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Santiago A. Barbini^{ab}; Luis O. Lucifora^{cd}; Natalia M. Hozbor^e

^a Laboratorio de Ictiología, Departamento de Ciencias Marinas, Universidad Nacional de Mar del Plata, Mar del Plata, Argentina ^b Comisión de Investigaciones Científicas (CIC), Provincia de Buenos Aires, La Plata, Argentina ^c Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Ciudad Autónoma de Buenos Aires, Argentina ^d Centro de Investigaciones Ecológicas Subtropicales (CIES), Centro de Investigaciones del Bosque Atlántico (CeIBA), Puerto Iguazú, Misiones, Argentina ^e Instituto Nacional de Investigación y Desarrollo Pesquero, Mar del Plata, Argentina

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ORIGINAL ARTICLE

Feeding habits and habitat selectivity of the shortnose guitarfish, *Zapteryx brevirostris* (Chondrichthyes, Rhinobatidae), off north Argentina and Uruguay

SANTIAGO A. BARBINI^{1,2*}, LUIS O. LUCIFORA^{3,4} & NATALIA M. HOZBOR⁵

¹Laboratorio de Ictiología, Departamento de Ciencias Marinas, Universidad Nacional de Mar del Plata, Mar del Plata, Argentina; ²Comisión de Investigaciones Científicas (CIC), Provincia de Buenos Aires, La Plata, Argentina; ³Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Ciudad Autónoma de Buenos Aires, Argentina; ⁴Centro de Investigaciones Ecológicas Subtropicales (CIES), Centro de Investigaciones del Bosque Atlántico (CeIBA), Puerto Iguazú, Misiones, Argentina, and ⁵Instituto Nacional de Investigación y Desarrollo Pesquero, Mar del Plata, Argentina

Abstract

Dietary shifts with size, maturity stage, season, and bottom type selection of *Zapteryx brevirostris* were evaluated, using generalized linear models. In terms of the index of relative importance, the most important prey were amphipods (39.17%), polychaetes (22.33%) and lancelets (20.33%), followed by decapods (8.93%), cumaceans (5.41%) and isopods (3.41%). *Z. brevirostris* consumed mainly polychaetes and amphipods in spring and summer, more cumaceans in winter, consumed more lancelets in spring, and preyed more heavily on decapods and isopods in summer. As *Z. brevirostris* increased in size, the consumption of decapods, polychaetes and isopods was higher, but the consumption of amphipods decreased. Mature individuals of *Z. brevirostris* consumed more lancelets than juveniles. *Z. brevirostris* selected sand over other bottom types. The diet of *Z. brevirostris* can be influenced by the selectivity of this species for sandy bottoms. As sandy bottoms are exposed to a high intensity of bottom trawling, the positive selection of sandy bottoms increases the vulnerability of *Z. brevirostris* by exposing it to fishing mortality.

Key words: Habitat selectivity, ontogenetic diet shift, Rhinobatidae, Southwest Atlantic, trophic ecology

Introduction

Resource selectivity – i.e. the use of resources in different proportions to those available in the environment (Chesson 1978; Jaksic 1989) – in elasmobranchs is becoming apparent for a number of species differing widely in morphology and ecology. Elasmobranchs are known to feed selectively (Harris et al. 1988; Heithaus et al. 2002; Heupel & Hueter 2002; Lucifora et al. 2006) and also to selectively use their habitats (Morrissey & Gruber 1993; Hopkins & Cech 2003; Campana & Joyce 2004; Robbins 2007; Conrath & Musick 2008; Powter & Gladstone 2008; Vögler et al. 2008).

Guitarfishes (Rhinobatidae) inhabit a variety of habitats, such as muddy and sandy bottoms, sea-grass beds and nearby reefs, but in all habitats they

feed in close association to the bottom (Compagno 1990; Kyne & Bennett 2002; White et al. 2004). Given this strong association to the bottom, diet and bottom type selectivity are expected to be closely linked in guitarfishes.

The shortnose guitarfish, *Zapteryx brevirostris* (Müller & Henle, 1841), is widely distributed in the coastal waters of the Western South Atlantic, from Rio de Janeiro (~23°S, Brazil), to southern Buenos Aires Province (~41°S, Argentina) (Castello 1971; Menni & Stehmann 2000). Its diet appears to vary geographically; off Mar del Plata (38°S, Argentina), *Z. brevirostris* feeds heavily on cephalochordates (Castello 1971), whereas off Rio de Janeiro and Ubatuba (Brazil), it feeds mainly on small crabs, other crustaceans and benthic invertebrates (Batista

*Correspondence: S. A. Barbini, Laboratorio de Ictiología, Departamento de Ciencias Marinas, Universidad Nacional de Mar del Plata, Funes 3350, Mar del Plata, B7602AYL, Argentina. E-mail: sbarbini@mdp.edu.ar

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1984; Soares et al. 1992). In Uruguayan and Argentinean waters, *Z. brevirostris* is a bycatch of bottom trawl fisheries that operate over smooth bottoms (Massa et al. 2004). As a result, the biomass of *Z. brevirostris* in this area decreased by 86% between 1994 and 1999, prompting the species to be categorized as Vulnerable by the International Union for Conservation of Nature (IUCN) (Vooren et al. 2006).

The marine ecosystem located off Uruguay and northern Argentina, between 34°S and 38°S, 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, and the world's largest estuary. This system is characterized by strong vertical stratification: freshwater flows on the surface, while dense shelf waters intrude at the bottom, taking the shape of a salt wedge. The dynamics of the upper layer is driven by wind stress, while the bottom layer is controlled by the bathymetry (Guerrero et al. 1997). The area contains a variety of bottom types including areas of mud, sand, sand and mud mixed, loose shells, gravel and scattered rocky areas (Brazeiro et al. 2003). While pollution, harmful algal blooms, benthic habitat alteration and biological invasions have been identified as threats, industrial fishing is regarded as the main threat to marine biodiversity in the area (Brazeiro et al. 2003). Industrial fishing effort on batoids in the area – almost exclusively bottom trawling – increased from zero to about 160,000 trawling hours per year between 1991 and 1999 (Massa et al. 2004).

In this paper, we present, for the first time, diet and habitat selectivity of *Z. brevirostris*, off Uruguay and northern Argentina, between 34°S and 38°S. For these reasons the aims were to: (1) describe the diet composition, (2) identify changes in the diet with seasons and ontogeny, (3) study relationship between prey size and predator size, and (4) determine selectivity of bottom types.

