

Feeding habits of *Bathyraco marri* (Pisces, Notothenioidei, Bathyracoidea) from the Ross Sea, Antarctica

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Abstract In comparison with other bathyracooids, all species of the genus *Bathyraco* are poorly known from an ecological perspective. The diet of juvenile *Bathyraco marri* Norman, 1938 was studied for the first time in specimens collected in the southwestern Ross Sea during summer 1998. Fish were collected in a single otter trawl catch at 330–340 m depth. The stomach content analysis showed that this species fed exclusively on crustaceans. Overall, 20 prey taxa were identified to genus or species level. Mysids, amphipods and copepods were the most important prey in decreasing order of importance. Other prey, such as *Euphausia superba*, isopods and tanaids were eaten occasionally and in very small amounts. A multivariate analysis was applied to feeding data to assess ontogenetic or sex-related changes in diet. No difference was detected between sexes, whereas diet of small and large fish differed in some degree. An ontogenetic shift from small and pelagic crustaceans such as copepods to benthic–benthopelagic prey such as amphipods and mysids was observed. Relating present results with published data on physiological characteristics of

B. marri, it was possible to infer their feeding behaviour and mode of life. Like other bathyracooids, this species appeared to be an inactive and sluggish fish, which relied on more or less motile benthic or epibenthic prey adopting a “sit and wait” feeding strategy. On the other hand, smaller fish seem to be more active, feeding also on pelagic prey such as copepods that can be seasonally abundant, thus reducing the intraspecific competition for food.

Keywords Diet · Bathyracooid · Ross Sea

Introduction

The Bathyracoidea (dragonfishes), one of the five Antarctic notothenioid families, includes 16 species and 11 genera (Eastman and Eakin 2000). They are plentiful in the coldest, deepest shelf waters at the highest latitudes (Eka 1988, 1990; Schwarzbach 1988; Kunzmann 1991) with only *Bathyraco joannae* found outside the Antarctic region on the Patagonian slope and near the Falkland Islands (Voskoboinikova and Balushkin 1998). Adult bathyracooids reach 13–59 cm SL, although most are less than 25 cm (Gon 1990). They have an elongated body and show only modest diversification in form, ranging from moderately robust and well muscled in the case of *Gymnodraco acuticeps* and *Cygnodraco mawsoni* to thin and delicate as exemplified by members of the deep-living tribe Bathyracoini including the genera *Akarotaxis*, *Prionodraco*, *Racovitzia*, *Vomeridens* and *Bathyraco* (Balushkin and Voskoboinikova 1995; Balushkin 2000). Most aspects of the biology of these relatively small thin-bodied species are unknown.

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With five species the genus *Bathyraco* is the most speciose in the family and also includes the deepest-living species (DeWitt 1971, 1985), with *B. scotiae* recorded from 2,950 m (Gon 1990), deeper than any other notothenioid. Since the Bathyracidae also contains shallow-living species, the family exhibits the greatest overall depth range among notothenioid families. *Bathyraco marri* is eurybathic with a range of 300–1,250 m (Gon 1990). It has been documented by bottom trawling as the most abundant bathyracoid in the western Ross Sea (Eastman and Hubold 1999) and it is also common in other high latitude shelf areas such as the Weddell, Lazarev and eastern Ross seas (Ekau 1990; Hubold 1992; Zimmermann 1997; Donnelly et al. 2004). Compared with other notothenioids, species in the tribe Bathyracini, including *B. marri*, possess a suite of sensory characters supplementing vision and reflecting their deep shelf and upper slope habitat (Eastman and Lannoo 2003).

Since bathyracoids have a reduced ascending process on the premaxilla, jaw protrusion is limited compared with phylogenetically basal notothenioids (Iwami 1985; Balushkin and Voskoboinikova 1995). Therefore, they are probably less efficient in bottom feeding and rooting for infauna and more reliant on food captured in the water column just above or on the substrate. For example, near the Antarctic Peninsula, *Prionodraco evansii* eats cumaceans, amphipods and euphausiids (Daniels 1982). In McMurdo Sound *G. acuticeps* lives in relatively shallow water under cover of heavy sea ice where they are ambush predators on other notothenioid fishes (Eastman 1985). In the Indian Ocean sector of the Southern Ocean, *G. acuticeps* and *C. mawsoni* have overlapping distributions at depths of 200–400 m. Although both species are piscivorous predators, *G. acuticeps* consumes mostly mesopelagic myctophids whereas *C. mawsoni* feeds opportunistically on young notothenioids, pelagic *Euphausia superba* and benthic crustaceans (Pakhomov 1998). Little is known about the diet and feeding habits of most species in the deep-living tribe Bathyracini (Gon 1990).

