

Trophic ecology of yellownose skate *Zearaja chilensis*, a top predator in the south-western Atlantic Ocean

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The diet and trophic level (T_L) of the yellownose skate *Zearaja chilensis* in the south-western Atlantic Ocean (35° – 54° S), and how these varied in relation to body size, sex, maturity stage, depth and region were determined by analysis of stomach contents. From 776 specimens analysed, 671 (86.5%) ranging from 180 to 1190 mm total length (L_T) had prey in their stomachs. The diet was dominated by fishes, mainly the notothenioid *Patagonotothen ramsayi* and the Argentine hake *Merluccius hubbsi*. The consumption of fishes and crabs increased with increasing predator size, and these preys were more important in the north than in the south. Isopods and other crustaceans were consumed more in the south and their consumption decreased as the size of *Z. chilensis* increased. The T_L of *Z. chilensis* increased with L_T from 4.29 to 4.59 (mean 4.53), confirming their ecological role as a top predator. The small and large size classes exhibited a low diet overlap and the highest spatial segregation, whereas medium and large specimens had higher co-occurrence and dietary overlap indices. A clear distinction in tooth shape was noted between sexes in adult specimens, with males having longer cusps. This sexual heterodonty may be related to reproductive behaviour, increasing the grasping ability of males during courtship, because there were no differences in diet between the sexes.

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Key words: dentition; diet; elasmobranchs; trophic level.

INTRODUCTION

The genus *Zearaja* Whitley 1939 consists of at least three valid species of hard-nose skates within Rajidae (Last & Gledhill, 2007). The members of the genus *Zearaja* have been consistently classified within *Dipturus* Rafinesque 1810 because of their superficial resemblance (Nelson, 2006; Last & Gledhill, 2007). The yellownose skate *Zearaja chilensis* (Guichenot 1848), also formerly assigned to the genus *Dipturus*, occurs in the south-west Atlantic Ocean (34° $35'$ – 55° S) and the south-east Pacific Ocean off Chile (30° $15'$ – 55° $13'$ S) (Cousseau & Perrota, 2004; Last & Gledhill, 2007). It is one of

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the most abundant deep-sea skates in the south-west Atlantic Ocean and also one of the most commercially valuable (Massa *et al.*, 2004; Patrucco *et al.*, 2011). Although *Z. chilensis* is subject to targeted longline fishing in this region (Colonello *et al.*, 2002), it is captured mainly as by-catch during groundfish trawling operations (Buratti, 2004; García de la Rosa *et al.*, 2004; Massa *et al.*, 2004).

Catches of skate species in Argentina have increased rapidly, from <1000 t during 1993 to 15 000 t in 2001 and 17 465 t in 2003 (Massa *et al.*, 2004). In 2014, 16 338 t of skates were landed (MINAGRI, 2015a). Because of their similar morphology, most skate landings were listed as rajid, until 2008 when the official statistics began to separate *Z. chilensis* from total landings (Sánchez *et al.*, 2012). In 2009 and 2010, 1331 and 1459 t of *Z. chilensis* were landed in Argentina (MINAGRI, 2015b). In 2013, the elasmobranch catch limit was set at 40% of the total catch (Consejo Federal Pesquero, 2013), which reduced *Z. chilensis* landings to 432 t in 2014 (MINAGRI, 2015a). In spite of the improvement in the quality of landings data, specific catch values were underestimated because of the confusion of common names and the inaccuracy of species identification in landings (Massa *et al.*, 2011). *Zearaja chilensis* is listed as a vulnerable species by the International Union for Conservation of Nature (Kyne *et al.*, 2007). The intrinsic characteristics of this species such as slow growth, long life (Licandeo *et al.*, 2006; Zavatteri & Hozbor, 2010) and relatively large and delayed maturity (Oddone *et al.*, 2005; Paesch & Oddone, 2008; Quiroz *et al.*, 2009; Colonello & Cortés, 2014) make it extremely vulnerable to exploitation. In addition, the decreasing stock abundance of large skates and some evidence of local extinctions (Brander, 1981; Casey & Myers, 1998; Dulvy *et al.*, 2000) have led to increased ecological attention being paid to the larger species of skates that are most vulnerable to exploitation (Dulvy *et al.*, 2000, 2014).

Because of their relatively high abundance, skates may play an important role in demersal food webs and benthic communities (Ebert & Bizzarro, 2007). The first step to determine how they can influence the dynamics of the community is to know the diet composition and trophic trends (Heithaus *et al.*, 2010). The diet of *Z. chilensis*, studied in Argentina from 1996 to 1998 from 41° to 46° S from commercial fishing catches, was composed mainly of fishes (Lucifora *et al.*, 2000; Koen Alonso *et al.*, 2001). This species is, however, widely distributed off South America and would benefit from a dietary analysis across its entire range of distribution. Top predators in marine ecosystems can play important roles in structuring communities of both fishes and invertebrates at lower trophic levels (T_L) (Heithaus *et al.*, 2010). The T_L of *Z. chilensis* has not been examined, so the effect that catches of this species may have on the community is unknown. Consequently, the diet of *Z. chilensis* was quantified here through stomach content analysis, based on substantial samples over space and time. The goals of this work were to (1) determine the diet composition of the *Z. chilensis* in the south-western Atlantic Ocean, (2) assess the effects of body size, sex, maturity stage, depth and region on diet, (3) determine the T_L and (4) examine the dentition by sex and maturity stage.

