Feeding ecology of the southern thorny skate, *Amblyraja doellojuradoi* on the Argentine Continental Shelf

G.E. DELPIANI[1,2], M.C. SPATH[1,2] AND D.E. FIGUEROA[1]

[1]Universidad Nacional de Mar del Plata (UNMdP), Facultad de Ciencias Exactas y Naturales, Laboratorio de Ictiología, Funes 3350, Mar del Plata (B7602AYL), Argentina, [2]Instituto de Investigaciones Marinas y Costeras (IIMyC), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Argentina.

The feeding ecology of the southern thorny skate, Amblyraja doellojuradoi, *on the Argentine Continental Shelf was evaluated using generalized linear models.* Amblyraja doellojuradoi *preyed mainly on crabs (85.41% index of relative importance (IRI)) and to a lesser extent on polychaetes (4.98% IRI), teleosts (3.28% IRI), isopods (2.03% IRI), other crustaceans (1.52% IRI) and other invertebrates (2.78% IRI). As individuals increased in size, the consumption of crabs also increased and the consumption of polychaetes and other invertebrates decreased. The study area was divided into a northern (36°–43°S) and a southern (43°–50°S) region. Regarding the latitude of capture, it was observed that* A. doellojuradoi *mainly fed on crabs in the north and on fish, isopods and other crustaceans in the south. Females of* A. doellojuradoi *had a stronger preference for fish and isopods than males. As to sexual maturity, immatures fed more on polychaetes and other crustaceans than did mature. The ontogenetic change in feeding habits could be attributed to body size and an increasing ability to capture larger prey, rather than to food availability. However, this point cannot be confirmed because little is known about the benthic fauna of this area.*

INTRODUCTION

Elasmobranchs are among the top predators in marine environments and have an important role in marine ecosystems in relation to both fish and lower trophic level invertebrate populations (Ellis *et al.*, 1996). In spite of the value of understanding the feeding relationships in food web dynamics, community conformation and the energy transfer in marine systems, knowledge of the dietary ecology of most elasmobranchs is poor. This applies particularly to batoids, which have received considerably less scientific attention than pelagic sharks (Bizarro *et al.*, 2007). Indeed, of the 245 species of skate described, fewer than 24% have had any quantitative dietary information published. There are many reasons why quantitative analyses are few. One is the lack of adequate systematic knowledge of the group. Another is the lack of financial resources to study either non-target species or species of low economic value. Yet another is that skates often live in habitats difficult to get at (Ebert & Bizarro, 2007).

The skates, as important predators and ground-fish competitors, have a significant impact on the benthic fauna, playing an essential role in structuring benthonic–demersal marine communities (Ebert & Bizarro, 2007; Treloar *et al.*, 2007). Even though the skates' diet is determined largely by

ontogenetic mechanisms, it is also influenced by environmental factors. Hence, it is important to identify those factors in order to evaluate the diet variation in terms of the environment (Jaworski & Ragnarsson, 2006). Factors such as body size, maturity stage, sex, season, bottom depth, region, habitat mobility, seasonal occurrence, potential prey abundance and distribution, as well as ecomorphology, are among potential factors influencing skate diets (Jaworski & Ragnarsson, 2006; Treloar *et al.*, 2007).

Ontogenetic dietary changes have been analysed in skates (Bizarro *et al.*, 2007; Barbini, 2011), since the predator size is one of the main causes behind diet composition changes during ontogeny (Lucifora *et al.*, 2009). Moreover, differences in feeding behaviour between sexes have been also found in some species (Orlov, 1998; San Martín *et al.*, 2007).

Amblyraja is a circumglobal genus, even though it most often is found at high latitudes and deep waters (McEachran & Miyake, 1990; Ebert & Compagno, 2007). It is composed of ten species, one of which, *Amblyraja doellojuradoi*, inhabits the south-west Atlantic (Menni & Stehmann, 2000; Cousseau *et al.*, 2007). Off the coast of Argentina it is distributed from 36° to 55°S along the outer shelf and the continental slope (80–600 m depth). Information about *A. doellojuradoi* is scarce and refers almost exclusively to taxonomy and distribution (Pozzi, 1935; Bellisio *et al.*, 1979; Menni *et al.*, 1984; Menni & Stehmann, 2000; Sánchez & Mabragaña, 2002; Cousseau *et al.*, 2007). The exception is a paper published by Sánchez & Mabragaña (2002) where, on the basis of few specimens, the diet of *A. doellojuradoi* was evaluated.

Corresponding author:
G.E. Delpiani
Email: gabriela.delpiani@gmail.com

They found that this species feeds mainly on crabs and, in a lesser proportion, on fish and polychaetes. Regarding the information on industrial fishing, *A. doellojuradoi* is considered a rare species (Colonello *et al.*, 2002).

The aim of the present work is to study the trophic aspects of *A. doellojuradoi* on the Argentine Continental Shelf. The specific objectives are to evaluate potential differences by sex, size, maturity stage, latitude and depth in feeding ecology. This study provides the first detailed contribution on the food habits of *A. doellojuradoi* in an extensive area of the south-west Atlantic in order to understand the role of the species in the regional food web.

MATERIALS AND METHODS

Study area and sampling

Skates were collected from research cruises carried out by the Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP) ($N = 167$), and from commercial vessels ($N = 102$) between the years 2005 and 2012 in the south-west Atlantic between 36° and 50°S, from 75 to 414 m deep (Figure 1).

Total length (TL) was measured to the nearest millimetre, and sex and maturity stage were recorded by macroscopic observation of the reproductive organs (Mabragaña *et al.*, 2002; Colonello *et al.*, 2007). The immature specimens were characterized by thin uteri, ovaries without visible oocytes, oviductal glands not fully developed in females; thin and straight spermatic ducts, underdeveloped testes and not calcified claspers in males. In contrast, mature females evidenced enlarged uteri, ovaries with vitellogenic oocytes, oviductal glands fully formed and possible presence of fully or partially formed egg-case; mature males showed meandered epididymides tightly filled with sperm, testes with vitelline vesicles and calcified claspers (Mabragaña *et al.*, 2002; Colonello *et al.*, 2007). The stomachs were dissected, labelled and fixed in 10% formaldehyde. In the laboratory, prey items were identified to the lowest possible taxonomic level using identification keys (Bastida & Torti, 1973; Menni *et al.*, 1984; Boschi *et al.*, 1992; Cousseau & Perrotta, 2000), illustrative guides and information from specialists. The numbers and weights of every prey item were recorded.

