Diet composition and feeding habits of the eyespot skate, *Atlantoraja cyclophora* (Elasmobranchii: Arhynchobatidae), off Uruguay and northern Argentina

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The eyespot skate, *Atlantoraja cyclophora,* is an endemic species from the southwestern Atlantic, occurring from Rio de Janeiro, Brazil, to northern Patagonia, Argentina. The feeding habits of this species, from off Uruguay and north Argentina, were evaluated using a multiple hypothesis modelling approach. In general, the diet was composed mainly of decapod crustaceans, followed by teleost fishes. Molluscs, mysidaceans, amphipods, isopods, lancelets and elasmobranchs were consumed in lower proportion. The consumption of shrimps drecreased with increasing body size of *A. cyclophora.* On the other hand, the consumption of teleosts increased with body size. Mature individuals preyed more heavily on crabs than immature individuals. Teleosts were consumed more in the south region (34º – 38ºS) and crabs in the north region (38º – 41ºS). Shrimps were eaten more in the warm season than in the cold season. Prey size increased with increasing body size of *A. cyclophora*, but large individuals also consumed small teleosts and crabs. *Atlantoraja cyclophora* has demersal-benthic feeding habits, shifts its diet with increasing body size and in response to seasonal and regional changes in prey availability and distribution.

La raya de círculos, *Atlantoraja cyclophora*, es una especie endémica del Atlántico Sudoccidental, que se distribuye desde Río de Janeiro, Brasil, hasta el norte de la Patagonia, Argentina. Los hábitos alimentarios de esta especie fueron evaluados frente a la costa de Uruguay y norte de Argentina, utilizando un enfoque de modelado de múltiples hipótesis. En general, la dieta estuvo compuesta principalmente por crustáceos decápodos (71,37 %IRI), seguido de peces teleósteos (28,54 %IRI). En menor proporción fueron consumidos moluscos, misidáceos, anfípodos, isópodos, anfioxos y elasmobranquios. El consumo de decápodos Natantia disminuyó con el incremento del tamaño del cuerpo de *A. cyclophora*. Por otro lado, el consumo de teleósteos se incrementó con el incremento del tamaño del cuerpo. Individuos maduros consumieron cangrejos en mayor proporción que individuos inmaduros. Los teleósteos fueron consumidos mayormente en la región sur (34º – 38ºS) y los cangrejos en la región norte (38º – 41ºS). Los decápodos Natantia fueron más consumidos en la estación cálida que en la estación fría. El tamaño de las presas consumidas se incrementó con el aumento del tamaño corporal de *A. cyclophora*, pero individuos de mayor tamaño no abandonadon el consumo de pequeños cangrejos y teleósteos. *Atlantoraja cyclophora* presenta hábitos alimentarios demersal-bentónicos, cambia su dieta con el incremento del tamaño corporal y en respuesta a cambios estacionales y regionales en la disponibilidad y distribución de las presas.

Keywords: Chondrichthyes, Ontogenetic shifts, Predation, Southwest Atlantic.

Introduction

The eyespot skate, *Atlantoraja cyclophora* (Regan, 1903), is a member of the family Arhynchobatidae and it is an endemic species from the southwestern Atlantic, occurring from Rio de Janeiro, Brazil (22º S) to northern Patagonia, Argentina (42º S) (Menni & Stehmann, 2000; Bovcon *et al.*, 2011). Typically, this species inhabits depths ranging from the shoreline to 150 m and it reaches a maximun total length of 695 mm (Cousseau *et al.*, 2007). Off Uruguay and southern Brazil waters, *A. cyclophora* matures at 463-485 mm and 528-532 mm total length for male and female, respectively (Oddone & Vooren 2005; Oddone *et al.*, 2008). Like other skate species along the coastal and continental shelf waters from north Argentina and Uruguay, *A. cyclophora* is subjected to heavy fishing

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pressure in multi-species fisheries for coastal demersal species (Tamini *et al.*, 2006), with a decreasing trend in population abundance (Massa *et al.*, 2006). Like most elasmobranchs, *A. cycplohora* may be particularly sensitive to fishing pressure, therefore this species is categorized as vulnerable by the International Union for the Conservation of Nature (IUCN) (Massa *et al.*, 2006).

Indirect effects of a heavy fishing pressure include disruption of trophic interactions through selective removal of predator or prey species, removal of competitors and species replacement (Stevens *et al.*, 2000; Bornatowaki *et al.*, 2014; Navia *et al.*, 2016). Thus, knowledge of potential ecological consequences of declines in the abundance of predators is critical for fisheries and marine ecosystem management (Heithaus *et al.*, 2008). For this reason, information on feeding habits and trophic interactions between species are very important and necessary ecological parameters for the correct management and protection of fisheries (Navia *et al.*, 2016). Despite that, catches of skates off Argentina increased markedly in recent years (Hozbor & Massa, 2012), fishery statistics and ecological traits of these species are scarcely known, specially for *A. cyclophora*.