MATERIALS AND METHODS

SAMPLE COLLECTION

Zearaja chilensis specimens were collected during five bottom-trawl research cruises conducted by the National Institute of Fisheries Research and Development (INIDEP) during October to November 2011, March to May and November 2012, and September to October

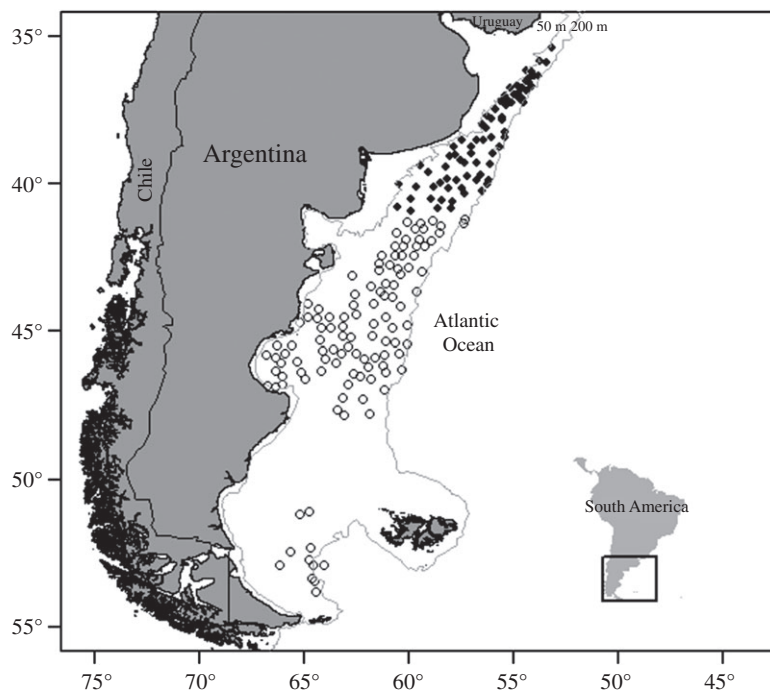


FIG. 1. Map of the study area showing sampling sites in each region (●, north region; ○, south region) for *Zearaja chilensis*.

2013. The study area comprised much of the Argentinean continental shelf and slope, between 35° and 54° S and from 40 to 293 m depth (Fig. 1). A stratified random sampling scheme (stratified on latitude and depth) was used to assess abundances of Argentine hake *Merluccius hubbsi* Marini 1933, southern blue whiting *Micromesistius australis* Norman 1937, long tail hake *Macruronus magellanicus* Lönnberg 1907 and Argentine squid *Illex argentinus*. Fishing was conducted during daylight hours (0700–1900 hours), at 5.6–7.4 km h⁻¹ (three to four knots) for 30 min at each sampling site, using an Engel bottom trawl (200 mm mesh in the wings, 103 mm in the codend, 4 m vertical opening and 15 m horizontal aperture). Specimens of *Z. chilensis* were sexed and the total length (L_T) was measured to the nearest mm. Maturity stage was recorded according to Walker (2005) and Colonello *et al.* (2011). Males were classified as juvenile or adult based on the development of the claspers and the testes, whereas females were classified based on the development of the oviducal gland, uteri and ovary. To describe dietary variation related to body size, specimens were sorted into small ($L_T \leq 450$ mm), medium ($451 \leq L_T \leq 699$ mm) and large ($L_T \geq 700$ mm) size classes. Stomachs were excised, labelled in plastic bags and frozen.

DIET COMPOSITION ANALYSIS

The stomachs of *Z. chilensis* were thawed and prey items were identified to the lowest possible taxonomic level using taxonomic keys (Bastida & Torti, 1973; Hobson & Banse, 1981; Menni *et al.*, 1984) and field guides (Boschi *et al.*, 1992; Cousseau & Perrota, 2004). Prey items were counted, weighed to the nearest 0.01 g and grouped into seven prey groups: fishes, crabs, isopods, other crustaceans, cephalopods, polychaetes and other invertebrates.

To assess whether the number of stomachs analysed was sufficient to accurately describe the diet of each group of specimens of *Z. chilensis* considered in the dietary analysis, the stomachs sampled were randomized 100 times, and the accumulation prey curve was constructed as a

function of stomach number. These cumulative prey curves were plotted with their 95% c.i. (Ferry & Cailliet, 1996; Cortés, 1997).

The diet composition was quantified by calculating for each prey and prey group, the percentage frequency of occurrence (%F, the total number of stomachs in which a given prey was found expressed as percentage of the total number of stomachs with food), the percentage by number (%N, the total number of a given prey as percentage of the total number of prey found), percentage by mass (%M, the mass of a given prey as percentage of the total mass of prey found) and index of relative importance: $I_{RI} = \%F \times (\%N + \%M)$ (Pinkas *et al.*, 1971), expressed as a percentage (% I_{RI} ; Cortés, 1997).

The multiple hypotheses that the diet of *Z. chilensis* changed with changes in body size, sex, maturity stage, depth and region were evaluated using generalized linear models (GLM) and information theory selection criteria (Venables & Ripley, 2002). The numbers of prey items from the most important prey groups (fishes, crabs, isopods and other crustaceans) were used as dependent variables. This kind of numerical data has many zeros resulting in variances much greater than the means, hence a negative binomial error distribution and a log link were assumed to fit GLMs (Crawley, 2005). The independent variables included in the GLMs were: L_T (mm), sex, maturity stage (juvenile, adults), depth and region (north–south). To test for a curvilinear relationship between L_T and the consumption of any prey, models including a quadratic term of L_T (L_T^2) as an independent variable were also fitted. The models were constructed with all possible combinations of two independent variables. A theoretical model without any independent variables was also constructed to test the hypothesis that none of the chosen independent variables influenced the consumption of any prey groups (Lucifora *et al.*, 2009). The Akaike's information criterion (AIC) and Akaike's weight (w) were used to compare and rank the models, and to estimate which of them best fitted the data (Franklin *et al.*, 2001; Johnson & Omland, 2004). The model with the lowest AIC was selected and plotted (Franklin *et al.*, 2001; Johnson & Omland, 2004). All analyses were performed using R 3.1.2 (www.R-project.org).

The T_L was calculated for all *Z. chilensis* and for each size class separately based on % I_{RI} from the full array of prey items in the diet following the method proposed by Cortés (1999) as: $T_L = 1 + \sum_{i=1}^n (p_i T_{Li})$, where T_L is the trophic level of *Z. chilensis*, T_{Li} is the trophic level of each prey item i and p_i is the proportion of each prey item i (using % I_{RI}) in the diet and n is the total number of prey items. The samples were bootstrapped a hundred times with replacement in order to find the 95% c.i. for the mean of T_L . The T_L of each prey item was obtained from the literature (Ebert & Bizzarro, 2007; Vögler *et al.*, 2009; Ainley & Pauly, 2014; Froese & Pauly, 2015; Sea Around Us, 2015).

