



# Feeding ecology of an inshore population of *Notothenia coriiceps* from the Argentine Islands, Bellingshausen Sea

Vladien Trokhymets<sup>1</sup> · Artem Zinkovskyi<sup>1</sup> · Ihor Dykyi<sup>2</sup> · Mario La Mesa<sup>3</sup>

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## Abstract

The inshore waters off the Argentine Islands host a diversified benthic fish community largely dominated by the black rockcod, *Notothenia coriiceps*. Compared to other areas along the western Antarctic Peninsula, the feeding habits of this species in this location are poorly known. Hence, the aim of the study is to assess food preferences by the stomach content examination, applying a sophisticated analytical approach. As reported elsewhere, the black rockcod is omnivorous, relying primarily on algae, gastropods, amphipods, euphausiids and fishes, each consumed with different foraging strategies. Based on multidimensional scaling statistical procedures, fish size and water depth are the primarily contributors to prey resource diversification and partitioning. Overall the sampled population of the black rockcod are generalist feeders with a relatively high between-phenotype component to the niche width, consisting of specialized individuals with little or no overlap in food resource use.

**Keywords** Diet · Feeding strategy · Antarctic fish · Black rockcod · Antarctic Peninsula

## Introduction

The black rockcod, *Notothenia coriiceps* Richardson, 1844 is one of the most common species in inshore waters of West Antarctica and adjacent islands, from surface waters to 550 m depth (Gon and Heemstra 1990). Its widespread distribution, large population size and wide food spectrum consisting of some of the most energy rich invertebrate prey make this species a stable and integral component of the Southern Ocean benthic communities (Marina et al. 2018; Barrera-Oro et al. 2019). The non-commercial status of black rockcod, interrupted by a period as by-catch of past commercial harvesting (Kock 1992), has contributed to its

survival and status as a healthy population. Indeed, mass commercial fisheries exploitation has led to a significant decrease in several sympatric species with a similar ecological niche to the black rockcod, with *Notothenia rossii* Richardson, 1844 and *Gobionotothen gibberifrons* Lönnberg, 1905 as examples. The progressive decline of these species reduced the competition for food with other closely related benthic feeders, such as *N. coriiceps*, whose populations are increasing, especially in inshore waters off the South Shetland Islands (Barrera-Oro et al. 2000, 2017; Marschoff et al. 2012).

The black rockcod is overwhelmingly the most abundant fish species collected in coastal waters off Argentine Islands, a group of small islands within the Wilhelm Archipelago located off the western Antarctic Peninsula (WAP) (Fig. 1). Considering interannual variability, this species represented approximately 50% to 91% of total catches obtained in inshore waters less than 50 m deep (Manilo et al. 2009; Trokhymets et al. 2022). Given its abundance and wide geographical distribution, the black rockcod is one of the key species of inshore areas along the southern Scotia Arc and off the WAP, relying on a wide variety of benthic and epibenthic prey, such as algae, polychaetes, gastropods, limpets, clams, bivalves, cephalopods, gammarideans, isopods, ascidians, krill, hyperiids and salps. In turn, it is the common