From a trophic viewpoint, skates may have an important role in structuring marine communities due to their wide distribution and high abundance (Ebert & Bizzarro, 2007). These roles in the marine communities can be influenced by traits of the predator (*e.g.* sex, maturity stage and body size) and extrinsic factors (*e.g.* season and region) (Di Giácomo & Perier, 1996; Lucifora, 2003). Therefore, there is a need to investigate the diet of skates with emphasis on ontogenetic, seasonal and regional variation. This information about life history and trophic interactions must be known and incorporated into future analyses, to accurately evaluate the population dynamics (Schmitt *et al.*, 2015). Information on the feeding habits of *A. cyclophora* is scarce. Diet composition has been studied in detail only off the southern coast of Rio de Janeiro, Brazil, near Ilha Grande, where *A. cyclophora* preys mainly on crustaceans and teleosts, with seasonal differences in diet composition (Viana & Vianna, 2014).

In coastal waters off Uruguay and northern Argentina, the skate species *Atlantoraja castelnaui* (Miranda Ribeiro, 1907), *Rioraja agassizii* (Müller & Henle, 1841) and *Sympterygia acuta* Garman, 1877, that co-occur in space and time with *A. cyclophora*, showed a consistent regional shift in the diet composition: teleosts were consumed more in the southern part of this region, whereas decapods were eaten more in the northern part (Barbini & Lucifora, 2011; 2012; 2016). Therefore, we expected to find the same spatial pattern in *A. cyclophora*.

We examined the food habits of *A. cyclophora* off Uruguay and north Argentina. The specific aims of the study were to: (1) describe diet composition; (2) identify changes in diet with sex, maturity stage, body size, season and region; and (3) examine relationships between predator size and prey size.

Material and Methods

Study area and sampling. The study area is located off Uruguay and northern Argentina, between 34º S and 41º S (Fig. 1). The northern area is characterized by a stratified coastal zone influenced by the discharge of the Río de la Plata. On the other hand, the southern area is a homogeneous coastal zone, that comprises an estuarine system, called El Rincón, characterized by the discharge of the Negro and Colorado Rivers and discharges of high salinity waters of the San Matías Gulf (Guerrero & Piola, 1997; Lucas *et al.*, 2005).

Samples of *A. cyclophora* were taken from scientific trawl surveys conducted by the Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP, Argentina) and from commercial landings of the coastal fleet of Mar del Plata harbour (Fig. 1) during December 2005, February, May, June, September and November 2006, April, May, July, August, October, November and December 2007. Total length (TL, mm), sex and maturity stage (juvenile or adult) of each individual were recorded. The maturity stage was determined according to the presence of eggs and observation of the uteri, oviducal glands and ovarian follicles in females and to the degree of calcification of the claspers and the development of testes and reproductive ducts in males (Colonello *et al.*, 2011). The stomachs were removed and stored at -20º 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). Whenever possible, carapace width (CW) of crabs, cephalothorax length (CL) of shrimps and total lenght (TL) of teleosts were measured.
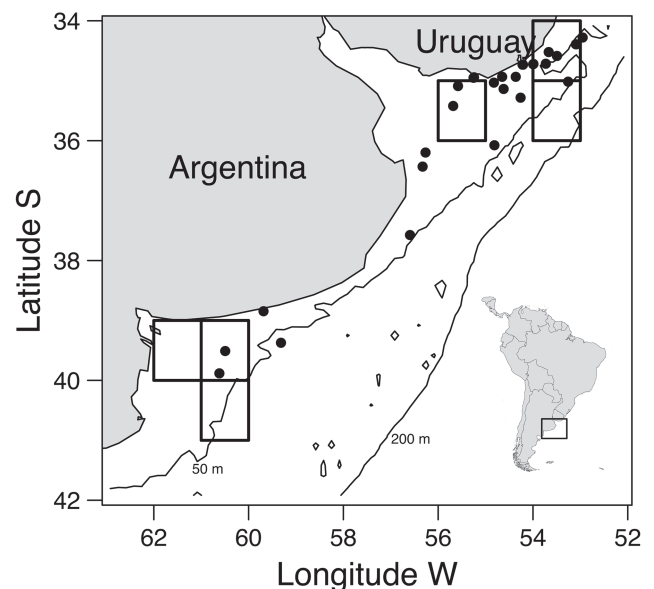
Fig. 1. Study area showing the location of trawl stations (black dots) and cells of the fishing grid (black rectangles) where individuals of *Atlantoraja cyclophora* were captured off North Argentina and Uruguay.

