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Feeding ecology of *Bathyraja macloviana* (Rajiformes: Arhynchobatidae): a polychaete-feeding skate from the South-west Atlantic*

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SUMMARY: The present paper analyses the diet, feeding strategy and niche width of *B. macloviana* in a sector of the Argentinean Continental Shelf (ACS). Individuals (n = 147) were collected from 43 sampling stations in late summer and autumn 2001. Thirty one alimentary items in the gut contents were found, with a clear dominance of polychaetes. Crustaceans were secondary alimentary items. The polychaete *Travisia kerguelensis* was the main food item ingested, followed by Nepthyidae, Sabellidae and Lumbrineridae, while Gammaridae and Cirolanidae were the main items among crustaceans. The niche width and feeding strategy displayed by *B. macloviana* support the specialisation towards polychaetes throughout this study. Slow motile and infaunal species constitute major preys. The results suggest that this skate actively selects worms, reflecting, in some sense, the composition of the polychaete assemblage, and allowing a low dietary overlap with other sympatric skates of the ACS.

Keywords: skates, feeding strategy, polychaetes, niche width, specialist, Argentina.

RESUMEN: ECOLOGÍA ALIMENTARIA DE *BATHYRAJA MACLOVIANA* (RAJIFORMES, ARHYNCHOBATIDAE): UNA RAYA CONSUMIDORA DE POLIQUETOS DEL ATLÁNTICO SUDOCCIDENTAL. – En el presente trabajo se analiza la dieta, estrategia alimentaria y amplitud del nicho trófico de *Bathyraja macloviana* en un sector de la Plataforma Continental Argentina (ACS). Los individuos (n = 147), fueron colectados en 43 estaciones de muestreo a fines de verano y otoño de 2001. Fueron encontrados 31 ítems en los contenidos estomacales con una clara dominancia de poliquetos. Los crustáceos constituyeron ítems secundarios. El poliqueto *Travisia kerguelensis* fue el principal ítem consumido seguido por Nepthyidae, Sabellidae y Lumbrineridae, mientras que Gammaridea y Cirolanidae fueron los ítems principales entre los crustáceos. En este estudio, la amplitud de nicho y la estrategia alimentaria de esta especie muestran su especialización hacia poliquetos. Especies de baja motilidad e infaunales constituyeron las presas fundamentales. Los resultados sugieren que esta raya selecciona activamente poliquetos, reflejando de algún modo las asociaciones de poliquetos, lo que permite un bajo solapamiento con otras especies de rayas simpátricas del Atlántico Sudoccidental.

Palabras clave: rayas, estrategia alimentaria, poliquetos, amplitud de nicho, especialista, Argentina.

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INTRODUCTION

Skates are a significant element of the trophic food webs in benthic and demersal communities (McEachran and Musick, 1975; Ajayi, 1982; Ebert *et al*., 1991; Orlov, 1998). Within the skates, *Bathyraja* is the most diversified genus and comprises about 45 species (McEachran and Dunn, 1998; Compagno, 1999). These fishes have a worldwide distribution, being present in temperate and cold waters from the continental shelf to the upper slope (McEachran and Miyake, 1990). In spite of this, the knowledge of the feeding ecology of this genus is scarce (Ebert *et al*., 1991; Orlov, 1998).

At least eight described species of *Bathyraja* are recorded on the Argentine Continental Shelf (ACS): *B. brachyurops* (Fowler, 1910), *B. magellanica* (Philippi, 1902), *B. scaphiops* (Norman, 1937), *B. multispinis* (Norman, 1937), *B. albomaculata* (Norman, 1937), *B. griseocauda* (Norman, 1937), *B. cousseauae* Díaz de Astarloa and Mabragaña, 2004 and *B. macloviana* (Norman, 1937). Previous studies on skates of the genus concentrated primarily on taxonomy and distribution (Menni, 1973; Cousseau *et al*., 2000; Menni and Stehmann, 2000 and references therein; Díaz de Astarloa and Mabragaña, 2004). Preliminary descriptions of the diet and reproduction of some species of *Bathyraja* were recently carried out (Sanchez and Mabragaña, 2002; Scenna, 2003; Ruocco, 2004).

