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Food habits of the broad nose skate, *Bathyraja brachyurops* (Chondrichthyes, Rajidae), in the south-west Atlantic

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SUMMARY: Food habits of *Bathyraja brachyurops* were studied based on stomach content analyses of 346 specimens collected from research cruises carried out from 2003 to 2005 on the Argentinean continental shelf (36ºS-55ºS). A total of 265 stomachs (76.6%) contained food, and thirty-five taxonomic levels of prey were identified. The most important prey were fishes followed by isopods. Trophic level analysis revealed that *B. brachyurops* is a tertiary consumer throughout its life history. There were no differences between sexes and regions in the diet composition, but dietary shifts with ontogeny were found. The Levins' standardized index indicated wider niche breadth for small skates, whereas larger skate specimens showed a narrow niche breadth with a specialization in fishes.

Keywords: *Bathyraja*, Argentina, broad nose skate, elasmobranchs, trophic ecology.

RESUMEN: Hábitos alimentarios de la raya de cola corta, *Bathyraja brachyurops* (Chondrichthyes, Rajidae), en el Atlántico Sudoccidental. – Se estudiaron los hábitos alimentarios de *Bathyraja brachyurops* en base al análisis de los contenidos estomacales de 346 ejemplares capturados en campañas de investigación realizadas durante el periodo 2003-2005 sobre la plataforma continental Argentina (36ºS-55ºS). Un total de 265 estómagos (76.6%) contenían alimento en los cuales se identificaron treinta y cinco ítems presa. Las presas más importantes fueron los peces, seguidos por los isópodos, ubicando a *B. brachyurops* como un consumidor terciario a lo largo de toda su historia de vida. No se hallaron diferencias en la composición de la dieta entre sexos y regiones, sin embargo se apreciaron cambios ontogenéticos en la alimentación. El índice de Levins' estandarizado indicó una mayor amplitud de nicho para las rayas de menor tamaño, mientras que los ejemplares de mayor tamaño mostraron una menor amplitud de nicho trófico y una especialización ictiófaga.

Palabras clave: *Bathyraja*, Argentina, raya de cola corta, elasmobranquios, ecología trófica.

INTRODUCTION

The skates of the family Rajidae are found worldwide in marine waters, and are distributed from shallow coastal shelves to abyssal regions (McEachran and Miyake, 1990). They are a significant link of food webs in benthic communities (Orlov, 1998) and may play influential roles in the food webs of demersal marine communities (Ebert and Bizzarro, 2007). *Bathyraja* is the most diverse genus of skates (Nelson, 2006; Ebert and Compagno, 2007) with eight species (*B. brachyurops, B. macloviana, B. albomaculata, B. magellanica, B. scaphiops, B. multispinis, B griseocauda* and *B. cousseauae*) present on the Argentinean continental shelf (Cousseau *et al.,* 2000; Menni and Stehmann, 2000; Díaz de Astarloa and Mabragaña, 2004). Of these, the broad nose skate *Bathyraja brachyurops* (Fowler, 1910) is widely distributed in Argentinean waters, from 36º to 55ºS (Menni and López, 1984; Cousseau *et al.,* 2000).

Skates, like other cartilaginous fishes, are characterized by slow growth, late attainment of sexual maturity and lower fecundity than teleost fishes (Stevens *et al*., 2000). Their life history characteristics make them particularly sensitive to overexploitation and once overfished, populations of skates need more time to recover than populations of teleost fishes (Stevens *et al.*, 2000; Stehmann, 2002). Skates are increasingly targeted in fisheries conducted on the Argentinean continental shelf (Massa and Hozbor, 2003); catches increased from 300 t in 1991 to 14856 t in 1998 (Cousseau *et al.,* 2000). In Argentinean harbours they are commonly landed with no species differentiation under the common name "skates". Therefore, further studies on the biology and ecology of skates are needed for proper management of these fisheries.

Despite the local diversity of *Bathyraja* in Argentinean waters, few studies have focused on the feeding habits and ecology of species of this genus. The diet of five species of *Bathyraja* have been briefly described on the Argentinean continental shelf (Sánchez and Mabragaña, 2002), and only the feeding habits of the Patagonian skate *B. macloviana* have been thoroughly studied (Mabragaña *et al*., 2005; Scenna *et al*., 2006). Brickle *et al*. (2003) provided some data on diet composition of *B. albomaculata, B. brachyurops* and *B. griseocauda* around the Malvinas Islands. The diet composition of skate species of other genera have been studied in the region (Lucifora *et* al., 2000; Koen Alonso *et al*., 2001; Sánchez and Mabragaña, 2002; Braccini and Perez, 2005; Mabragaña *et al*., 2005; Mabragaña and Gilberto, 2007; San Martín *et al*., 2007). Although understanding a predator's trophic interactions is crucial for developing sustainable management strategies (Robinson *et al*., 2007), trophic relationships among skate species in Argentinean waters remain unknown.