Habitat and resource partitioning among the size classes of *Z. chilensis* were investigated with the Schöener index for niche overlap (Schöener, 1970) and the percentage of co-occurrence for each size class (Lopez-Lopez *et al.*, 2011). The Schöener index was calculated with the following formula, $S = 1 - 0.5 \times \sum (|pX_i - pY_i|)$, where pX_i and pY_i represent the proportion of each prey item i (using % I_{RI}) of the diet of the size classes X and Y, respectively (Schöener, 1970). The percentage of co-occurrence was calculated as the number of sampling sites in which the size classes X and Y were captured simultaneously divided by the total number of sampling sites in which any of them were found.

Finally, the jaws of juvenile and adult specimens from both sexes were dissected, cleaned and dried to describe the dentition. Differences in tooth arrangement and external tooth morphology among sexes and maturity stages were determined and described. Digital photographs were taken.

RESULTS

A total of 776 *Z. chilensis* stomachs were analysed, with 671 (86.5%) fish ranging from 180 to 1190 mm L_T (Fig. 2) containing prey. The size distributions were significantly different between regions [Kolmogorov–Smirnov (K–S) test: $D = 0.19$, $P < 0.001$] (Fig. 2). Male and female size distributions were not different in the northern (K–S test: $D = 0.15$, $P > 0.01$) or southern (K–S test: $D = 0.10$, $P > 0.01$) regions (Fig. 2). Furthermore, male and female size distributions were different

between regions (female K–S test, $D=0.19$, $P<0.001$; male K–S test: $D=0.21$, $P<0.001$) (Fig. 2), with larger male and female specimens in the northern region (male t -test, $t=3.71$, $P<0.001$; female t -test, $t=3.21$, $P<0.001$). The sample sizes were sufficient to describe diets in all cases considered and to make statistical analyses because the cumulative prey curves reached an asymptote (Fig. 3).

Fishes were the main prey of *Z. chilensis* (Table I). The notothenioid *Patagonotothen ramsayi* (Regan 1913) and *M. hubbsi* were the most common identified fish species (Table I). Secondary prey groups in decreasing order of importance were crabs, other crustaceans, isopods, cephalopods, other invertebrates and polychaetes. Small *Z. chilensis* fed on fishes followed by isopods, mainly *Acanthoserolis schythei* (Table I). Medium and large specimens also fed primarily upon fishes, but the former fed mainly on *P. ramsayi*, whereas the large specimens preferred *M. hubbsi* (Table I). Cannibalism and predation on other skate species were observed in medium and large size classes (Table I).

The ontogenetic changes in diet, along with regional variations, were also reflected by the GLMs. The consumption of fishes and crabs increased with the L_T of *Z. chilensis*, and both prey groups were more important in the north than in the south (Fig. 4 and Table II). Isopods and other crustaceans were also consumed more in the south, but their consumption decreased with L_T (Fig. 4 and Table II).

The T_L of all *Z. chilensis* was 4.53 (95% c.i.: 4.52–4.53). The T_L increased progressively with L_T from 4.29 (4.27–4.32) to 4.42 (4.41–4.43) and 4.59 (4.58–4.60) in small, medium and large size classes of *Z. chilensis*, respectively (Fig. 5).

Small and large size classes of *Z. chilensis* showed a low diet overlap and the highest habitat partitioning (Table III). The medium size class of *Z. chilensis* showed a high habitat overlap with both small and large specimens (Table III), but the degree of dietary overlap between medium and small was low in relation to the highest dietary overlap found between medium and large specimens (Table III).

There were differences in the dentition of male and female adults (Fig. 6). A clear distinction in tooth shape was noted between adult females and males; adult male teeth developed distinctly longer cusps (Fig. 6). In contrast, juvenile teeth showed no variation in shape between sexes (Fig. 6).

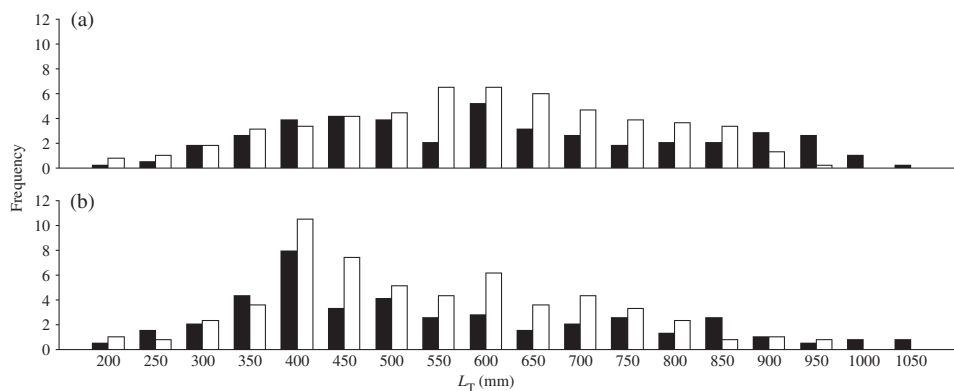


FIG. 2. Total length (L_T) frequency distributions of male (□) and female (■) *Zearaja chilensis* from (a) north region and (b) south region (see Fig. 1).