Diet and data analysis. Percentage by frequency of occurrence (%O), number (%N), weight (%W) and index of relative importance (%IRI; Pinkas *et al.*, 1971; Cortés, 1997) for each prey were used to describe the diet of *A. cyclophora*. To determine whether a sufficient number of individuals was sampled to conduct statistical analyses, the order of stomachs was randomised 100 times and the mean cumulative Shannon 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).

Prey were grouped into four categories for the statistical analyses: shrimps, crabs, teleosts and cephalopods. mysidaceans, amphipods, isopods, lancelets, gastropods, polychaetes and elasmobranchs were excluded from the comparative analysis because they had %N < 1. For each prey category, we fitted generalized linear models (GLM) (Venables & Ripley, 2002), where response variable was the number of prey consumed by *A. cyplophora*, and independent variables were sex, body size (TL), matury stage (immature and mature), season (warm = October-March; cold = April-September) and region (north = 34º-38º S; south = 38º-41º S). Also, models with combinations among independent variables were fitted. A model without any of the independent variables (*i.e.* null model) was fitted to assess if none of the tested variables had an effect on the consumption of prey categories. All models had a negative binomial error distribution and a log link (Venables & Ripley, 2002).

The significance of each model was tested using a multiple-hypothesis modelling approach (Anderson *et al.*, 2000; Franklin *et al.*, 2001), therefore each model was considered as a hypothesis explaining the consumption of a particular prey category. For each model fitted, the Akaike information criterion (AIC) and the Akaike's weight (*w*) were calculated. The value of the AIC for a given model represents the information lost, so the model with the lowest AIC was selected as the best model among all within the set of candidate models. *w* provides a measure of the strength of evidence for each model and represents the probability that the model is the best among the whole set of candidate models (Franklin *et al.*, 2001; Johnson & Omland, 2004). If *w* did not provide strong support for any particular model, we used model averaging to stimate the parameters of the variables included in the best model (Symonds & Moussalli, 2011).

To examine the relationships between predator size and prey size, we used TL of *A. cyclophora* and CW of crabs, LC of shrimps and TL of teleosts. Regressions on the 5, 50 and 95% quantiles were fitted in order to test an increase in minimum, medium and maximum prey size with increasing TL of *A. cyplophora*, respectively (Scharf *et al.*, 1998). All statistical analyses were performed using the R statistical software, version 3.1.0. (R Development Core Team, 2012).

Results

Overall, 442 individuals were sampled and the 75.8% (335) contained food. Of the individuals with stomachs containing food, 176 were females (245-686 mm TL) and 159 were males (210-670 mm TL). Cumulative mean Shannon diversity index curves for all the groups considered reached an asymptote, indicating that sample sizes were sufficient for comparisons (Fig. 2).

In terms of %IRI, the diet from *A. cyclophora* included mainly decapods, followed of teleost fishes. Molluscs, mysidaceans, amphipods, isopods, lancelets and elasmobranchs were also consumed but in lower proportion (Table 1). Among decapods, *Artemesia longinaris, Pleoticus muelleri* and *Pontocaris boschii* were the most consumed prey species in terms of %N and %O. *Dules auriga* was the most important prey species among teleosts in terms of %N, %W and %O.

Several patterns were found between the number of prey consumed and maturity stage, TL, season and region (Table 2; Fig. 3). All prey categories were independent of sex. The consumption of shrimps decreased with TL and it was more important in the warm season than in the cold season. In the warm season, the most important shrimps in the diet were *Artemesia longinaris* and *Pleoticus muelleri* (Fig. 4). Mature individuals of *A. cyplophora* preyed more heavily on crabs than immatute individuals, and this consumption was higher in the north region than in the south region. On the other hand, the consumption of teleosts increased with TL of *A. cyplophora* and they were more consumed in the south region than in the north region. The teleost species more consumed in the south region were *Dules auriga*, *Porichthys porosissimus*, *Trachurus lathami*, *Mullus argentinae*, *Etropus longimanus* and *Symphurus* spp.; unidentified teleosts had also a great contribution (Fig. 4). Cephalopods had no significant relationship with any of the independent variables evaluated. As shrimps and crabs had a low *w*, model averaging was computed. The averaged coefficients for shrimps were -0.0016 (s.e. = 0.0014) for TL (*w* = 0.60) and -0.366 (s.e. = 0.237) for cold season (*w* = 0.82). For crabs the averaged coefficient were -0.179 (s.e. = 0.276) for immature (*w* = 0.36) and -0.611 (s.e. = 0.302) for south region (*w* = 0.90).