The objectives of this paper were to describe the diet composition and trophic level of *B. brachyurops* on the Argentinean continental shelf, evaluate whether there is sexual, regional and ontogenetic variation in their feeding habits and determine their feeding strategy. This study provides the first detailed information on food habits of *B. brachyurops* in an extensive area of the south-west Atlantic in order to understand the role of the species in the food web of this region.

MATERIALS AND METHODS

Sample collection

Specimens of *B. brachyurops* were collected from ten research cruises on the RVs "Dr. E. L. Holmberg" and "Capitán Oca Balda" of the Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP, Mar del Plata, Argentina), between 2003 and 2005 on the Argentinean continental shelf (36ºS-55ºS) (Fig. 1). Skates were captured using a bottom trawl of 200 m mesh in the wing and 103 mm in the codend.

Disc width (DW) of each specimen was measured to the nearest millimetre and sex was recorded. Stomachs were excised, fixed in 4% formaldehyde and analyzed in the laboratory.

Diet composition

Prey items were identified to the lowest possible taxonomic level using keys, field guides (Bastida and Torti, 1973; Menni *et al*., 1984; Boschi *et al*., 1992; Cousseau and Perrotta, 2000) and reference collections at the Ichthiological Laboratory of the University of Mar del Plata. Each prey item was counted and weighed to the nearest 0.01 g using a digital top loading balance. Diet composition was assessed according to the percentage frequency of occurrence (%F), the percentage of wet weight (%W), the percentage of number (%N) and the Index of Relative Importance (IRI = %F (%N + %W)) (Pinkas *et al.,* 1971) expressed as a percentage (Cortés, 1997).

Prey were assigned to seven taxonomic categories (Pisces, Brachyura, Isopoda, Mollusca, Polychaeta, Anomura and Amphipoda) to analyze sexual, regional and ontogenetic variation in the diet. Regional dietary difference was assessed by comparing two study regions (Fig. 1): northern (35ºS-43ºS) and southern (43ºS-55ºS). The northern region is more influenced by the warm, salty waters of the Brazil Current which flows southward adjacent to the east-

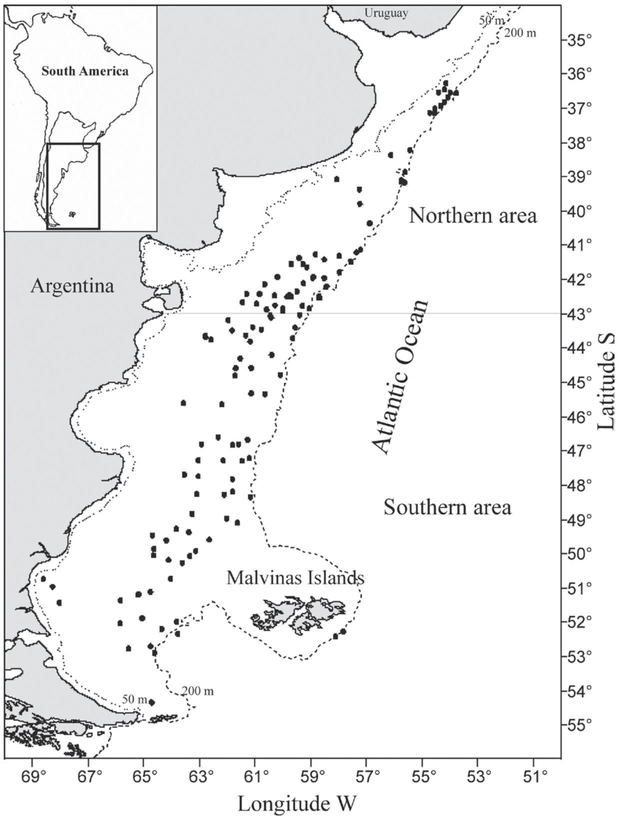

FIG. 1. – Study area showing the location of sampling sites where *Bathyraja brachyurops* were collected on the Argentinean continental shelf. The rectangle in the inset represents the study area.

ern South American continental shelf. The southern region is characterized by the cold and relatively fresh subantarctic waters of the equatorward Malvinas Current (Boltovskoy, 1981; Olson *et al.,* 1988). Ontogenetic variations were determined by analyzing the following size classes: I (<400 mm DW), II (400-500 mm DW) and III (>500 mm DW).

