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Effects of intrinsic and extrinsic factors on the diet of *Bathyraja macloviana*, a benthophagous skate

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The effects of intrinsic (sex, maturity stage and body size) and extrinsic (depth and region) factors on the diet of *Bathyraja macloviana*, in the south-west Atlantic Ocean, were evaluated using a multiple-hypothesis modelling approach. *Bathyraja macloviana* fed mainly on polychaetes followed by amphipods, isopods and decapods. Effects of intrinsic and extrinsic factors on diet composition of this species were found. The consumption of polychaetes had a humped relationship with total length (L_T), and isopods and decapods increased with increasing L_T . Immature individuals preyed on amphipods more heavily than mature individuals. Furthermore, region and depth had an important effect on the consumption of isopods, decapods and amphipods. Such ontogenetic changes and spatial patterns may provide insights into understanding the regulatory mechanisms of marine communities.

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Key words: feeding habits; ontogenetic shifts; Rajidae; south-west Atlantic; spatial variation.

INTRODUCTION

Feeding habits of a predator may be affected by many factors. The intrinsic factors are traits related to the predator, such as sex, maturity stage and body size, and the extrinsic factors are those characteristics related to the prey or the environment that affects the availability and distribution of prey (Di Giacomio & Perier, 1996; Lucifora, 2003). It is well documented among elasmobranchs species that the predator response to these factors may cause ontogenetic (Braccini & Perez, 2005; Lucifora *et al.*, 2006, 2009; Bethea *et al.*, 2007; Barbini *et al.*, 2010; Barbini & Lucifora, 2012), seasonal (Cortés *et al.*, 1996; Braccini & Perez, 2005; Lucifora *et al.*, 2006; San Martín *et al.*, 2007; Rinewalt *et al.*, 2009; Barbini & Lucifora, 2012) and spatial (Bethea *et al.*, 2007; Barbini & Lucifora, 2012; Yick *et al.*, 2012) dietary shifts. These shifts do not,

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however, only affect individuals, but also have consequences for marine populations and communities (Werner & Gilliam, 1984; Mittelbach & Persson, 1998). Therefore, evaluating the importance of these factors on the diet will improve understanding of the foraging behaviour of a predator and of those mechanisms that control and regulate the distribution and abundance of prey.

Rajidae may play an influential role in structuring marine communities where they occur (Ebert & Bizzarro, 2007). Given this, and from a viewpoint of marine conservation, knowledge of how diet composition of rajids changes in response to intrinsic and extrinsic factors has important implications for understanding marine community dynamics, which is necessary for developing adequate management and species conservation planning. For example, knowledge about the spatial plasticity of a species in terms of its diet will be important for evaluating the ecological role of a predator from one area to another. Besides, if body size and reproductive condition of a predator are an important determinant of the consumption of a particular prey, then the overfishing of the larger or sexually mature individuals will affect the predator–prey relationship (Stevens *et al.*, 2000). Therefore, studies on dietary shifts of predators are needed to establish a clearer picture of the ecological consequences of spatial differences in fishing effort and the removal of the large individuals in a population, on consumption of a given prey.

The Patagonian skate *Bathyraja macloviana* (Norman 1937) is a relatively small rajid (maximum total length, L_T , 675 mm) that occurs from 36° S in the south-western Atlantic Ocean to 51° S in the Pacific Ocean (Cousseau *et al.*, 2007). On the Argentine continental shelf, this species is one of the most common rajids in the region and inhabits depths between 63 and 509 m (Menni & Stehmann, 2000; Cousseau *et al.*, 2007). It is targeted by the skate fishery in the Falkland (Malvinas) Islands (Agnew *et al.*, 2000) and is commonly caught as by-catch in bottom trawling fisheries (Buratti, 2004). Females mature between 520 and 540 mm L_T , whereas males mature between 519 and 535 mm L_T (Paesch & Oddone, 2009). *Bathyraja macloviana* is a benthophagous fish that feeds mainly on polychaete worms and a small proportion of amphipods, isopods and decapods (Mabragaña *et al.*, 2005; Scenna *et al.*, 2006; Ruocco *et al.*, 2012). Although these studies provide important data on the diet composition of *B. macloviana*, no information about the interactions among intrinsic and extrinsic factors (*e.g.* the influence of sex, maturity stage, body size, space and dietary) is documented.

In this study, the effect of intrinsic and extrinsic factors on the feeding habits of *B. macloviana* in the south-western Atlantic Ocean are assessed to determine whether change in diet is associated with sex, maturity stage, body size, depth and region. This species is categorized as near threatened by International Union for Conservation of Nature (IUCN) (McCormack *et al.*, 2007). Therefore, studies on the life history of this species are needed for the management and effective conservation of the fishery.

MATERIALS AND METHODS

STUDY AREA AND SAMPLING

The study area was located in the south-west Atlantic Ocean between 36° and 55° S, and over a depth range of 66–340 m (Fig. 1). Water mass on the continental shelf in this region are of sub-Antarctic origin (Guerrero & Piola, 1997). The northern area of the continental shelf is characterized, however, by an alternation throughout the year, between warm coastal