Materials and methods

Feeding ecology

Sampling. Individuals of *Zapteryx brevirostris* which were used for dietary analysis ($n=332$) were obtained from eight research cruises between July 2001 and February 2006, using standard bottom trawls with an Engels trawl net (200 mm stretched mesh in the wings and 120 mm stretched mesh in the cod end), towed at 4 knots for 15 min (Figure 1). Trawl depth was 6–70 m.

For each individual captured, total length (TL), sex and maturity stage were recorded. Females were considered mature when exhibiting enlarged uteri

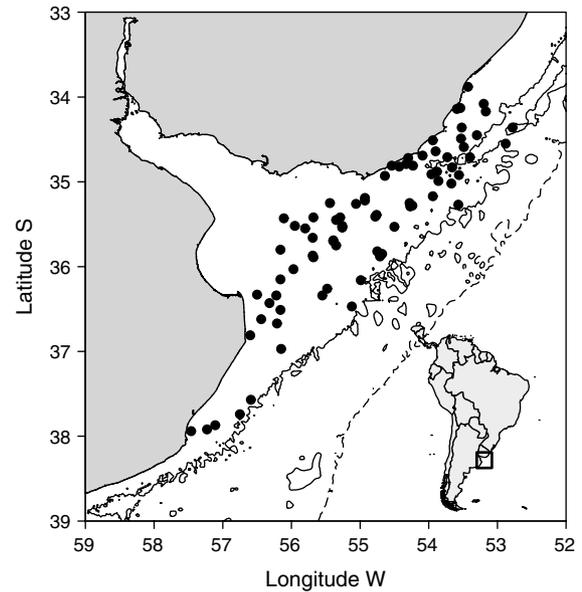


Figure 1. Map of the study area showing the locations (black circles) where the shortnose guitarfish, *Zapteryx brevirostris*, was collected. The 50- and 200-m isobaths are shown as solid and dashed lines, respectively. The inset shows the location of the study area in South America.

and oviducal glands, yolked oocytes in the ovary or the presence of embryos in the uterus, while both the presence of convoluted epididymi and the degree of clasper calcification were used to determine maturity in males (Stehmann 2002; Walker 2005).

Diet composition. Stomachs were removed and stored at -20°C . In the laboratory, stomach contents were sorted and identified to the lowest possible taxonomic level, using published catalogues (Boschi et al. 1992; Cousseau & Perrotta 2000; Rouse & Pleijel 2001) and reference collections. Prey were counted and their wet weight was recorded. When possible, the carapace width (CW) of brachyuran crab prey was measured. To quantify the diet composition for comparison with published studies, percentage weight ($\%W_i$: weight of a particular prey i expressed as percentage of total weight of consumed prey), percentage number ($\%N_i$: number of a particular prey i expressed as percentage of total number of consumed prey), percentage of frequency of occurrence ($\%F_i$: percentage of stomachs which contained a particular prey i) (Hyslop 1980), and the index of relative importance ($\text{IRI} = \%F_i \times (\%W_i + \%N_i)$) (Pinkas et al. 1971), expressed as a percentage (Cortés 1997), with the contents of all stomachs pooled were calculated.

The degree of digestion of the polychaetes made it difficult to count some of these prey. For this reason, a relationship (linear regression) between weight (W) and number of polychaetes (N) was estimated. Only undigested, whole polychaetes were used to

estimate this relationship. Polychaetes of very small size (i.e. the family Glyceridae and *Armandia loboï*) were not used for this relationship because it was not possible to estimate individual weight of such small individuals. This relationship was significant (Student's t ; $P < 0.05$) with the following equation: $\ln(N) = 0.022344 \times \ln(W) + 0.92143$; with weight expressed in g.

To determine if an adequate number of stomachs had been collected to accurately describe the diets of *Z. brevirostris* and to conduct statistical analyses, the order of stomachs sampled was randomized 100 times and the mean cumulative Shannon Wiener diversity index was plotted as a function of sample size. When the curve reached a stable asymptote, sample size was considered sufficient.

For the purpose of statistical analysis, prey were grouped into seven taxonomic categories: polychaetes, lancelets, decapods, amphipods, cumaceans, isopods and other. This latter category included prey species with less than 1% IRI, i.e. tanaids, mollusks, ophiuroids, sipunculids and teleosts. These categories were chosen because they reflected the taxonomic and ecological variability of the diet of *Z. brevirostris*.

Diet shifts. Dietary variability with *Zapteryx brevirostris* size (TL), maturity stage (juvenile, mature female and mature male) and season (winter, spring and summer) were evaluated, using generalized linear models (GLM) (Venables & Ripley 2002). Individuals captured in autumn were not included in the analysis due to low sample size. For each prey type, models were built where occurrence (presence or absence) and number of each prey type was employed as the response variable, and TL, maturity stage or season as the explanatory variables (Lucifora et al. 2009). As the response variable of models with occurrence of prey type had a binary nature, then a binomial error distribution and a logit link were specified. In the same way, since models with number of prey individuals had a large variance due to the large number of zero values in the samples, then a negative binomial error distribution and a log link were specified. Model parameters were obtained by maximizing the maximum likelihood.

Generalized additive models were also fitted between prey consumption (number and presence or absence) and predator size for assessing possible curvilinear relationships (Wood 2006). If this was the case, then quadratic terms were included in the GLM (Crawley 2005). If a significant relationship between prey type and *Z. brevirostris* size was detected, we assessed whether the relationship was continuous or discrete, i.e. we tested if there was a threshold size at which *Z. brevirostris* started to

consume that prey (Lucifora et al. 2009). To do this, GLMs were fitted varying the threshold at intervals of 1 mm and the model with the threshold that gave the lowest deviance was selected (Crawley 2005).

We used Information Theory to identify the best model explaining the consumption of a given prey. For each prey, we calculated the Akaike Information Criterion (AIC) of all models considered. AIC measures the amount of information lost when fitting a model, so that the model with the lowest AIC is the one that best describes the data (Anderson et al. 2000; Franklin et al. 2001; Johnson & Omland 2004). Each model was weighed against the others using Akaike weights (w), which give an estimation of the likelihood of the model given the data (Anderson et al. 2000; Franklin et al. 2001; Johnson & Omland 2004).

Predator-prey size relationships. For brachyuran crab prey (the only prey for which size data could be accurately taken in sufficient numbers), the relationship between *Zapteryx brevirostris* length and prey size was assessed using total length (TL) of *Z. brevirostris* and carapace width (CW) of prey. Quantile regressions of CW on TL of 5%, 50% and 95% quantiles were estimated in order to test an increase in minimum, median and maximum size of consumed prey with an increase in predator's size (Scharf et al. 1998).