To assess sample size sufficiency (Ferry and Caillet, 1996; Cortés, 1997), the order of stomachs sampled were randomized 100 times, and the mean cumulative diversity of stomach contents (Shannon-Wiener diversity index) plotted as a function of stomach number. Cumulative curves were built separately for each combination of specimen groups considered in the comparative analyses.

Diet comparisons

Similarity in the composition of the diet (%W and %N of each taxonomic category) between regions and size classes was assessed using the multivariate statistical software PRIMER v5 (Clarke and Warwick, 2001). Similarity matrices were constructed using the Bray-Curtis similarity coefficient. Two-way nested analyses of similarities (ANOSIM) using regions and size classes as factors were used to determine whether the dietary composition of *B. brachyurops* was significantly influenced by location or ontogeny. One-way ANOSIMs were performed to identify any paired relationships. Similarity percentages (SIMPER) were used to identify which taxonomic categories characterized the dietary composition of each sample and which taxonomic categories made the greatest contributions to any dissimilarity.

Preliminary multivariate analysis indicated that there were no significant differences between the diets of females and males (ANOSIM %W: R statistic = 0.01, p = 0.069; ANOSIM %N: R statistic = 0.003, p = 0.254) and thus dietary data from both sexes were pooled for subsequent analyses.

Trophic level and feeding strategy

Trophic level (TL) was estimated to determine the position of *B. brachyurops* within the food web and was calculated following Cortés (1999) as:

$$TL = 1 + (\sum_{j=1}^{n} P_j \times TL_j)$$

where TL_j is the trophic level of each prey category j, P_j is the proportion of each prey category j (using %IRI) in the diet of *B. brachyurops*, and n is the total number of prey categories. The taxonomic categories used to calculate the standardized trophic level of *B. brachyurops* were Teleosts, Chondrichthyes, Cephalopoda, Mollusca (excluding cephalopods), Brachyura, Isopoda, Polychaeta, Anomura and Amphipoda. The trophic level of each prey category was obtained from Ebert and Bizarro (2007).

In order to analyze the feeding strategy of each size class of *B. brachyurops,* the graphic method proposed by Amundsen *et al.* (1996) was used by plotting the prey-specific abundance (%Pi) of each prey category against %F. Pi was calculated as the weight of prey category i, divided by the total weight of prey in the stomachs that contained prey category i, expressed as a percentage. Prey points located at the upper right of the diagram are indicative of specialization of the predator population. In contrast, all prey points located along or below the diagonal from the upper left to the lower right reflect a generalized feeding strategy of the predator population. Furthermore, the distribution of points along the diagonal from the lower left to the upper right corner provides a measure of prey importance, with dominant prey at the upper and rare prey at the lower end.

Levins' measure (B) was used for calculating niche breadth of each size class of *B. brachyurops* using the following equation (Krebs, 1989):

$$B = 1 / \sum_{i=1}^{n} pi^{2}$$

where p_i is the proportion of each prey category i in the diet and n is the total number of prey categories in the diet of *B. brachyurops*. The standardized Levins' index ($B_{est} = (B - 1) / (n - 1)$) was used to express niche breadth on a scale from 0 (a narrow niche breadth) to 1 (a broad niche breadth).

RESULTS

Diet composition

All the cumulative diversity curves reached an asymptote, which indicates that the sample sizes were sufficient for describing and comparing the diets (Fig. 2). A total of 346 skates was examined, of which 265 (76.6%) were found with stomachs containing prey items at different stages of digestion. Males (n=125) ranged from 245 to 567 mm DW, while females (n=140) ranged from 268 to 692 mm DW.

Thirty-five taxonomic levels of prey were identified (Table 1): 10 teleosts, 1 condrichthyan, 4 polychaetes, 4 molluscs and 16 crustaceans. The most important dietary component was teleosts, followed by crustaceans (isopods, amphipods and crabs). Among identified teleosts, notothenids, Argentine hake (*Merluccius hubbsi*), and scorpaenids (*Helicolenus dactylopterus*) occurred most frequently and contributed most to the weight. The isopod *Serolis schythei* was the second most dominant prey among crustaceans in terms of %IRI (16.59%) and number (20.65%), and the third most important in terms of occurrence (22.26%) and weight (3.37%). *Libidoclea granaria* was the fourth most dominant prey among crustaceans according to %IRI (8.98%), and contributed the highest values of %F (24.91%) and %W (6.94%) in the diet of *B. brachyurops*. Amphipods were the second most dominant prey in terms of occurrence (23.4%), but the most important according to number (28.53%) and %IRI (20.89%). Unidentified *Serolis* spp. and *Peltarion spinosolum* were also important prey according to occurrence (22.26 and 12.83%), number (14.78 and 2.3%), weight (1.79 and 4.6%) and %IRI (11.44 and 2.74%) respectively. Molluscs (except *Illex argentinus*), polychaetes and chondrichthyans were not important in the diet (<1 %IRI).