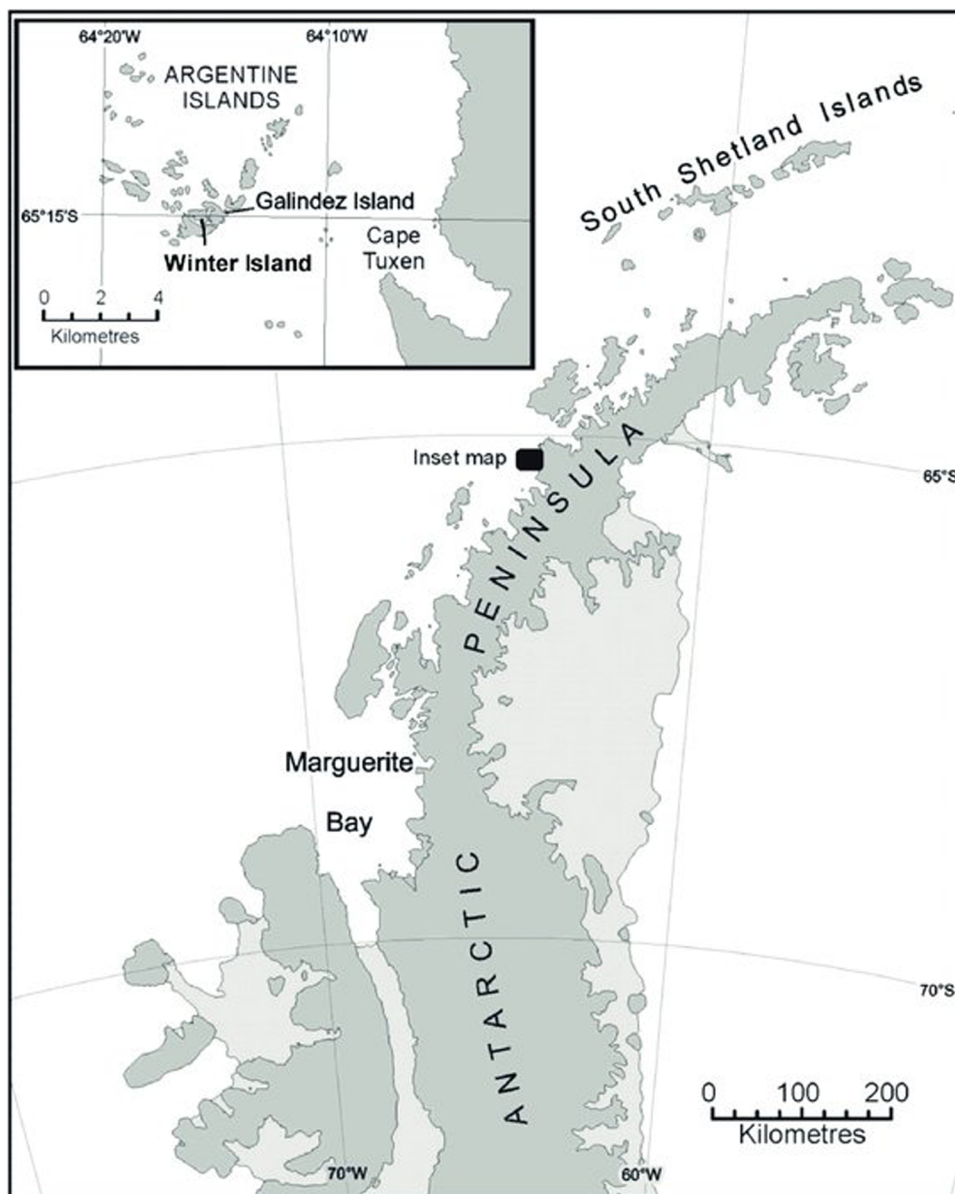
✉ Mario La Mesa  
mario.lamesa@cnr.it

<sup>1</sup> Department of Ecology and Zoology, Taras Shevchenko National University of Kyiv, Educational and Scientific Center «Institute of Biology and Medicine», Hlushkova Avenue 2, Kiev 03127, Ukraine

<sup>2</sup> Department of Zoology, Faculty of Biology, Ivan Franko National University of Lviv, Mykhaila Hrushevskoho Street, 4, Lviv 79005, Ukraine

<sup>3</sup> CNR, Institute of Polar Sciences (ISP), c/o Area di Ricerca di Bologna, via P. Gobetti 101, 40129 Bologna, Italy

**Fig. 1** Topographic map of the Argentine Islands showing the sampling area and its position along the western Antarctic Peninsula. Vernadsky Station is located at Marina Point on Galindez Island



prey of several top predators, such as sea birds and seals (reviewed in Barrera-Oro 2002 and references therein).

The Argentine islands ecosystem is important from an ecological perspective, hosting a diverse vertebrate fauna including fishes and breeding colonies of birds and mammals (Polishuk et al. 2009), whose protection has been recently ensured through the establishment of a marine-protected area (Utevsky et al. 2014; Fedchuk et al. 2020). Before planning and enforcement of any rules for conservation of this area, an annual monitoring programme was adopted in 2003 to provide more insight on the structure and function of the most common species (Fedchuk et al. 2020). In particular, monthly samples of the black rockcod have been collected all the year around during the XI, XII, and XIV Ukrainian

Antarctic Expeditions carried out in 2006–2007, 2007–2008, and 2009–2010, respectively.

In this study we focus on the feeding habits of the black rockcod population living in inshore waters off the Argentine Islands. We use stomach content analysis to assess the variability of diet in relation to biotic and environmental characteristics. Applying a multidimensional scaling statistical procedure, we evaluate the role of population parameters (fish size) and environmental factors (water depth, sampling month) in prey resource partitioning to prevent intraspecific competition. Finally, we described the feeding strategy at the population level and the individual fish contributions to feeding niche breadth by applying a graphical method (Costello 1990; Amundsen et al. 1996).

## Materials and methods

### Fish sampling

Black rockcod were collected in inshore waters off the Argentine islands during the XI (2006–2007, February to February), XII (2007–2008, April to January) and XIV (2009–2010, April to March) Ukrainian Antarctic Expeditions. Due to rugged, rocky bottoms and frequent floating ice, most specimens were caught by hook and line (94%), whereas the remaining fish were captured by hand net and traps. The severe environmental constraints (sunlight, ice cover, cold temperature, etc.) and their variability throughout the year did not enable us to follow a precise sampling design, and our collections should be considered as opportunistic. Sampling activities were carried out in several sites, although fishes were disproportionately collected in a few sites in proximity to the Vernadsky Station. For this reason, the sampling site was not taken into account in the dietary analyses. Fishes were unevenly sampled over a depth range between 1.5 and 50 m (Table 1). Fishing depth was measured by an echosounder.