Habitat selection

Data from 619 sampling stations from eight research cruises conducted between 1994 and 2004 were used to assess bottom type selectivity by *Zapteryx brevirostris*. At each sampling station we recorded number of individuals of *Z. brevirostris* captured, year, Julian day, depth, swept area, latitude and longitude. Bottom types were determined from a map of the distribution of bottom sediments of the Río de la Plata and adjacent marine areas from Brazeiro et al. (2003).

For analysing habitat selection, we fitted GLMs with a negative binomial error distribution and a log link (Venables & Ripley 2002). The full model had number of individuals of *Z. brevirostris* as the dependent variable, and bottom type (class variable: sand; mud; sand/mud mixed; tuff; sand, shell rest and/or tuff), year, longitude, latitude, Julian day, depth (in m), and squared depth as independent variables. The log of swept area (in square nautical miles) was included as an offset term to account for the different size of samples (Shepherd & Myers 2005). The random error (ϵ_i) was specified as negative binomial due to the high number of zero values, and a log link was used. While we were

interested mainly in the effect of bottom type, the rest of the independent variables were considered in order to standardize the data by taking into account the effect of those variables in our model (Shepherd & Myers 2005). Similar to the procedure for prey consumption, the best minimum adequate model was selected as that with the lowest AIC (Crawley 2005).

In this study, we included availability by using data from all trawl stations (i.e. samples) regardless of the number of *Z. brevirostris* caught in them. All the samples with zero *Z. brevirostris*, i.e. available but not used, were included, as well as samples with positive numbers of *Z. brevirostris*, i.e. used habitat (Vilchis et al. 2006). In our model, we expect that, if no habitat is selected by *Z. brevirostris*, the term for habitat will be dropped in the best model because there will be no relationship between habitat type and the abundance of *Z. brevirostris*. Alternatively, if any habitat type is used selectively by *Z. brevirostris*, then the term for habitat type will be retained in the best model, and the parameters for each habitat type will provide an estimation of the relative selectivity of each habitat type.

Results

Feeding ecology

Diet composition. Of the 332 individuals examined, 279 (84.04%) contained food. Of the individuals with food, 67 were juveniles (201–620 mm TL), 120 were mature females (435–670 mm TL) and 92 were mature males (462–630 mm TL). The number of individuals within each group was as follows: 16 juvenile-winter, 26 juvenile-spring, 21 juvenile-summer, 32 mature female-winter, 47 mature female-spring, 30 mature female-summer, 33 mature male-winter, 29 mature male-spring, and 19 mature male-summer. The cumulative curves of diversity reached an asymptote for all the groups, indicating that the number of stomachs analysed was sufficient, except for mature males in winter, where the asymptote was not as clearly reached as in the remaining groups (Figure 2).

In general, the most important prey of *Zapteryx brevirostris*, in terms of %IRI, were amphipods (39.17%), followed by polychaetes (22.33%) and lancelets (20.33%). Decapods (8.93%), cumaceans (5.41%) and isopods (3.41%) were less important in the diet. Other prey items represented less than 1% of %IRI, like teleosts, ophiuroids, mollusks, tanaidaceans and sipunculids (Table I). Amphipods had the highest values of %N (44%), followed by lancelets (27.25%) and cumaceans (10.25%). Polychaetes and amphipods had the highest %W (26.41 and 20.14%, respectively). The third most dominant

prey by weight were decapods (18.01%) followed by lancelets (17.05%). Polychaetes were the dominant prey by %F (66%) followed by amphipods (62.01%); lancelets (46.60%), decapods (40.86%), cumaceans (37.63%) and isopods (32.26%) had high %F values as well.

Diet shifts. Several patterns were found in the relationships between occurrence and number of prey type with season, predator size and maturity stages (Table II).

Seasonal shifts. In number, *Zapteryx brevirostris* preyed more heavily on polychaetes and amphipods in spring and summer than in winter (Figure 3a,b), while in winter it consumed more cumaceans than in spring and summer (Figure 3c). The occurrence of decapods in the diet was higher in summer than in winter and spring (Figure 3d).

Shifts with season and predator's size. The number of decapods in the diet increased with increasing size of *Z. brevirostris*. This increase was higher in summer than in winter and spring (Figure 4a). In terms of occurrence, polychaetes were more common in the diet of *Z. brevirostris* in spring and summer than in winter and were consumed in higher proportion with increasing size of *Z. brevirostris* (Figure 4b), isopods were increasingly consumed with increasing size of *Z. brevirostris*, and were consumed more often in summer than in winter or spring (Figure 4c). Amphipods were preyed upon more often in spring and summer than in winter, but their consumption decreased with increasing size of *Z. brevirostris* (Figure 4d).

Shifts with season and predator's maturity stage. The number and occurrence of lancelets preyed upon by *Z. brevirostris* were higher in spring than in winter or summer and both mature females and mature males consumed more lancelets than juveniles (Figure 5a,b). The consumption of isopods in number was higher in summer than in winter and spring and both juveniles and mature males consumed more isopods than mature females (Figure 5c).

Shifts with maturity stages. In occurrence, mature females preyed on cumaceans more heavily than juveniles and mature males (Figure 6).

Predator-prey size relationships. As TL increased, both the minimum and median prey size consumed did not increase significantly (5% quantile regression slope = 0.00429, Student's *t*, $P > 0.05$; 50% quantile regression slope = 0.0295, Student's *t*, $P > 0.05$). However, the maximum prey size consumed increased significantly with increased TL of the predator (95% quantile regression slope = 0.1, Student's *t*, $P < 0.001$) (Figure 7).