Here, we report for the first time a detailed taxonomic description of the diet of juvenile *B. marri* Norman, 1938 from the southwestern Ross Sea, focusing on diet and niche breadth variability between the sexes and fish size and its role in reducing intra-specific competition for food resources.

Materials and methods

Specimens of *B. marri* analysed in the present study were collected in the southwestern Ross Sea during

cruise 97–9 of the RV *Nathaniel B. Palmer*. Forty-eight specimens were caught in a single haul (station 58, 74°21'S; 176°28'E, 2 January 1998) carried out by an otter trawl deployed at 333–344 m depth. The trawling area had a benthic fauna composed mainly of bryozoans and sponges. Further details on sampling at sea are reported elsewhere (see Eastman and Hubold 1999). Specimens were identified according to Gon (1990) and preserved in formalin aboard the vessel.

In the laboratory, each fish was measured to the nearest mm (total length, TL), weighed to the nearest 0.1 g, sexed and staged according to a five-point scale of gonad maturity (Everson 1977; Kock and Kellermann 1991). After dissection, the stomach content of each specimen was washed out into a petri dish and sorted under a dissecting microscope. Whenever possible, each prey item was identified to the species level and the number of individuals recorded. Unfortunately, we were unable to determine with reliability the weight of each prey item owing to their small size and different degree of digestion. To evaluate the rate of feeding activity, the coefficient of emptiness $V = N_e / N_s$, where N_e is the number of empty stomachs and N_s is the total number of stomachs examined, was calculated.

The dietary analysis was carried out evaluating each prey type by the percentage by number ($N\%$) and by the frequency of occurrence ($O\%$), defined as the number of stomachs containing a particular prey as percentage of the total number of stomachs examined (Hyslop 1980). The dietary diversity or feeding niche breadth of the species was expressed by the Shannon–Wiener diversity index H' (Colwell and Futuyma 1971), whereas the Pielou evenness index J' was calculated to measure the extent the different prey are evenly distributed (Pielou 1966). One-way analysis of variance (ANOVA) was applied to test for differences in the diversity index H' between sex and fish size. Normality and constant variance of the H' values distribution across the samples were tested by the non-parametric test of Kolmogorov–Smirnov and by the F distribution, respectively.

In order to assess the feeding strategy and the inter/intra individual components of niche width of *B. marri*, a modified Costello graphical method was applied to the data set of prey taxa identified at genus/species level (Costello 1990; Amundsen et al. 1996). In the graphical methods, the prey-specific abundance, defined as the percentage of a prey taxon calculated considering only those predators in which the prey taxon actually occurs, is plotted against the frequency of occurrence, providing a two-dimensional diagram (Amundsen et al. 1996). In detail, the prey-specific

abundance is calculated as follows: $P_i = (\sum S_i / \sum S_{ii}) \times 100$, where P_i is the prey-specific abundance of prey i , S_i the stomach content (as number of individuals) composed of prey i and S_{ii} the total stomach content in only those fish with prey i in their stomachs.

Ontogenetic and sex-related changes in diet were assessed using a multivariate analysis of data. The fish sample was split into two size groups, small (≤ 115 mm TL) and large fish (> 115 mm TL) in order to have samples of comparable number of individuals. A Bray–Curtis coefficient similarity matrix was obtained from the full-standardized data set. A non-metric multidimensional scaling (MDS) was then applied to the similarity matrix to order fishes in a two-dimensional plane according to their relevant diet similarity. Sex and fish size were “superimposed” on the MDS plot, to see the relevant pattern of distribution. To determine relevant contributions of each prey species to fish distribution in the two-dimensional plot, an analysis of dissimilarity was carried out using the SIMPER routine. Finally, a one-way statistical analysis (ANOSIM routine, test R) was performed to test the null hypothesis (i.e. no statistical difference in diet between sex and fish size). All statistical analyses were performed using the PRIMER software package developed at the Plymouth Marine Laboratory (Clarke and Warwick 1994; Clarke and Gorley 2001).