The Patagonian skate *B. macloviana* is endemic to South America, distributed along the Atlantic and Pacific Oceans (Pequeño and Lamilla, 1993; Menni and Stehmann, 2000). In the ACS, it is distributed from 35°S to 55°S, between 80 and 250 m depth. It was also recorded in the Beagle Channel (Norman, 1937; Bellisio *et al*., 1979).

B. macloviana is the smallest species of the genus in the ACS, reaching 67 cm in total length (*TL*) (Cousseau *et al*., 2000), and it is one of the most important skates in terms of biomass in Patagonian waters (Sanchez and Mabragaña, 2002). In this area, *B. macloviana* matures at 53-58 cm of *TL*, suggesting a late maturity. Preliminary analysis of the diet suggested that this skate feeds on polychaetes (Sanchez and Mabragaña, 2002; Scenna, 2003).

Skates as a whole are becoming target species in South-west Atlantic fisheries (Agnew *et al*., 1998; Paesch and Meneses, 1999; Cousseau *et al*., 2000). The general low fecundity and late maturity typical of most rajid species would indicate that they are particularly sensitive to fishing pressure and overexploitation (Walker and Hislop, 1998). Most of the demersal fisheries in Argentina include by-catches of skates that were mostly discarded until the early 1990s. This situation changed and catches increased from 300 tons in 1991 to 14,856 tons in 1998 (Cousseau *et al*., 2000). Therefore, further studies on the biology and ecology of this group are needed for the proper management of the fishery.

The main goals of this work are to analyse the diet, feeding strategy and niche width of *B. macloviana* in the ACS.

MATERIALS AND METHODS

Study area

The study area comprises a sector of the ACS, between 37ºS and 50ºS and 80 and 400 m depth in the southwest Atlantic (Fig. 1). The water masses of the shelf are of subantarctic origin. Subantarctic waters enter the shelf mainly between the Malvinas Islands and Tierra del Fuego. These water masses are modified substantially by the contribution of diluted waters from the Magellan Strait and freshwater from Negro River and La Plata River. Bottom temperature ranges from 4 to 15°C. The general pattern of circulation of marine currents follows the continental shelf with NNE direction (Guerrero and Piola, 1997).

Data collection

Bathyraja macloviana individuals were collected during the day from 43 sampling stations on two research cruises designed to assess demersal fish stocks in late summer (southern locations) and autumn (northern locations) 2001 by the R/V “Eduardo L. Holmberg” (INIDEP) (Fig. 1). Skates (n=147) were captured using a bottom trawl performed with an Engel mesh type. Total length (*TL*) and disc width (*DW*) of each specimen were measured to the nearest millimetre (mm), weight was measured to the nearest gram (g) and sex was recorded. Some stomach contents were analysed on board and prey items were identified and assigned to major taxonomic groups. In order to identify the prey groups to a lower specific level, 108 stomachs were frozen and analysed in the laboratory.

As part of a usual sampling regime carried out at each station, biological data (abundance, *TL*, sex