### Laboratory analyses

After taxonomic identification according to Gon and Heemstra (1990), the black rockcod were sorted, measured as total length (TL) and standard length (SL) to the nearest mm and weighed as total weight (TW) and eviscerated weight (EW) to the nearest gram. Sex was determined macroscopically after evisceration, and gonads were weighed to 0.01 g. Soon after capture, fresh stomachs were removed from each specimen and their contents put in a petri dish. Prey were identified to main categories and counted. Unfortunately, the lack of an accurate electronic balance in the Base laboratory did not allow us to record prey weight. Fish eggs and algae found in the

stomachs were considered as single items, as they would have been overestimated or eaten in an unknown number, respectively.

### Data processing

The structure of sampled population was analysed in terms of length frequency distributions calculated for each sex and sampling year. Each paired comparison was performed applying the Kolmogorov–Smirnov two-sample test. Sex ratio departure from 1:1 was assessed by a chi-square goodness of fit test. Fish body growth was modelled by an exponential function, in the form  $TW = aTL^b$ , where TW and TL are total weight (g) and total length (cm) of fishes, respectively, and  $a$  and  $b$  are the fitting parameters. Isometric growth departure ( $b \neq 3$ ) is assessed by a  $t$  test using the equation  $t = (b - 3) SE^{-1}$ , where SE is the standard error of  $b$ . Paired comparisons of allometric indices ( $b$ ) calculated for each sex and sampling years were performed by a Fisher test (Sokal and Rohlf 1995). As a measure of individual fish condition, the relative condition factor  $K_{rel} = a (TW/TL^b)10^5$  (Bolger and Connolly 1989) was calculated using the above-mentioned parameters and compared between sexes and sampling years by ANOVA. Finally, the gonadosomatic index (GSI) was estimated as the proportion of gonad to somatic weight. All statistical tests were performed with a significance level of 0.05.

Based on the analysis of stomach contents, food composition was assessed in terms of numerical abundance of each prey category ( $N\%$ ) and frequency of occurrence ( $O\%$ ), excluding fishes with empty stomachs (Hyslop 1980). The percentage of empty stomachs of the total number of stomachs analysed was calculated. Dietary diversity was assessed separately for each sampling year by calculating the number of prey taxa ( $S$ ) and the feeding niche breadth through the Shannon–Wiener index ( $H' = -\sum_i^S pi(\log pi)$ ), where  $pi$  is the percentage by number of the  $i$ th prey and the evenness index ( $J' = H'/\log S$ ) (Shannon and Weaver 1963; Pielou 1966). A modified Costello method was applied to the entire prey dataset to assess the feeding strategy and individual contribution to niche breadth (Costello 1990; Amundsen et al. 1996). The prey-specific abundance ( $P_i$ ), defined as the numerical percentage of a prey taxon calculated considering only those fish containing it, was plotted against the frequency of occurrence ( $O\%$ ) to produce a two-dimensional diagram.

To evaluate the influence of biotic (fish size) and environmental parameters (sampling month, fishing depth) on diet composition, a multivariate analysis was performed using the whole prey dataset (Marshall and Elliott 1997). To reduce individual variability, the mean abundance of prey was calculated by pooling fish within 1 cm size classes to evaluate diet shift during the ontogeny in 25 size categories.

**Table 1** Fish samples of the black rockcod collected by depth and year of sampling

Depth range (m)	2006–2007	2007–2008	2009–2010
0–5	16		4
5–10	13	2	
15–20	22	58	5
20–25	7	25	48
25–30	80	70	
30–35	2	20	35
40–45		14	
45–50	3	3	

Similarly, the influence of sampling period and fishing depth was assessed by pooling fish for each month of sampling (from January to December) and for eight depth strata arbitrarily chosen (0–5 m, 5–10 m, 15–20 m, 20–25 m, 25–30 m, 30–35 m, 40–45 m, 45–50 m), respectively. A non-metric multidimensional scaling (MDS) was applied to a pair-wise Bray–Curtis coefficient similarity matrix derived from the numerical data set of prey (previously standardized), producing a two-dimensional plot. An analysis of dissimilarity was carried out through the SIMPER routine to evaluate the relative contribution of each prey taxon to fish categories distribution within the plot. Finally, a one-way statistical analysis (ANOSIM routine, test *R*) was performed to test the role of biotic and environmental factors in diet diversification. 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