Diet comparisons

Two-way nested analyses of similarities showed that there were no significant differences in overall diet between northern (n=118) and southern (n=147) populations (ANOSIM %W: R statistic = -0.037, p = 0.5; ANOSIM %N: R statistic = 0.037, p = 0.5). However, significant differences in the dietary composition of the size classes categorized according to percent of weight and percent of number were ob-

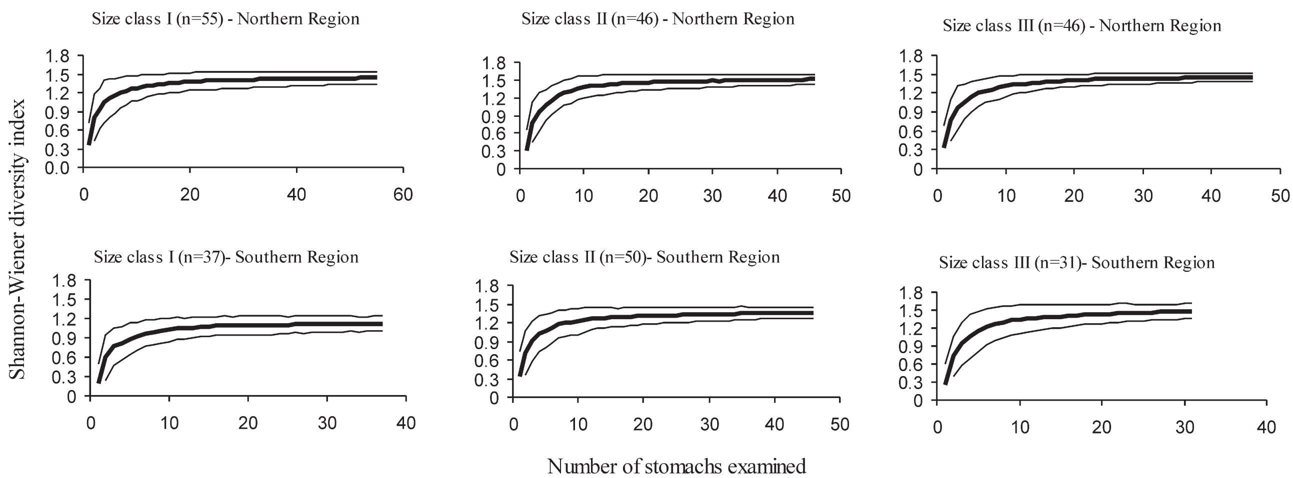

FIG. 2. – Cumulative prey diversity curves for each trophic group of *Bathyraja brachyurops* on the Argentinean continental shelf. The dark line indicates the mean diversity estimated by the Shannon-Wiener diversity index as a function of sample size, and the light lines indicate the standard deviations.

Table 1. – Percentage of occurrence (%F), number (%N), wet weight (%W) and percentage of the Index of Relative Importance (%IRI) for each prey present in the diet of *Bathyraja brachyurops.*