Analysis of diet

DIET COMPOSITION
In order to quantify the diet composition and its comparison with published studies, percentage by weight (%W), percentage by number (%N) and percentage of frequency of occurrence (%F) were calculated. From these values the index of relative importance (IRI = %F(%N + %W)) was estimated (Pinkas *et al.*, 1971) and then expressed as a percentage value (%IRI, Cortés, 1997). For statistical purposes, prey items were grouped into six categories: teleosts, crabs, isopods, other crustaceans (other decapods, gammarids, cumacea and mysidacea), polychaetes and other invertebrates (pycnogonids, cephalopods, sipunculids, asteroids, hydrozoans and ophiuroids). The variables considered in assessing the consumption of different prey categories were: TL, sex, maturity stage (immature and mature), and longitude and

latitude as geographical variables. Latitudinally, the study area was divided into a northern region from 36° to 43°S and a southern region from 43° to 50°S. Since the depth of capture of the totality of specimens was unknown, the geographical variable longitude was considered to supply missing data. In agreement with the spatial layout of the Argentine coast, as the geographical variable longitude decreases from 69° to 51°W, the platform depth increases.

The minimum number of stomachs needed to describe the diet of each group of individuals considered, was assessed using cumulative diversity curves (Magurran, 2004). In order to minimize bias, the order in which stomachs were sampled was randomized 100 times. Then, the cumulative number of stomachs sampled at random was plotted in relation to the average cumulative diversity index of the stomach contents. Where the average value of the diversity index (Shannon–Wiener) reached an asymptote, the sample size was considered sufficient to describe the dietary composition of the group of individuals considered.

DIET SHIFTS
By means of a multiple hypothesis modelling approach (Franklin *et al.*, 2001), variations in consumption of prey categories in terms of sex, maturity stage, TL, the geographical variables longitude (depth) and latitude (taking into account both the northern and southern regions) were evaluated. For each prey category, generalized linear models were built where the number of each prey category was taken as the response variable, and sex, maturity stage, TL, deepness and regions as the explanatory variables (Venables & Ripley, 2002). A model with no independent variables (null model) was also fitted to test the hypothesis that no one variable had an effect on the consumption of each prey category (Lucifora *et al.*, 2009). Furthermore, models were made with combinations of some of the variables: sex and TL, sex and depth, sex and regions, sex and maturity stage, TL and depth, TL and regions, TL and maturity stage, depth and regions, maturity stage and depth, maturity stage and regions. Whenever too many zeros were present and the variance was often much greater than the mean, models with prey number as the response variable had a binomial error distribution and a log link (Crawley, 2005). For each prey category, the Akaike information criterion (AIC) of all models considered was calculated. The AIC indicates the amount of information lost in each model fit; therefore, the model with the lowest value of AIC was the one that best described the data (Anderson *et al.*, 2000; Franklin *et al.*, 2001; Johnson & Omland, 2004). Each model was weighed against the others using the Akaike weights (w) which give an estimation of the likelihood of the model (Anderson *et al.*, 2000; Franklin *et al.*, 2001; Johnson & Omland, 2004).

RESULTS

Diet composition

Of 306 specimens examined, 269 (87.9%) contained food, 158 of which were males (209–710 mm TL) and 111, females (275–515 mm TL). Cumulative curves reach the asymptote diversity in all specimens with 84 stomachs, with 60 and 96 in females and males, respectively, with 20 in immature and
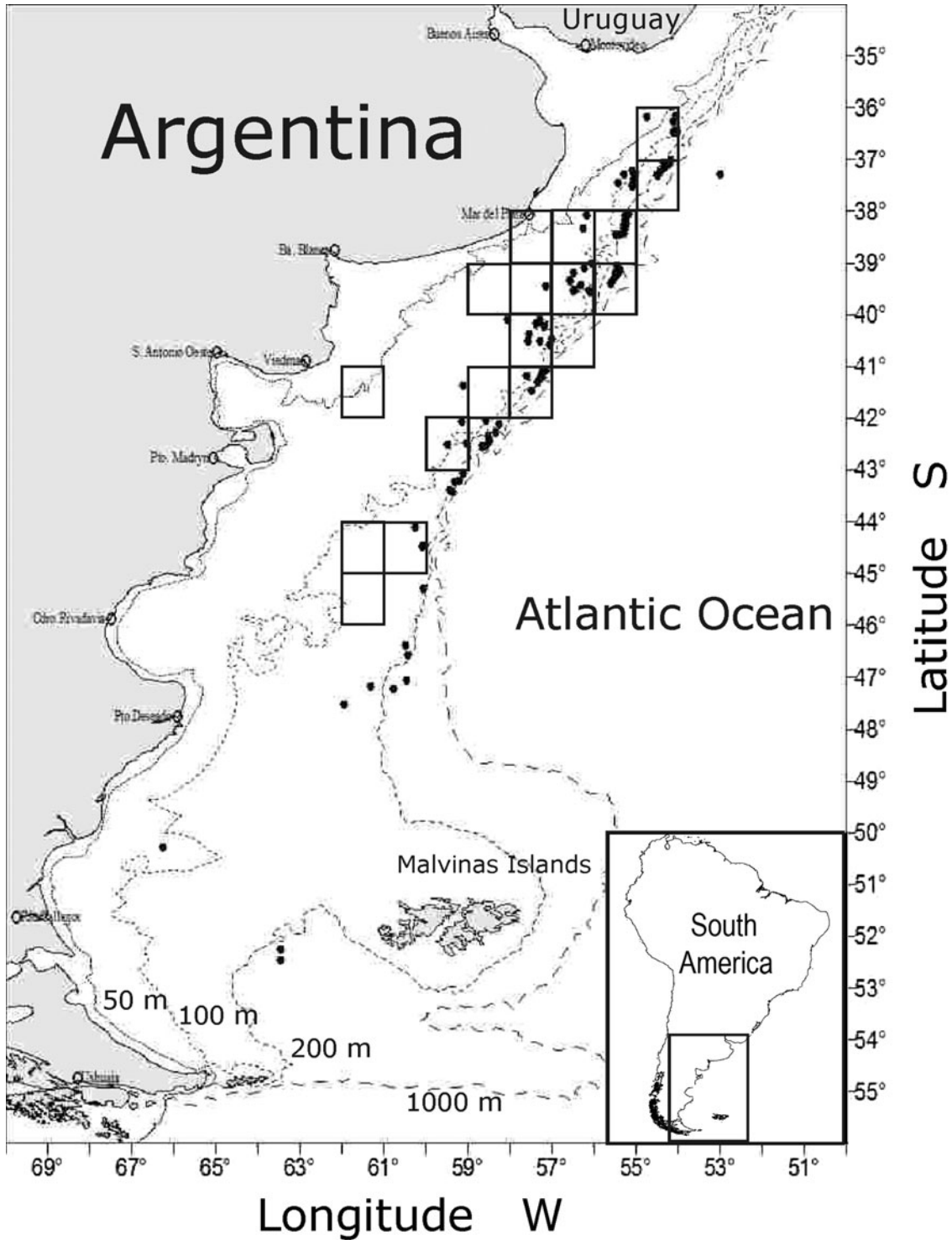
Fig. 1. Map of the study area showing positions of trawl stations and cells of fishing grid (black rectangles) where specimens of *Amblyraja doellojuradoi* were captured.