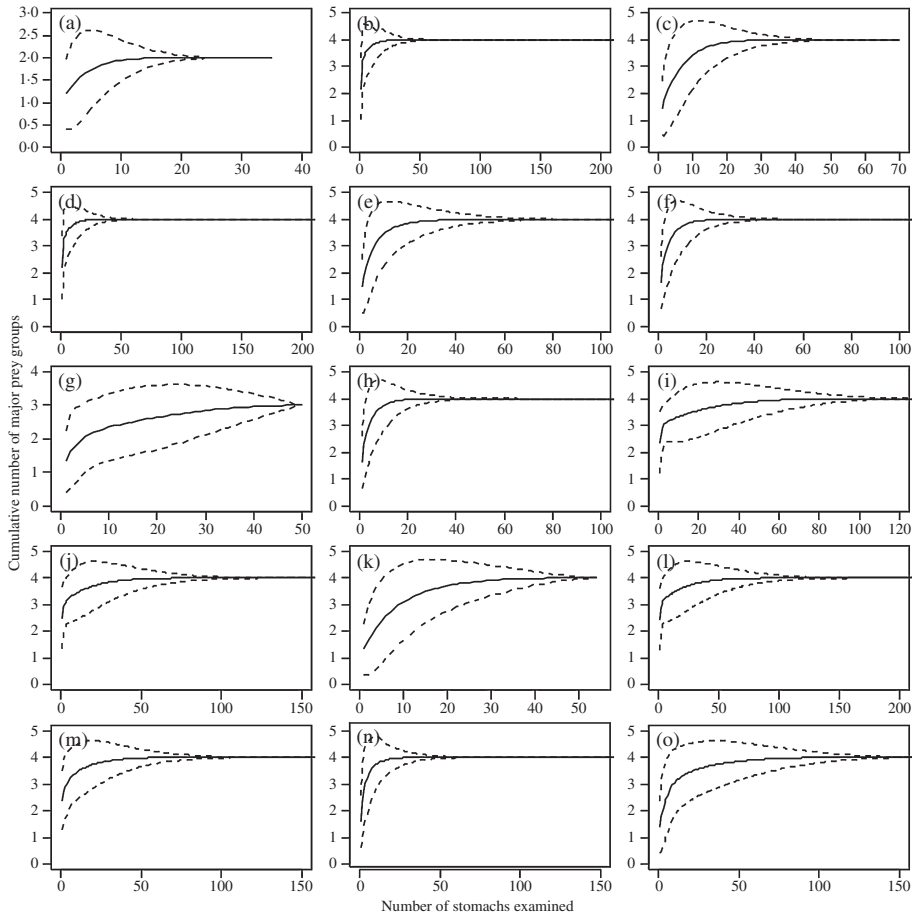


FIG. 3. Cumulative prey curves as a function of sample size for each group of specimens of *Zearaja chilensis* considered in the dietary analysis: (a) adult females $n = 35$, (b) juvenile females $n = 252$, (c) adult males $n = 70$, (d) juvenile males $n = 314$, (e) female north $n = 150$, (f) male north $n = 188$, (g) adult north $n = 51$, (h) juvenile north $n = 287$, (i) female south $n = 137$, (j) male south $n = 196$, (k) adult south $n = 54$, (l) juvenile south $n = 279$, (m) small size class $n = 182$, (n) medium size class $n = 289$ and (o) large size class $n = 200$. Mean (—) and $\pm 95\%$ C.I. (---) are plotted.

DISCUSSION

Zearaja chilensis in the south-western Atlantic Ocean is an ichthyophagous species that feeds on demersal fishes, mainly *P. ramsayi* and *M. hubbsi*. Small *Z. chilensis* also fed on benthic prey, primarily the same fish species as the medium and large groups, but also with a substantial component of *A. schythei*. This fish-based diet is similar to diets reported for other similar-sized hard-nose species from the genus *Dipturus* off Tasmania (Treloar *et al.*, 2007), New Zealand (Forman & Dunn, 2012) and South Africa (Ebert *et al.*, 1991). In contrast, the diets of smaller hard-nose skates such as argus skate *Dipturus polymmata* (Ogilby 1910) (Kyne *et al.*, 2008), white-spotted skate *Dipturus cerva* (Whitley 1939) and thornback skate *Dipturus lemprieri* (Richardson 1845) (Treloar *et al.*, 2007), and even other skates similar in size to *Z.*

TABLE 1. Diet composition of *Zearaja chilensis* from the Argentinean continental shelf. The diet was quantified for all stomachs sampled (general) and for the three size classes considered (small, medium and large), and expressed as percentage of frequency of occurrence (%F), percentage of wet mass (%M), percentage number (%N) and percentage index of relative importance (%IRI)