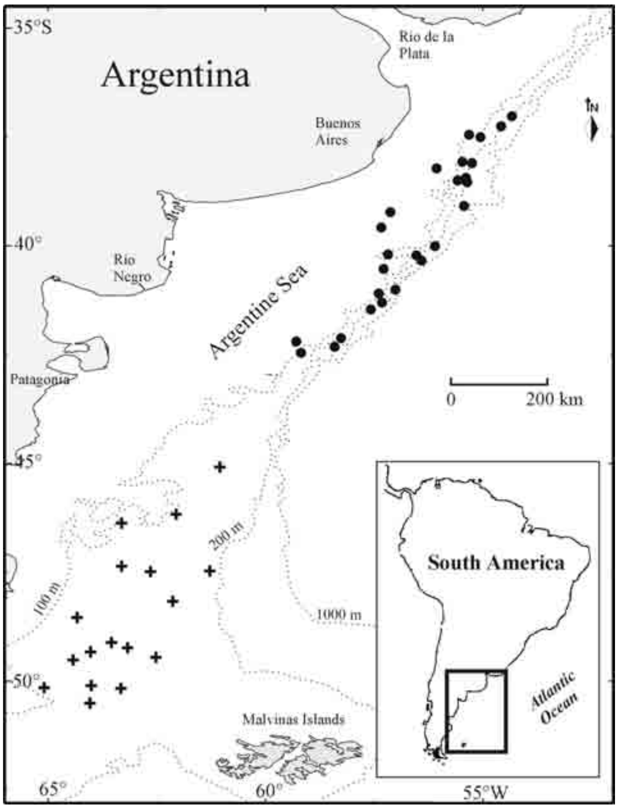

FIG. 1. – Location of sampling sites of stomach contents of *Bathyraja macloviana*, corresponding to southern (+) and northern (•) regions of the study area.

and gut contents assigned to major taxonomic groups) of other rajids collected (n= 491) from the 43 sampling stations were recorded on board.

Data analysis

The diet was expressed as frequency of occurrence of major groups for all the skates collected on board (n= 638). On the other hand, prey items of *B. macloviana* analysed in the laboratory (n = 108) were identified to the lowest taxa possible, counted and weighed (wet weight) to the nearest 0.01 g. We assessed the prey importance by percentage frequency of occurrence (%F), numerical abundance (%A) and percentage of biomass (%B). An index of relative prey importance (IRI) was calculated for each prey category *i* as the product of $\%F_i$ and $\%B_i$ and expressed as a percentage, where:

$$\%\text{IRI} = 100\ \text{IRI}_i \Big/ \sum_{i=1}^{n} \text{IRI}_i$$

and *n* is the total number of food categories considered at a given taxonomic level (Cortes, 1997; Griffiths, 1997). Numerical percentage contribution was excluded in this analysis because it is biased towards small prey items (e.g. amphipods and isopods), and because it is difficult to estimate numbers in each category when there is mastication of food items (Hyslop, 1980; Griffiths, 1997).

The analysis was carried out at two levels: the lowest taxonomic groups possible and functional groups. To evaluate the potential vulnerability to fish predation, prey items were assigned into functional groups from specific literature using aspects of life habits (mobility as the major criteria: motile, discretely motile and sessile) related to particular traits that influence invertebrate conspicuousness (Fauchald and Jumars, 1979; Boschi *et al.*, 1992; Wolff, 1992). Stomachs with prey items that showed a high degree of digestion (e.g. only "polychaete remains") were removed to perform this analysis (n=21).

Similarity in the composition of the diet (% IRI of each prey item) between stations was determined by a non-parametric multivariate analysis (Field *et al.*, 1982; Clarke, 1993; Clarke and Warwick, 2001) and the ANOSIM (Analysis of similarities) test (Clarke and Green, 1988; Clarke and Warwick, 2001). The ANOSIM test was used to search for differences in the diet between northern and southern sectors defined in the study area. This permutation test analyses differences between replicates within sites contrasted with differences between sites, computing an R statistic under the null hypothesis "no difference between sites". R falls between -1 and 1, so R is approximately 0 if the null hypothesis is true and R= 1 if all replicates within sites are more similar to each other than any replicates from different sites. Classification (group average sorting of the Bray-Curtis similarity measures based on 4th root transformed %IRI data) and ordination (multidimensional scaling (MDS) on the above similarity matrices) were performed using the PRIMER software (Clarke and Warwick, 2001). Niche width was analysed by the reciprocal of Simpson's diversity index (λ_i), the Levins index B (Levins, 1968)

$$B = 1 / \lambda_i = 1 / \Sigma\ p_{ij}^2$$

where p_{ij} is the proportion of utilisation of resource *j* by species *i*.