117 in mature, and finally with 131 stomachs in the northern area and 24 in the southern area (Figure 2).

A total of 53 different prey items were identified in the *Amblyraja doellojuradoi* stomachs (Table 1). The most important prey in terms of %IRI were crabs (85.47%); less important were polychaetes (4.71%), isopods (1.89%), other crustaceans (1.39%), other invertebrates (3.00%) and teleosts (3.51%). Among the crabs, *Libidoclea granaria* was the most consumed

species, followed by remains of brachyuran crabs and *Peltarion spinulosum*.

Diet shifts

The consumption of prey categories presented some changes depending on variables such as total length, sex, maturity and regions (Table 2). As the *A. doellojuradoi* body size
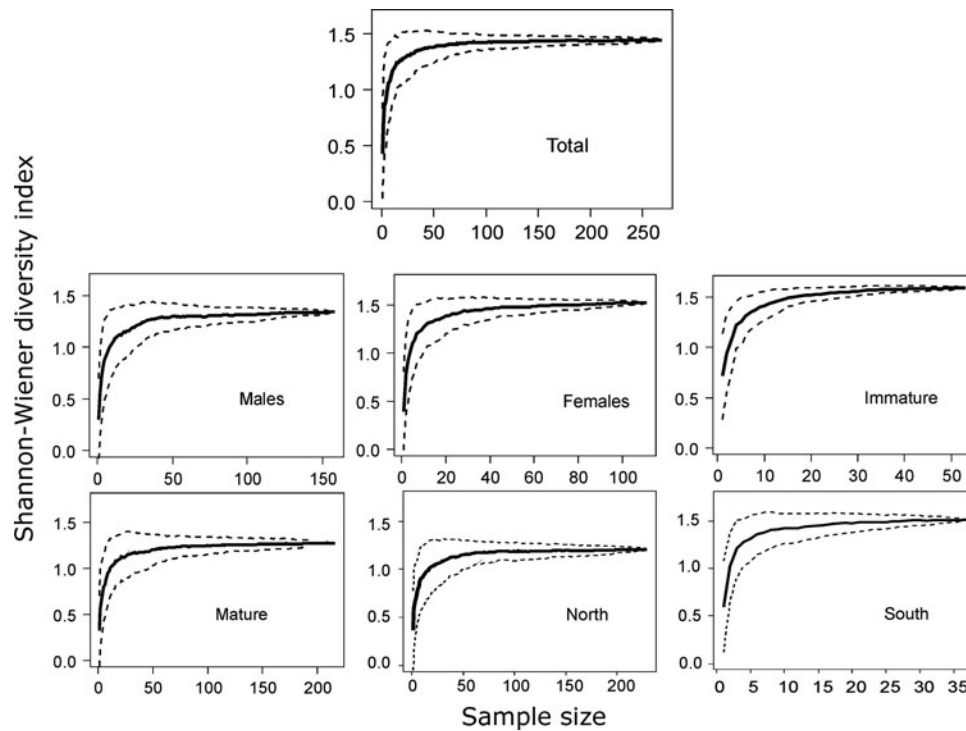
Fig. 2. Curves of cumulative mean diversity (Shannon–Wiener index) for each group of specimens considered for the dietary analysis of *Amblyraja doellojuradoi*. Mean, continuous line; standard deviation, dashed lines.

rose, the number of crabs consumed increased and consumption was higher in the northern than in the southern region (Figure 3A). The polychaetes consumption decreased as specimens gained size, and it was higher in immatures than in matures (Figure 3B). Females of *A. doellojuradoi* consumed more isopods than males, and that consumption was higher in the southern than in the northern region (Figure 3C; Table 2). On the other hand, immatures fed more on the 'other crustaceans' prey category, and consumption was also higher in the southern region (Figure 3D). The consumption of other invertebrates decreased in number as *A. doellojuradoi* increased in size (Figure 3E). Finally, feeding on teleosts was determined by the sex variable, showing females having higher consumption than males, and that consumption was higher in the southern than in the northern region (Figure 3F; Table 2).

DISCUSSION

Since it fed mainly on crabs, polychaetes and bottom fish, *Amblyraja doellojuradoi* evidenced benthic feeding habits on the Argentine Continental Shelf.

In addition, it was clear that this species was capable of capturing benthic–demersal prey items like *Merluccius hubbsi* and *Patagonotothen ramsayi*, although not main components of the skate diet. Of minor significance were polychaetes, represented by errant and sedentary worms. Crustaceans and fish constituted the most important prey items of the region, observed in the majority of skates (García de la Rosa & Sánchez, 1999; Koen Alonso *et al.*, 2001; Brickle *et al.*, 2003; Mabragaña & Giberto, 2007; Belleggia *et al.*, 2008). Even though *A. doellojuradoi* consumed a great variety of prey, it

showed a specialized consumption of crabs, and therefore is carcinophaga in its feeding habits.

Sánchez & Mabragaña (2002) found that the diet of *A. doellojuradoi* in Patagonian waters was dominated by crustaceans, and occasionally by fish, polychaetes and molluscs. Besides, Bizikov *et al.* (2004) in the Malvinas (Falkland) Islands reported for the early stages a diet based mostly on euphausids, shifting, close to adulthood, to isopods and polychaetes, as well fish and other benthic prey items. The results of the present work showed that the most important prey was crabs, while the less important were polychaetes, other invertebrates and teleosts. Also, in agreement with Bizikov *et al.* (2004), a dietary shift was evident in *A. doellojuradoi*. Smaller individuals consumed chiefly polychaetes, isopods and other invertebrates, and larger individuals consumed mostly crabs. Differences between the diet reported by Bizikov *et al.* (2004) and the one here stated result from difference of the sampling areas. It is well known the significance of krill as an abundant resource in the Malvinas Islands (Volkman *et al.*, 1980; Main & Collins, 2011); thereby, the skates of smaller size are better able to capture these prey items. The consumption of krill has not been reported by other authors.