Prey items	General				Small size class				Medium size class				Large size class			
	%F	%W	%N	%IRI	%F	%W	%N	%IRI	%F	%W	%N	%IRI	%F	%W	%N	%IRI
All fishes combined	67.36	87.98	29.71	87.98	29.12	51.92	4.34	51.92	78.89	89.07	53.47	89.07	85.50	90.53	75.06	90.53
Scyliorhinidae	0.30	0.08	0.09	0.08					0.35	0.19	0.16	0.19	0.50	0.02	0.26	0.02
Narcinidae	0.15	1.26	0.04	1.26									0.50	2.06	0.26	2.06
Rajidae	0.15	0.82	0.04	0.82					1.73	0.17	0.81	0.17	0.50	1.34	0.26	1.34
Rajidae unidentified	2.24	1.26	0.66	1.26									5.00	1.96	2.60	1.96
<i>Bathyraja</i> spp.	0.15	0.09	0.04	0.09									0.50	0.14	0.26	0.14
Congridae	0.30	1.65	0.09	1.65									1.00	2.68	0.52	2.68
<i>Bassanago albescens</i>	8.20	25.19	3.48	25.19	1.65	23.68	0.24	23.68	8.30	15.74	4.68	15.74	14.00	30.44	12.21	30.44
<i>Macruronus magellanicus</i>	0.15	0.54	0.04	0.54									0.50	0.87	0.26	0.87
<i>Raneya brasiliensis</i>	1.64	1.95	0.53	1.95					1.73	2.96	0.97	2.96	3.00	1.56	1.56	1.56
Ophidiidae	0.15	0.28	0.04	0.28									0.50	0.46	0.26	0.46
<i>Gonypterus blacodes</i>	0.15	0.05	0.04	0.05									0.50	0.08	0.26	0.08
Congiopodidae	0.30	0.12	0.09	0.12	0.55	1.21	0.08	1.21	0.35	0.17	0.16	0.17	0.50	0.02	0.26	0.02
<i>Agonopsis chilensis</i>	0.15	0.01	0.04	0.01									1.00	3.46	0.52	3.46
<i>Trachurus lathami</i>	0.30	2.12	0.09	2.12									1.50	0.41	0.78	0.41
Cheilodactylidae	0.60	0.40	0.18	0.40					0.35	0.46	0.16	0.46	1.00	3.37	0.78	3.37
<i>Bucoetes fimbriatus</i>	0.30	2.07	0.13	2.07									0.50	0.66	0.26	0.66
<i>Cottoperca gobio</i>	0.15	0.19	0.04	0.19									0.50	0.02	0.26	0.02
<i>Dissostichus eleginoides</i>	16.54	31.43	8.76	31.43	6.59	12.92	1.26	12.92	21.45	43.97	17.29	43.97	18.50	26.23	19.74	26.23
<i>Patagonotothen ramsayi</i>	0.30	0.68	0.09	0.68					0.35	0.02	0.16	0.02	0.50	1.11	0.26	1.11
<i>Trichiurus lepturus</i>	0.30	0.82	0.09	0.82					0.35	1.24	0.16	1.24	0.50	0.66	0.26	0.66
<i>Xystreutys rasile</i>	0.15	0.01	0.04	0.01									0.50	0.02	0.26	0.02
Paralichthyidae unidentified	41.43	16.97	15.05	16.97	19.78	14.22	2.76	14.22	51.90	23.58	28.76	23.58	46.00	13.62	33.51	13.62
Actinopterygii unidentified	11.48	3.68	4.31	3.68	4.40	2.05	0.79	2.05	11.07	4.07	6.30	4.07	18.50	3.60	12.73	3.60
All crab species combined	5.37	2.12	2.16	2.12	0.55	0.10	0.24	0.10	4.84	2.29	3.07	2.29	10.50	2.20	7.01	2.20
Ateleocyidae	0.15	0.02	0.04	0.02					0.35	0.07	0.16	0.07				
<i>Platyanthus crenulatus</i>	5.96	1.40	1.89	1.40	3.85	1.92	0.47	1.92	5.88	1.67	2.91	1.67	8.00	1.21	4.94	1.21
<i>Libinia clava granaria</i>																

TABLE I. Continued

Prey items	General				Small size class				Medium size class				Large size class			
	%F	%W	%N	%IRI	%F	%W	%N	%IRI	%F	%W	%N	%IRI	%F	%W	%N	%IRI
Majidae unidentified	0.75	0.13	0.22	0.13	0.55	0.03	0.08	0.03	0.35	0.05	0.16	0.05	1.50	0.19	0.78	0.19
All other crustaceans	25.63	2.79	34.02	2.79	50.55	16.33	51.89	16.33	20.76	2.76	13.89	2.76	10.00	1.63	7.53	1.63
Galatheidae	5.22	0.68	2.99	0.68	7.14	3.56	2.60	3.56	5.88	0.89	3.55	0.89	2.50	0.32	3.38	0.32
<i>Munida subrugosa</i>	1.79	0.49	0.75	0.49	3.30	3.33	0.71	3.33	1.38	0.37	0.81	0.37	1.00	0.32	0.78	0.32
<i>Pagurus gaudichaudii</i>	0.15	0.19	0.04	0.19					0.35	0.57	0.16	0.57				
Nephropidae	0.15	0.20	0.04	0.20									0.50	0.32	0.26	0.32
<i>Thymops birsteini</i>	0.15	0.20	0.04	0.20									0.50	0.32	0.26	0.32
Squillidae	1.34	0.30	0.00	0.30	3.30	1.74	0.00	1.74	0.69	0.16	<0.01	0.16				
<i>Pterygosquilla armata</i>	1.34	0.30	0.00	0.30	3.30	1.74	0.00	1.74	0.69	0.16	<0.01	0.16				
Euphausiidae	5.81	0.10	14.57	0.10	18.13	1.77	24.29	1.77	2.08	0.01	3.72	0.01				
<i>Euphausia</i> spp.	5.81	0.10	14.57	0.10	18.13	1.77	24.29	1.77	2.08	0.01	3.72	0.01				
Hyperiidae	3.87	0.06	11.80	0.06	13.74	1.09	21.06	1.09	0.35	<0.01	0.16	<0.01				
<i>Themisto gaudichaudii</i>	3.87	0.06	11.80	0.06	13.74	1.09	21.06	1.09	0.35	<0.01	0.16	<0.01				
Sergestidae	0.15	<0.01	0.04	<0.01	0.55	0.06	0.08	0.06								
<i>Peisos petrunkevitchii</i>	0.15	<0.01	0.04	<0.01	0.55	0.06	0.08	0.06								
Solenoceridae	1.64	0.38	0.57	0.38	2.75	0.61	0.47	0.61	0.69	0.35	0.48	0.35	2.00	0.37	1.04	0.37
<i>Pleoticus muelleri</i>	1.64	0.38	0.57	0.38	2.75	0.61	0.47	0.61	0.69	0.35	0.48	0.35	2.00	0.37	1.04	0.37
Pandalidae	1.79	0.05	0.70	0.05					2.42	0.07	1.62	0.07	2.50	0.04	1.56	0.04
<i>Austropandalus grayi</i>	1.79	0.05	0.70	0.05					2.42	0.07	1.62	0.07	2.50	0.04	1.56	0.04
<i>Pandalopsis ampla</i>	0.15	0.01	0.04	0.01	0.55	0.16	0.08	0.16								
<i>Pandalopsis ampla</i>	0.15	0.01	0.04	0.01	0.55	0.16	0.08	0.16								
Caridea unidentified	0.30	<0.01	0.09	<0.01	0.55	0.01	0.08	0.01	0.35	<0.01	0.16	<0.01				
Caridea unidentified	0.30	<0.01	0.09	<0.01	0.55	0.01	0.08	0.01	0.35	<0.01	0.16	<0.01				
Crustaceans unidentified	7.00	0.34	2.38	0.34	13.74	4.03	2.52	4.03	6.92	0.32	3.23	0.32	1.00	0.02	0.52	0.02
Crustaceans unidentified	7.00	0.34	2.38	0.34	13.74	4.03	2.52	4.03	6.92	0.32	3.23	0.32	1.00	0.02	0.52	0.02
All isopods combined	19.67	2.15	29.71	2.15	50.00	29.15	41.80	29.15	12.11	1.73	22.46	1.73	3.00	0.03	1.56	0.03
<i>Acanthoserolis</i> spp.	3.43	0.11	1.80	0.11	7.69	0.95	1.89	0.95	2.42	0.15	2.42	0.15	1.00	0.01	0.52	0.01
<i>Acanthoserolis schyithi</i>	3.43	0.11	1.80	0.11	7.69	0.95	1.89	0.95	2.42	0.15	2.42	0.15	1.00	0.01	0.52	0.01
<i>Cirrolana</i> spp.	15.65	1.96	26.80	1.96	42.31	27.20	38.56	27.20	8.65	1.51	18.90	1.51	1.50	0.01	0.78	0.01
<i>Cirrolana</i> spp.	15.65	1.96	26.80	1.96	42.31	27.20	38.56	27.20	8.65	1.51	18.90	1.51	1.50	0.01	0.78	0.01
All cephalopods combined	2.83	0.08	1.10	0.08	6.59	1.05	1.34	1.05	2.08	0.06	1.13	0.06	0.50	0.01	0.26	0.01
<i>Illex argentinus</i>	2.83	0.08	1.10	0.08	6.59	1.05	1.34	1.05	2.08	0.06	1.13	0.06	0.50	0.01	0.26	0.01
Ommastrephidae	0.89	1.56	0.31	1.56	2.20	0.26	0.32	0.26	2.77	0.65	1.45	0.65	2.50	2.83	1.30	2.83
<i>Illex argentinus</i>	0.89	1.56	0.31	1.56	2.20	0.26	0.32	0.26	2.77	0.65	1.45	0.65	2.50	2.83	1.30	2.83
Loliginidae	0.75	0.36	0.22	0.36	1.10	0.14	0.16	0.14	0.69	0.33	0.32	0.33	2.00	2.43	1.04	2.43
<i>Loligo</i> spp.	0.75	0.36	0.22	0.36	1.10	0.14	0.16	0.14	0.69	0.33	0.32	0.33	2.00	2.43	1.04	2.43
Octopodidae	0.15	<0.01	0.04	<0.01	0.55	0.01	0.08	0.01	0.35	>0.01	0.16	>0.01				
<i>Octopus</i> spp.	0.15	<0.01	0.04	<0.01	0.55	0.01	0.08	0.01	0.35	>0.01	0.16	>0.01				
<i>Semirostris</i> spp.	0.15	<0.01	0.04	<0.01	0.55	0.01	0.08	0.01	0.35	>0.01	0.16	>0.01				
Cephalopoda unidentified	0.60	0.04	0.18	0.04	4.40	0.20	0.79	0.20	3.11	0.04	2.10	0.04	0.50	0.10	0.52	0.10
Cephalopoda unidentified	0.60	0.04	0.18	0.04	4.40	0.20	0.79	0.20	3.11	0.04	2.10	0.04	0.50	0.10	0.52	0.10
All ptychaetes combined	2.68	0.08	1.10	0.08												

