Idotea baltica	1.68	0.12	3.65	6.59	
Macrochiriditea spp.	0.55	0.02	2.66	1.52	
Cephalochordata	0.43	0.03	1.99	0.93	0.01
Branchiostomidae					
Branchiostoma platae	0.43	0.03	1.99	0.93	
Mysidacea	9.47	0.36	3.99	39.19	0.51
Polychaeta	1.79	1.04	11.96	33.92	0.44
Unidentified polychaetes	0.74	0.36	5.98	6.61	
Flabelligeridae	0.74	0.35	3.98	4.36	
Maldanidae	0.08	0.25	0.66	0.22	
Nephthyidae	0.04	0.05	0.33	0.03	
Onuphidae	0.16	0.02	1.33	0.23	

Table 1. Continued

prey	%N	%M	%FO	IRI	%IRI
Opheliidae					
Armandia loboi	0.04	<0.01	0.33	0.01	
Mollusca	0.12	0.25	0.99	0.36	<0.01
Bivalvia					
Unidentified bivalves	0.04	0.05	0.33	0.03	
Solenidae					
Solen tehuelchus	0.04	0.09	0.33	0.05	
Cephalopoda					
Octopodidae					
Octopus tehuelchus	0.04	0.10	0.33	0.05	

However, *S. acuta* has a higher trophic level than expected from its body size, especially for mature individuals, with similar values to large-bodied marine predators, such as some mammals (Pauly *et al.* 1998; Tucker & Rogers 2014) and large skates and sharks (Cortés 1999; Ebert & Bizzarro 2007). This unexpectedly high trophic level for a small elasmobranch suggests that *S. acuta* may play a unique functional role in Southwest Atlantic food webs.

Ontogenetic diet shifts in many skates are usually a function of body size (Bizzarro *et al.* 2007; Robinson *et al.* 2007) and the effect of reproductive condition (*i.e.* maturity stage) on feeding habits is less known. In *S. acuta,* maturity stage has a strong effect in producing ontogenetic dietary shifts: invertebrates (*i.e.* shrimps, crabs, isopods, and cumaceans) are preyed upon by immature individuals, while teleosts are consumed mainly by mature individuals. This pattern may occur by the combination of an improved ability to capture prey and a change in energy demand of large individuals. Mature individuals may be more efficient predators than immature individuals. An increase in the metabolic requirements that mature individuals need for reproductive success may also contribute to generate the observed pattern. There is no single explanation for this pattern, but the effect of maturity stage on dietary shifts may be part

of a more complex behavioral response to maturation (Koen Alonso *et al.* 2001). This pattern is reflected in the higher trophic level of mature individuals compared with immature individuals.

Spatial and seasonal differences in the diet composition of *S. acuta* were found. In the study area, the same spatial patterns in diet composition were found for both the Rio skate, *Rioraja agassizii* (Barbini & Lucifora 2011), and the spotback skate, *Atlantoraja castelnaui* (Barbini & Lucifora 2012b): crustaceans were consumed more in the north region and teleosts were more preyed upon in the south region. Possible regional differences in prey availability resulting from differences in environmental conditions and oceanographic characteristics between the north and south regions (Acha *et al.* 2004; Giberto *et al.* 2004) may explain this dietary pattern. Seasonal variations in the diet composition of skates have also been found previously in the study area (*e.g. Psammobatis extenta*, Braccini & Perez 2005; *R. agassizii*, Barbini & Lucifora 2011; *A. castelnaui*, Barbini & Lucifora 2012b). Seasonal fluctuations in the abundance and distribution of prey may explain this pattern (Muto *et al.* 2001).

The feeding activity of *S. acuta* varied clearly between seasons and regions. The effect of season in producing a shift in feeding activity cannot be explained by the seasonal reproductive cycle. The level of feeding activity of *S. acuta* was independent of maturity stage. Spatially, the higher feeding activity in the north region than in the south region might be explained by the same reason as the spatial differences in diet composition described above.

The responses of prey to predators can have important effects on prey refuge use, activity, vigilance, and feeding and mating behavior (Sih *et al.* 2000). Besides, the level of perceived predation risk by prey can vary over time owing to seasonal changes in predator occurrence (Lima & Dill 1990; Sih *et al.* 2000). From a trophic viewpoint, some times are more dangerous for feeding than others, influencing foraging activity of prey because predation

Table 2. Best models explaining the consumption (in number of individuals) of the prey categories of *Sympterygia acuta*.

prey	intercept	coefficients	AIC	w
teleosts	−0.444	−1.181 immature + 0.534 south	513.85	0.671
shrimps	−0.286	1.403 immature − 0.457 south	913.99	0.428
crabs	−0.646	1.155 immature − 1.981 south	616.92	0.836
amphipods	3.545	−0.012 TL	229.66	0.458
cumaceans	−22.314	22.031 immature + 2.609 cold	633.26	0.882
isopods	−4.541	3.789 immature + 1.039 cold	425.18	0.845
polychaetes	−3.788	1.606 immature + 1.254 cold	245.49	0.477

The coefficients of Maturity stage and Region are relative to Mature and North, respectively.
AIC = Akaike information criterion; w = Akaike's weight; TL = total length.