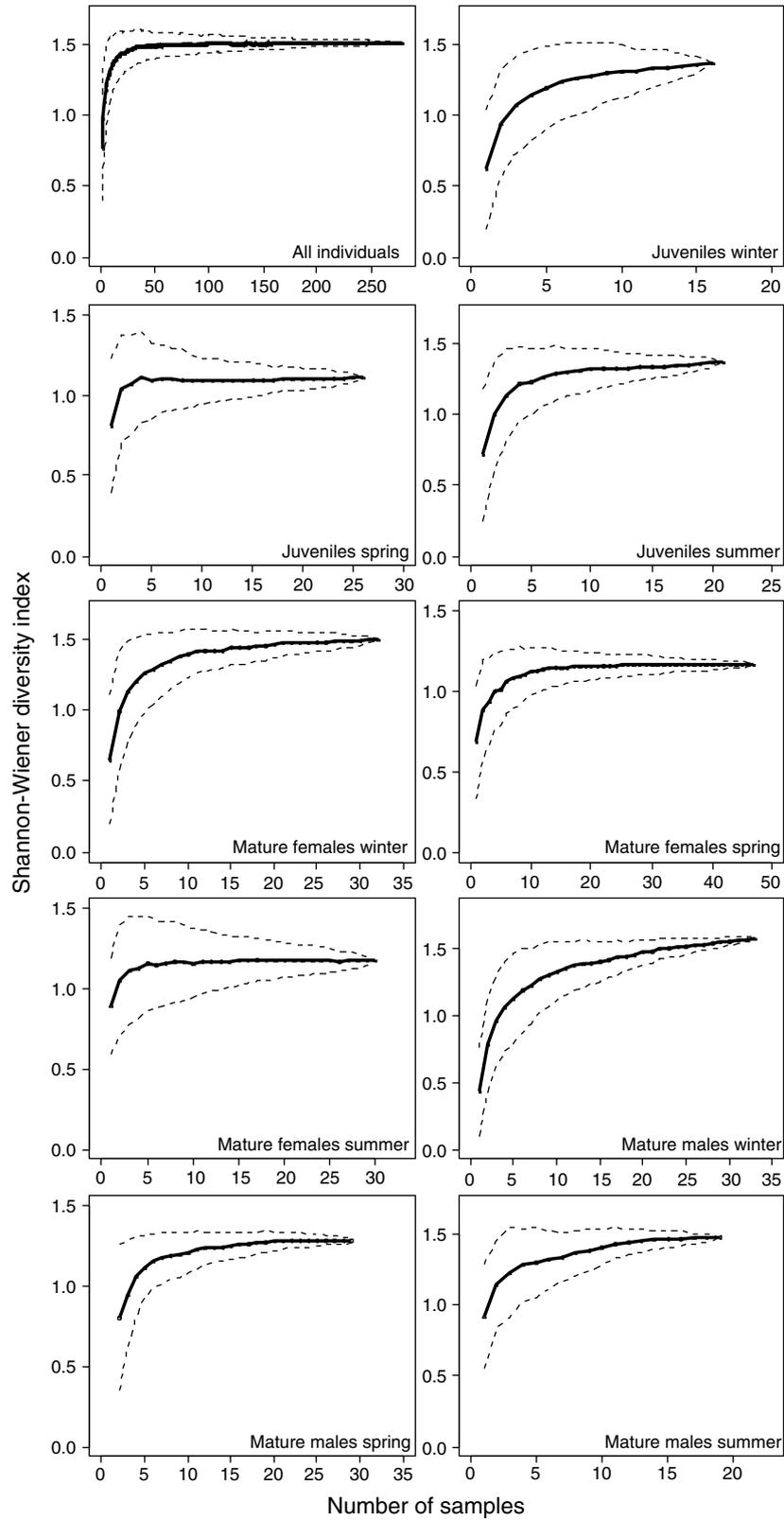


Figure 2. Curves of cumulative mean Shannon–Wiener diversity index as function of sample size for the food consumed by shortnose guitarfish, *Zapteryx brevirostris*, off Uruguay and north Argentina. Dashed lines represent the standard deviation.

Table I. Diet composition of *Zapteryx brevirostris* by percentage number (%N_i), percentage of weight (%W_i), percentage of frequency occurrence (%F_i), index of relative importance (IRI) and IRI expressed as a percentage (%IRI).

Prey items	%N _i	%W _i	%F _i	IRI	%IRI
Polychaeta	7.97	26.41	66.00	2267.41	22.33
Unidentified polychaetes	4.04	20.17	53.05	1284.21	
Opheliidae					
<i>Travisia</i> spp.	0.31	0.50	5.73	4.60	
<i>Armandia loboii</i>	2.48	1.00	14.00	48.14	
Aphroditiformia	0.03	0.20	0.72	0.16	
Eunicomorpha	0.40	1.95	5.73	13.30	
Glyceridae	0.30	0.40	4.30	3.00	
Onuphidae	0.20	0.24	4.30	1.90	
Orbinidae	0.10	0.16	1.80	0.50	
Nephtyidae	0.03	0.50	0.72	0.36	
Maldanidae	0.10	0.80	2.15	1.95	
Phyllodocidae	0.03	0.54	0.72	0.41	
Cephalochordata					
<i>Branchiostoma plataea</i>	27.25	17.05	46.60	2064.40	20.33
Crustacea					
Decapoda	4.18	18.01	40.86	907.00	8.93
Unidentified Natantia	0.01	0.03	0.36	0.02	
<i>Artemesia longinaris</i>	0.82	1.25	5.37	11.14	
<i>Pleoticus muelleri</i>	0.55	1.30	6.45	12.00	
Unidentified crabs	1.34	6.33	22.22	170.71	
<i>Libinia spinosa</i>	0.38	4.64	5.02	25.20	
<i>Panopeus</i> spp.	0.07	0.16	1.80	0.42	
<i>Leucipa pentagona</i>	0.12	0.56	2.51	1.70	
<i>Pinnixa brevipolex</i>	0.25	1.31	2.86	4.48	
<i>Peisos</i> spp.	0.04	0.09	0.36	0.05	
<i>Corystoides abbreviatus</i>	0.17	0.63	3.60	2.88	
<i>Ovalipes trimaculatus</i>	0.30	1.10	2.15	3.00	
<i>Cyrtograpsus affinis</i>	0.07	0.30	1.43	0.54	
Pinnotheridae	0.01	0.02	0.36	0.01	
Unidentified hermit crabs	0.01	0.26	0.36	0.10	
<i>Loxopagurus loxochelis</i>	0.01	0.02	0.36	0.01	
Amphipoda	44.00	20.14	62.01	3976.86	39.17
Cumacea	10.25	4.33	37.63	549.02	5.41
Tanaidacea	0.30	0.22	1.07	0.55	<0.01
Isopoda	5.16	5.57	32.26	346.17	3.41
Unidentified isopods	0.85	1.21	4.00	8.11	
<i>Serolis</i> spp.	1.00	1.45	15.05	37.00	
<i>Exocirrolana armata</i>	3.20	2.41	13.62	76.23	
<i>Cirolana</i> spp.	0.13	0.49	2.87	1.80	
Teleostea	0.22	6.31	5.38	35.10	0.34
Unidentified teleosts	0.15	3.04	3.60	11.42	
<i>Engraulis anchoita</i>	0.04	2.13	1.07	2.34	
<i>Anchoa maringii</i>	0.03	1.13	0.72	0.83	
Mollusca					
Cephalopoda	0.06	1.07	1.43	1.63	0.01
<i>Octopus tehuelchus</i>	0.04	1.07	1.07	1.20	
Beaks of squids	0.01	<0.01	0.36	<0.01	
Unidentified bivalvia	0.13	0.18	3.22	1.00	0.01
Ophiuroidea	0.45	0.67	3.22	3.62	0.03
Sipunculida	0.03	0.03	0.72	0.04	<0.01