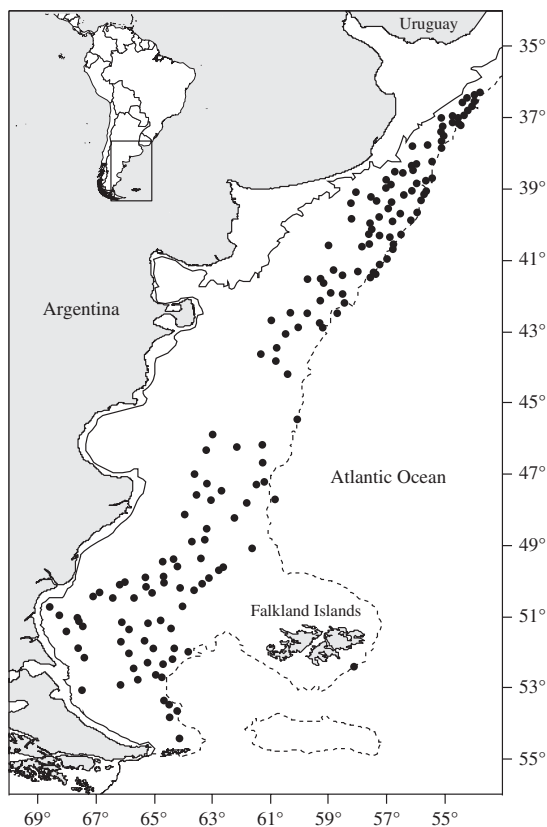


FIG. 1. Study area showing the location of trawl stations (●) where individuals of *Bathyraja macloviana* were captured in the south-west Atlantic Ocean. The continuous and dashed lines represent the 50 and 200 m isobaths, respectively.

waters and temperate–cold waters. On the other hand, the southern area is dominated by sub-Antarctic cold water throughout the year (Balech & Ehrlich, 2008).

Individuals of *B. macloviana* were caught from 12 research cruises carried out by the Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP, Argentina), between October 2003 and October 2006, and designed for assessment of Argentine hake *Merluccius hubbsi* Marini 1933, southern blue whiting *Micromesistius australis* Norman 1937, hoki *Macruronus magellanicus* Lönnberg 1907 and Argentine squid *Illex argentinus*. All specimens were captured using an Engel-type bottom trawl (200 mm stretched mesh in the wings and 103 mm in the codend), towed at a speed of 4 knots (7.41 km h^{-1}) for 30 min.

For each captured individual, sex, maturity stage and L_T (mm) were recorded. Sexual maturity stage of each individual was determined by visual examination of reproductive organs (Stehmann, 2002). Males were categorized as: immature (non-calcified claspers with length shorter than the length of the pelvic fins; alar thorns not yet developed; testes small; straight and filiform sperm ducts) and mature (long fully calcified claspers; developed alar thorns; highly coiled sperm ducts). Females were sorted into: immature (small ovaries with undifferentiated ovarian follicles or all uniformly small; hardly recognizable oviducal glands; narrow and thread-like uteri) and mature (enlarged ovaries with yolked ovarian follicles; wide, large and heart-shaped oviducal glands; wide uteri over their entire length, with and without egg cases). The stomachs were removed and fixed in 4% formalin. In the laboratory, stomach contents were sorted and identified to the lowest possible taxonomic level using published

catalogues (Bastida & Torti, 1973; Boschi *et al.*, 1992) and a voucher collection was deposited at the Laboratorio de Ictiología, Universidad Nacional de Mar del Plata (Argentina). Prey were counted and their wet mass was recorded (g).

DATA ANALYSIS

To determine the importance of each prey in the diet, the following indices were estimated: percentage by number (%N), percentage by mass (%M), percentage frequency of occurrence (%F_O) and the index of relative importance (I_{RI}) was calculated from $I_{RI} = \%F_O (\%N + \%M)$ (Pinkas *et al.*, 1971; Hyslop, 1980), which was also expressed as a percentage (% I_{RI} ; Cortés, 1997).

Cumulative prey curves were generated to assess whether the number of *B. macloviana* analysed was sufficient to accurately describe the diet and to perform statistical analyses. The order of sampled stomachs was randomized 100 times, and the sample size was plotted against the mean cumulative Shannon–Wiener diversity index (Magurran, 2004). An asymptotic curve is indicative that the sample size was sufficient. The curves were generated to the lowest taxonomic level of the prey.

For the statistical analyses, the prey were grouped in the following zoological categories: polychaetes, amphipods, decapods and isopods. These categories were chosen because they reflected the ecological variability of the diet of *B. macloviana*. The effect of both intrinsic (L_T , sex and maturity stage) and extrinsic (region and depth) factors on the diet composition of *B. macloviana* were evaluated using generalized linear models (GLM) (Venables & Ripley, 2002). For each prey category, GLMs were built in which the number of consumed prey was the response variable and the sex, L_T , maturity stage (immature and mature), region (north = 36°–45° S; south = 45°–55° S) and depth (m) were the independent variables. Furthermore, models with combinations and interactions among independent variables were fitted (Table I). A null model (*i.e.* model without any of the independent variables) was fitted to assess if none of the tested variables had an effect on the consumption of prey categories. All models had a negative binomial error distribution and a log link because the number of prey as response variable had a high number of zero values and the variance was much greater than the mean (Crawley, 2005).

Possible curvilinear relationships between the response variable and independent variables were assessed by fitting generalized additive models (GAM) (Crawley, 2005). Therefore, GAMs were built among the number of prey consumed, L_T and depth. If GAMs detected a significant non-linear relationship, then quadratic functions were included in the GLMs.

The best model was selected using a multiple-hypothesis modelling approach (information theory) (Anderson *et al.*, 2000; Franklin *et al.*, 2001). The magnitude of the effect of each independent variable on the response variable is measured by the estimation of its coefficient (either an intercept or a slope) in the best model (Franklin *et al.*, 2001). For each model fitted within a prey category, the Akaike information criterion (AIC) was calculated and the model with the lowest AIC was selected as the best model. AIC is a numerical value that measures the amount of information lost when fitting a model (Crawley, 2005). Akaike's weight (w) was calculated to obtain the relative likelihood of each model fitted given the data (Franklin *et al.*, 2001; Jonson & Omland, 2004). If the best model is not strongly weighted, the model averaging was computed to measure the effects of the variable explaining most of the variation (Symonds & Moussalli, 2011). All statistical analyses were conducted with the statistical software R version 2.15.1 (R Development Core Team; www.r-project.org/).