As TL of *A. cyclophora* increased, minimum, medium and maximum LC of shrimps increased (slopes and intercepts of 5, 50 and 95% quantile regressions = 0.022 and -3.513; 0.032 and -3.761; 0.019 and 10.789, respectively, p < 0.01). However, only maximun CW of crabs increased significantly with TL of *A. cyclophora* (slope and intercept of 95% quantile regressions = 0.405 and -113.968, p < 0.05). Further, as TL of *A. cyclophora* increased, maximum TL of teleosts increased significantly (slope and intercept of 95% quantile regressions = 0.303 and -21.621, p < 0.05) (Fig. 5).
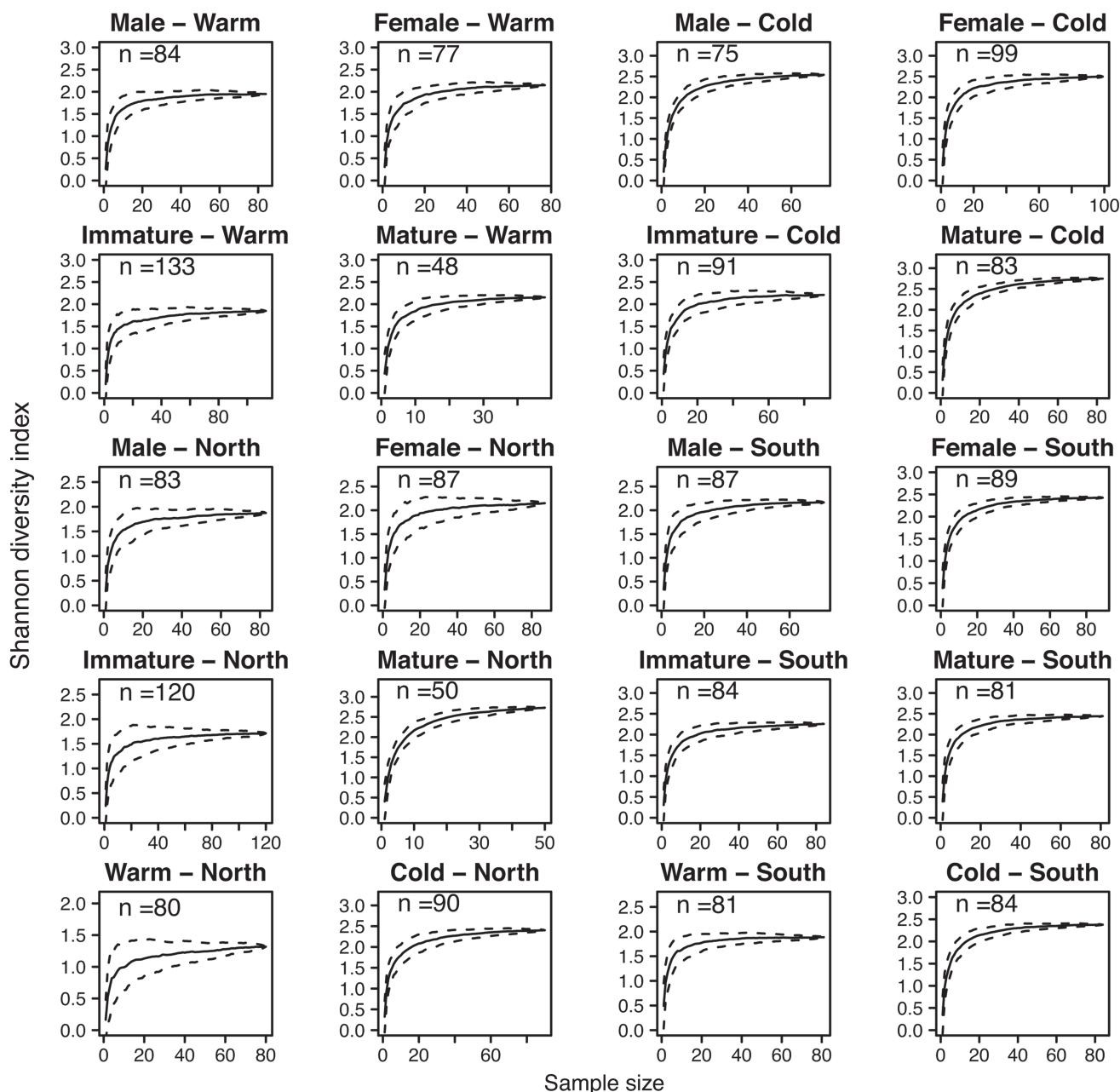
Fig. 2. Cumulative mean Shannon diversity index as a function of sample size for prey of *Atlantoraja cyclophora* from off Uruguay and northern Argentina. Dashed lines indicate standard deviation.

Table 1. Diet composition of *Atlantoraja cyclophora* off Uruguay and northern Argentina. %O, percentage frequency of occurrence; %N, percentage by number; %W, percentage by weight; IRI, index of relative importance; %IRI, percentage IRI.