Some species of the genus *Amblyraja*, such as *A. radiata*, were studied in detail. The diet of this species was studied by Skjæraasen & Bergstad (2000) in the Norwegian Sea, Norway, and Pedersen (1995) in the Davis Strait, Greenland. The first authors found fish, decapods and polychaetes in the diet, and the second one, copepods, gammarids, mysids and squid. Another species of the genus with known dietary habits is *A. georgiana* of South Georgia, which when young feeds on amphipods and polychaetes and when it matures, on fish (Main & Collins, 2011). Bizikov *et al.* (2004) found that *A. georgiana* of the Malvinas Islands preyed on fish,

Table 1. Diet composition of *Amblyraja doellojuradoi*. %N, percentage by number; %W, percentage by weight; %F, percentage frequency of occurrence; IRI, index of relative importance; %IRI, percentage of IRI.

Prey	%N	%W	%F	IRI	%IRI	%IRI prey categories
TELEOSTEI	**2.59**	**38.93**	**0.41**	**17.04**	**0.17**	
Notothenidae	0.06	6.55	0.16	1.05		
Patagonotothen ramsayi	0.57	9.88	0.63	6.61		
Bassanago spp.	0.06	3.66	0.16	0.59		3.51
Merluccius hubbsi	0.32	9.09	0.79	7.44		
Unidentified teleosts	1.58	9.75	3.96	44.82		
CRUSTACEA	**75.52**	**68.66**	**65.19**	**9399.11**	**95.62**	
BRACHYURA						
Majidae	1.08	2.27	0.63	2.12		
Libidoclea granaria	36.24	34.1	25.32	1780.9		
Eurypodius laterillei	0.38	1.15	0.63	0.97		
Leucippa pentagona	0.06	0.62	0.16	0.11		
Peltarion spinulosum	5.12	8.56	7.12	97.45		85.47
Unidentified brachiuran	5.44	10.49	13.61	216.71		
ANOMURA						
Munida subrugosa	0.7	2.81	1.11	3.88		
Sympagurus dimorphus	0.63	5.03	1.58	8.95		
ISOPODA						
Arcturidae	8.98	1.19	1.74	17.71		
Serolidae	1.96	1.00	3.01	8.89		
Serolis schytei	2.40	0.49	1.11	3.20		1.89
Cirolanidae	0.38	0.08	0.95	0.44		
Sphaeroma serratum	0.32	<0.01	0.16	0.05		
Macrochiridotea spp.	0.25	0.06	0.47	0.15		
CARIDEA						
Campylonotus vagans	5.95	0.4	4.11	26.09		
Callianassa sp.	0.06	0.23	0.16	0.05		
Unidentified decapods	0.32	0.02	0.79	0.27		
AMPHIPODA						
Gammaridea	4.55	0.13	1.58	7.42		
Tryphosella sp.	0.13	<0.01	0.16	0.02		1.39
Ampheliscidae spp.	0.38	0.01	0.32	0.12		
CUMACEA	0.06	<0.01	0.16	0.01		
MYSIDA						
Mysidae	0.13	0.01	0.32	0.04		
ANNELIDA						
POLYCHAETA	**13.03**	**4.27**	**18.35**	**317.5**	**3.23**	
Onuphiidae	2.53	0.33	1.58	4.52		
Onuphis eremita	0.57	0.05	0.47	0.29		
Terebellidae	0.32	0.17	0.16	0.08		
Phyllodocidae	0.25	0.05	0.16	0.05		
Eunicemorpha	0.38	0.01	0.16	0.06		
Glyceridae	0.13	0.14	0.32	0.08		
Nereididae	0.19	0.06	0.32	0.08		
Maldanidae	1.27	0.29	0.79	1.23		
Serpulidae	0.06	<0.01	0.16	0.01		4.72
Terebelomorpha	0.06	0.10	0.16	0.03		
Ophellidae	0.06	0.03	0.16	0.01		
Nephthyidae	1.20	0.10	0.79	1.03		
Lumbrineridae	0.25	0.03	0.47	0.13		
Orbiniidae	0.19	0.02	0.32	0.06		
Capittelidae	0.19	0.03	0.32	0.07		
Aphroditiformia	0.19	0.07	0.47	0.12		
Unidentified polychaetes	5.19	2.80	11.55	92.27		
CHELICERIFORMES	**0.06**	**0.003**	**0.16**	**0.01**	**<0.01**	
PYCNOGONIDA						
Tanystylum orbiculare	0.06	<0.01	0.16	0.01		
MOLLUSCA	**6.64**	**7.24**	**6.17**	**85.67**	**0.87**	
CEPHALOPODA						
Octopoda	0.19	0.53	0.47	0.34		
Loligo gahi	2.59	0.51	1.74	5.40		
Teuthoidea	0.95	0.20	1.90	2.17		3.00
Illex argentinus	2.91	6.01	2.06	18.34		

Continued

Table 1. Continued.

Prey	%N	%W	%F	IRI	%IRI	%IRI prey categories
SIPUNCULA	**0.63**	**0.07**	**0.63**	**0.44**	**<0.01**	
CNIDARIA						0.1
Hydrozoa	1.90	0.13	4.75	9.64		
ECHINODERMATA	**0.13**	**0.01**	**0.32**	**0.04**	**<0.01**	
Asteroidea	0.06	<0.01	0.16	0.01		
Ophiuroidea	0.06	0.01	0.16	0.01		

shrimps, crabs and squids. As discussed so far, it can be concluded that *Amblyraja* is a genus that feeds mainly on fish and crabs, but does not exclude other prey items from its diet. In addition, it appeared that this genus also undergoes ontogenetic shift in its diet.