Habitat selection

Individuals of *Zapteryx brevirostris* were found on all bottom types (Figure 8). The AIC of the full model was 1533.26. The best minimum model (Table III) retained the class variable S_b , indicating that bottom type had a significant effect on abundance of *Z. brevirostris*. *Z. brevirostris* selected significantly sand over sand-mud (t -value = -4.327 ; $P < 0.001$),

mud (t -value = -5.358 ; $P < 0.001$) and tuff bottoms (t -value = -2.328 ; $P < 0.05$). No differences were detected between sand and sand-shell rest-tuff bottom types.

The best model also retained year of capture as a significant variable affecting the abundance of *Z. brevirostris* in the study area. The coefficient for year can be interpreted as an estimate of the

Table II. Best models used to explain consumption of prey type in number (a) and in presence or absence (b) in *Zapteryx brevirostris*. TL total length in mm, *w* Akaike weight, AIC Akaike's information criteria, standard errors in brackets. The parameters for seasonal and maturity stage are given as relative to winter and mature female, respectively.

Prey	Intercept	Coefficient	AIC	<i>w</i>
a				
Polychaetes	-0.103 (0.210)	1.123 (0.262) Spring 0.803 (0.287) Summer	937.14	0.594
Lancelets	1.452 (0.279)	1.508 (0.305) Spring -1.023 (0.337) Juvenile 1.508 (0.305) Spring -0.272 (0.304) Mature male -1.452 (0.355) Summer -1.023 (0.337) Juvenile -1.452 (0.355) Summer -0.272 (0.304) Mature male	1221.2	0.648
Decapods	-3.931 (1.340)	-0.155 (0.302) Spring+0.006 (0.002) TL 1.241 (0.297) Summer+0.006 (0.002) TL	613.01	0.846
Amphipods	1.777 (0.226)	0.854 (0.302) Spring 0.883 (0.332) Summer	1523.8	0.450
Cumaceans	1.551 (0.261)	-1.286 (0.359) Spring -0.602 (0.388) Summer	893.21	0.509
Isopods	-0.449 (0.316)	-0.694 (0.352) Spring+0.510 (0.368) Juvenile -0.694 (0.352) Spring+0.918 (0.368) Mature male 1.031 (0.362) Summer+0.510 (0.368) Juvenile 1.031 (0.362) Summer+0.918 (0.368) Mature male	679.03	0.663
b				
Polychaetes	-3.304 (1.411)	1.459 (0.326) Spring+0.005 (0.002) TL 1.634 (0.371) Summer+0.005 (0.002) TL	301.13	0.742
Lancelets	-0.223 (0.287)	1.792 (0.337) Spring -0.952 (0.369) Juvenile 1.792 (0.337) Spring -0.381 (0.329) Mature male -0.487 (0.364) Summer -0.952 (0.369) Juvenile -0.487 (0.364) Summer -0.381 (0.329) Mature male	301.9	0.756
Decapods	-1.066 (0.253)	0.328 (0.329) Spring 1.846 (0.361) Summer	314.87	0.495
Amphipods	4.342 (1.625)	0.929 (0.315) Spring -0.008 (0.002) TL 0.978 (0.352) Summer -0.008 (0.002) TL	325.14	0.832
Cumaceans	0.128 (0.192)	-0.614 (0.322) Juvenile 1.070 (0.311) Mature male	337.71	0.865
Isopods	-3.666 (1.486)	-0.052 (0.333) Spring+0.005 (0.002) TL 1.157 (0.347) Summer+0.005 (0.002) TL	319.81	0.665

instantaneous population rate of change (Shepherd & Myers 2005).

Discussion

Our results show that *Zapteryx brevirostris* inhabits selectively sandy bottoms and feeds mainly on amphipods, lancelets and polychaetes, with significant variation between seasons, ontogenetic stages and size. The main prey in the diet composition of *Z. brevirostris* were amphipods, polychaetes and lancelets, with a low contribution of decapods and cumaceans, indicating benthic feeding habits, as is common among guitarfishes (Talent 1982; White et al. 2004; Marshall et al. 2007; Navia et al. 2007). This pattern is consistent with that recorded for *Z. brevirostris* off Mar del Plata, Argentina (38°S) (Castello 1971). However, it contrasts with the pattern found in other regions, where the main prey of *Z. brevirostris* are decapod crustaceans. In Ubatuba Bay, Brazil (24°S), *Z. brevirostris* preyed mainly on decapods, followed by polychaetes, amphipods, isopods and cumaceans (Soares et al.

1992), and off Rio de Janeiro, Brazil (23°S), it consumed decapods and polychaetes, followed by lancelets, mollusks and fish (Batista 1984). Our results also contrast with the diet of other species of guitarfishes. The diet of other species of Rhinobatidae are mainly composed of decapod crustaceans, while polychaetes, amphipods and lancelets are little represented or absent (Talent 1982; Harris et al. 1988; Soares et al. 1992; Kyne & Bennett 2002; White et al. 2004; Mejía-Falla et al. 2006; Marshall et al. 2007; Navia et al. 2007).