Prey		%O	%N	%W	IRI	%IRI
TELEOSTEI		42.98	19.28	59.78	3398.4	28.54
Unidentified teleosts		24.18	8.34	15.29	571.38	
Engraulidae	*Anchoa marinii*	0.30	0.18	0.45	0.19	
	Engraulis anchoita	0.60	0.18	0.42	0.36	
Ophidiidae	*Raneya brasiliensis*	2.98	1.11	3.12	12.64	
Batrachoididae	*Porichthys porosissimus*	2.69	0.83	5.31	16.50	
Triglidae	*Prionotus nudigula*	1.19	0.37	0.74	1.33	
Serranidae	*Dules auriga*	9.55	4.17	16.21	194.71	

Table 1. (conclusion).

Prey		%O	%N	%W	IRI	%IRI
Carangidae	*Trachurus lathami*	2.69	1.02	5.51	17.54	
Mullidae	*Mullus argentinae*	1.19	0.37	5.58	7.10	
Pinguipedidae	*Pinguipes brasilianus*	0.30	0.09	0.79	0.26	
Paralychthyidae	*Etropus longimanus*	2.69	1.30	2.52	10.27	
Cynoglossidae	*Symphurus* spp.	3.28	1.30	3.83	16.85	
ELASMOBRANCHII						
Rajidae		0.89	0.56	0.19	0.67	<0.01
CRUSTACEA						
Decapoda		73.43	77.57	38.18	8500.1	71.37
Lysiosquillidae	*Heterosquilla platensis*	0.30	0.09	0.05	0.04	
Unidientified shrimps		17.31	13.44	4.81	315.98	
Penaeidae	*Artemesia longinaris*	22.10	30.12	7.23	825.14	
Solenoceridae	*Pleoticus muelleri*	13.73	13.44	9.12	309.82	
Caridae		0.30	0.46	0.01	0.14	
Crangonidae	*Pontocaris boschii*	13.13	5.84	2.86	114.28	
Unidentified Brachyura		16.42	8.34	4.26	206.82	
Majidae	*Eurypodius latreillei*	0.30	0.18	0.09	0.08	
	Leurocyclus tuberculosus	5.37	2.04	4.28	33.97	
	Libinia spinosa	1.79	0.74	1.73	4.43	
Atelecyclidae	*Peltarion spinosulum*	3.28	1.11	2.74	12.65	
Portunidae	*Callinectes sapidus*	1.79	1.02	0.75	3.18	
	Ovalipes trimaculatus	0.30	0.09	0.12	0.06	
	Coenophtalmus tridentatus	0.30	0.18	0.05	0.07	
Xanthidae		0.30	0.18	0.03	0.06	
Pinnotheridae	*Pinnixa patagoniensis*	0.30	0.09	<0.01	0.03	
	Pinnixa brevipollex	0.60	0.18	0.02	0.12	
Mysidacea		0.60	0.28	<0.01	0.17	<0.01
Amphipoda		0.60	0.28	<0.01	0.17	<0.01
Isopoda		1.50	0.46	0.05	0.76	<0.01
Serolidae	*Serolis* spp.	0.60	0.18	0.01	0.12	
	Serolis marplatensis	0.30	0.09	0.01	0.03	
	Serolis polaris	0.60	0.18	0.02	0.12	
MOLLUSCA						
Cephalopoda		2.98	1.02	1.75	8.27	0.07
Unidentified cephalopods		0.60	0.18	0.07	0.15	
Octopodidae	*Octopus tehuelchus*	2.69	0.83	1.68	6.75	
Gasteropoda		0.30	0.09	<0.01	0.03	<0.01
POLYCHAETA		0.89	0.28	0.02	0.27	<0.01
CEPHALOCHORDATA						
Branchiostomidae	*Branchiostoma platae*	0.60	0.18	<0.01	0.11	<0.01

Table 2. Best models explaining the consumption in number of the main prey category of *Atlantoraja cyclophora* off Uruguay and northern Argentina. TL: total length; AIC: Akaike Information criterion; *w*: Akaike weights. The coefficients of the models are relative to mature individuals, north region and warm season. Standard error in parentheses.