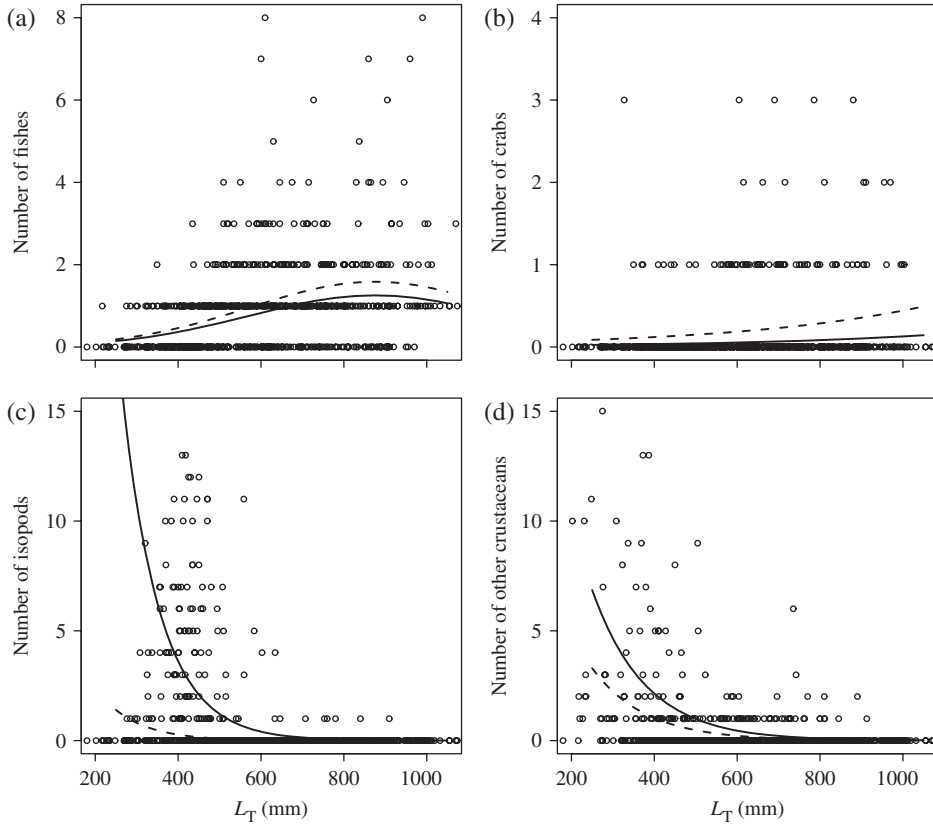


FIG. 4. Generalized linear models (GLM) fitted for the number (○) of the most important prey groups of *Zeoraja chilensis*: (a) fishes, (b) crabs, (c) isopods and (d) other crustaceans, as a function of total length (L_T) of the predator and region: south (—) and north (---). The models had a log link and a negative binomial error distribution.

chilensis such as longnosed skate *Dipturus oxyrinchus* (L. 1758) in the Mediterranean Sea (Mulas *et al.*, 2015), are dominated by crustaceans. Given the high importance of fish prey, the ontogenetic shifts and the high T_L observed here, *Z. chilensis* may play an important role in the demersal and benthic community of the south-western Atlantic Ocean.