In rhinobatids, the sensory system organs (ventral lateral line and ampullae of Lorenzini) allows for the detection of small infaunal and cryptic organisms (Wueringer & Tibbetts 2008). However, some authors have suggested that the low occurrence of polychaetes or deep-burrowing prey in the diet of guitarfishes may be caused by morphological limitations that do not allow guitarfishes to dig into the bottom sediments (Talent 1982; Kyne & Bennett 2002). *Z. brevirostris* differs from other guitarfishes because 42.66% IRI belongs to prey that live buried or semiburied in the substratum, like polychaetes

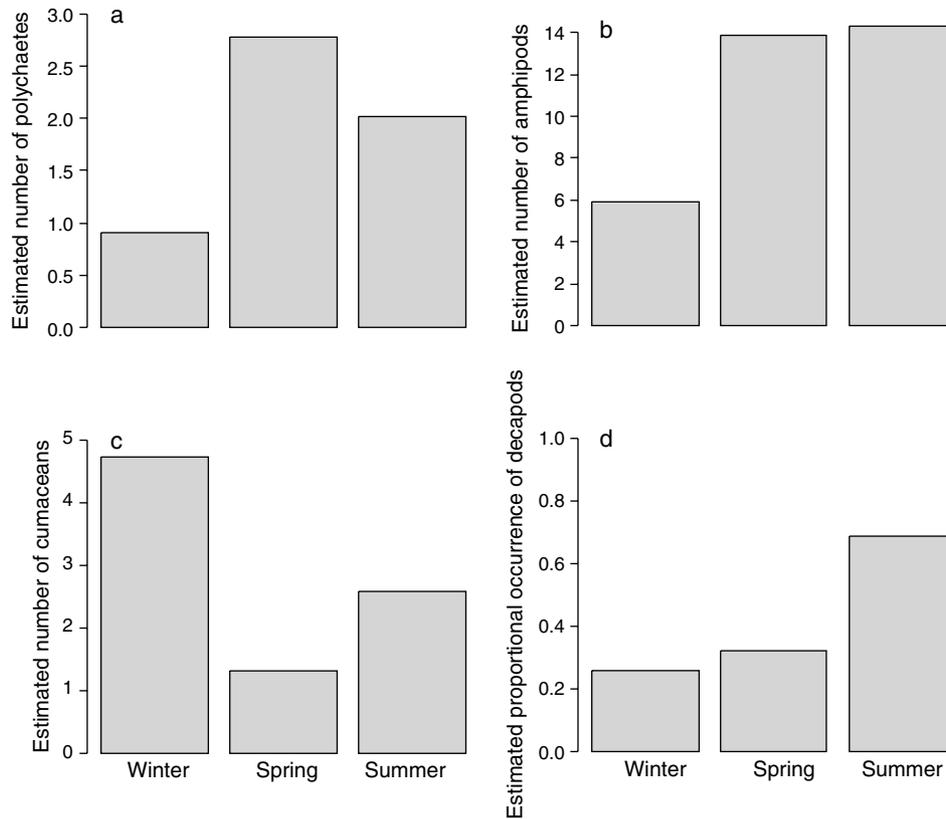


Figure 3. Shifts with season of *Zapteryx brevirostris* off Uruguay and northern Argentina estimated by generalized linear models for number of polychaetes (a), amphipods (b), and cumaceans (c), and for occurrence of decapods (d). Models in (a), (b) and (c) had a log link and a negative binomial error distribution; models in (d) had a logit link and a binomial error distribution.

(Rouse & Pleijel 2001) and lancelets (Lambert 2005). For this reason, we propose that *Z. brevirostris* has the capacity to dig into the bottom in search of prey, causing disturbances on the surface of the substratum.

The diet of different species of elasmobranchs varies from highly specialized to very generalized (Wetherbee & Cortés 2004); for *Z. brevirostris*, and if diet is compared to the abundance of prey in the environment, there is an evident tendency toward trophic specialization. In the study area, bivalve mollusks are the most abundant of all benthic invertebrates (65.9%), followed by echinoderms (18.42%), decapod crustaceans (13%), cnidarians (2%) and lastly, polychaetes (0.61%) (Giberto et al. 2004). Consequently, *Z. brevirostris* most likely does not feed in an opportunistic way, since its main prey (e.g. polychaetes and lancelets) have a very low abundance in the environment and they do not consume the most abundant prey (e.g. mollusks and echinoderms) (Giberto et al. 2004). This selective consumption pattern is also characteristic of other guitarfish, *Rhinobatos annulatus*, from the west coast of South Africa, which rejects echinoderms, mollusks and polychaetes, the organisms with the highest abundance in the environment (Harris et al. 1988).

Seasonal differences in the use of some trophic resources may be related to a seasonal peak in abundance of different prey (Muto et al. 2001). This could explain the clear seasonal pattern observed in the diet composition of *Z. brevirostris*. There is no available information on seasonal variation in abundance of invertebrate benthic species in the study area, but the higher consumption of polychaetes, amphipods, lancelets, decapods and isopods in spring and summer may suggest that *Z. brevirostris* is feeding on them when these invertebrates are more abundant or active. Seasonal variation in the dietary composition is not exclusive to *Z. brevirostris* and has been reported in skates of the same study area, i.e. *Psammobatis extenta* (Braccini & Perez 2005) and *Psammobatis bergi* (San Martín et al. 2007), which suggest that prey availability may be a factor explaining diet variation.

Body size and maturity stage have an important effect on diet composition in *Z. brevirostris*, as observed in other guitarfishes (Talent 1982; Abdel-Aziz et al. 1993; Kyne & Bennett 2002; Ismen et al. 2007). Smaller individuals consume a higher proportion of amphipods (small prey) than larger individuals. Polychaetes and decapods increase as prey for large individuals and lancelets increase