RESULTS

A total of 637 individuals of *B. macloviana* were examined, of which 596 (93.56%) contained food. Of the individuals with stomach contents, 118 were immature females (378–605 mm L_T), 180 were mature females (500–674 mm L_T), 89 were immature males (152–631 mm L_T) and 209 were mature males

TABLE I. Models fitted between the number of consumed prey (N) by *Bathyraja macloviana* and the independent variables. The categorical variables were maturity stage (immature and mature) and region (north and south)

Number	Models
1	$N \sim \text{sex}$
2	$N \sim \text{maturity stage}$
3	$N \sim L_T$
4	$N \sim \text{region}$
5	$N \sim \text{depth}$
6	$N \sim \text{sex} + \text{region}$
7	$N \sim \text{sex} + \text{depth}$
8	$N \sim \text{maturity stage} + \text{region}$
9	$N \sim \text{maturity stage} + \text{depth}$
10	$N \sim L_T + \text{region}$
11	$N \sim L_T + \text{depth}$
12	$N \sim \text{region} + \text{depth}$
13	$N \sim \text{sex} + \text{region} + \text{depth}$
14	$N \sim \text{maturity stage} + \text{region} + \text{depth}$
15	$N \sim L_T + \text{region} + \text{depth}$
16	$N \sim \text{sex} \times \text{region}$
17	$N \sim \text{sex} \times \text{depth}$
18	$N \sim \text{maturity stage} \times \text{region}$
19	$N \sim \text{maturity stage} \times \text{depth}$
20	$N \sim L_T \times \text{region}$
21	$N \sim L_T \times \text{depth}$
22	$N \sim \text{region} \times \text{depth}$
23	$N \sim \text{sex} \times \text{region} \times \text{depth}$
24	$N \sim \text{maturity stage} \times \text{region} \times \text{depth}$
25	$N \sim L_T \times \text{region} \times \text{depth}$
26	$N \sim L_T + L_T^2$
27	$N \sim \text{depth} + \text{depth}^2$
28*	$N \sim 1$

L_T , total length; *, null model.

(495–645 mm L_T) (Fig. 2). The cumulative diversity curves reached an asymptote for all the groups considered, indicating that the sample size was large enough to describe and compare the diets (Fig. 3).

The stomachs contained 36 taxonomic categories of prey: 17 polychaetes, six amphipods, five decapods, five isopods, and one cumacean, one sipunculid and one cephalopod (Table II). Overall, polychaetes were the most important prey in the diet of *B. macloviana*, showing the highest values of % N , % M , % F_O and % I_{RI} . They were followed by amphipods, isopods and decapods. Cumaceans, sipunculids and cephalopods were less important in the diet composition. Among 16 families of polychaetes identified, Opheliidae (*Travisia* spp.) was the most consumed by *B. macloviana* in terms of % N , % M , % F_O and I_{RI} , followed by Capitellidae, Orbiniidae and Maldanidae. Ampeliscidae was the most important amphipod consumed, whereas the crab *Peltarion spinosulum* was the most ingested among decapods. *Cirolana* was the most important isopod genus preyed by *B. macloviana*.

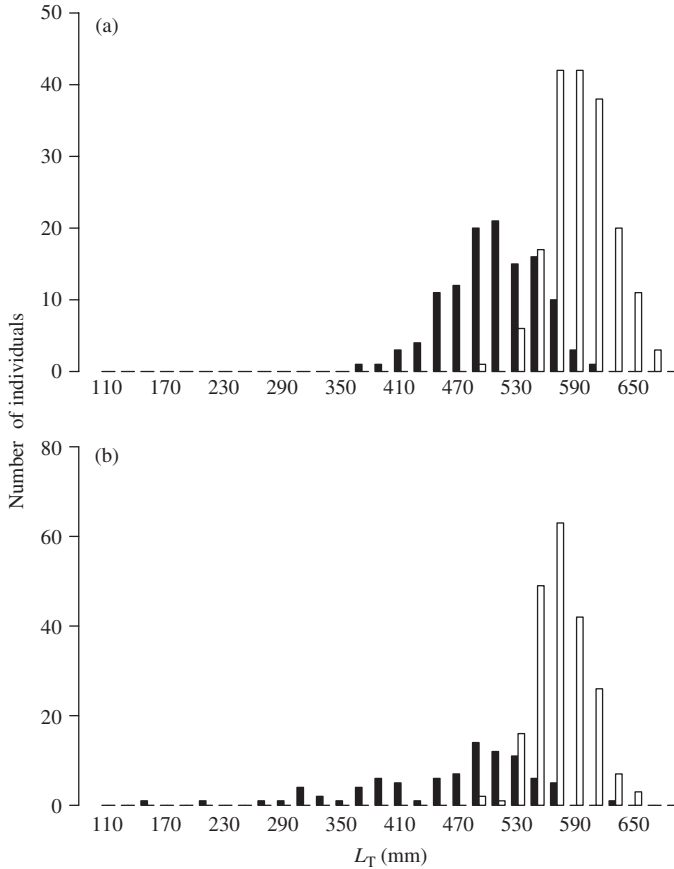


FIG. 2. Total length (L_T) frequency distributions of *Bathyraja macloviana* (a) females and (b) males (■, immature individuals; □, mature individuals).