Amblyraja doellojuradoi showed changes in diet composition between sexes, with increasing body size, maturity stage, and also between regions (northern–southern). Ontogenetic changes in diet composition had been reported in several studies of skates, in different parts of the world including those skates that inhabit the Argentine Continental Shelf (McEachran et al., 1974; Pedersen, 1995; Lucifora et al., 2000; Skjæraasen & Bergstad, 2000; Kohen Alonso et al., 2001; Brickle et al., 2003; Belleggia et al., 2008; Barbini, 2011). According to Jaworski & Ragnarsson (2006) the size of the skates is the most important variable in determining the composition of their diet. Most of the observed changes in several skates were from crustaceans to fish (Orlov, 1998; Lucifora et al., 2000; Koen Alonso et al., 2001; Brickle et al., 2003; Treloar et al., 2007). Considering the aforementioned and evaluating the diet of skates that inhabit the Argentine Continental Shelf, it is observed that those specimens between 75 and >100 cm maximum total length (*Bathyraja griseocauda*, *B. scaphiops*, *B. cousseauae*, *B. brachyurops*, and *Zearaja chilensis*) changed their diet from invertebrates, mainly isopods, amphipods and crabs, to fish (García de la Rosa & Sanchez, 1999; Lucifora et al., 2000; Koen Alonso et al., 2001; Brickle et al., 2003; Belleggia et al., 2008). In contrast, species who reach around 60 cm of total length (*B. macloviana*, *Psammobatis normani* and *P. rudis*) in the same area, fed mainly on polychaetes and small crustaceans (Mabragaña & Giberto, 2007; Ruocco et al., 2009). *Amblyraja doellojuradoi* is part of this group since the maximum reported size is 60 cm and in the ontogeny it preys on polychaetes and other invertebrates to later feed mainly on crabs. This change is due to the increasing size of the predators, since with a gradual increase in total length, swimming capabilities increase, permitting the capture of bigger and faster prey items, and also to the techniques related to the feeding system, like gape size (Scharf et al., 2000) and to the strength of biting or sucking (Motta, 2004).

Another variable that determines the consumption of polychaetes and other crustaceans is the maturation of the specimens. Immatures of *A. doellojuradoi* showed an increased consumption of polychaetes and other crustaceans. This is hypothesized to be a result of the higher vulnerability of small prey compared to large prey due to higher encounter rates and the higher probability of capture once detected (Lucifora et al., 2006). Within the species, reduced competition between mature and immature would increase survivorship for the latter during the critical early stages of life. Mature elasmobranchs of many species feed on larger, more active prey items that immatures cannot obtain, thereby reducing intraspecific competition with smaller, younger conspecifics (Olsen, 1954; Springer, 1960; Lowe et al., 1996; Gray et al., 1997).

It was also noted that consumption of some prey items varied depending on the regions. Crabs were consumed mostly in the north rather than in the south; fish, isopods and other crustaceans were consumed chiefly in the south rather than in the north. The lack of detailed quantitative information on the distribution and availability of potential benthic prey on the Argentine Continental Shelf prevents an assessment of prey selectivity by *A. doellojuradoi*. Mabragaña & Giberto (2007) found a similar feeding pattern in *P. normani* and *P. rudis*, species both inhabiting the same environment as *A. doellojuradoi*. These authors state that between 35 and 41°S, the most consumed prey were crabs, and between 48 and 55°S were isopods and amphipods. The benthic communities may differ among regions in relation to abundance, dynamics and arrangement. In the north, the inner limit of the Argentine Continental Shelf is forming a highly productive front inhabited by large numbers of benthic prey (Acha et al., 2004; Mabragaña & Giberto, 2007).

Another variable that determined the consumption of a prey category was sex. Dietary analysis of *A. doellojuradoi* showed an increased consumption of fish and isopods in females. It was known that some female sharks grew to bigger sizes than males (Cortés, 2000) and exhibited sexual segregation (Springer, 1967). Hence, it could be presumed that females of shark species with sexual size dimorphism and spatial segregation would have a different dietary composition than males. However, skates inhabiting the same habitat, that reached equal size and possessed similar capture capabilities, are expected to exhibit diets and ecological roles alike in both sexes (San Martín et al., 2007). Nevertheless, Ezzat et al. (1987) reported sexual differences in the diet of *R. miraletus* in the Egyptian Mediterranean waters. Commonly, these disparities appeared as higher frequencies of occurrence of crustaceans and fish in female stomachs, and worms and molluscs in those of males (Ezzat et al., 1987). In some species of the genus *Bathyraja* from the North Pacific, sexual differences in food composition were also found and they have been associated with sexual size dimorphism (Orlov, 1998). Diet of skates might vary between sexes either as a result of sexual dimorphism and differences in the predatory capacity of males and females, and/or because of differences in the spatio-temporal foraging activity (San Martín et al., 2007). In the case of *A. doellojuradoi*, differences in the spatio-temporal foraging activity of males and females should be ruled out (Braccini et al., 2005) because both sexes had the same distribution. Sexual size dimorphism should also be ruled out (Begg et al., 2003) because, beyond the existence of dimorphism, it is contrary to what had been expected, males being larger than females.
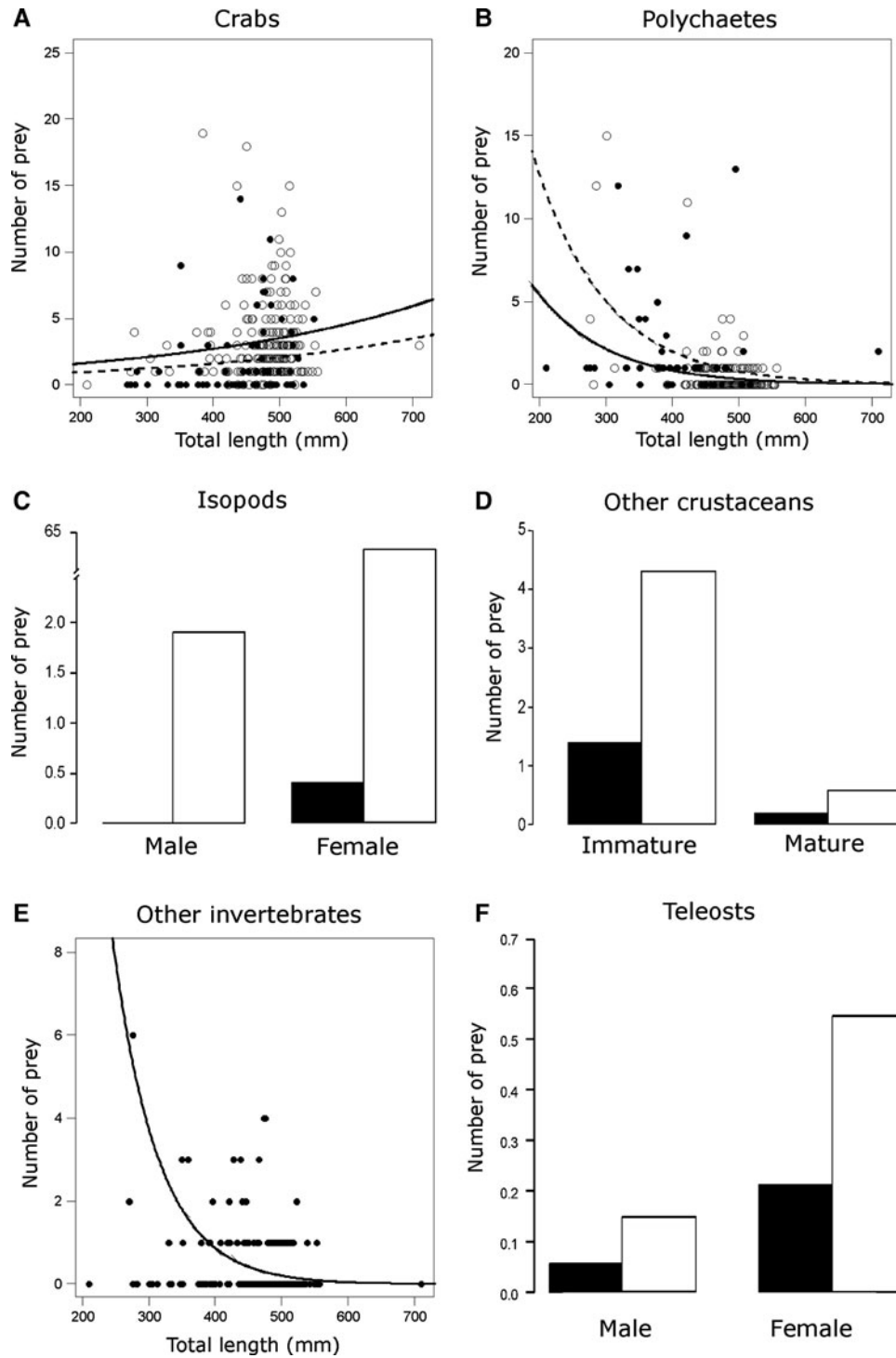
Fig. 3. Shift in consumption of different prey categories of *Amblyraja doellojuradoi* in the Argentinean Continental Shelf in function of the total length, sex, latitude and longitude, estimated by a generalized linear model: (A) shift in consumption of crabs in function of the total length and regions (north: solid line and solid circles; south: dotted line and open circles); (B) shift in consumption of polychaetes in function of the total length and maturity (mature: solid line and solid circles; Immature: dotted line and open circles); (C) shift in consumption of isopods in function of sex and regions (north: black; south: white); (D) shift in consumption of other crustaceans in function of the maturity and regions (north: black; south: white); (E) shift in consumption of other invertebrates in function of the total length; (F) shift in consumption of teleosts in function of sex and regions (north: black; south: white). The models had a log link and a negative binomial error distribution.