Prey items	%F	%N	%W	%IRI
Pisces				
Congridae				
Bassanago albescens	0.75	0.09	0.45	0.01
Merlucciidae				
Merluccius hubbsi	4.53	0.71	19.1	2.78
Macruronidae				
Macrorunus magellanicus	0.38	0.04	1.87	0.02
Ophidiidae				
Genypterus blacodes	0.38	0.04	1.22	0.01
Raneya brasiliensis	0.38	0.04	0.14	< 0.01
Zoarcidae	1.13	0.18	0.15	0.01
Nototheniidae				
Patagonotothen spp.	10.94	6.41	26.01	11.01
Scorpaenidae				
Helicolenus dactylopterus	2.26	0.4	9.88	0.72
Sebastes capensis	0.38	0.04	0.24	< 0.01
Unidentified teleosts	32.08	8.27	13.43	21.59
Chondrichthyes				
Rajidae				
Bathyraja brachyurops	0.38	0.04	0.37	< 0.01
Polychaeta				
Nepthtyidae	2.64	0.62	0.01	0.05
Lumbrineridae	1.89	0.75	0.02	0.05
Maldanidae	3.4	1.37	0.09	0.15
Unidentified polychaetes	3.02	0.44	0.2	0.01
Mollusca				
Cephalopoda				
Illex argentinus	4.53	0.84	5.99	0.96
Loligo gahi	0.75	0.13	<0.01	< 0.01
Unidentified cephalopods	6.79	0.84	2.25	0.65
Gasteropoda				
Volutidae				
Odontocymbiola magellanica	0.75	0.09	0.26	0.01
Crustaceans				
Unidentified crustaceans	1.13	0.22	0.01	0.01
Amphipoda	23.40	28.25	0.53	20.89
Isopoda				
Cirolana spp.	7.92	1.41	0.26	0.41
Arcturus spp.	4.53	5.13	0.34	0.77
Serolis elliptica	0.38	0.04	<0.01	< 0.01
Serolis paradoxa	1.51	0.27	0.04	0.01
Serolis polaris	1.51	0.18	0.03	0.01
Serolis schythei	22.26	20.65	3.37	16.59
Serolis vemae	0.38	0.09	0.01	< 0.01
Serolis spp.	22.26	14.78	1.79	11.44
Anomura				
Munida subrugosa	1.13	0.13	0.12	0.01
Munida spinosa	0.75	0.09	0.1	< 0.01
Munida spp.	1.13	0.13	0.14	0.01
Brachyura				
Libidoclaea granaria	24.91	4.69	6.94	8.98
Peltarion spinosulum	12.83	2.3	4.6	2.74
Unidentified brachyurans	0.38	0.13	< 0.01	< 0.01

served (ANOSIM %W: R statistic = 0.14, p = 0.001; ANOSIM %N: R statistic = 0.137, p = 0.01).

Pairwise comparisons within ANOSIM in terms of %W and %N showed significant differences between size class I (n= 92) and size class II (n= 96) and size class III (n= 77), but not between size class II and size class III. According to the ANOSIM test, larger differences occurred between size classes I and III (Table 2). SIMPER analyses showed that the

Table 2. – One-way ANOSIM results for *Bathyraja brachyurops* between diets of different size classes analyzed according to percent of weight and percent of number.

	ANOSIM %W	*p*- value	ANOSIM %N	*p*- value
Size I vs. Size II	0.149	0.001	0.14	0.001
Size I vs. Size III	0.204	0.001	0.194	0.001
Size II vs. Size III	0.005	0.261	0.001	0.391
	Global R = 0.12 p = 0.01		Global R = 0.114 p = 0.01	

average dissimilarity between size class I and size class II was high (76.45% by %W and 79.4% by %N). This is mainly due to differences in the importance of isopods and fishes in the diet of the two size classes, although crabs also contributed considerably to the dietary dissimilarity (Table 3). Average dissimilarity between size class I and size class III categorized by %W and %N were 79.33% and 82.13% respectively. SIMPER identified isopods, fishes and crabs as the prey categories responsible for these differences (Table 3).

The diet of size class I consisted largely of isopods. Individuals of size class II fed more frequently on fishes, followed by crabs. In size class III, fish was the most important prey category, followed by amphipods. Fish prey became increasingly important in the diet of larger specimens of *B. brachyurops* (Table 4).

Trophic level and feeding strategy

The trophic level of *B. brachyurops* was 4.16. The three size classes had similar values and were all tertiary consumers ($TL_{\text{size class I}}$= 4.14, $TL_{\text{size class II}}$= 4.12 and $TL_{\text{size class III}}$= 4.19). However, %P*i*-%F plots showed a pronounced and progressive change in diet of *B. brachyurops* with increased size, from a mixed dietary composition in the smallest skates to one dominated almost entirely by fishes in size classes II and III. Individuals of size classes II and III fed mainly on teleosts but small proportions of other prey categories were included in the diet of some specimens (Fig. 3, Table 4). The niche breadths in both classes were narrow (Fig. 3). Conversely, the graphical method proposed by Amundsen *et al.* (1996) demonstrated a more mixed feeding strategy for individuals of size class I, with a certain preference for isopods (Fig. 3, Table 4). Furthermore, the niche breadth value of small skates of *B. brachyurops* was wider (Fig. 3), which suggests a more generalized feeding strategy.

Table 3. – The contribution of prey categories to observed dietary differences among *B. brachyurops* size classes determined by SIMPER analyses. Prey categories are listed in descending order of percentage contribution and only categories contributing >2% to the observed differences are shown.