This analyses detected several effects of intrinsic and extrinsic factors on the number of prey consumed by *B. macloviana* (Table III). No prey categories had a significant relationship with sex. The number of polychaetes consumed had a significant curvilinear relationship with L_T . According to this model, the consumption of polychaetes had a humped relationship with L_T (Fig. 4). The consumption of isopods and decapods changed significantly with L_T : the number of these prey in the diet increased with increasing L_T of *B. macloviana*. Immature individuals preyed on amphipods more heavily than mature individuals.

Region and depth had an important effect on the consumption of isopods, decapods and amphipods (Table III). *Bathyraja macloviana* preyed more heavily on isopods and amphipods in the southern region than in the northern region. On the other hand, decapods were more consumed in the north than in the south. As depth increased, the consumption of amphipods and decapods increased, while the number of isopods decreased with increasing depth.

The best model for amphipods was not strongly weighted, thus model averaging was computed. The estimated mean \pm s.e. coefficients were -0.819 ± 1.680 for

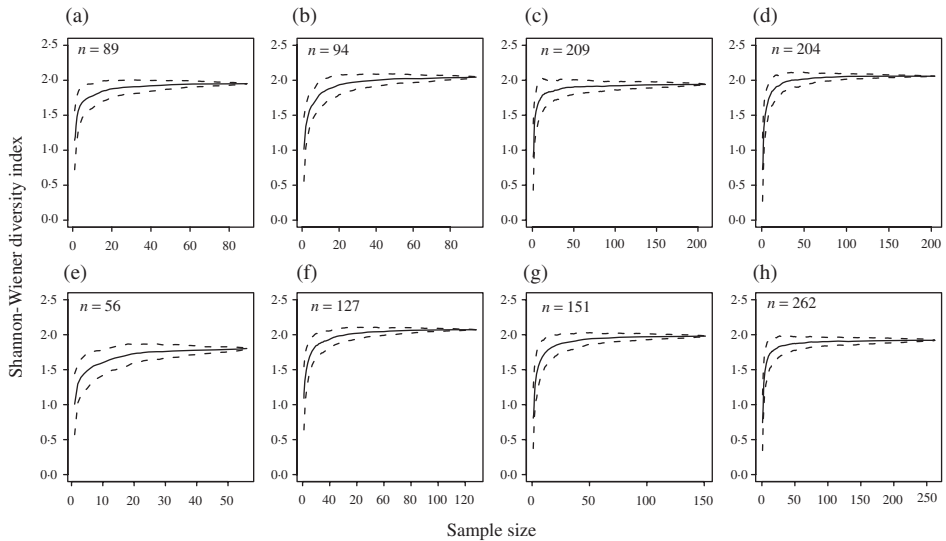


FIG. 3. Curves of cumulative mean diversity index (—) and s.d. (- - -) of prey as a function of sample size (n) for each group of specimens considered in the dietary analyses of *Bathyraja macloviana*: (a) female and south, (b) male and south, (c) female and north, (d) male and north, (e) immature and south, (f) mature and south, (g) immature and north and (h) mature and north.

mature individuals, 1.458 ± 3.483 for the southern region and 0.008 ± 0.002 for depth, with a combined w of 0.998.

DISCUSSION

Bathyraja macloviana is a benthic predator that feeds mainly on polychaetes followed by amphipods, isopods and decapods. This results agree with published information on diet composition of this species in the same region (Mabragaña *et al.*, 2005; Scenna *et al.*, 2006; Ruocco *et al.*, 2012). Many species of elasmobranchs such as *B. macloviana* are not top predators, and have received little attention, with the potential effects of these predators dismissed in ecological systems (Vaudo & Heithaus, 2011). Mesopredators, defined as mid-level predators, however, can have profound effects on ecosystem structure, because they provide a crucial link between upper and lower trophic levels (Ritchie & Johnson, 2009). Furthermore, elasmobranch mesopredators, batoids in particular, may influence community structure through predation and bioturbation (Peterson *et al.*, 2001; O'Shea *et al.*, 2012). Feeding behaviour of some batoids (*i.e.* digging in the bottom in search of prey) can result in physical disturbance to soft-bottoms, hence determining benthic community structure by removing prey species, providing secondary predators with access to normally unavailable prey and creating new opportunities for colonization (VanBlaricom, 1982; Thrush *et al.*, 1991; O'Shea *et al.*, 2012). The dominant polychaetes in the diet of *B. macloviana* were *Travisia* spp. (Opheliidae); Opheliidae are burrowers, commonly found in soft-bottoms (Rouse & Pleijel, 2001). This pattern indicates that *B. macloviana* has the capacity to dig into the bottom in search

TABLE II. Diet composition of *Bathyrāja macloviana* presented as percentage by number (%N), mass (%M), frequency of occurrence (%F_O), index of relative importance (*I*_{RI}) and *I*_{RI} expressed as a percentage (%*I*_{RI})