### Population structure

The sample of black rockcod consisted of 427 specimens collected in three different sampling years (Table 2). The

sex ratio differed significantly from 1:1, with males more abundant than females (246 vs 181,  $\chi^2 = 9.89$ ,  $p = 0.002$ ). The condition factor did not change across fish size range, and any comparison between sexes or sampling years was not statistically significant (Table 3). As expected, GSI values in males were generally lower than in females and rarely they exceeded 5% in either sex, suggesting the absence of specimens in spawning condition. The length frequency distributions (Fig. 2) did not differ significantly between sexes within each sampling year or between sampling years

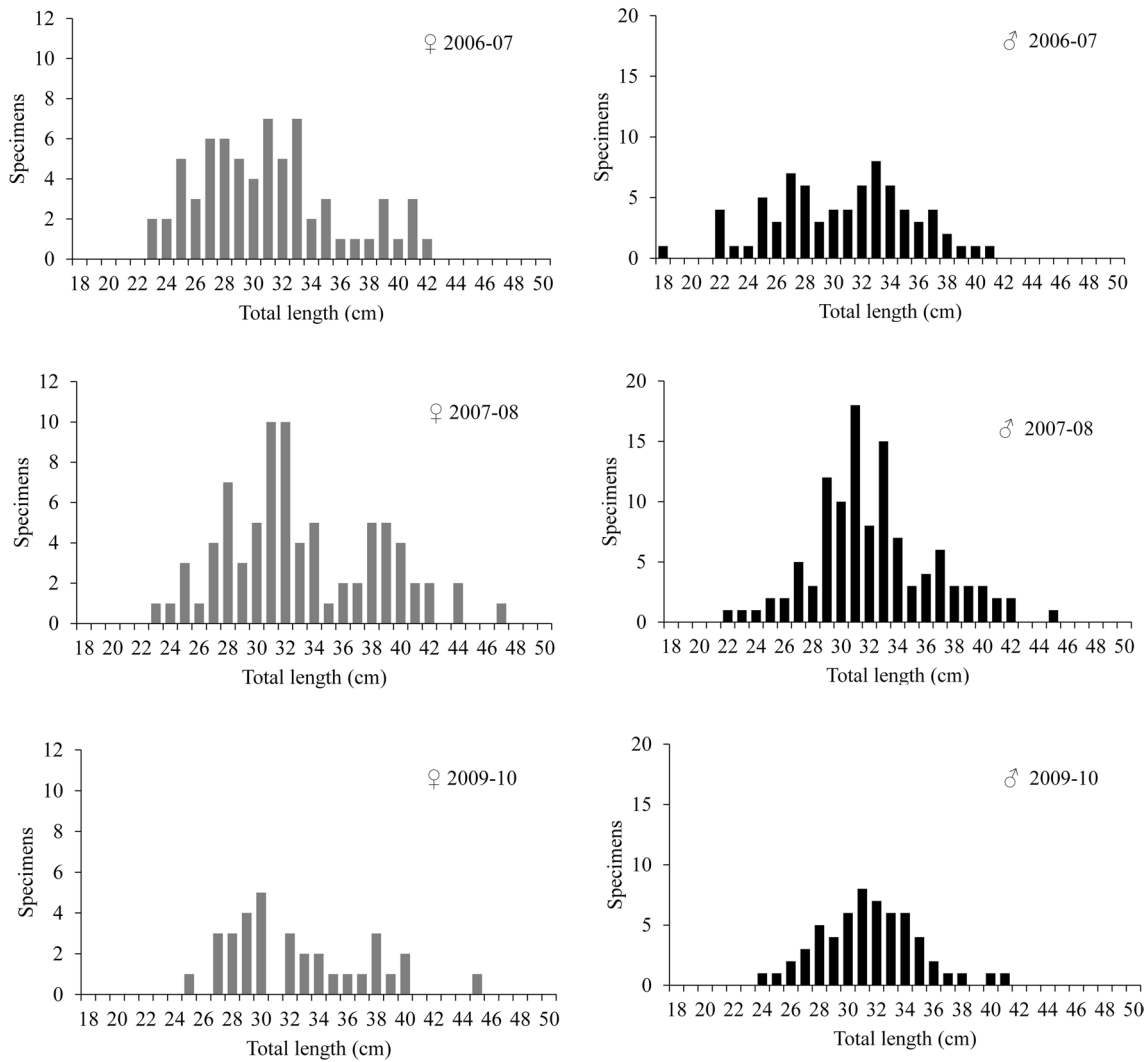
**Table 3** ANOVA table of the relative condition factor ( $K_{rel}$ ) in relation to sex and sampling year