In this region, two previous works on the feeding habits of *Z. chilensis* examined samples from commercial fishing vessels targeting Patagonian scallop *Zygochlamys patagonica* (Lucifora *et al.*, 2000) and *M. hubbsi* (Koen Alonso *et al.*, 2001). The authors reported some pelagic fishes and the Argentine squid *I. argentinus*, generally with cut marks, indicating that they were discarded from fishing vessels and scavenged by *Z. chilensis* (Lucifora *et al.*, 2000). The New Zealand smooth skate *Dipturus innominatus* (Garrick & Paul 1974) is also a scavenger-consuming discarded fish heads, tails or skeletal remains after filleting, often from pelagic species (Forman & Dunn, 2012). The fish prey in this work was identified from specimens sampled on research vessels, not commercial vessels, and were not believed to be scavenged discards. The three studies of the diet of *Z. chilensis* suggest that the diet may vary in time and space

TABLE II. The best generalized linear models (GLM) explaining the consumption of the most important prey groups by *Zearaja chilensis* in the south-western Atlantic Ocean. The intercept and parameters with s.e. (in parentheses) and Akaike's information criterion weights (w) for each model are given

Prey group	Intercept	Parameters	w
Fish	-3.73 (0.51)	0.009 $(1.5 \times 10^{-4})L_T - 5.5 \times 10^{-6}$ $(1.1 \times 10^{-6})L_T^2 - 0.23$ $(0.08) R_S$	0.99
Crabs	-2.98 (0.43)	0.002 $(6 \times 10^{-4})L_T - 1.23$ $(0.27) R_S$	0.99
Isopods	3.07 (0.46)	-0.011 $(9.2 \times 10^{-4})L_T + 2.59$ $(0.27) R_S$	0.60
Other crustaceans	3.13 (0.40)	-0.007 $(7 \times 10^{-4})L_T + 0.73$ $(0.21) R_S$	0.99

L_T , total length; R_S , south region (south of 41° S).

with commercial fleets supplying an easy food source in regions with high fishing intensities.

Zearaja chilensis showed an ontogenetic shift in diet. Isopods and small crustaceans decreased in importance as the predator increased in size, while the consumption of fishes and crabs increased. Such ontogenetic differences in diet composition have been

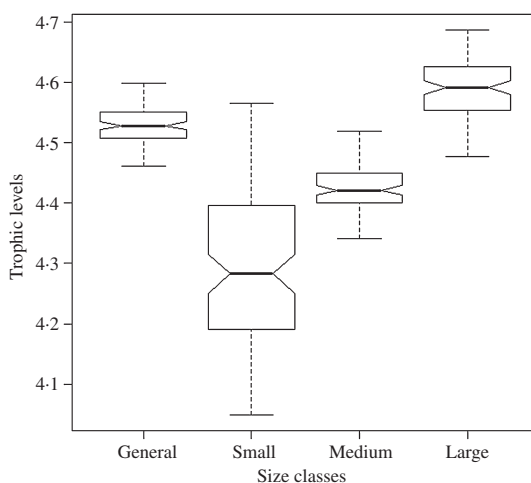


FIG. 5. Boxplot of bootstrapped trophic levels of *Zearaja chilensis* for all specimens sampled (general) and for each size class. The boxes represent 25th and 75th trophic level percentiles, and whiskers the 95th and 5th percentiles. The notches (V-shaped cut in the edge) represent 95% C.I. for the median are plotted on each side of the boxes giving strong evidence for the statistical difference among median trophic levels as they do not overlap.

TABLE III. Schöener index for niche overlap and the percentage of co-occurrence between different size classes: small (total length, $L_T \leq 450$ mm), medium ($451 \leq L_T \leq 699$ mm) and large ($L_T \geq 700$ mm) to represent the dietary and habitat overlap

	Size classes	Schöener index		
		Small	Medium	Large
Percentage of co-occurrence	Small	–	0.49	0.53
	Medium	40.25	–	0.64
	Large	28.14	39.52	–