Results

We analysed the stomach contents of 48 specimens caught in a single haul (Fig. 1). The sample was composed of 24 females ranging between 100 and 166 mm TL and 2.1 and 12.4 g, and 17 males ranging between

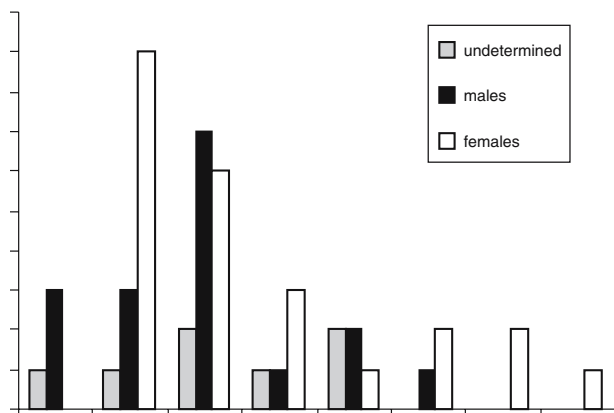


Fig. 1 Length frequency distribution and sex composition of *B. marri* sample investigated in the present study

91 and 143 mm TL and 1.7 and 7.9 g. Seven specimens were sexually undetermined. The coefficient of emptiness (V) was relatively low, being about 10% in the whole sample (8 and 12% in females and males, respectively).

Diet

The food composition of *B. marri* is reported in Table 1. Overall 20 prey taxa were identified, most of them at genus or species level. Dietary diversity (H') and evenness (J') for the whole fish sample were 2.44 and 0.81, respectively. Interestingly, all prey taxa found in the stomach contents were crustaceans. In terms of percentage by number and frequency of occurrence (Table 1), the most important taxa were mysids, amphipods and copepods. The other prey taxa, such as euphausiids, isopods and tanaids, were eaten

Table 1 Food composition of juvenile *B. marri* from the southwestern Ross Sea

Prey taxon	O (%)	N (%)
Euphausiids	2.3	1.0
<i>E. superba</i>	2.3	1.0
Mysids	58.1	36.8
<i>Mysidopsis</i> sp.	2.3	1.0
<i>Pseudomma</i> spp.	25.6	13.3
<i>Antarctomysis</i> spp.	16.3	9.2
<i>Mysidetes</i> spp.	9.3	7.2
Undetermined	9.3	6.1
Amphipods	48.8	29.6
<i>Liljeborgia</i> cf. <i>georgiana</i>	11.6	5.1
<i>Hippomedon</i> cf. <i>kerueleni</i>	2.3	1.0
<i>Lepidepcreum urometacarinatum</i>	14.0	7.2
<i>Orchomenella franklini</i>	14.0	7.2
<i>Tryphosella macropareia</i>	2.3	1.0
<i>Eusirus</i> cf. <i>antarcticus</i>	7.0	3.1
<i>Tryphosella intermedia</i>	2.3	1.0
<i>Gammaropsis</i> sp.	2.3	1.0
<i>Rhachotropis</i> sp.	2.3	1.0
Lysianassoidea gen. sp.1	4.7	2.0
Copepods	46.5	28.6
<i>Calanus</i> sp.	2.3	1.0
<i>Aetideopsis</i> sp.	39.5	22.5
Undetermined	9.3	5.1
Isopods	7.0	3.0
<i>Serolis</i> sp.	4.7	2.0
<i>Eurycope</i> sp.	2.3	1.0
Tanaids	2.3	1.0
<i>Leptognatia</i> sp.	2.3	1.0
N of full stomachs	45	
N of empty stomachs	3	
N of prey taxa	20	
N of prey	87	
J'	0.81	
H'	2.44	

O Frequency of occurrence; N percentage by number; J' Pielou evenness index; H' Shannon–Wiener diversity index