Crossed comparisons	<i>F</i>	<i>p</i>
♂ vs ♀ 2006–2007	0.0038	0.9567
♂ vs ♀ 2007–2008	0.0009	0.9754
♂ vs ♀ 2009–2010	0.0013	0.9712
♀ 2006–2007 vs 2007–2008	0.0002	0.9871
♀ 2007–2008 vs 2009–2010	0.0006	0.9802
♀ 2006–2007 vs 2009–2010	0.0013	0.9704
♂ 2006–2007 vs 2007–2008	0.0115	0.9144
♂ 2007–2008 vs 2009–2010	0.0028	0.9573
♂ 2006–2007 vs 2009–2010	0.0204	0.8866

**Table 2** Biological data of the black rockcod samples collected off the Argentine islands

Month/data	2006–2007		2007–2008		2009–2010	
	♀	♂	♀	♂	♀	♂
February	17	23				
March	6	14				
April	4	2	7	13	7	16
May			15	21	2	4
June	4	3	20	32	7	12
July	4	2	9	20	4	4
August	13	11	1	1	1	
September	4	4	3	2		1
October	4	3	14	10	6	9
November	5	7	4	8		
December	6	3	3	1	1	1
January			4	4	1	1
February	1	3				6
March					4	5
<i>n</i>	68	75	80	112	33	59
Size (TL, cm)	22.5–42.0	17.5–40.5	22.5–46.7	22.0–45.0	24.4–45.0	23.1–40.4
Weight (TW, g)	141–1108	66–847	122–1242	117–958	188–1390	152–940
GSI	0.28–10.96	0.14–5.73	0.18–17.30	0.11–3.38	0.71–11.71	0.10–9.22
Mean	1.37	0.84	1.72	0.37	2.09	0.56
$K_{rel}$	0.81–1.28	0.82–1.26	0.73–1.31	0.82–1.35	0.75–1.26	0.83–1.36
Mean	1.004	1.003	1.004	1.005	1.005	1.006

*n* number of specimens, *TL* total length, *TW* total weight, *GSI* gonadosomatic index,  $K_{rel}$  relative condition factor



**Fig. 2** Length frequency distributions of the black rockcod collected off the Argentine islands

**Table 4** Kolmogorov–Smirnov test results applied to the length frequency distributions in relation to sex and sampling year

Crossed comparisons	<i>D</i>	<i>p</i>
♂ vs ♀ 2006–2007	0.077	1.30
♂ vs ♀ 2007–2008	0.137	0.34
♂ vs ♀ 2009–2010	0.174	0.54
♀ 2006–2007 vs 2007–2008	0.176	0.20
♀ 2007–2008 vs 2009–2010	0.172	0.50
♀ 2006–2007 vs 2009–2010	0.146	0.76
♂ 2006–2007 vs 2007–2008	0.239	0.01
♂ 2007–2008 vs 2009–2010	0.112	0.75
♂ 2006–2007 vs 2009–2010	0.174	0.26

**Table 5** Length–weight relationships parameters and *t* test for allometry results

Parameters	<i>a</i>	<i>b</i>	<i>r</i> <sup>2</sup>	<i>t</i>	<i>p</i>
♂ 2006–2007	0.0096	3.09	0.97	1.52	0.1326
♀ 2006–1007	0.0049	3.29	0.96	3.85	0.0003
♂ 2007–1008	0.0085	3.09	0.94	1.21	0.2284
♀ 2007–2008	0.0048	3.26	0.96	3.71	0.0004
♂ 2009–2010	0.0084	3.15	0.91	1.17	0.2431
♀ 2009–2010	0.0051	3.29	0.95	2.28	0.0291

within the same sex, except for the comparison between males collected in 2006–2007 and 2007–2008 (Table 4). The length–weight relationship was calculated separately for each sex and sampling year. Fish body growth was different between sexes and was consistently isometric and positively

allometric in males and females, respectively (Table 5). Nevertheless, all paired comparisons of the allometric indices were not statistically significant, except for males and females sampled in 2006–2007 (Table 6).

### Diet composition

The stomach contents analysis was performed on the entire available fish sample. One hundred thirteen of 427 specimens (26.5%) had empty stomachs. A total of 14 prey taxa were recognized, mostly crustaceans or molluscs (Table 7). The most abundant prey by number were relatively small items, such as amphipods (mainly *Paraceradocus gibber* Andres, 1984), gastropods (limpets, *Nacella concinna*) and euphausiids, followed by fishes (mainly *Lepidonotothen* spp. and *Trematomus* spp.) and algae. Conversely, the most frequently eaten organisms were algae, followed in decreasing order by amphipods, gastropods, fishes, euphausiids and isopods (Table 7). Indices of dietary diversity and evenness were comparable in the first two sampling years, increasing slightly in the third year (Table 8).