Generally, species that consume fish have sharp teeth to capture these prey items more successfully (Feduccia & Slaughter, 1974). However, teeth of *A. doellojuradoi* were sharper in males than in females, in opposition to the difference reported in diet (Delpiani *et al.*, 2012). Thayer *et al.*

(1973) proposed that prey consumption is determined by the calorific value. In this case, the total caloric content of small crustaceans is lower than that of teleost fish. Therefore, increased consumption of fish by females could be due to an energy demand for the reproductive processes

Table 2. Best models explaining the consumption in number of prey categories of *Amblyraja doellojuradoi*. The intercept and coefficient for the variables are given. TL, total length (mm); AIC, Akaike information criterion; w, Akaike's weights; standard errors in parentheses.

Prey categories	Intercept	Coefficients	AIC	w
Crabs	−0.1670(0.6308)	0.00276(0.0013) TL − 0.6157(0.236) south	1165	0.4961
Polychaetes	3.617(1.207)	−0.0093(0.0025) TL + 0.8184(0.360) immature	573.75	0.7503
Isopods	−7.9084(1.4903)	3.5202(0.8227) females + 5.0339(0.9236) south	325.68	0.5281
Other crustaceans	−1.6276(0.2519)	1.9706(0.4876) immature + 1.3746(0.5620) south	416.13	0.4091
Other invertebrates	5.941(1.2945)	−0.01512(0.0028) TL	412.95	0.300
Teleosts	−4.139(0.6445)	1.2997(0.366) females + 0.937(0.4171) south	225.73	0.4086

such as gonadal development, egg formation and gestation (King & Murphy, 1985). A qualitative or quantitative shift in their diets for meeting these growing requirements could be expected (Cooper *et al.*, 2007).

Finally, several factors might influence the feeding of *A. doellojuradoi*. This species occurred sympatrically with many similar-sized species and consumed the same prey categories. Hence, few species could be main trophic competitors for the species under study. Another factor that could have modified the diet of *A. doellojuradoi* was the commercial fishing. From 1992 to 2006, skate fisheries in Argentina became strongly important, and capture rose from 761 t to 23,618 t (Cousseau *et al.*, 2007). This activity may affect marine populations both directly through removal of individuals and indirectly through loss of habitat and modification of the trophic structure (Cousseau & Perrotta, 2000). Therefore, due to these factors, the environment can be constantly altered, making it difficult to determine the causes of food preference.

ACKNOWLEDGEMENTS

FINANCIAL SUPPORT

REFERENCES

Acha E.M., Mianzan H.W., Guerrero R.A., Favero M. and Bava J. (2004) Marine fronts at the continental shelves of austral South America physical and ecological processes. *Journal of Marine Systems* 44, 83–105.

Anderson D.R., Burnham K.P. and Thompson W.I. (2000) Null hypothesis testing problems, prevalence, and an alternative. *Journal of Wildlife Management* 64, 912–923.

Barbini S.A. (2011) *Ecología trófica de las rayas (Chondrichthyes, Rajidae) en el ecosistema costero bonaerense y uruguayo.* PhD thesis. Universidad Nacional de Mar del Plata, Argentina.

Bastida R. and Torti M.R. (1973) Los isópodos Serolidae de la Argentina. Clave para su reconocimiento. *Physis Sección A* 32, 19–46.

Begg C.M., Begg K.S., Du Toit J.T. and Mills M.G.L. (2003) Sexual and seasonal variation in the diet and foraging behavior of a sexually dimorphic carnivore, the honey badger (*Mellivora capensis*). *Journal of Zoology* 260, 301–316.

Belleggia M., Mabragaña E., Figueroa D.E., Scenna L.B., Barbini S.A. and Díaz de Astarloa J.M. (2008) Food habits of the broad nose skate, *Bathyraja brachyurops* (Chondrichthyes, Rajidae), in the southwest Atlantic. *Scientia Marina* 72, 701–710.