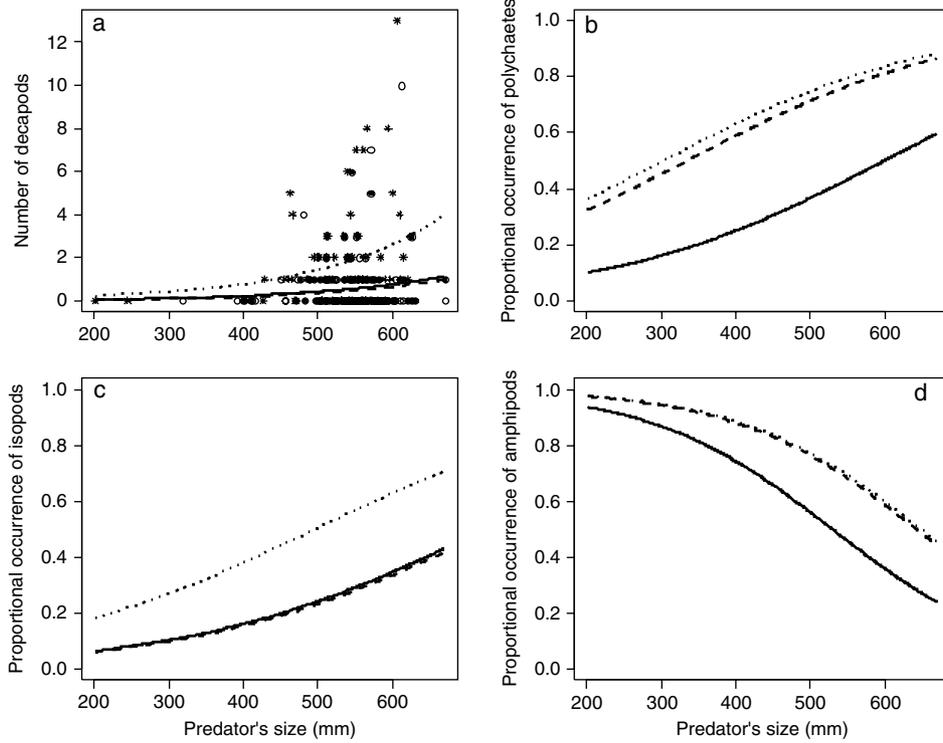


Figure 4. Shifts with season and size of *Zapteryx brevirostris* off Uruguay and northern Argentina estimated by a generalized linear model for number of decapods (a), and for occurrence of polychaetes (b), isopods (c), and amphipods (d). Winter: solid lines and open circles; spring: dashed lines and solid circles; summer: dotted lines and asterisk. The model in (a) had a log link and a negative binomial error distribution; models in (b), (c) and (d) had a logit link and a binomial error distribution.

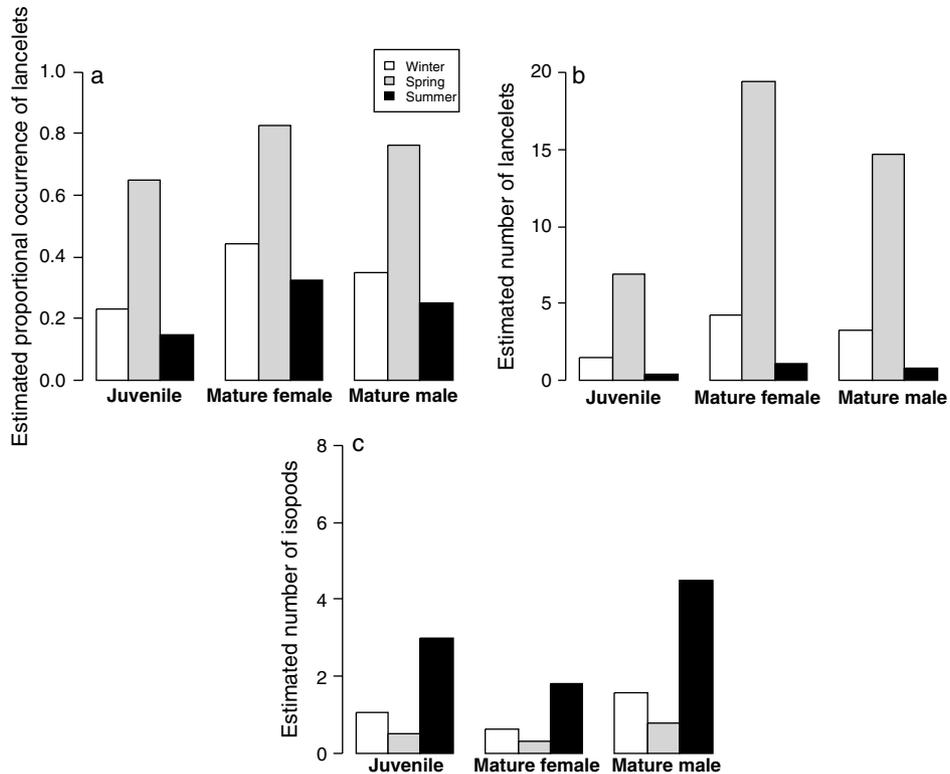


Figure 5. Shifts with season and maturity stage of *Zapteryx brevirostris* off Uruguay and northern Argentina, estimated by a generalized linear model for occurrence of lancelets (a), and for number of lancelets (b) and isopods (c). The model in (a) had a logit link and a binomial error distribution; models in (b) and (c) had a log link and a negative binomial error distribution.

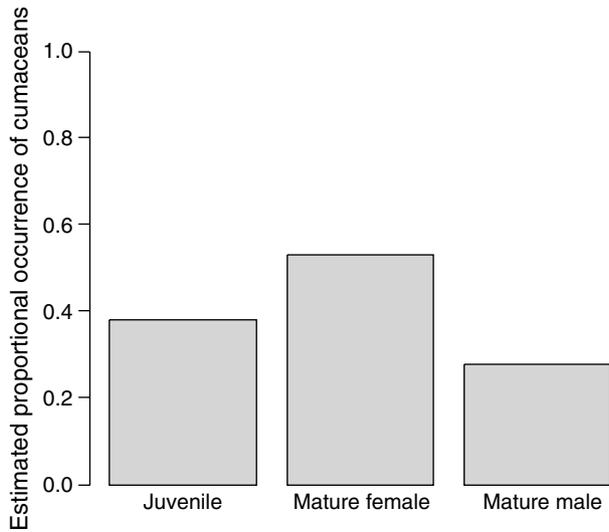


Figure 6. Shifts with maturity stage of *Zapteryx brevirostris* off Uruguay and northern Argentina, estimated by a generalized linear model with a logit link and a binomial error distribution for occurrence of cumaceans.

as prey for mature individuals. On the other hand, cumaceans are highly preyed on by mature females and isopods are heavily consumed by large individuals and mature males. In other guitarfishes, like *Rhinobatos rhinobatos* in Egyptian Mediterranean waters, teleosts, cephalopods and polychaetes were more commonly consumed by adults than by juveniles (Abdel-Aziz et al. 1993). A similar pattern was found in *Aptychotrema rostrata* from Moreton Bay, Australia, where crabs and teleosts were more important in the diet of adults than juveniles (Kyne & Bennett 2002). An explanation for these differences may be that large individuals (adults) have a greater ability to capture more active and/or larger

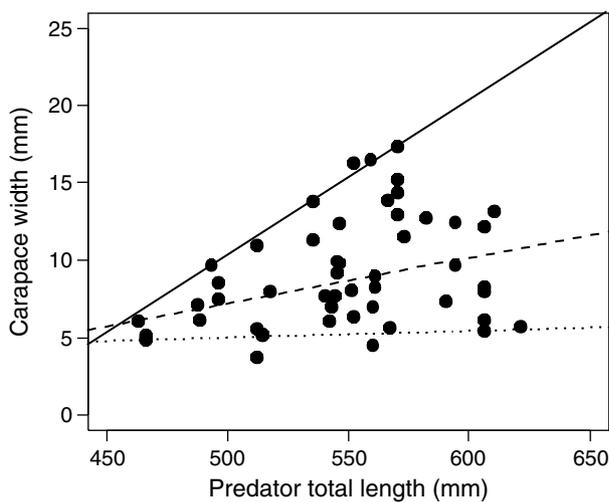


Figure 7. Quantile regressions of carapace width of brachyuran crab prey and total length of *Zapteryx brevirostris* off Uruguay and north Argentina. The dotted, dashed and solid lines are 5%, 50% and 95% quantile regressions, respectively.