### Feeding strategy

The two-dimensional modified Costello diagram shows the pattern of distribution of prey taxa based on their own frequency of occurrence and prey-specific abundance (Fig. 3). The feeding strategy axis indicates that the black rockcod is a generalist feeder, relying on several prey taxa with a relatively low prey-specific abundance, being mainly located in the lower part of the diagram. Considering the prey importance and niche width contribution axes, the diet consists of rare prey items eaten in small amount (low *N%*) and occasionally (low *O%*), with a relatively high between-phenotype component to the niche width (Fig. 3). In other words, the sampled fish population includes primarily specialized individuals with little or no overlap in food resource use.

**Table 6** Fisher test results applied to the allometric indices (*b*) in relation to sex and sampling year

Crossed comparisons	<i>F</i>	<i>p</i>
♂ vs ♀ 2006–2007	4.5032	0.0356
♂ vs ♀ 2007–2008	2.8092	0.0953
♂ vs ♀ 2009–2010	0.5849	0.4464
♀ 2006–2007 vs 2007–2008	0.1157	0.7341
♀ 2007–2008 vs 2009–2010	0.0691	0.7931
♀ 2006–2007 vs 2009–2010	0.0002	0.9882
♂ 2006–2007 vs 2007–2008	0.0004	0.9839
♂ 2007–2008 vs 2009–2010	0.2040	0.6520
♂ 2006–2007 vs 2009–2010	0.2265	0.6349

**Table 7** Diet composition of the black rockcod from the Argentine Islands

Prey taxa	<i>N%</i>	<i>O%</i>
Algae	11.56	61.15
Sponges	0.06	0.32
Nemertean	0.12	0.64
Polychaetes	2.59	7.64
Gastropods	21.73	27.07
Bivalves	0.12	0.32
Cephalopods	0.12	0.64
Amphipods	29.44	41.08
Isopods	3.55	14.65
Euphausiids	17.76	19.43
Decapods	0.12	0.64
Echinoderms	0.06	0.32
Fishes	12.04	25.48
Fish eggs	0.54	2.87

*N%* numerical percentage, *O%* frequency of occurrence

### Biotic and environmental parameters influencing diet

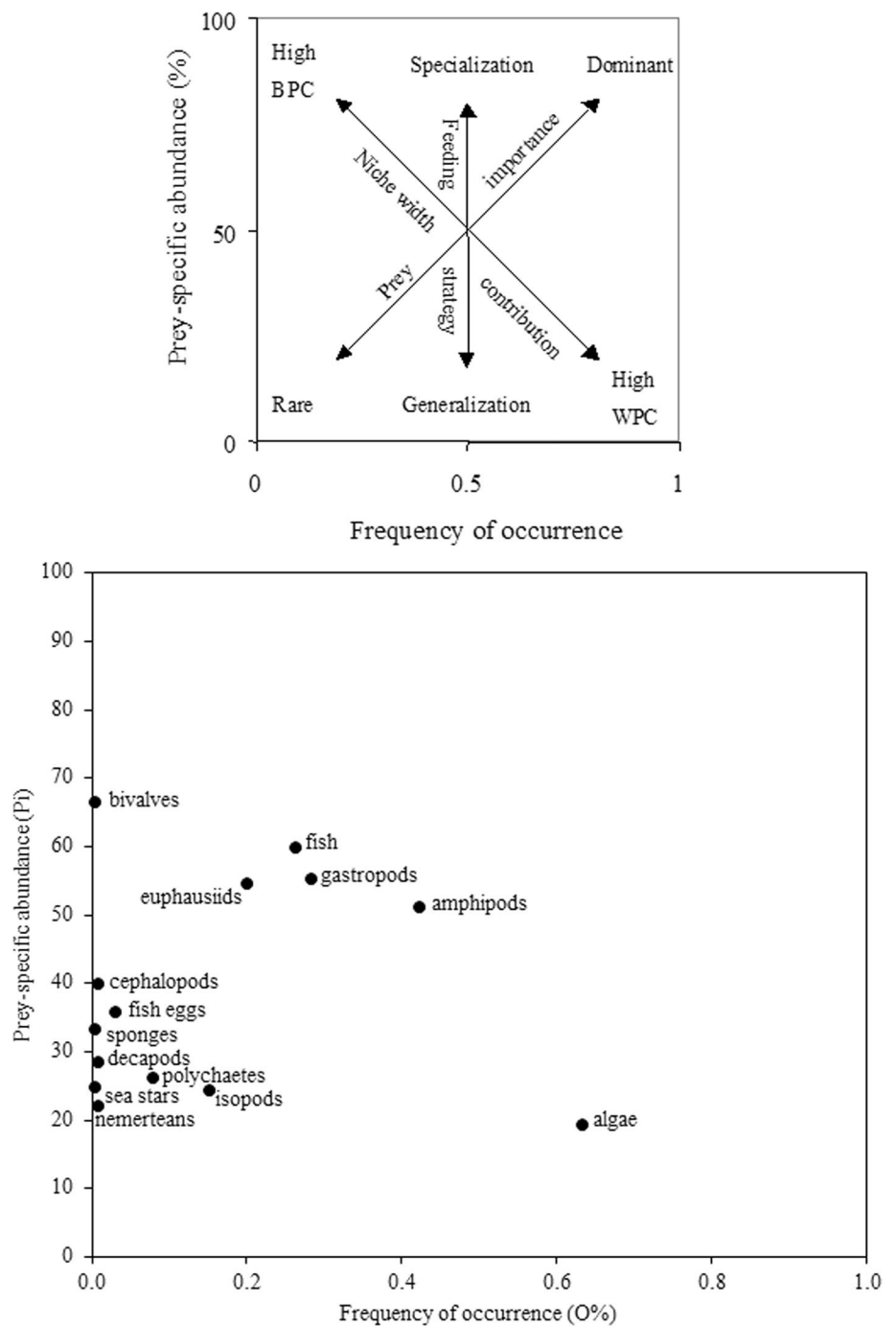
Food composition was influenced primarily by the fish size and sampling depth, whereas no significant diet changes were detected in relation to month of sampling. Size-related changes in diet are shown in the MDS two-dimensional plot (Fig. 4a). The 25 size categories consisted of small (< 30 cm TL), medium (≥ 30 and < 40 cm TL) and large fish (≥ 40 cm TL), labelled within the plot as “s”, “m” and “l”. Based on the ANOSIM results, the size groups were clearly different although partially overlapping ( $R > 0.5$  in all comparisons, Table 9). The stress value of the ordination was relatively low (0.08), indicating a good representation of diet similarities within groups in the two-dimensional scale. The SIMPER analysis provided information on the relevant contribution of the most important prey taxa to the ordination plot (Fig. 4b–f). Five prey taxa contributed to 86–92% of average dissimilarity amongst fish size groups. Algae were present in all groups, although with an increasing trend from small to large fishes (Fig. 4b). Gastropods were eaten primarily by the marginal size classes of each group located on the lower left side of the plot (Fig. 4c). Finally, crustaceans such as