Prey	%N	%M	%F _O	<i>I</i> _{RI}	% <i>I</i> _{RI}
Polychaeta	68.06	76.67	96.31	13938.80	87.14
Unidentified polychaetes	16.24	33.50	85.57	4257.03	
Opheliidae					
<i>Travisia</i> spp.	33.65	28.38	63.42	3934.03	
Onuphidae	0.97	0.36	9.23	12.33	
Maldanidae	1.36	3.14	10.40	46.81	
Nephtyidae	0.99	1.68	7.05	18.80	
Lumbrineridae	1.52	0.86	12.58	29.97	
Aphroditidae					
<i>Aphrodite</i> spp.	0.04	0.30	0.50	0.17	
Glyceridae	1.29	0.51	8.89	18.04	
Eunicidae	0.02	0.01	0.17	<0.01	
Orbinidae	4.57	3.34	6.88	54.50	
Polynaidae	0.17	0.22	1.01	0.40	
Terebellidae	0.09	0.20	0.84	0.25	
Nereidae	0.01	<0.01	0.17	<0.01	
Ampharetidae	0.01	0.05	0.17	0.01	
Gonianidae	0.07	0.13	1.01	0.20	
Sabellidae	0.01	0.14	0.17	0.02	
Capitellidae	6.85	3.20	17.28	173.82	
Tube of polychaetes	0.16	0.62	2.18	1.71	
Amphipoda	22.42	4.61	48.82	1320.07	8.25
Unidentified amphipods	17.64	3.80	41.44	888.61	
Ampeliscidae	4.42	0.67	8.56	43.66	
Lysianassidae	0.14	0.05	0.84	0.15	
Phoxocephalidae	0.14	0.07	0.33	0.07	
Aoridae	0.01	<0.01	0.17	<0.01	
Hyperiididae					
<i>Themisto gaudichaudii</i>	0.07	0.01	1.01	0.08	
Decapoda	1.88	7.46	13.92	130.13	0.81
Unidentified decapods	0.09	0.14	1.17	0.27	
Solenoceridae					
<i>Pleoticus muelleri</i>	0.06	0.08	0.84	0.11	
Atelecyclidae					
<i>Peltarion spinosulum</i>	1.51	6.66	10.90	89.09	
Majidae					
<i>Libidoclaea granaria</i>	0.21	0.47	2.52	1.71	
<i>Eurypodius latreillei</i>	0.01	0.12	0.17	0.02	
Isopoda	7.09	9.89	35.57	604.11	3.77
Unidentified isopods	0.03	0.02	0.50	0.03	
<i>Cirolana</i> spp.	6.22	9.57	33.05	521.90	
<i>Arcturus</i> spp.	0.78	0.29	3.35	3.60	
Serolidae	0.05	0.01	0.50	0.03	
Idoteidae	0.01	<0.01	0.17	<0.01	
Cumacea	0.45	0.04	4.53	2.24	0.01
Sipunculida	0.06	0.20	0.50	0.13	<0.01
Cephalopoda	0.03	1.12	0.50	0.58	<0.01

TABLE III. Best models used to explain prey categories consumption in number by *Bathyraja macloviana* (s.e. in parentheses). Mature (M_a) and south (S) are factor levels of maturity stage and region

Prey categories	Intercept	Coefficient	AIC	w
Polychaeta	-6.43 (1.69)	0.03 (0.01) L_T $- 2.85 \times 10^{-5}$ $(6.41 \times 10^{-6}) L_T^2$	3936.9	0.60
Amphipoda	0.81 (0.34)	-1.28 (0.20) M_a + 0.68 (0.22) S + 0.01 (0.00) D	2372.5	0.35
Decapoda	-7.44 (1.46)	0.001 (0.00) L_T - 1.60 (0.34) S + 0.02 (0.00) D	678.6	0.75
Isopoda	-3.71 (1.02)	0.001 (0.00) L_T + 2.07 (0.22) S - 0.01 (0.00) D	1443.6	0.77

L_T , total length; AIC, Akaike information criterion; w , Akaike's weight; D , depth

of prey (Mabragaña *et al.*, 2005; Scenna *et al.*, 2006), suggesting that this mesopredator could have strong effect on the benthic invertebrate community. Therefore, the ecological role of *B. macloviana* as for other benthophagous species, and other mesopredators, could be very important in the marine community where they occur.

The results of this article highlight the influence of intrinsic and extrinsic factors on the feeding habits of *B. macloviana*. Ontogenetic dietary shifts were found, where the smallest individuals fed on amphipods, individuals from 500 to 600 mm L_T preyed on polychaetes and large individuals incorporated isopods and decapods in

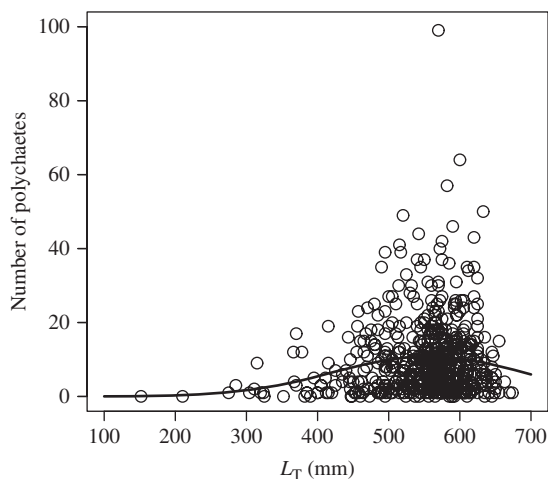


FIG. 4. Shifts in consumption of polychaetes with total length (L_T) of *Bathyraja macloviana* estimated by generalized linear models. The models had a log link and a negative binomial error distribution.

their diet. A similar pattern was found in another specialized rajid in the same region: as white-dotted skate *Bathyraja albomaculata* (Norman 1937) increases in size, the consumption of amphipods decreases and the consumption of polychaetes increases (Brickle *et al.*, 2003; Ruocco *et al.*, 2009). For several species of rajids, the ontogenetic dietary shifts can be attributed to morphological limitations (*e.g.* limited mouth size) (Braccini & Perez, 2005). The prey consumed by *B. macloviana*, however, are mainly small benthic invertebrates, suggesting that these hypotheses do not explain diet variation in this species. Therefore, ontogenetic differences in *B. macloviana* could be associated with the possibly better foraging ability of large individuals and to changes in energy requirements with increasing body size.