Percent of Weight Prey categories	Mean ± S.D. Dissimilarity	Contribution to dissimilarity %	Cumulative percentage
Size I vs. Size II (76.45%)			
Isopoda	25.22 ± 1.15	32,99	32,99
Pisces	24.17 ± 1.15	31,61	64,6
Brachyura	17.65 ± 0.85	23,08	87,69
Polichaeta	3.17 ± 0.33	4,15	91,84
Size I vs. Size III (79.33%)			
Pisces	27.49 ± 1.21	34,65	34,65
Isopoda	25.39 ± 1.14	32,01	66,66
Brachyura	15.11 ± 0.74	19,05	85,71
Squids	4.32 ± 0.35	5,44	91,16
Percent of Number Prey categories	**Mean ± S.D. Dissimilarity**	**Contribution to dissimilarity**	**Cumulative percentage**
Size I vs. Size II (79,40%)			
Isopoda	24.52 ± 1.18	30,87	30,87
Pisces	20.07 ± 1.01	25,27	56,15
Brachyura	15.20 ± 0.79	19,15	75,29
Amphipoda	10.84 ± 0.63	13,65	88,94
Polychaeta	4.48 ± 0.42	5,64	94,58
Size I vs. Size III (82.13%)			
Isopoda	24.79 ± 1.15	30,18	30,18
Pisces	22.05 ± 1.07	26,85	57,03
Brachyura	12.74 ± 0.70	15,21	72,54
Amphipoda	11.72 ± 0.68	14,26	86,81
Polychaeta	5.54 ± 0.43	6,74	93,55

Table 4. – Percentage of occurrence (%F), number (%N), wet weight (%W) and percentage of the Index of Relative Importance (%IRI) for each taxonomic category present in the diet of different *Bathyraja brachyurops* size classes.

Prey categories	Size class I (n = 92)				Size class II (n = 96)				Size class III (n = 77)			
	%F	%N	%W	%IRI	%F	%N	%W	%IRI	%F	%N	%W	%IRI
Pisces	31.52	10.06	50.61	22.29	62.50	28.50	72.96	69.40	62.34	18.83	87.62	79.02
Polychaeta	18.48	5.57	0.90	1.39	4.17	1.47	0.70	0.10	5.19	1.16	0.08	0.08
Mollusca	7.61	0.63	1.58	0.20	4.17	0.65	0.94	0.07	9.09	1.86	3.40	0.57
Amphipoda	18.48	18.86	1.39	4.36	13.54	25.08	0.47	3.79	19.48	44.86	0.35	10.49
Isopoda	63.04	59.82	28.54	64.93	30.21	30.78	3.43	11.31	15.58	24.87	1.75	4.94
Anomura	3.26	0.64	0.80	0.05	2.08	0.33	0.24	0.01	3.90	0.74	0.20	0.04
Brachyura	28.26	4.41	16.18	6.78	40.63	13.19	21.26	15.32	28.57	7.67	6.60	4.86

DISCUSSION

Stomach content analysis of *Bathyraja brachyurops* showed that it is a piscivorous predator that feeds largely on benthic and demersal fishes on the Argentinean continental shelf. Other benthic invertebrates are present in the diet but in lower proportions. The dominance of fishes and cephalopods in the diet of large individuals of larger skate species has been reported by several authors (Ebert *et al.*, 1991; Smale and Cowley, 1992; Orlov, 1998; Lucifora *et al.*, 2000; Koen Alonso *et al.*, 2001; Brickle *et al.*, 2003). Koen Alonso *et al.* (2001) noted that smaller specimens of the long nose skate *Dipturus chilensis* in the Argentinean Sea preyed on benthic crustaceans, whereas larger individuals foraged mostly on fishes and molluscs. A general pattern for the feeding habits of skates was suggested by Braccini and Perez (2005), in which small individuals (either smaller species or young individuals of larger species) prey mainly on crustaceans and thus are secondary consumers (TL<4), while larger individuals feed on fishes and cephalopods and thus are tertiary consumers that occupy higher trophic levels (TL>4). Nevertheless, no differences were found between the trophic levels of the three size classes of *B. brachyurops* analyzed here, which ranged between 4.12 and 4.19. Ebert and Bizarro (2007) estimated the trophic level for 60 skate species, based on quantitative data obtained from different studies.