Finally, the feeding strategy was analysed with the graphical method proposed by Amundsen *et al.* (1996), which incorporated the prey-specific biomass into Costello's (1990) analysis. This new parameter is defined as the percentage that a prey taxon comprises of all items in only those predators in which the actual prey occurs, or in mathematical terms:

TABLE 1. – Stomach contents of *Bathyraja macloviana* (n = 108) from the study area, presented as percentage of occurrence (%F), abundance (%A), wet biomass (%B), and percentage of the index of relative importance IRI (%F x %B) for each prey taxa (%IRI) (see text for details).

Taxa	%F	%A	%B	IRI	%IRI
Polychaeta	*96.55*	*60.26*	*85.02*	*8208.54*	*88.03*
Polychaeta remains	66.67	4.03	22.99	1532.49	37.982
Travisia kerguelensis	56.67	23.80	26.61	1507.78	37.369
Nephtyidae	40.00	6.39	8.87	354.92	8.796
Sabellidae	6.67	9.15	11.83	78.86	1.954
Lumbrineridae	38.89	5.65	1.98	76.91	1.906
Capitellidae	14.44	2.42	2.67	38.52	0.955
Terebellidae	8.89	1.55	3.22	28.66	0.710
Ampharetidae	7.78	3.23	2.10	16.31	0.404
Polynoidae	6.67	0.61	2.06	13.75	0.341
Onuphiidae	15.56	1.88	0.81	12.64	0.313
Maldanidae	3.33	0.47	0.94	3.12	0.077
Eunicemorfa	2.22	0.20	0.36	0.80	0.020
Nereididae	1.11	0.20	0.34	0.37	0.009
Ophelina sp.	3.33	0.20	0.08	0.27	0.007
Glyceriidae	3.33	0.14	0.06	0.20	0.005
Owenia sp.	2.22	0.20	0.04	0.09	0.002
Arabellidae	1.11	0.07	0.04	0.05	0.001
Phyllodocidae	1.11	0.07	0.02	0.02	0.001
Crustacea	*74.71*	*39.47*	*14.94*	*1116.57*	*11.97*
Gammaridae	52.22	30.80	3.45	180.12	4.464
Cirolanidae	21.11	5.78	8.32	175.54	4.351
Idotheidae	5.56	0.94	1.50	8.31	0.206
Peltarium spinulosum	3.33	0.20	0.98	3.26	0.081
Isopoda	6.67	0.54	0.11	0.76	0.019
Sphaeroma sp.	1.11	0.13	0.28	0.31	0.008
Macrochiridotea stebbingi	4.44	0.27	0.06	0.27	0.007
Cumacea	3.33	0.27	0.05	0.18	0.004
Lepadidae	1.11	0.34	0.15	0.17	0.004
Crustacean remains	2.22	0.13	0.03	0.06	0.001
Serolis polaris	1.11	0.07	0.02	0.02	<0.001
Echinodermata	*1.85*	*0.13*	*0.02*	*0.04*	*<0.001*
Ophiura unid.	1.85	0.13	0.02	0.04	<0.001
Mollusca	*0.93*	*0.13*	*0.02*	*0.02*	*<0.001*
Hyatella solida	0.93	0.13	0.02	0.02	<0.001

$$Pi= (SBi/SBt_i) \times 100$$

where P*i* is the prey-specific biomass of prey *i*, B*i* the stomach content (weight) comprised of prey *i*, and Bt_i the total stomach content in only those predators with prey *i* in their stomach. Then this value is plotted against the frequency of occurrence on a two-dimensional graph and information about feeding strategies in terms of specialisation (narrow dietary niche width) and generalisation (broad dietary niche width) can be extracted. Additional information about the method is available in Costello (1990) and Amundsen *et al*. (1996).

RESULTS

Analysed skates of *B. macloviana* (n = 147) were mostly adults, with a *TL* range of 34-66 cm. More than 98% contained food in the stomach. They fed on four main groups, expressed in frequency of occurrence: Polychaeta (95.15%), Crustacea (72.82%), Echinodermata (3.88%) and Mollusca (0.97%).