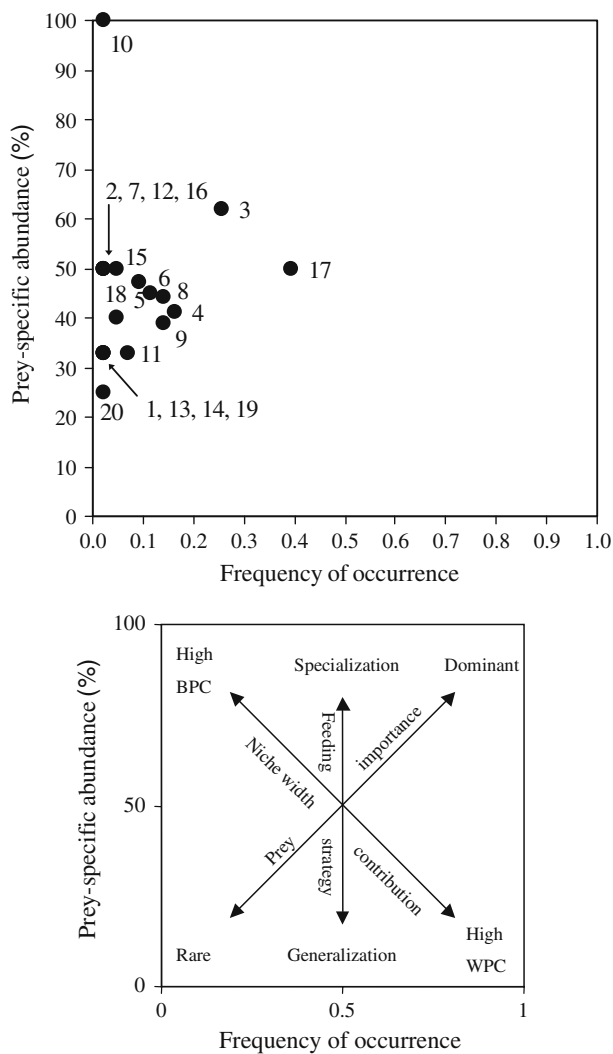


Fig. 2 Feeding strategy and importance of prey items in the diet of *B. marri* caught in the southwestern Ross Sea, as determined by the modified graphical method of Costello. Prey taxa: 1 *E. superba*, 2 *Mysidopsis* sp., 3 *Pseudomma* spp., 4 *Antarctomysis* spp., 5 *Mysidetes* spp., 6 *Liljeborgia* cf. *georgiana*, 7 *Hippomedon* cf. *kerueleni*, 8 *Lepidepecreum urometacarinatum*, 9 *Orchomenella franklini*, 10 *Tryphosella macroporeia*, 11 *Eusirus* cf. *antarcticus*, 12 *Tryphosella intermedia*, 13 *Gammaropsis* sp., 14 *Rhachotropis* sp., 15 *Lysianassoidea* gen. sp. 1, 16 *Calanus* sp., 17 *Aetideopsis* sp., 18 *Serolis* sp., 19 *Eurycope* sp., 20 *Leptognatia* sp. A guide to the interpretation of the Costello method is shown in the small diagram below

occasionally in very small amounts. Comparing prey taxa in more detail, mysids were represented by four genera, i.e. *Pseudomma*, *Antarctomysis*, *Mysidetes* and *Mysidopsis*, in decreasing order of importance. Amphipods were the most speciose prey group, being represented by ten species. Within this group, the most important species were *Lepidepecreum urometacarinatum*, *Orchomenella franklini* and *Liljeborgia* cf. *georgiana*. Copepods were represented by only two species, *Calanus* sp. and *Aetideopsis* sp., the latter

constituting the most numerous and frequent item preyed on by *B. marri* ($N\% = 22$; $FO\% = 39.5$). Isopods and tanaids were composed of two and one species, namely, *Serolis* sp. and *Eurycope* sp. and *Leptognatia* sp., respectively. Finally, a single specimen of *E. superba* was found in the stomach content of a fish.

The graphic representation of dietary composition of *B. marri* based on the modified Costello method is summarized in Fig. 2. According to Amundsen et al. (1996), the two-dimensional plot provides information on prey importance, feeding strategy and niche width contribution of between and/or within phenotype components. As for prey importance, most items are located in the lower-left corner of plot, thus representing rare prey with a low frequency of occurrence and a relatively low prey-specific abundance. The less rare prey were *Pseudomma* spp. and *Aetideopsis* sp., owing to their relatively high frequency of occurrence compared with other taxa. In relation to the feeding strategy axis, *B. marri* can be considered a generalist feeder, as most of prey are located in the lower part of diagram, attaining a low prey-specific abundance. The position of *Tryphosella macroporeia* in the upper part of diagram can lead to a misinterpretation of its relative importance, as it was found in a single stomach. As far as the niche width contribution is concerned, the location of most prey within the two-dimensional plot indicates a relatively higher between-phenotype component in the utilization of food resources than within phenotype component. Summarizing the aforementioned results, *B. marri* is a crustacean feeder that has a broad food niche width at the population level, but with single individuals relying on a small number of prey which are different from each other.