The humped relationship between the consumption of polychaetes and body size could be the result of an increasing energy demand in response to changes in reproductive condition coupled with an increase in the search for highly available prey. This humped relationship coincides with sexual maturation and includes the range between the smallest mature (female = 500 mm; male = 495 mm) and the largest immature individual (female = 605 mm; male = 631 mm). Polychaetes could be readily available to benthophagous rajids (Ruocco *et al.*, 2009) because in the benthic communities of the Argentine continental shelf, polychaetes have a very high frequency of occurrence in benthic samples (Roux *et al.*, 1993; Bremec *et al.*, 2000). Therefore, it is hypothesized that *B. macloviana* possibly feeds mainly on polychaetes between 500 and 600 mm L_T as behavioural response to an increasing energy demand.

Recently, with the application of a model selection approach in diet studies using GLM and GAM, curvilinear relationships between prey consumption and explanatory variables (*i.e.* body size and age) for elasmobranchs have been identified. In Anegada Bay, Argentina, pelagic teleosts were consumed mostly by medium aged individuals of copper shark *Carcharhinus brachyurus* (Günther 1870) (Lucifora *et al.*, 2009). In the south-western Atlantic Ocean (between 34 and 41° S), the Patagonian smoothhound *Mustelus schmitti* Springer 1939 the consumption of crustaceans increased from small to medium size individuals but decreased in large individuals (Belleggia *et al.*, 2012). In the same region, for the smallnose fanskate *Sympterygia bonapartii* Müller & Henle 1841, a humped relationship of consumption of bivalve molluscs with body size was found (Barbini, 2011). The detection of these patterns is dependent on the statistical methods used. It is believed that a model selection approach is a very useful statistical tool to identify and analyse different dietary changes related to body size and age of marine predators.

This results show that the diet of *B. macloviana* varied in relation to depth and region. As the depth increased, the consumption of amphipods and decapods increased and the consumption of isopods decreased. Regionally, the isopods and amphipods were the most important prey in the southern region and the decapods in the northern region. The spatial variation found in this study is not consistent with the observations in a previous study in the same area. Mabrugaña *et al.* (2005) assessed differences between northern and southern regions and they noted that the diet of *B. macloviana* was similar throughout the study area. These different results between studies may be associated with differences in methodological approach, to differences in sample size (present study = 596; previous study = 108) and to seasonal differences in the sampling. Despite the fact that benthic invertebrates are important prey of mesopredators, information on the distribution and composition

of benthic communities in the south-west Atlantic Ocean is scarce and scattered. Bastida *et al.* (1992), on the basis of the assemblages of molluscs, bryozoans and echinoderms, covered all the Argentine continental shelf and found three main areas differing in their benthic composition. This pattern suggests a heterogeneous distribution of benthic fauna. Such changes in available resources could explain the spatial variation (*i.e.* depth and region) observed in the diet composition of *B. macloviana*.

From a viewpoint of management and conservation planning, studies on trophic ecology are crucial for understanding ecosystem functioning. The results of this study highlight the importance of the relative effects of intrinsic and extrinsic factors on diet composition, and will assist in predicting the differential roles of the predators. Therefore assessment of such feeding patterns is a first step in the development of hypotheses about the mechanisms regulating marine communities (Koen Alonso, 1999).

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References

- Agnew, D. J., Nolan, C. P., Beddington, J. R. & Baranowski, R. (2000). Approaches to the assessment and management of multispecies skate fisheries using the Falkland Islands fishery as an example. *Canadian Journal of Fisheries and Aquatic Sciences* **57**, 429–440. doi: 10.1139/f99-264
- Anderson, D. R., Burnham, K. P. & Thompson, W. L. (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.
- Barbini, S. A. & Lucifora, L. O. (2012). Feeding habits of a large endangered skate from the south-west Atlantic: the spotback skate *Atlantoraja castelnaui*. *Marine and Freshwater Research* **63**, 1–9. doi: 10.1071/MF11170
- Barbini, S. A., Scenna, L. B., Figueroa, D. E., Cousseau, M. B. & Díaz de Astarloa, J. M. (2010). Feeding habits of the Magellan skate: effects of sex, maturity stage, and body size on diet. *Hydrobiologia* **641**, 275–286. doi: 10.1007/s10750-010-0090-5
- Balech, E. & Ehrlich, M. D. (2008). Esquema biogeográfico del Mar Argentino. *Revista de Investigación y Desarrollo Pesquero* **19**, 45–75.
- Bastida, R. & Torti, M. R. (1973). Los isópodos Serolidae de la Argentina. Clave para su reconocimiento. *Physis A* **32**, 19–46.
- Bastida, R., Roux, A. & Martínez, D. E. (1992). Benthic communities of the Argentine continental shelf. *Oceanologica Acta* **15**, 687–698.
- Belleggia, M., Figueroa, D. E., Sánchez, F. & Bremec, C. (2012). The feeding ecology of *Mustelus schmitti* in the southwestern Atlantic: geographic variations and dietary shifts. *Environmental Biology of Fishes* **95**, 99–114. doi: 10.1007/s10641-011-9874-3
- Bethea, D. M., Hale, L., Carlson, J. K., Cortés, E., Manire, C. A. & Gelsleichter, J. (2007). Geographic and ontogenetic variation in the diet and daily ration of the bonnet-head shark, *Sphyrna tiburo*, from the eastern Gulf of Mexico. *Marine Biology* **152**, 1009–1020. doi: 10.1007/s00227-007-0728-7
- Boschi, E. E., Fischbach, C. E. & Iorio, I. M. (1992). Catálogo ilustrado de los crustáceos estomatópodos y decápodos marinos de Argentina. *Frente Marítimo* **A10**, 7–94.
- Braccini, J. M. & Perez, J. E. (2005). Feeding habits of the sand skate *Psammobatis extenta* (Garman, 1913): sources of variation in dietary composition. *Marine and Freshwater Research* **56**, 395–403. doi: 10.1071/MF04205