All stomachs analysed in the laboratory (n= 108) contained food. Thirty one alimentary items were found, with a clear dominance of polychaetes (17 species). Crustaceans appeared as secondary alimentary item (10 species) (Table 1). The polychaete Opheliidae *Travisia kerguelensis* was the main item ingested, reaching a percentage IRI of 37.7%, followed by Nepthyidae (8.8%), Sabellidae (1.95%) and Lumbrineridae (1.91%), while Gammaridae (4.46%) and Cirolanidae (4.35%) were the main items among crustaceans (Table 1).

Regarding functional groups, *B. macloviana* preyed upon infaunal and slow motile invertebrates, mainly discretely motile polychaetes and crustaceans (Table 2). Epibenthic crustaceans and motile polychaetes were also included, but in lower proportions (Table 2).

TABLE 2. – Stomach contents of *Bathyraja macloviana* (n = 87) from the study area presented as percentage of occurrence (%F), wet biomass (%B) and percentage of the index of relative importance IRI (%F x %B) for each functional groups (%IRI) (see text for details).

GROUP	F	B	%F	%B	IRI	%IRI
POLYCHAETA						
Discretely motile	51	84.64	58.62	35.19	2,062.87	40.19
Motile or discretely motile	52	17.82	59.77	7.41	442.85	8.63
Motile	46	33.11	52.87	13.77	727.92	14.18
Sessile	21	57.44	24.14	23.88	576.45	11.23
CRUSTACEA						
Discretely motile (infaunal)	63	43.79	72.41	18.20	1,318.29	25.68
Motile (epibenthic)	3	3.11	3.45	1.29	4.46	0.09
ECHINODERMATA						
Discretely motile	2	0.06	2.30	0.03	0.06	< 0.01
MOLLUSCA						
Discretely motile	1	0.06	1.15	0.02	0.03	< 0.01

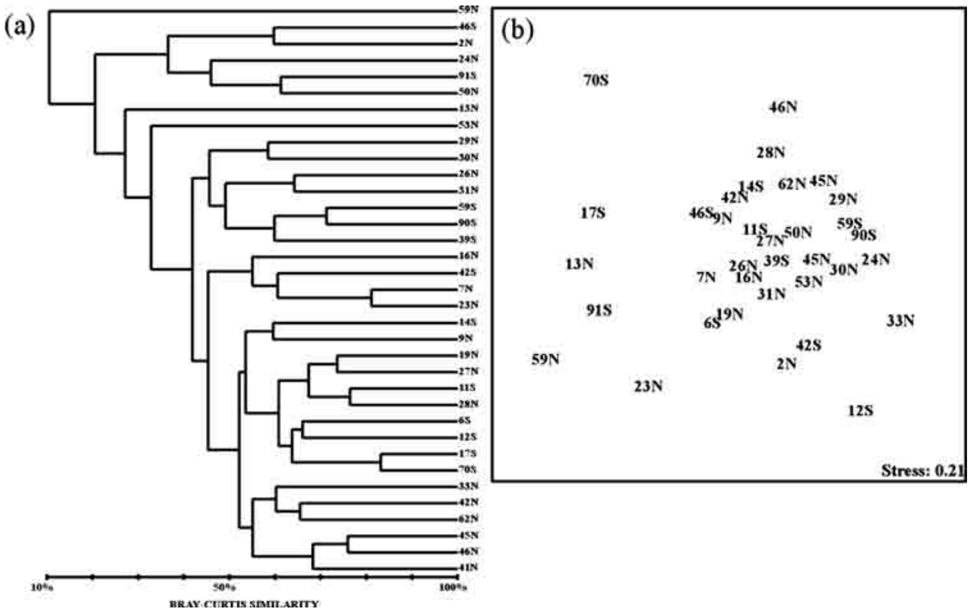

FIG. 2. – Feeding patterns of *Bathyraja macloviana* in relation to the region of the ACS analysed. (a) Classification of stations using %IRI of prey taxa, (b) MDS ordination of stations using %IRI of prey taxa (Stress: 0.21). S = southern stations, N = northern stations.