Ontogenetic and sex-related changes

Multidimensional scaling ordination of the sample on the basis of stomach contents is reported in Fig. 3. In the first plot (Fig. 3a), sex was “superimposed” on each point. Although the value of “stress” (0.08) was low, a measure of the goodness-of-fit of data to MDS representation, the spatial distribution of points in relation to this parameter showed no clear trend or, in other words, there was a strong food overlap between sexes. On the other hand, the pattern of distribution of points in relation to size gave rise to two more homogeneous groups (Fig. 3b), evidence of an ontogenetic shift of diet. These results were statistically tested using the ANOSIM routine (test R). As expected, dietary differences between sexes were not

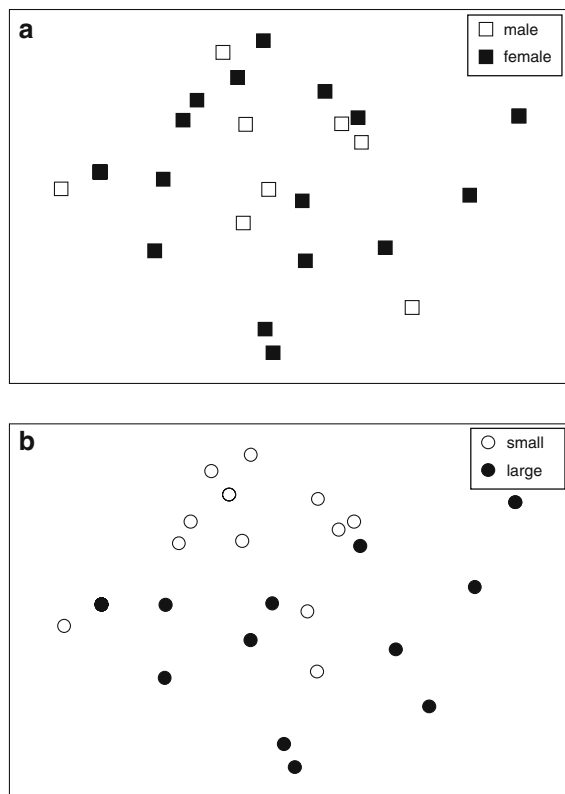


Fig. 3 MDS plot of *B. marri* sample on the basis of stomach content analysis, with sex (a) and fish size (b) superimposed, respectively

statistically significant, R being close to 0 ($P > 0.5$). Conversely, the differences between small and large fish were statistically significant, although the two groups were barely separable from each other ($R = 0.16$, $P < 0.01$).

Applying the SIMPER analysis to fish size, we obtained the relative contributions of each prey taxon to average dissimilarity between small and large fishes (Table 2). The copepod *Aetideopsis* sp. and the mysids *Pseudomma* spp. were the main contributors, together attaining a cumulative percentage of 36%. In detail, *Aetideopsis* sp. was consumed by small fishes, whereas

Pseudomma spp. were eaten preferentially by large fishes. The other three prey taxa, namely, the amphipods *O. franklini*, *Liljeborgia* cf. *georgiana* and *L. urometacarinatum* each contributed to 10% of the cumulative percentage (Table 2), and all were mainly preyed on by large fishes.

Finally, we compared univariate indices of dietary diversity (H') and evenness (J') calculated for each sex and fish size group. All the comparisons were not statistically significant ($P > 0.1$), giving evidence of a considerable food overlap between the selected groups of fishes.

Discussion

Compared with other congeneric species, *B. marri* inhabits relatively shallow waters ranging from 300 to 1,250 m depth (DeWitt 1985; Gon 1990; Miller 1993). This species was quite common in bottom trawling catches carried out between 300 and 450 m depth, although it was caught also in waters as deep as 1,200 m (Eastman and Hubold 1999; Donnelly et al. 2004). Juveniles may live in shallower waters (< 500 m) than adult fish, which are mainly distributed from 400 to 1,200 m. In the Weddell Sea, for example, *B. marri* preferentially inhabits the area of the Filchner depression (Gould Bay), which is a deep trench under the Filchner ice shelf where water temperature drops to -2.2°C (Ekau 1988, 1990; Hubold 1992). The preference for deep and cold waters would imply specific physiological adaptations in terms of antifreeze molecules in body fluids. Indeed, *B. marri* possess further antifreeze compounds in addition to the common antifreeze glycopeptides (AFGP) that characterize all other species of notothenioids (Wöhrmann 1996).