Prey categories	Intercep	Coefficients	AIC	*w*
Shrimps	− 2.176 (0.327)	− 0. 002 (0.0006) TL − 0.375 (0.159) cold	1252.6	0.42
Crabs	− 0.195 (0.209)	− 0.499 (0.231) immature − 0.736 (0.233) south	593.6	0.35
Teleosts	− 2.947 (0.399)	0.003 (0.0007) TL + 0.924 (0.166) south	649.1	0.98
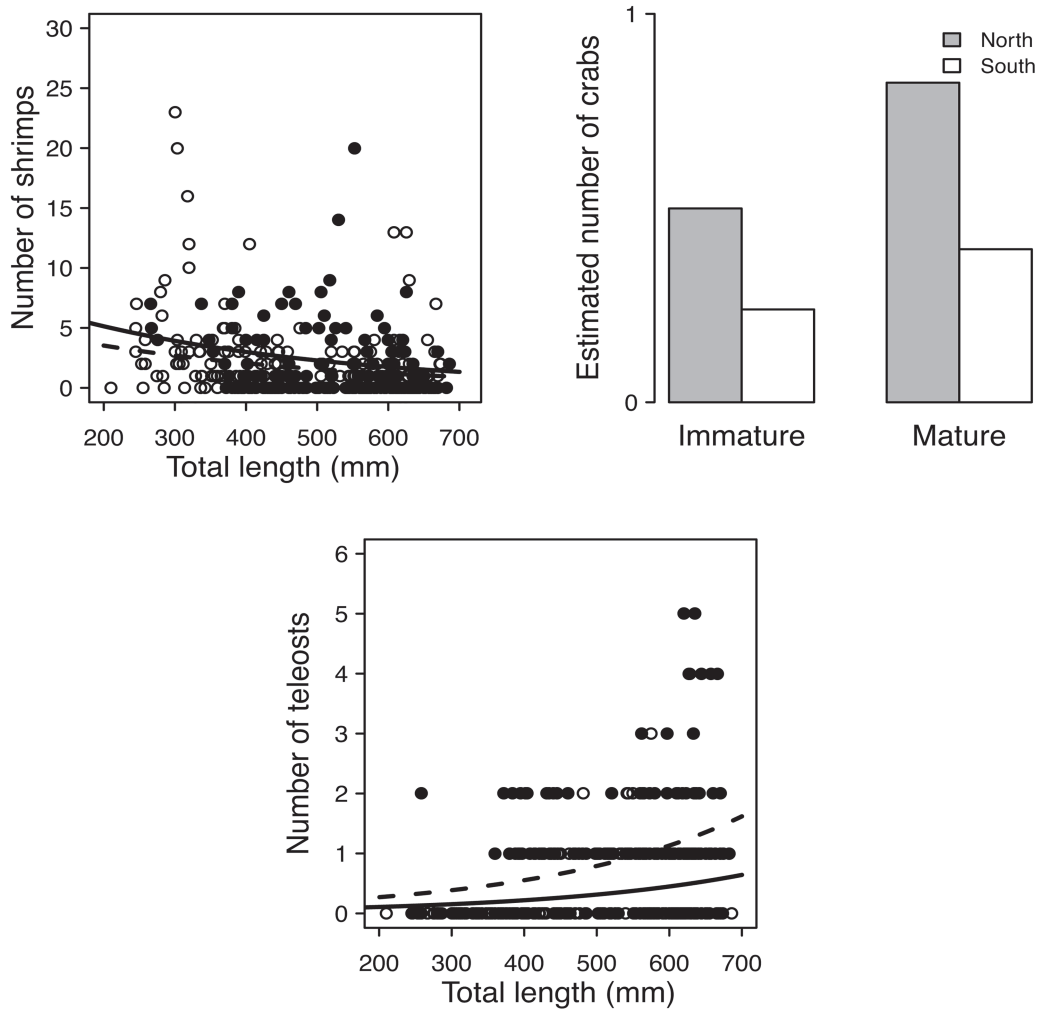
Fig. 3. Changes in consumption of different prey with body size, maturity stage, season and region of *Atlantoraja cyclophora* from off Uruguay and northern Argentina estimated by generalized linear models for number of shrimps, crabs and teleosts. In shrimps: warm season with solid lines and open circles; cold season with dashed