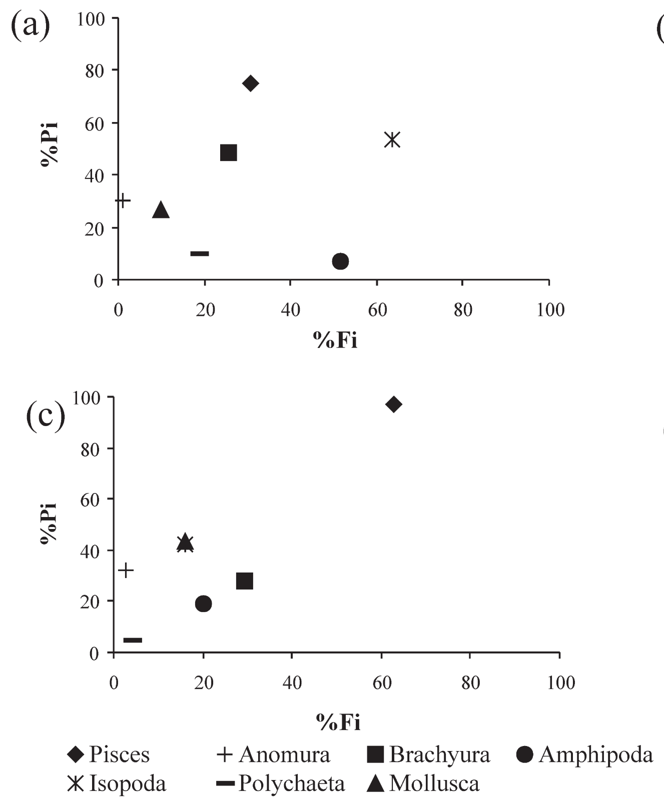

FIG. 3. – Prey-specific abundance (%*Pi*) plotted against frequency of occurrence (%Fi) of prey categories of *Bathyraja brachyurops* from the south-west Atlantic. (a) <400 mm DW (n= 92), (b) 400-500 mm DW (n= 96), (c) >500 mm DW (n= 77), and (d) Standardized Levins' measure for the three size classes considered.

Values ranged from 3.48 (*Rajella caudaspinosa*) to 4.22 (*D. chilensis*) and the greatest values for species of *Bathyraja* were 4.09 (*B. griseocauda*) and 4.08 (*B. brachyurops*). In our study the trophic level of *B. brachyurops* was 4.16 and thus conformed to the feeding pattern hypothesis as a tertiary consumer which occupies trophic positions similar to other upper trophic level predators e.g. marine mammals, seabirds (Wetherbee and Cortés, 2006), large teleosts and some shark species (Ebert and Bizzarro, 2007).

One case of cannibalism was found in our study and this behaviour has been observed in other skates (Ellis *et al.*, 1996). Ebert *et al.* (1991) analyzed the diet of several species of skates from the south eastern Atlantic, including one species of the genus *Bathyraja* (*B. smithii*), and found, similarly to the present study, that the most important prey were crustaceans and teleosts. In this study the most frequently consumed teleosts that contributed most to the diet in terms of weight were *Patagonotothen* spp., Argentine hake, and scorpaenids (*Helicolenus dactylopterus*). The Argentine hake is the most important demersal fishing resource on the Argentinean shelf (Bezzi *et al.*, 2004). Furthermore, the Argentine hake is consumed by a lot of organisms, such as *Illex argentinus* (Santos and Haimovici, 1997), *Squalus acanthias* (García de la Rosa and Sánchez, 1997), *Dipturus chilensis* (Lucifora *et al.*, 2000; Koen Alonso *et al.*, 2001), dusky dolphins *Lagenorynchus obscurus* (Alonso *et al.*, 1998) and 20 other fish species (García de la Rosa and Sánchez, 1997), which prey on different stages of ontogeny.

There were no sexual differences in the dietary composition of *B. brachyurops*, which indicates that males and females consume similar prey and occupy similar trophic roles. Similar findings have been reported in other studies (Braccini and Perez, 2005; Scenna *et al.*, 2006; San Martín *et al.*, 2007). Conversely, sexual differences in the diet have been found in other skate species of *Bathyraja* in the western Bering Sea (e.g. *B. parmifera*, *B. aleutica*, *B. maculata*, *B. matsubarai*, *B. minispinosa*) (Orlov, 2001). Sexual heterodonty has been investigated in *B. brachyurops* and it was found that females have wider, more rounded teeth on both the upper and lower jaws than males (Belleggia, 2007). Dental sexual dimorphism was originally proposed to be a result of feeding segregation among sexes (Du Buit, 1978). It is also well known that elasmobranchs exhibit complex reproductive behaviour in which the teeth are used by males for firmly gripping the female during copulation (Price, 1967; McEachran, 1977; Kajiura *et al*., 2000). Males and females of *B. brachyurops* have a similar diet, which suggests that differences in tooth morphology could be related more to reproductive behaviour than to feeding.