Table 3. Best models explaining the number of prey species consumed ($N_{species}$), number of prey consumed (N_{prey}) and proportion of empty stomachs of *Sympterygia acuta*.

response variable	intercept	coefficients	AIC	w
$N_{species}$	0.338	0.235 cold − 0.235 south + 0.244 log(N_{prey})	855.05	0.297
N_{prey}	2.251	0.636 cold − 1.538 south	1788.8	0.875
proportion of empty stomachs	−1.333	−1.087 cold + 1.090 south	453.74	0.989

AIC = Akaike information criterion; w = Akaike's weight.
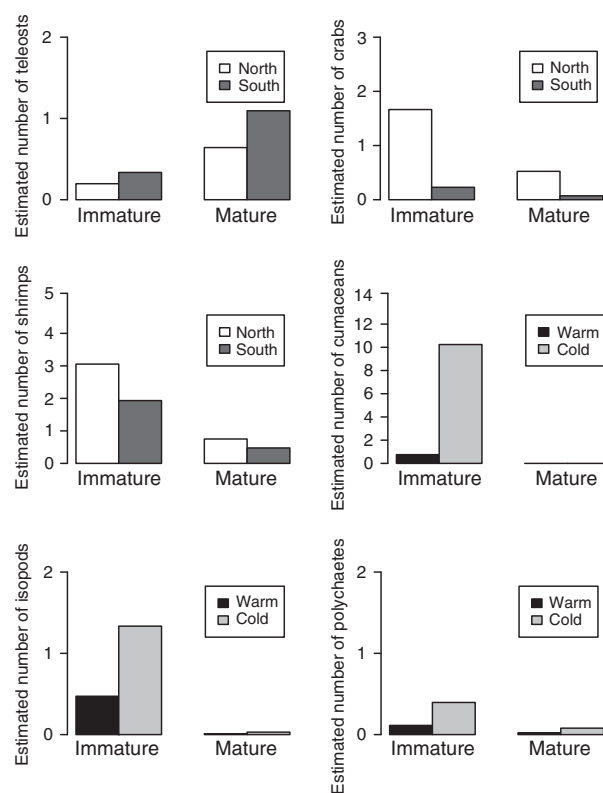
Fig. 3. Changes in consumption of prey categories (by number) with maturity stage, season and region of *Sympterygia acuta* from off Uruguay and North Argentina estimated by generalized linear models. The models had a log link and a negative binomial error distribution.

risk varies seasonally (Lima & Dill 1990). Off North Argentina, *S. acuta* is subject to the threat of predation by large sharks, such as the broadnose sevengill shark, *Notorynchus cepedianus* (Lucifora *et al.* 2005), the school shark, *Galeorhinus galeus* (Lucifora *et al.* 2006), and the sand tiger shark, *Carcharias taurus* (Lucifora *et al.* 2009). In the Southwest Atlantic, these sharks migrate seasonally

in coastal waters among Brazil, Uruguay and Argentina, being present during spring and summer in shallow waters off Northern Argentina (Lucifora 2003). *Sympterygia acuta* may reduce its feeding activity seasonally as a response to the presence of these large predators in the warm season. Possibly, this pattern may be associated with a change in foraging behavior (*i.e.* less frequent feeding activity) as a predator avoidance response.

Uruguayan and Northern Argentinean coastal waters are among the most heavily impacted by fisheries in the Southwest Atlantic (Tyedmers *et al.* 2005). *Sympterygia acuta* is captured by the multi-species fleet that exploits the coastal demersal fish assemblage (Massa *et al.* 2004). In addition, this species is caught commonly by recreational fishermen along the coast of Buenos Aires Province, Argentina (Cedrola *et al.* 2011). The coastal habitat of *S. acuta* is exposed to a high intensity of bottom trawling (Brazeiro *et al.* 2003) that alters the physical structure of the bottom, affecting indirectly the benthic community (Kaiser 1998; Watling & Norse 1998). *Sympterygia acuta* completes its life cycle from egg to adult in very shallow waters (Mabragaña *et al.* 2014) and feeds mainly on benthic prey. Therefore, this species is threatened by both heavy fishing and habitat destruction. Consequently, its biomass has declined (Massa & Hozbor 2004, 2011) and the International Union for Conservation of Nature has assessed this species as Vulnerable (Massa & Hozbor 2004). All of this increases the concern and the need for appropriate measures for the conservation of this species.

Conclusions

Our results indicate that *Sympterygia acuta* feeds on a broad spectrum of prey, but teleosts are the most important followed by decapods. In this skate, maturity stage is a strong determinant of the ontogenetic diet shift that is associated with region and season. The level of feeding activity is also associated with season and region. *Sympterygia acuta* is peculiar among the skates studied so far in having a high trophic level despite its rather small body size, which indicates that it may have a unique functional role in Southwest Atlantic food webs.

Acknowledgements

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