Skates showed similar values in diet composition (% IRI) throughout the study area. The global test of the ANOSIM (R = 0.065, p= 79.3%) indicated no difference between sites. This similar diet was also evident in the classification (Fig. 2a) and ordination (Fig. 2b) analyses performed, in which all sampling sites were clustered together, from the coast of Buenos Aires (northern stations) to Patagonia (southern stations) (Figs. 1, 2).

A specialisation of *B. macloviana* was found, with most of the prey points positioned towards the upper right corner of the graph (Fig. 3). Typically, all individuals had been feeding on the dominant prey taxon, polychaetes, but small proportions of other prey types, like crustaceans, were included in the diet of some individuals. Echinoderms and molluscs were rarely found. At specific level, there was

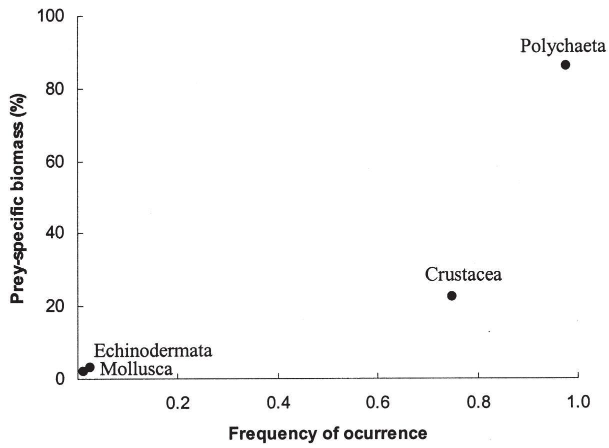

FIG. 3. – Feeding strategy plot for *Bathyraja macloviana*. Contribution of prey groups expressed as percentage of prey-specific biomass. Points represent different prey types.

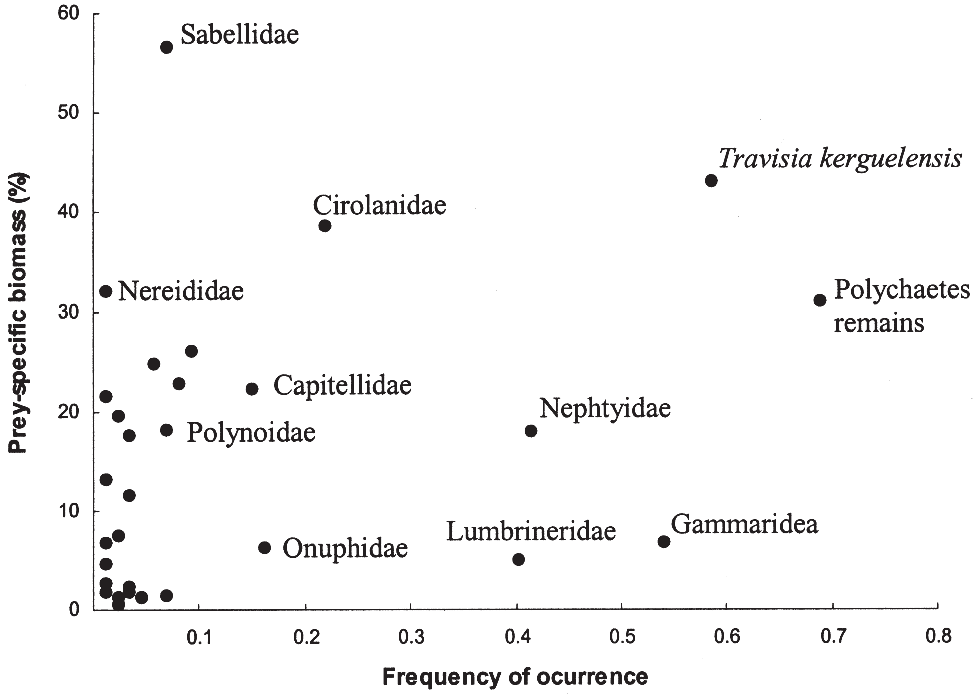

FIG. 4. – Feeding strategy plot for *Bathyraja macloviana*. Contribution of prey taxa expressed as percentage of prey-specific biomass. Points represent different prey types.

a tendency to specialisation towards the discretely motile worm *T. kerguelensis*, while other prey types showed a low average contribution to the stomach contents (mainly amphipods Gammaridae and polychaetes Lumbrineridae and Nephtyidae) (Fig. 4). The value of niche breadth (B= 3.37) for *B. macloviana*, calculated on the lowest specific level of preys, indicates a relative low variability in its diet.