**Table 8** Dietary diversity indices of the black rockcod from the Argentine Islands

Sampling year	<i>S</i>	<i>H'</i>	<i>J'</i>
2006–2007	9	0.67	0.70
2007–2008	10	0.65	0.65
2009–2010	11	0.78	0.75

*S* number of prey taxa, *H'* Shannon–Wiener index, *J'* Pielou index

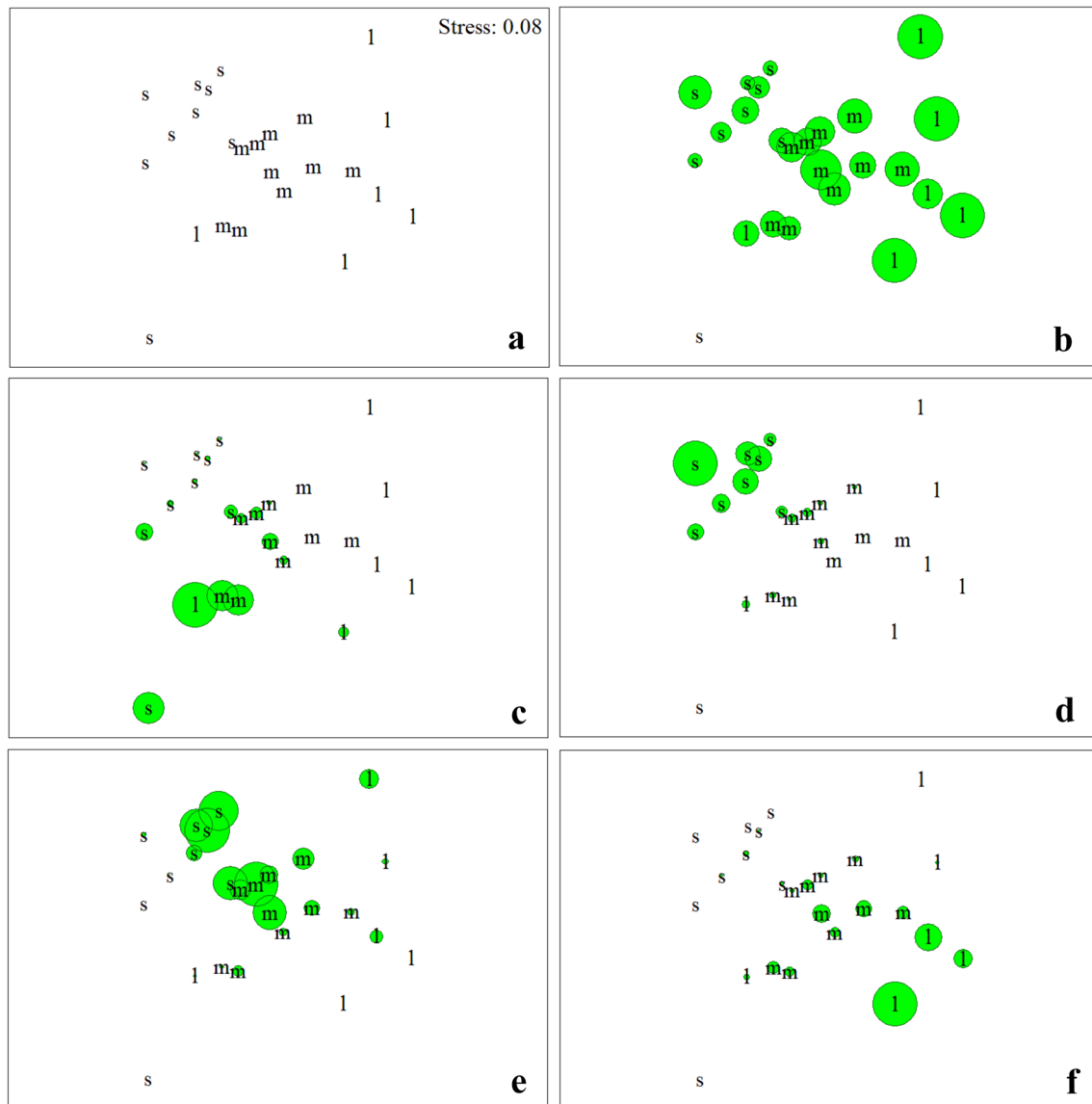
**Fig. 3** Modified Costello plot applied to the prey taxa consumed by the black rockcod collected off the Argentine Islands. Upper diagram shows the main axes and their significance, and the lower diagram indicates the taxa of prey