- Bremec, C., Elías, R. & Gami, M. C. (2000). Comparison of the polychaete fauna composition from the Patagonian shelf and the Strait of Magellan. Preliminary results from cruises Shinkai Maru IV, V, X and XI (1978-1979) and second Italian oceanographic cruise (1991). *Bulletin of Marine Science* **67**, 189–197.
- Brickle, P., Laptikhovskiy, V., Pompert, J. & Bishop, A. (2003). Ontogenetic changes in the feeding habits and dietary overlap between three abundant rajid species on the Falkland Island' shelf. *Journal of the Marine Biological Association of the United Kingdom* **83**, 1119–1125. doi: 10.1017/S0025315403008373h
- Buratti, C. C. (2004). Fauna acompañante de la merluza (*Merluccius hubbsi*) en la Zona Común de Pesca Argentino-Uruguaya y Mar Argentino hasta 41°S, en 1994, 1999 y 2001. *INIDEP Informe Técnico* **10**, 1–90.
- 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. doi: 10.1139/f96-316
- Cortés, E., Manire, C. A. & Huerter, R. E. (1996). Diet, feeding habits, and diel feeding chronology of the bonnethead shark, *Sphyrna tiburo*, in Southwest Florida. *Bulletin of Marine Science* **58**, 353–367.
- Cousseau, M. B., Figueroa, D. E., Díaz de Astarloa, J. M., Mabrugaña, E. & Lucifora, L. O. (2007). *Rayas, chuchos y otros batoideos del Atlántico Sudoccidental (34° S – 55° S)*. Mar del Plata: Instituto Nacional de Investigación y Desarrollo Pesquero.
- Crawley, W. F. (2005). *Statistics. An Introduction using R*. Chichester: Wiley.
- Di Giácomo, E. E. & Perier, M. R. (1996). Feeding habits of cockfish, *Callorhynchus callorhynchus* (Holocephali: Callorhynchidae), in Patagonian Waters (Argentina). *Marine and Freshwater Research* **47**, 801–808. doi: 10.1071/MF9960801
- Ebert, D. A. & Bizzarro, J. J. (2007). Standardized diet compositions and trophic levels of skates (Chondrichthyes, Rajiformes, Rajoidei). *Environmental Biology of Fishes* **80**, 221–237. doi: 10.1007/s10641-007-9227-4
- Franklin, A. B., Sheik, T. M., Anderson, D. R. & Burnham, K. P. (2001). Statistical model selection: an alternative to null hypothesis testing. In *Modeling in Natural Resources Management: Development, Interpretation, and Application* (Shenk, T. M. & Franklin, A. M., eds), pp. 75–90. Washington, DC: Island Press.
- Guerrero, R. A. & Piola, A. R. (1997). Masas de aguas de la plataforma continental. In *El Mar Argentino y sus recursos pesqueros. Antecedentes históricos de las exploraciones en el mar y las características ambientales*, Tomo I (Boschi, E. E., ed), pp. 107–118. Mar del Plata: INIDEP.
- Hyslop, E. J. (1980). Stomach contents analysis a review of methods and their applications. *Journal of Fish Biology* **17**, 411–429. doi: 10.1111/j.1095-8649.1980.tb02775.x
- Jonson, J. B. & Omland, K. S. (2004). Model selection in ecology and evolution. *Trends in Ecology & Evolution* **19**, 101–108. doi: 10.1016/j.tree.2003.10.013
- Koen Alonso, M. (1999). Estudio comparativo de la alimentación entre algunos predadores de alto nivel trófico de la comunidad marina del norte y centro de Patagonia. PhD Thesis, Universidad de Buenos Aires, Argentina.
- Lucifora, L. O. (2003). Ecología y conservación de los grandes tiburones costeros de Bahía Anegada, Provincia de Buenos Aires. PhD Thesis, Universidad Nacional de Mar del Plata, Argentina.
- Lucifora, L. O., García, V. B., Menni, R. C. & 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. & 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. doi: 10.1007/s11284-008-0487-z
- Mabrugaña, E., Giberto, D. A. & Bremec, C. S. (2005). Feeding ecology of *Bathyraja macloviana* (Rajiformes: Arhynchobatidae): a polychaete-feeding skate from the South-west Atlantic. *Scientia Marina* **69**, 405–413.
- Magurran, A. E. (2004). *Measuring Biological Diversity*. Malden: Blackwell Publishing.
- Menni, R. C. & Stehmann, M. F. W. (2000). Distribution, environment and biology of batoid fishes off Argentina, Uruguay and Brazil. A review. *Revista del Museo Argentino de Ciencias Naturales* **2**, 69–109.