Bellisio N.B., López R.B. and Torno A. (1979) *Peces Marinos Patagónicos.* Buenos Aires: Ministerio de Economía, Subsecretaría de Pesca, Argentina.

Bizarro J.J., Robinson H.J., Rinewalt C.S. and Ebert D.A. (2007) Comparative feeding ecology of four sympatric skates species off central California, USA. *Environmental Biology of Fishes* 80, 197–220.

Bizikov V.A., Arkhipkin A.I., Laptikhovski V.V. and Pompert J. (2004) *Identification guide and biology of the Falkland Islands skates.* Port Stanley: Fisheries Department, Falkland Islands Government.

Boschi E.E., Fischbach C.E. and Iorio M.I. (1992) Catálogo ilustrado de los crustáceos estomatópodos y decápodos marinos de Argentina. *Frente Marítimo Sección A* 10, 7–94.

Braccini J.M., Gillanders B.M. and Walker T.I. (2005) Sources of variation in the feeding ecology of the piked spurdog (*Squalus megalopus*): implications for inferring predator–prey interactions from overall diet composition. *ICES Journal of Marine Science* 62, 1076–1094.

Brickle P., Laptikhovsky V., Pompert J. and Bishop A. (2003) Ontogenetic changes in the feeding habits and dietary overlap between three abundant rajid species on the Falkland Island's shelf. *Journal of the Marine Biological Association of the United Kingdom* 83, 1119–1125.

Colonello J.H., Massa A. and Lucifora L.O. (2002) Composición de la captura de rayas del buque palangrero 'Sureste 501' en el norte del Mar Argentino. *INIDEP, Informe Técnico interno*, no. 107.

Colonello J.H., García M.L. and Lasta C.A. (2007) Reproductive biology of *Rioraja agassizi* from the coastal southwestern Atlantic ecosystem between northern Uruguay (34°S) and northern Argentina (42°S). *Environmental Biology of Fishes* 80, 277–284.

Cooper A.B., Pettorelli N. and Durant S.M. (2007) Large carnivore menus: factors affecting hunting decisions by cheetahs in the Serengeti. *Animal Behaviour* 73, 651–659.

Cortés E. (1997) A critical review of methods of studying fish feeding based on analysis of stomach contents: application to elasmobranch fishes. *Canadian Journal of Fisheries and Aquatic Sciences* 54, 726–738.

Cortés E. (2000) Life history patterns and correlations in sharks. *Reviews in Fisheries Science* 8, 299–344.

Cousseau M.B. and Perrotta R.G. (2000) *Peces marinos de Argentina: biología, distribución y pesca.* Mar del Plata: INIDEP.

Cousseau M.B., Figueroa D.E., Díaz de Astarloa J.M., Mabragaña E. and Lucifora L.O. (2007) *Rayas, chuchos y otros batoideos del Atlántico Sudoccidental (34°S–55°S).* Mar del Plata: INIDEP.

Crawley M.J. (2005) *Statistics: an introduction using R.* Chichester: John Wiley & Sons.

Delpiani G., Figueroa D.E. and Mabragaña E. (2012) Dental abnormalities of the southern thorny skate *Amblyraja doellojuradoi* (Chondrichthyes, Rajidae). *Revista de Biología Marina y Oceanografía* 47, 135–140.

Ebert D.A. and Bizzarro J.J. (2007) Standardized diet composition and trophic levels in skates. *Environmental Biology of Fishes* 80, 221–237.

Ebert D.A. and Compagno L.J.V. (2007) Biodiversity and systematics of skates (Chondrichthyes: Rajiformes: Rajoidei). *Environmental Biology of Fishes* 80, 111–124.

Ellis J.R., Pawson M.G. and Shackley S.E. (1996) The comparative feeding ecology of six species of shark and four species of ray in the north-east Atlantic. *Journal of the Marine Biological Association of the United Kingdom* 76, 89–106.

Ezzat A., Abd El-Aziz S.H., El-Gharabawy M.M. and Hussein M.O. (1987) The food of *Raja miraletus* Linnaeus, 1758, in Mediterranean waters off Alexandria. *Bulletin of the Institute of Oceanography and Fisheries* 13, 59–74.

Feduccia A. and Slaughter B.H. (1974) Sexual dimorphism in skates (Rajidae) and its possible role in differential niche utilization. *Evolution* 28, 164–168.

Franklin A.B., Shenk T.M., Anderson D.R. and Burnham K.P. (2001) Statistical model selection: an alternative to null hypothesis testing. In Shenk T.M. and Franklin A.B. (eds) *Modeling in natural resource management: development, interpretation and application.* Washington: Island Press, pp. 75–90.

García de la Rosa S.B. and Sánchez F. (1999) Ecología trófica de la raya (*Dipturus chilensis*) y predación sobre merluza común (*Merluccius hubbsi*) en el Atlántico sudoccidental. *VIII Congreso Latinoamericano sobre Ciencias del Mar, 17–21 October 1999.* Perú, pp. 152–154.

Gray A.E., Mulligan T.J. and Hannah R.W. (1997) Food habits, occurrence, and population structure of the bat ray, *Myliobatis californica*, in Humboldt Bay, California. *Environmental Biology Fishes* 49, 227–38.

Jaworski A. and Ragnarsson S.A. (2006) Feeding habits of demersal fish in Icelandic waters: a multivariate approach. *ICES Journal of Marine Science* 63, 1682–1694.

Johnson J.B. and Omland K.S. (2004) Model selection in ecology and evolution. *Trends in Ecology and Evolution* 19, 101–108.

King J.R. and Murphy M.E. (1985) Periods of nutritional stress in the annual cycles of endotherms: fact or fiction? *American Zoologist* 25, 955–964.

Kohen Alonso M., Crespo E.A., García N.A., Pedraza S.N., Mariotti P.A., Beron Vera B. and Mora N.J. (2001) Food habitats of *Dipturus chilensis* (Pisces: Rajidae) off Patagonia, Argentina. *ICES Journal of Marine Science* 58, 288–297.

Lowe C.G., Wetherbee B.M., Crow G.L. and Tester A.L. (1996) Ontogenetic dietary shifts and feeding behavior of the tiger shark, *Galeocerdo cuvier*, in Hawaiian waters. *Environmental Biology of Fishes* 47, 203–11.