lines and solid circles. In teleosts: north region with solid lines and open circles; south region with dashed lines and solid circles.
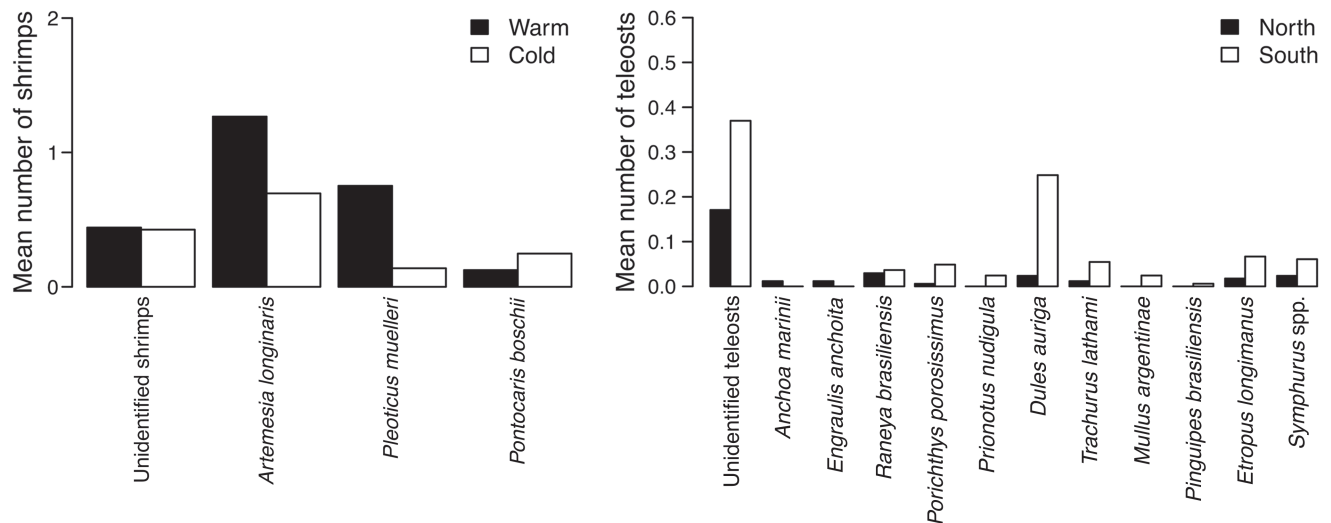
Fig. 4. Mean number of shrimps and teleosts consumed for *Atlantoraja cyclophora* from off Uruguay and northern Argentina by season and region, respectively.
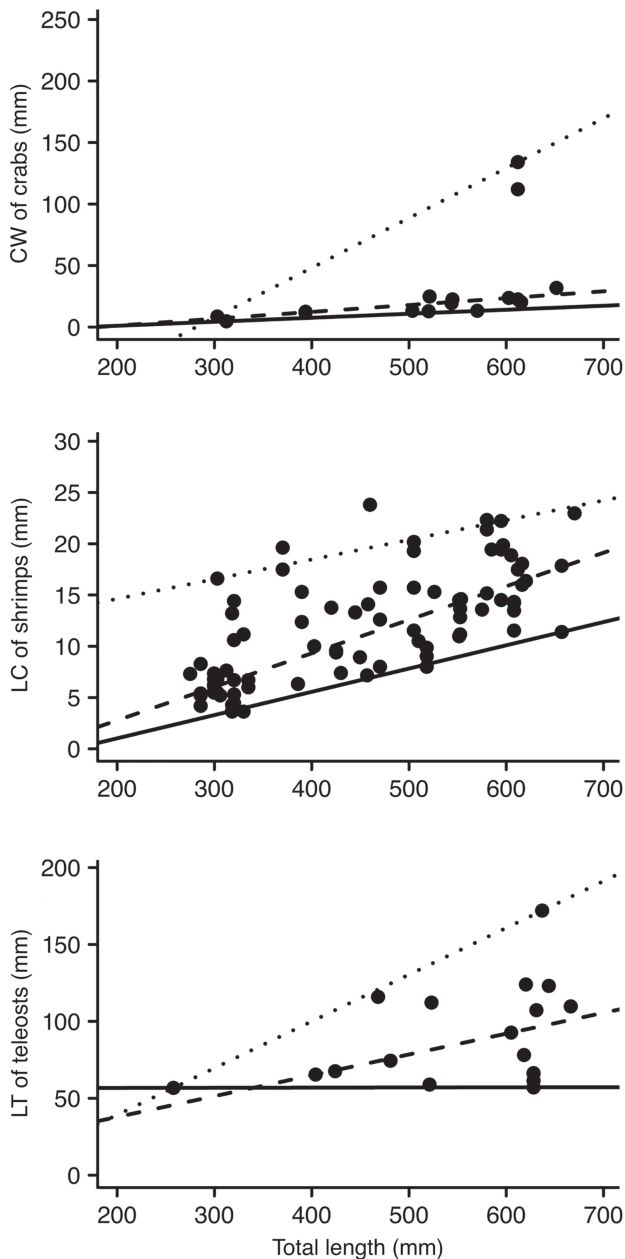
Fig. 5. Quantile regressions of carapace width (CW) of crabs, cephalothorax length (CL) of shrimps and total length (TL) of teleosts and total length of *Atlantoraja cyclophora*. The solid, dashed and dotted lines are 5%, 50% and 95% quantile regressions, respectively.