Although all size classes of *B. brachyurops* occupy similar trophic roles and are tertiary consumers (TL>4), ontogenetic shifts in the diet composition were found in this work. Small specimens of *B. brachyurops* predominantly fed upon isopods, whereas fishes and crabs became important in the diet of larger skates. Small individuals of *B. brachyurops* that occurred around Malvinas Islands mostly foraged on benthic gammarid amphipods and isopods, whereas larger skates consumed fish and cephalopods (Brickle *et al*., 2003). Orlov (1998) found that larger species of *Bathyraja* in the northern Pacific (*B. aleutica*, *B. maculata*, *B. parmifera*, and *B. matsubarai*) preyed on large crustaceans, cephalopods and fishes, while smaller species (*B. interrupta*, *B. minispinosa* and *B. violacea*) fed on benthic invertebrates. Ontogenetic changes in the diet composition of skates have been reported for several other species (Pedersen, 1995; Skjaeraasen and Bergstad, 2000; Brickle *et al*., 2003), and may be attributed to morphological constraints (McEachran *et al*., 1976) or may simply reflect differences in the foraging ability of larger individuals. Dietary changes associated with the ontogeny of *B. brachyurops* may, in part, explain how food resources within a given area are partitioned to minimize competition between co-specifics at different life-history stages, as Ebert (2002) proposed for *Notorynchus cepedianus*. Ontogenetic change in feeding habits is an almost universal phenomenon in fishes and thus its occurrence in elasmobranchs is not surprising. Although many species of skates increase in size, there are also changes in habitat, movement patterns, swimming speed, size of jaws, teeth and other factors that result in variable exposure to prey or improved ability to capture different prey (Wetherbee and Cortés, 2006).

Some studies on the feeding habits of skates have described them as generalist predators (McEachran *et al*., 1976; Orlov, 1998), although some species have been regarded as specialist predators (Ebert *et al*., 1991; Braccini and Perez, 2005; Scenna *et al*., 2006; San Martín *et al*., 2007). A generalist predator has a broad dietary niche, in contrast to the small variety of prey found in the stomach contents of a specialist predator. In our study, the Levins' standardized index indicated that the niche breadth was widest for small skates, whereas the niche breadth of the larger skates was relatively narrow. The analysis of the prey-specific abundance in relation to frequency of occurrence showed that small individuals of *B. brachyurops* have a generalist strategy with isopods as the main prey. However, larger skates, demonstrated a marked specialization in teleosts.

As in this study, Brickle *et al.* (2003) found that adult specimens of *Bathyraja brachyurops* were active predators and preyed mainly on fishes and cephalopods. However, the Argentine short fin squid *Illex argentinus* appeared to be the most important prey among cephalopods in the diet of *B. brachyurops* on the Argentinean continental shelf (the present study) and the loliginid squid *Loligo gahi* was the most common (in terms of numbers and frequency of occurrence) in the diet around the Malvinas Islands (Brickle *et al.,* 2003). The difference would be attributed to different distribution patterns observed in these two species of cephalopods. *Loligo gahi* is the coldest water dwelling loliginid species, and reaches its highest abundance in waters associated with the Malvinas Current which derives from the Antarctic Circumpolar Current (Hatfield and Des Clers, 1998). In contrast, *I. argentinus* presents latitudinal migrations and its concentrations during different times of the year are governed by feeding, sexual maturation and egg-laying (Brunetti *et al.,* 1998). It is a species associated mainly with waters of the Patagonian shelf (Haimovici *et al*., 1998).

Bathyraja brachyurops occurs sympatrically with *B. macloviana* and *B. albomaculata* along the Argentinean continental shelf (Cousseau *et al.,* 2000), which have been reported to be polychaete consumers (Sánchez and Mabragaña, 2002; Mabragaña *et al.*, 2005; Scenna *et al*., 2006). Species that share the same habitat may rely on differences in the utilization of food resources to avoid competition (Schoener, 1974). In our study we found that polychaetes made a low contribution to the diet of *B. brachyurops* (%IRI =0.44). The differences in feeding habits between these two polychaete consumers and *B. brachyurops* would indicate low feeding competition among these species.

Prior to this diet study, no published information was available on the food habits of *B. brachyurops* on the Argentinea continental shelf. To date our understanding of the Argentinean benthic ecosystem is scant. Although the results of this research will contribute to increasing our knowledge about benthic communities, further studies are warranted to fully understand the food webs of benthic and demersal communities on the Argentinean continental shelf.

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