Ten species of skates (n= 491) were collected together with *B. macloviana*. The most important prey items, except for *Bathyraja albomaculata,* were crustaceans, mainly burrowing isopods Cirolanidae, decapods and amphipods (Table 3). Demersal fishes, mainly Nototheniidae, were observed in high frequencies in two abundant and large species *Dipturus chilensis,* and *Bathyraja brachyurops*. On the other hand, *Illex argentinus,* the most abundant cephalopod in the ACS (Brunetti *et al*., 1998), was consumed by three large species *B. griseocauda, B. brachyurops and D. chilensis*. Finally, although reaching similar sizes and feeding primarily on crustaceans, two small skates, *Psammobatis rudis* and *P. normani,* showed differences in the other taxa consumed. In *P. rudis* fishes (juveniles of Nototheniidae) constituted the secondary item, and polychaetes and molluscs were of minor importance, whereas in *P. normani* polychaetes were consumed in high frequency, fishes were of minor importance and molluscs were absent from the diet.

TABLE 3. – Stomach contents presented as percentage of occurrence (%F) of major taxa and range *TL* (cm) of rajids (n = 491) collected simultaneously with the patagonian skate *B. macloviana* in the study area.

Species	n	*TL* (cm)	Fish	Crustaceans	Molluscs	Polychaetes
A. doellojuradoi	15	34 - 50	20.0	73.3	-	13.3
B. albomaculata	60	19 - 81	-	51.7	1.7	63.3
B. brachyurops	102	16 - 88	31.4	42.2	19.6	5.9
B. griseocauda	37	33 - 118	21.6	54.1	16.2	2.7
B. magellanica	15	33 - 69	20.0	53.3	-	6.7
B. multispinis	4	72 - 89	-	75.0	-	-
B. scaphiops	12	39 - 86	16.7	25.0	-	16.7
D. chilensis	101	34 - 102	40.6	46.5	10.9	-
P. normani	113	32 - 55	0.9	61.9	-	44.2
P. rudis	33	23 - 51	27.3	84.8	6.1	9.1

DISCUSSION

The present study on the feeding ecology of *Bathyraja macloviana* showed its narrow food niche and a marked tendency to specialisation on polychaetes of low motility in the southwest Atlantic. The most important prey items observed in 9 other species of skates in ACS (see Table 3) were crustaceans, squids and fishes; only *Bathyraja albomaculata* also consumed polychaetes in high frequency.

A central aspect of niche theory and feeding strategies is the generalist-specialist dichotomy (Pianka, 1988). A generalist predator has a broad dietary niche, whereas the food niche of a specialist is narrow. To our knowledge, no record of specialisation on worms has been reported for skates. However, specialisation on crustaceans and fishes is known for several skates from the eastern north Atlantic (Ajayi, 1982; Ellis *et. al.*, 1996), north Pacific (Orlov, 1998), southeast Atlantic (Ebert *et al.*, 1991) and southwest Atlantic (Lucifora *et al.*, 2000; García de la Rosa, 1998). Polychaetes were found in some generalist feeders but mostly constituted secondary items in the diet (McEachran *et al.*, 1976; Orlov, 1998). In *Raja radiata*, for example, worms were found in the diet, together with other items, and varied among areas of the east coast of North America (McEachran *et al.*, 1976).