On the basis of stomach content analysis, juveniles of *B. marri* relied on a relatively wide spectrum of prey, consisting entirely of crustaceans. In decreasing order, mysids, amphipods and copepods were the most important taxa in terms of number of individuals and

Table 2 Relative contributions of each prey taxon to Bray–Curtis dissimilarities between small (S) and large fish groups (L)

Prey taxon	SIMPER data		
	Average dissimilarity = 83.43		
	Average abundance, S	Average abundance, L	Cumulative percentage
<i>Aetideopsis</i> sp.	0.83	0.25	18.2
<i>Pseudomma</i> spp.	0.39	0.42	36.3
<i>Orchomenella franklini</i>	0.00	0.50	47.5
<i>Liljeborgia</i> cf. <i>georgiana</i>	0.11	0.25	58.3
<i>Lepidepcreum urometacarinatum</i>	0.17	0.33	68.7

frequency of occurrence. The other prey taxa, namely, euphausiids, isopods and tanaids were preyed on in very small amounts. As far as mysids are concerned, *Pseudomma* and *Mysidetes* are the most speciose Antarctic and Subantarctic genera, whereas *Antarctomysis* comprises only three species all endemic to the Southern Ocean. All mysids found in the stomach contents of *B. marri* live hyperbenthically (i.e. above but close to the bottom), and are distributed on the shelf or at the shelf break (Brandt et al. 1998). Except for *Eusirus* cf. *antarcticus*, which is a benthopelagic species, all other amphipods preyed on by *B. marri* were benthic or epibenthic gammarideans, most of them belonging to Lysianassoidea (De Broyer and Jazdzewski 1993; De Broyer et al. 2001). Among calanoid copepods, most prey belonged to the genus *Aetideopsis* (family Aetideidae), which is composed of mesopelagic species commonly caught on the Ross Sea continental shelf (Razouls et al. 2000; P. Licandro, personal communication). The remaining prey taxa were strictly benthic, such as isopods and tanaids, or pelagic–benthopelagic (euphausiid).

Our data indicate that *B. marri* fed primarily on small benthic and hyperbenthic invertebrates, which are more or less motile on the sea bottom or in close proximity to it. However, they may switch their usual diet to alternative food resources which become seasonally abundant in the water column, copepods for example. The overall low lipid contents and the relatively higher phospholipid and lower triacylglycerol levels found in *B. marri* (Hagen et al. 2000) are in accordance with their reliance on benthic prey organisms.

The study of blood parameters provides some insight on the activity level and possible lifestyle of *B. marri* (Kunzmann et al. 1991). In comparison with other bathydraconids, one of the most inactive groups amongst notothenioids, the number of erythrocytes and the haematocrit of *B. marri* was quite low, although their haemoglobin concentration was comparable. On the basis of these data and on the type of prey identified in the present study, a “sit and wait” feeding strategy on or just above the substrate can be tentatively hypothesized for *B. marri*.

In general terms, the food preferences of this species agree with those observed in several bathydraconids, which rely mainly on crustaceans, such as mysids, amphipods, decapods and euphausiids, and fish (Targett 1981; Daniels 1982; Kompowski 1992; Gröhsler 1994; Takahashi and Iwami 1997; Pakhomov 1998; Barrera-Oro 2003; Casaux et al. 2003; La Mesa et al. 2004). The absence of relatively large prey such as decapods and fish in the stomachs of *B. marri* was probably due to the

small size of specimens investigated. Indeed, an ontogenetic shift in diet from small crustaceans, like amphipods and mysids, to decapods and fish was found in large-sized bathydraconids, such as *C. mawsoni* and *G. acuticeps* from the Cosmonaut and Commonwealth Seas (Pakhomov 1998) and *Parachaenichthys georgianus* from South Georgia (Kompowski 1992). Our analysis of stomach contents, despite it is based on few specimens caught in a single haul, also provided evidence of an ontogenetic dietary change in juveniles of *B. marri*, supporting the existence of some food partitioning; copepods were primarily preyed on by small fish, while amphipods and mysids were eaten preferentially by large fish.

Considering the main prey taxa, the diet of *B. marri* closely resembles those of some bathydraconids of comparable size and morphology, such as *Akarotaxis nudiceps*, *Gerlachea australis*, *Racovitzia glacialis* and *Vomeridens infuscipinnis*, which rely almost exclusively on crustaceans (Schwarzbach 1988).

Unfortunately, the lack of data on diet of congeneric species of *B. marri* does not allow a comparison among them. Further studies should focus attention on feeding habits of either adults of *B. marri* or on other species of *Bathydraco*, in order to provide new insight on feeding strategies that mitigate intra- and/or inter-specific food competition within the demersal fish community of the high-Antarctic Zone.

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