- Mittelbach, G. G. & Persson, L. (1998). The ontogeny of piscivory and its ecological consequences. *Canadian Journal of Fisheries and Aquatic Sciences* **55**, 1454–1465. doi: 10.1139/f98-041
- O’Shea, O. R., Thums, M., van Keulen, M. & Meekan, M. (2012). Bioturbation by stingray at Ningaloo Reef, Western Australia. *Marine and Freshwater Research* **63**, 189–197. doi: 10.1071/MF11180
- Paesch, L. & Oddone, M. C. (2009). Size at maturity and egg capsules of the skates *Bathyrāja brachyurops* (Fowler, 1910) and *Bathyrāja macloviana* (Norman, 1937) (Elasmobranchii: Rajidae) in the SW Atlantic (37°00’–39°30’S). *Journal of Applied Ichthyology* **25**, 66–71. doi: 10.1111/j.1439-0426.2008.01114.x
- Peterson, C. H., Frodie, F. J., Summerson, H. C. & Powers, S. P. (2001). Site-specific and density-dependent extinction of prey by schooling rays: generation of a population sink in top-quality habitat for bay scallops. *Oecologia* **129**, 349–356. doi: 10.1007/s004420100742
- Pinkas, L. M., Oliphant, S. & Iverson, I. L. K. (1971). Food habits of albacore, bluefin tuna and bonito in Californian waters. *California Fish and Game* **152**, 1–105.
- Rinewalt, C. S., Ebert, D. A. & Cailliet, G. M. (2009). Food habits of the sandpaper skate, *Bathyrāja kincaidii* (Garman, 1908) off central California: seasonal variation in diet linked to oceanographic conditions. *Environmental Biology of Fishes* **27**, 41–57. doi: 10.1007/s10641-007-9218-5
- Ritchie, E. G. & Johnson, C. N. (2009). Predator interactions, mesopredators release and biodiversity conservation. *Ecology Letters* **12**, 982–998. doi: 10.1111/j.1461-0248.2009.01347.x
- Rouse, G. W. & Pleijel, F. (2001). *Polychaetes*. London: Oxford University Press.
- Roux, A., Bastida, R. & Bremen, C. (1993). Comunidades bentónicas de la plataforma continental Argentina. Campañas transacción BIP “Oca Balda” 1987/88/89. *Boletim do Instituto Oceanográfico Sao Paulo* **41**, 81–94.
- Ruocco, N. L., Lucifora, L. O., Díaz de Astarloa, J. M. & Bremec, C. S. (2009). Diet of the white-dotted skate, *Bathyrāja albomaculata*, in waters of Argentina. *Journal of Applied Ichthyology* **25**, 94–97. doi: 10.1111/j.1439-0426.2008.01081.x
- Ruocco, N. L., Lucifora, L. O., Díaz de Astarloa, J. M., Menni, R. C., Mabragaña, E. & Giberto, D. (2012). From coexistence to competitive exclusion: can overfishing change the outcome of competition in skates (Chondrichthyes, Rajidae)? *Latin American Journal of Aquatic Research* **40**, 102–112. doi: 10.3856/vol40-issue1-fulltext-10
- San Martín, M. J., Braccini, J. M., Tamini, L. L., Chiaramonte, G. E. & Perez, J. E. (2007). Temporal and sexual effects in the feeding ecology of the marbled sand skate *Psammodontus bergi* Marini, 1932. *Marine Biology* **151**, 505–513. doi: 10.1007/s00227-006-0499-6
- Scenna, L. B., García de la Rosa, S. B. & Díaz de Astarloa, J. M. (2006). Trophic ecology of the Patagonian skate, *Bathyrāja macloviana*, on the Argentine continental shelf. *ICES Journal of Marine Science* **63**, 867–874. doi: 10.1016/j.icesjms.2006.02.002
- Stehmann, M. F. W. (2002). Proposal of a maturity stages scale for oviparous and viviparous cartilaginous fishes (Pisces, Chondrichthyes). *Archive of Fishery and Marine Research* **50**, 23–48.
- Stevens, J. D., Bonfil, R., Dulvy, N. K. & Walker, P. A. (2000). The effects of fishing on sharks, rays, and chimaeras (chondrichthyans), and the implications for marine ecosystems. *ICES Journal of Marine Science* **57**, 476–494. doi: 10.1006/jmsc.2000.0724
- Symonds, M. E. & Moussalli, A. (2011). A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike’s information criterion. *Behavioral Ecology and Sociobiology* **65**, 13–21. doi: 10.1007/s00265-010-1037-6
- Thrush, S. F., Pridmore, R. D., Hewitt, J. E. & Cummings, V. J. (1991). Impact of ray feeding disturbances on sandflat macrobenthos: do communities dominated by polychaetes or shellfish respond differently? *Marine Ecology Progress Series* **69**, 245–252.
- VanBlaricom, G. R. (1982). Experimental analysis of structural regulation in a marine sand community exposed to oceanic swell. *Ecological Monographs* **52**, 283–305. doi: 10.2307/2937332

- Vaudo, J. J. & Heithaus, M. R. (2011). Dietary niche overlap in a nearshore elasmobranch mesopredators community. *Marine Ecology Progress Series* **425**, 247–260. doi: 10.3354/meps08988
- Venables, W. N. & Ripley, D. B. (2002). *Modern Applied Statistics with S-Plus*, 4th edn. New York, NY: Springer.
- Werner, E. E. & Gilliam, J. F. (1984). The ontogenetic niche and species interactions in size-structured populations. *Annual Review of Ecology and Systematics* **15**, 393–425. doi: 10.1146/annurev.es.15.110184.002141
- Yick, J. L., Barnett, A. & Tracey, S. R. (2012). The trophic ecology of two abundant mesopredators in south-east coastal waters of Tasmania, Australia. *Marine Biology* **159**, 1183–1196. doi: 10.1007/s00227-012-1899-4

Electronic Reference

- McCormack, C., Lamilla, J., San Martín, M. J. & Stehmann, M. (2007). *Rhinoraja macloviana*. In *IUCN Red List of Threatened Species*. Available at <http://www.iucnredlist.org/details/63117/0> (accessed 15 November 2012).