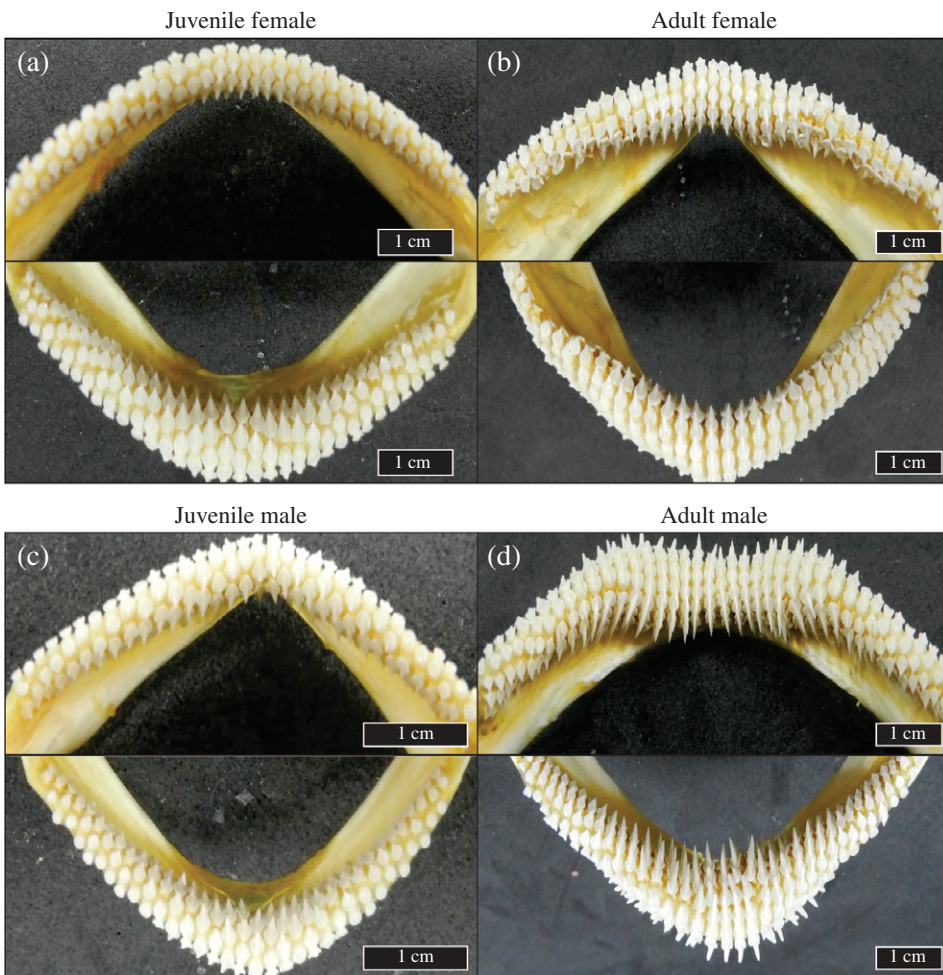


FIG. 6. Digital photographs of the external morphology of the upper and lower jaws of (a) juvenile female (685 mm total length, L_T), (b) adult female (1055 mm L_T), (c) juvenile male (542 mm L_T) and (d) adult male (905 mm L_T) *Zearaja chilensis*, from the Argentinean continental shelf.

demonstrated for many skate species (Orlov, 1998; Brickle *et al.*, 2003; Barbini *et al.*, 2010) and are a widespread phenomenon in elasmobranchs (Heithaus, 2004). In general, some hard-nose skate species exhibit a transition from small benthic crustaceans to larger crustaceans with more robust exoskeletons, whereas others consume more teleosts with increasing size (Treloar *et al.*, 2007). *Zearaja chilensis* exhibited a combination of both patterns, increasing the consumption of crabs and fishes, which might be linked to changes in foraging ability because of increased gape size and swimming speed. Moreover, dietary changes associated with changes in body size show how food resources within a given area are partitioned to minimize competition for food (when scarce) between different life stages (Ebert & Ebert, 2005).

Regional differences in the diet of *Z. chilensis* were found here: fishes and crabs were more important prey in the north region, and isopods and other crustaceans were consumed more in the south. Isopods, crabs, other crustaceans and fishes are widely distributed over the Argentinean continental shelf (Bastida & Torti, 1973; Boschi *et al.*, 1992; Cousseau & Perrota, 2004), but the lack of quantitative data on benthic species abundance in the region means that changes in the diet in response to prey availability could not be analysed. In the study area, previous work on the diet of shortfin sand skate *Psammobatis normani* McEachran 1983 and smallthorn sand skate *Psammobatis rudis* Günther 1870 showed the same patterns: crabs were the main prey group in the northern region, whereas isopods were most important in the south (Mabragaña & Giberto, 2007). In this context, it is possible to surmise that regional differences in *Z. chilensis* diet reflect geographical variation in benthic prey composition. The higher consumption of fishes in the north could be also related to the larger predators caught in the northern region, as the importance of fishes in the diet increased with predator length.

The T_L of *Z. chilensis* estimated here demonstrates their ecological role as a top predator. The T_L of all size classes was higher than 4, which confirms that over the entire ontogeny it is a tertiary consumer. These results show that *Z. chilensis* occupies a trophic role similar to that of marine mammals such as the southern sea lion *Otaria flavescens* (Lucifora *et al.*, 2000; Koen Alonso *et al.*, 2001). Studies focused on the T_L of *Dipturus* species and their position within the food web reveal that of the 14 species analysed, half are tertiary consumers and the rest are secondary consumers (Ebert & Bizzarro, 2007; Treloar *et al.*, 2007; Mulas *et al.*, 2015). In general, the maximum length of the species and the T_L were positively correlated (Ebert & Bizzarro, 2007), but the T_L value of the small size class of *Z. chilensis* may be overestimated, because isopods were their most important prey category, and the scavenging behaviour of amphipods and isopods results in high isotopic ratios (Hobson & Welch, 1992; Nyssen *et al.*, 2002), and therefore high T_L (3.18; Ebert & Bizzarro, 2007). These results highlight the importance of refining the T_L of prey items in order to accurately assess the trophic role of the predators.

The greatest overlap in both habitat and diet was observed between medium and large size classes, whereas diet overlap was low between the small and other size classes. Moreover, habitat partitioning was greatest between small and large size classes. The more extreme resource partitioning exhibited by small *Z. chilensis* may be related to their smaller mouth, less developed teeth and slower swimming speed. Habitat partitioning was also higher for small individuals, which were mainly segregated from large size class, probably reducing potential competition for food resources and the risk of intraspecific predation. During the more vulnerable early life stage of *Z. chilensis*,

high habitat partitioning and the low diet resource overlap with larger size classes may increase survival, and positively affect the recruitment of young *Z. chilensis* into the adult population.

The dentition of adult *Z. chilensis* showed sexual dimorphism, with larger and pointed cusps in mature males. This pattern is widespread in skates (Bigelow & Schroeder, 1953; Herman *et al.*, 1995; Sáez & Lamilla, 1997; Braccini & Chiaramonte, 2002; Scenna *et al.*, 2006) and was inaccurately attributed to differential foraging by the sexes to alleviate intraspecific competition for food (Feduccia & Slaughter, 1974). Tooth differentiation in adult males may, however, be related to reproductive behaviour, increasing their grasping ability during courtship (McEachran, 1977; Kajiura *et al.*, 2000). The results from this work showed that the dental sexual dimorphism in *Z. chilensis* was not accompanied by differences in diet between sexes, providing support for it being related to reproductive behaviour rather than to feeding.

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