Discussion

The diet of *Atlantoraja cyclophora* consists mainly of decapod crustaceans (shrimps and crabs), benthic teleosts (such as *Dules auriga*, *Porichthys porosissimus* and *Raneya brasiliensis*) and other benthic invertebrates, which implies that this species has demersal-benthic feeding habits. Further, the diet of *A. cyplophora* changes with ontogeny, season and region, and with size of both predator and prey.

In general, the diet composition of *A. cyclophora* off Uruguay and northern Argentina is consistent with the results obtained in Brazil (Ubatuba Bay, Soares *et al.*, 1992; southern coast of Rio de Janeiro, Viana & Vianna, 2014), where decapods and teleosts are the most consumed prey. This pattern indicates that *A. cyclophora* maintains its feeding habits along its distribution range in the Southwest Atlantic, using similar food resources and likely having the same trophic role.

Ontogenetic variations in the diet composition of elasmobranchs may be attributed to a combination of different processes: different foraging ability between small and larger individuals, morphological constraints such as gape limitation, and an increase in the metabolic requirements with mature individuals (Wetherbee & Cortés, 2004). As with another skate species, *A. cycplophora* showed ontogenetic shifts in the diet composition: small individuals consumed largely shrimps, but large individuals preyed mainly on crabs and teleosts. In southeastern Brazil, the diet of immature and mature individuals was similar, but shrimps were more common in immature individuals and teleosts and crabs were more consumed by mature individuals (Viana & Vianna, 2014). In general terms, the ontogenetic pattern of *A. cyclophora* is consistent between regions, which would reflect an identical use of trophic resources throughout its distribution range.

In benthic and demersal coastal communities, species composition is variable, because environmental conditions change seasonally (Jaureguizar *et al.*, 2006). Thus, seasonal changes in the diet are often related with differences in prey abundance between seasons (Muto *et al.*, 2001). In the study area, shrimps are more abundant in the warm season than in the cold season (Iorio *et al.*, 1996; Scelzo *et al.*, 2002), indicating that *A. cyclophora* may be adapting its feeding habits to seasonal changes in prey abundance. In southeastern Brazil, diet composition of *A. cyclophora* is also related to seasonal prey abundance, but the most important prey consumed in summer were crabs (Viana & Vianna, 2014). Also, seasonal changes in predation risk may be affecting the feeding habits of *A. cyclophora*, as it is preyed upon by large sharks during the warm season (Lucifora *et al.*, 2009).

An important and consistent pattern found off Uruguayan and northern Argentinean coastal waters is the difference in the diet composition of skates between regions. In several species of skate, the consumption of teleosts fishes is more important in the south region than in the north and the consumption of crustaceans is high in the north region (*Rioraja agassizii* in Barbini & Lucifora, 2011; *Atlantoraja castelanui* in Barbini & Lucifora, 2012; *Sympterygia acuta* in Barbini & Lucifora, 2016). This pattern is identical to the one in *A. cyclophora*. These spatial dietary changes could be attributed to differences in the structure and abundance of the benthic community between north and south region, caused by

distinct environmental conditions: in the north area, the Río de la Plata estuary, bottom type, salinity and the presence of a turbidity front structures the benthic communities (Giberto *et al.*, 2004); in the south area, vertical homogeneity due to tidal forcing and a salinity coastal front are the main environment factors (Acha *et al.*, 2004).

Our results show that as *A. cyclophora* increases its body size, the size of shrimps, crabs and teleosts consumed increases too, but larger individuals do not abandon the consumption of small crabs and teleosts. The same pattern is present in other skates that co-occur in time and space, such as *Rioraja agassizii* (Barbini & Lucifora, 2011). For both species, we hypothesized that this pattern could be a result of differences in prey availability. Elasmobranchs may be more selective predators in environments with a greater choice of prey (Lucifora *et al.*, 2006). Shrimps (*i.e. Artemesia longinaris* and *Pleoticus muelleri*) are abundant species in this region, therefore large individuals of *A. cyclophora* and *R. agassizii* could be more selective, consuming mainly large shrimps. On the other hand, the lower availability of crabs and teleosts may explain the inclusion in the diet of small individuals of these prey by large skates. The predator-prey size pattern found in *A. cyclophora* and *R. agassizii* (*i.e.* consuming both small and large prey) is the most common among elasmobranchs, specially in piscivorous predators (Scharf *et al.*, 2000; Lucifora *et al.*, 2006).

In conclusion, the ontogenetic diet shifts observed in *A. cyclophora* could be due to a combination of different processes, as improved ability of larger skates, morphological constraints of smaller skates and energy requirements. Seasonal and regional diet shifts could be associated to changes in the prey abundance between seasons and to differences in the environmental conditions between regions, respectively. Differences in availability among prey may explain the pattern that large skates do not abandon the consumption of small individuals of crabs and teleosts. These results bring information on the ecology of an important predator in an ecosystem highly impacted by fishing. Despite this, the life history of *A. cyclophora* is little known, therefore studies on reproductive aspects and estimates of age and growth parameters are very relevant for the suitable conservation of a vulnerable species that is commercially fished.

Acknowledgements

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