Lucifora L.O., Valero J.L., Bremec C.S. and Lasta M.L. (2000) Feeding habits and prey selection by the skate *Dipturus chilensis* (Elasmobranchii: Rajidae) from the south-western Atlantic. *Journal of the Marine Biological Association of the United Kingdom* 80, 953–954.

Lucifora L.O., García V.B., Menni R.C. and Escalante A.H. (2006) Food habits, selectivity, and foraging modes of the school shark *Galeorhinus galeus*. *Marine Ecology Progress Series* 315, 259–270.

Lucifora L.O., García V.B., Menni R.C., Escalante A.H. and Hozbor N.M. (2009) Effects of body size, age and maturity stage on diet in a large shark: ecological and applied implications. *Ecological Research* 24, 109–118.

Mabragaña E. and Giberto D.A. (2007) Feeding ecology and abundance of two sympatric skates, the shortfin sand skate *Psammobatis normani* (McEachran) and the smallthorn sand skate *P. rudis* (Günther) (Chondrichthyes, Rajidae), in the southwest Atlantic. *ICES Journal of Marine Science* 64, 1017–1027.

Mabragaña E., Lucifora L.O. and Massa M.A. (2002) The reproductive ecology and abundance of *Sympterygia bonapartii* endemic to the south-west Atlantic. *Journal of Fish Biology* 60, 951–967.

Magurran A.E. (2004) *Measuring biological diversity.* Malden: Blackwell.

Main C.E. and Collins M.A. (2011) Diet of the Antarctic starry skate *Amblyraja georgiana* (Rajidae, Chondrichthyes) at South Georgia (Southern Ocean). *Polar Biology* 34, 389–396.

McEachran J.D. and Miyake T. (1990) Zoogeography and bathymetry of skates (Chondrichthyes, Rajoidei). In Pratt H.L., Taniuchi J.R.T. and Gruber S.H. (eds) *Elasmobranchs as living resources: advances in the biology, ecology, systematics, and the status of the fisheries. NOAA Technical Report NMFS 90.* Silver Spring, MD: NOAA Fisheries, pp. 305–326.

McEachran J.D., Boesch D.F. and Musick J.A. (1974) Food division within two sympatric species-pairs of skates (Pisces: Rajidae). *Marine Biology* 35, 301–317.

Menni R.C. and Stehmann M.F.W. (2000) Distribution, environment and biology of batoid fishes of Argentina, Uruguay and Brazil. A review. *Revista del Museo Argentino de Ciencias Naturales* 2, 69–109.

Menni R.C., Ringuelet R.A. and Aramburu R.H. (1984) *Peces marinos de la Argentina y Uruguay.* Buenos Aires: Editorial Hemisferio Sur.

Motta P.J. (2004) Prey capture behavior and feeding mechanics of Elasmobranchs. In Carrier J.C., Musick J.A. and Heithaus M.R. (eds) *Biology of sharks and their relatives.* Boca Raton, FL: CRC Press, pp. 165–195.

Olsen A.M. (1954) The biology, migration, and growth rate of the school shark, *Galeorhinus australis* (Macleay) (Carcharhinidae) in south-eastern Australian waters. *Australian Journal of Marine and Freshwater Research* 5, 353–410.

Orlov A.M. (1998) On feeding of mass species of deep-sea skates (*Bathyraja* spp., Rajidae) from the Pacific waters of northern Kurils and southeastern Kamchatka. *Journal of Ichthyology* 38, 635–644.

Pedersen S.A. (1995) Feeding habits of the starry ray (*Raja radiata*) in West Greenland waters. *ICES Journal of Marine Science* 52, 43–53.

Pinkas L.M., Oliphan S. and Iverson I.L.K. (1971) Food habits of albacore, bluefin tuna and bonito in California waters. *California Fish and Game* 152, 1–105.

Pozzi A.J. (1935) Comunicación preliminar sobre una nueva especie de raya de la costa Atlántica Argentina *Raia doello-juradoi*. *Anales del Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia'* 37, 418–422.

Ruocco N.L., Lucifora L.O., Díaz de Astarloa J.M. and Bremec C. (2009) Diet of the white-dotted skate, *Bathyraja albomaculata*, in waters of Argentina. *Journal of Applied Ichthyology* 25(Supplement 1), 94–97.

San Martin M.J., Braccini J.M., Tamini L.L., Chiaramonte G.E. and Perez J.E. (2007) Temporal and sexual effects in the feeding ecology of the marbled sand skate *Psammobatis bergi* (Marini, 1932). *Marine Biology* 151, 505–513.

Sánchez F. and Mabragaña E. (2002) Características biológicas de algunas rayas de la región sud patagónica. INIDEP, Informe Técnico interno, no. 48.

Scharf F.S., Juanes F. and Rountree R.A. (2000) Predator size–prey size relationships of marine fish predators: interspecific variation and effects of ontogeny and body size trophic–niche breadth. *Marine Ecology Progress Series* 208, 229–248.

Skjæraasen J.E. and Bergstad O.A. (2000) Distribution and feeding ecology of *Raja radiata* in the northeastern North Sea and Skagerrak (Norwegian Deep). *ICES Journal of Marine Science* 57, 1249–1260.

Springer S. (1960) Natural history of the sandbar shark, *Eulamia milberti*. Washington, DC: United States Fish and Wildlife Service, Fisheries Bulletin No. 61.

Springer S. (1967) Social organization of shark populations. In Gilbert P.W., Mathewson R.F. and Rall D.P. (eds) *Sharks, skates, and rays.* Baltimore, MD: Johns Hopkins University, pp. 149–174.

Thayer G.W., Schaff W.E., Angelovic J.W. and LaCroix M.W. (1973) Caloric measurements of some estuarine organisms. *Fishery Bulletin* 71, 289–296.

Treloar M.A., Laurenson L.J.B. and Stevens J.D. (2007) Dietary comparisons of six skate species (Rajidae) in south-eastern Australian waters. *Environmental Biology of Fishes* 80, 181–196.

Venables W.N. and Ripley B.D. (2002) *Modern applied statistics with S-Plus.* 4th edition. New York: Springer.

and

Volkman N.J., Presler P. and Trivelpiece W. (1980) Diets of Pygoscelid penguins at King George Island, Antarctica. *Condor* 82, 373–378.

Correspondence should be addressed to:
G.E. Delpiani
Universidad Nacional de Mar del Plata (UNMdP), Facultad de Ciencias Exactas y
Naturales, Laboratorio de Ictiología, Funes 3350, Mar del Plata (B7602AYL)
Argentina
email: gabriela.delpiani@gmail.com