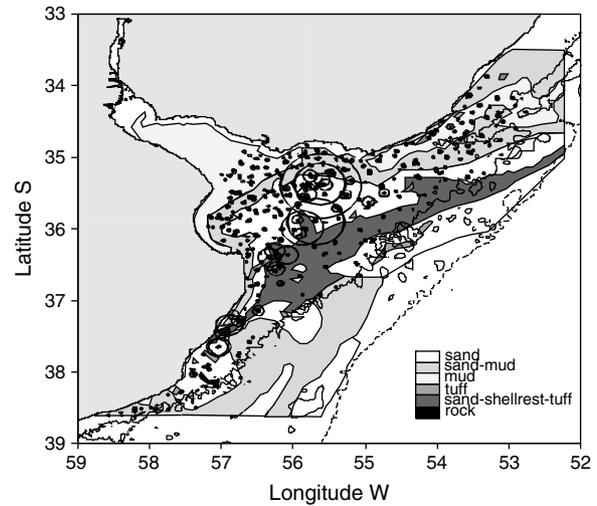


Figure 8. Map of the study area showing the abundance (in number of individuals per nautical mile square) of the shortnose guitarfish, *Zapteryx brevirostris*, off Uruguay and north Argentina. Abundance numbers range from 0 to 11,066.8 individuals per nautical mile square, from the smallest to the largest circle, respectively. The 50- and 200-m isobaths are shown as solid and dashed lines, respectively.

prey (Abdel-Aziz et al. 1993; Kyne & Bennett 2002). In *Z. brevirostris*, diet shifts with increasing size may be caused by an increase in physical strength in larger individuals, which allows them to hunt for larger prey (i.e. decapods) or prey buried in the bottom (i.e. polychaetes and lancelets). The reasons for diet shifts with maturity stage are not clear, but they could be the result of a possible shift in habitat use with maturity. Studies of shifts in habitat use with maturity stage will be helpful for testing this hypothesis.

As the size of *Z. brevirostris* increases, the size of consumed crabs does too. However, large individuals do not abandon the consumption of small prey, a pattern observed in other elasmobranchs (Braccini et al. 2005; Lucifora et al. 2006, 2009). This pattern

Table III. The best minimum model (AIC = 1530.3) used to explain habitat selection of *Zapteryx brevirostris*. S_i , bottom types; Y_i , year; Lo_i , longitude; La_i , latitude; D_i , Julian day; De_i^2 , depth. Standard errors in brackets.

Variables	Class variable	Coefficient
Intercept		310.324 (88.65)
S_i	Mud	-1.934 (0.435)
	Sand-mud	-1.378 (0.348)
	Tuff	-2.044 (0.941)
	Sand-gravel-tuff	0.091 (0.522)
Y_i		-0.135 (0.0043)
Lo_i		1.731 (0.281)
La_i		-1.771 (0.348)
$senD_i$		-1.095 (0.548)
$cosD_i$		-1.264 (0.446)
De_i^2		-0.0024 (0.00047)

could be related to the relative size of the mouth of small individuals, which is comparatively smaller than the mouth of larger individuals (Juanes et al. 2002). The selection of small prey by small individuals may be result of morphological limitations (Scharf et al. 2000). The trend of larger prey to be eaten by larger predators could be partly related to the type and strength of the exoskeleton in crustaceans (Smale & Compagno 1997). Small individuals of *Z. brevirostris* may be unable to both handle and crush the exoskeleton of large crabs.

Bottom type has a significant influence on the distribution of *Z. brevirostris*, selecting sandy bottoms over other bottom types. This selection may be partly due to the distribution of their prey. The offshore region of the study area, formed mainly by sandy bottoms, is characterized by a higher diversity of benthic invertebrates with a greater abundance of polychaetes and crustaceans than the inshore region, where the substrate consists mainly of muddy bottoms and the benthic fauna is dominated by bivalve mollusks (Giberto et al. 2004). Sandy bottoms are the preferred habitat of lancelets (Lambert 2005). In this way, it is possible that the distribution and abundance of its main prey (polychaetes and lancelets) influence the distribution of *Z. brevirostris*. Alternatively, the diet of *Z. brevirostris* can be shaped by the selection of this species for sandy bottoms. If *Z. brevirostris* selects sandy bottoms, regardless of the distribution of its prey (for example, if sandy bottoms are a better option to hide from predators), then diet composition will be determined by the selected bottom type. If this were the case, it would be expected that the diet of *Z. brevirostris* would vary between regions according to differences in prey availability, while bottom type remained less variable. Further research is needed to know which is the case, but thus far it has been shown that the diet of *Z. brevirostris* does vary between regions (Batista 1984; Soares et al. 1992), supporting selection by bottom type.

Coastal areas of the Río de la Plata estuary and adjacent marine areas are exposed to a high intensity of bottom trawling and this activity alters the physical structure of the habitat, directly affecting both the diversity and abundance of benthic communities and generating potential indirect effects on fish communities (Brazeiro et al. 2003). In this study, we showed that *Z. brevirostris* selectively uses sandy bottoms, which constitute one of the most heavily trawled bottom types in the area (Brazeiro et al. 2003). In addition to exposing *Z. brevirostris* to increased fishing mortality, the selection for sandy bottoms may increase the vulnerability of this species by the degradation and the loss of this habitat. Even though *Z. brevirostris* is not harvested commercially, a

significant impact by trawl fisheries on its population appears to exist, with estimated declines in the biomass of *Z. brevirostris* of 86% between 1994 and 1999 in this area (Vooren et al. 2006). Our results – showing that some areas (i.e. sandy bottoms) are especially relevant for the survival of *Z. brevirostris* – highlight the importance of detailed ecological studies for the design of conservation and management plans of species affected by fisheries.

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