Ebert *et al.* (1991) described the diet of several species of skates from southwest Africa, including other species of the genus *Bathyraja* (*B. smithii*), and observed that the most important prey items were crustaceans and fishes, whereas polychaetes were not important food items. In the same way, on the other side of the southern Atlantic (the ACS), crustaceans and fishes constituted the most important prey items observed in the majority of the skates. However, in contrast to southwest African skates, two worm-consumers were reported in the ACS, the Patagonian skate *B. macloviana* and the white spots skate *B. albomaculata* (Sanchez and Mabragaña, 2002; Scenna, 2003; Ruocco, 2004 and present study). Similar values of %IRI and a relative low niche width were estimated from spring *B. macloviana* samples taken in the northern ACS (38-44°S) (Scenna, 2003).

Records of specialisation on worms in the ACS are not common. Two coastal fishes, the hawkfish *Cheilodactylus bergi* (Bruno *et al.*, 2000) and the apron ray *Discopyge tschudii* (Garcia, 1984) displayed analogous values of polychaete preys to *B. macloviana*, feeding almost exclusively on worms. Previous studies on the diet of skates (not only *Bathyraja*) from outer ACS revealed that the largest species usually preyed on fishes and molluscs (squids), while the smallest ones included crustaceans and polychaetes in the diet (García de la Rosa, 1998; Lucifora *et al.*, 2000; Paesch *et al.*, 2000; Kohen Alonso *et al.*, 2001; Sanchez and Mabragaña, 2002 and present study). Studies from South Patagonian waters (48-55°S) indicated that of 11 skate species, only *B. albomaculata* (n= 10) and *B. macloviana* (n= 45) showed occurrence frequency of polychaetes > 65%, and *Psammobatis normani* (n= 60) contained worms as secondary items (Sanchez and Mabragaña, 2002). These species displayed a similar feeding pattern in the present study (Table 3).

Despite the fact that polychaetes species richness is considerable in benthic communities of the ACS, they comprise no more than 20% of the total invertebrate abundance in different regions (Roux *et al.*, 1993; Roux and Bremec, 1996; Bremec and Lasta, 2002; Bremec *et al.*, 2000 a, b). The family Opheliidae (including *Travisia* sp.) reached the highest frequency of occurrence in benthic samples off Buenos Aires (37°S), followed by Nephtyidae and Maldanidae (Roux *et al.*, 1993). In southern areas of the Patagonian shelf (50-55°S), several families (Onuphidae, Nephtyidae, Ampharetidae, Opheliidae and Maldanidae) were conspicuously represented although their percentage of abundance reached 9% (Bremec *et al.*, 2000b).

The results of the MDS (which presented a low resolution plot with no segregation of clear sites groups) and the ANOSIM test (R value close to zero implying little or no segregation of groups) indicated that the diet of *B. macloviana* was similar throughout the study area, consisting mainly of the Opheliidae *T. kerguelensis*. Opheliidae are found worldwide, usually in sandy sediments and muds. These worms are burrowers, feeding on detritus in sediment (Fauchald and Jumars, 1979). The dominance of *T. kerguelensis* in the diet suggested that *B. macloviana* fed deep in the substrate. On the other hand, Mianzan *et al.* (1996) found that this species may also feed on ctenophores, a feeding behaviour that can be explained by the later finding of near-bottom aggregations of these planktonic organisms (Costello and Mianzan, 2003; Colombo *et al.*, 2003).

Species sharing the same habitat may rely on differences in the utilisation of food resources to avoid competition (Schoener, 1974). Several species of skates occur sympatrically with *B. macloviana* along the ACS (Cousseau *et al.*, 2000). Most of them are potential food competitors, being typically benthophagous and reaching similar sizes during the ontogeny. *Bathyraja macloviana* feeds particularly on discretely motile polychaetes, excluding other macrobenthic invertebrates present in higher abundances on the bottom, while most of the sympatric skates of similar sizes prey mainly on crustaceans. *B. macloviana* preyed on polychaetes, a faunistic group characterised by low relative abundance in the ACS. The feeding pattern displayed by *B. macloviana* might reflect morphological differences in the structures involved in detection, capture and digestion of preys as well as different alimentary behaviours, allowing a low dietary overlap with other sympatric skates in the ACS.

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