amphipods and euphausiids were consumed almost exclusively by small or by small- and medium-sized fish (Fig. 4d, e), whereas fishes were preyed on primarily by large black rockcod individuals (Fig. 4f).

The eight depth strata were associated with three depth groups, defined as shallow ( $\leq 10$  m), medium ( $\geq 15$  and  $\leq 30$  m) and deep waters ( $> 30$  m) as labelled within the plots (Fig. 5a). Based on the ANOSIM results, the

different groups were clearly separated, with some overlap ( $R \cong 0.5$ ), as well as any pair-wise comparison except for the medium deep waters (Table 9). Five prey taxa accounted for 83–93% of average dissimilarity amongst depth groups. Algae were well represented in all groups, with a slightly higher abundance at medium depths (Fig. 5b). Gastropods were primarily represented in shallow and medium depths (Fig. 5c), whereas amphipods exhibited a decreasing trend



**Fig. 4** Multi-dimensional scaling (MDS) and SIMPER analyses performed on the mean numerical abundance of prey taxa of each fish size classes. MDS ordination plot (**a**) of fish size categories (25) labelled according to three size groups arbitrarily defined as small

(s), medium (m) and large (l); bubble plots show mean numerical abundance (increasing with bubble diameter) pattern of the following main contributing prey taxa (superimposed on the relevant MDS plot): **b** algae, **c** gastropods, **d** amphipods, **e** euphausiids and **f** fishes

from shallow to deep waters (Fig. 5d). Euphausiids were overwhelmingly consumed in the shallower waters at 0–5 m (Fig. 5e), and fish prey clearly showed an increasing trend from shallow to deep water groups (Fig. 5f).

## Discussion

In the Antarctic marine ecosystem, the dominant and endemic coastal demersal group Notothenioidei are the key components in inshore food webs, feeding on a variety of

benthic organisms below their trophic level, spanning algae to fish, as well as on zooplanktonic prey in the water column (Barrera-Oro 2002). To reduce food overlap at interspecific level and, hence, to limit competition under conditions of limited resource availability, notothenioids have evolved a wide range of feeding strategies and foraging behaviour (Daniels 1982; Kock 1992; Barrera-Oro 2003). By foraging on different prey items or on different amounts of the same prey and adopting specialized or generalized feeding mode,



**Table 9** Analyses of diet similarity (ANOSIM) of the black rockcod from the Argentine Islands

Groups	<i>R</i> statistic	Signifi- cance level (%)
<i>Size</i>		
Global	0.556	<< 0.001
Small, medium	0.585	<< 0.001
Small, large	0.605	0.001
Medium, large	0.522	0.001
<i>Depth</i>		
Global	0.483	0.004
Shallow, medium	0.500	0.1
Shallow, deep	0.583	0.1
Medium, deep	0.333	0.1

different species of notothenioid fish occupy an array of different food niches (Targett 1981; Gröhsler 1994).

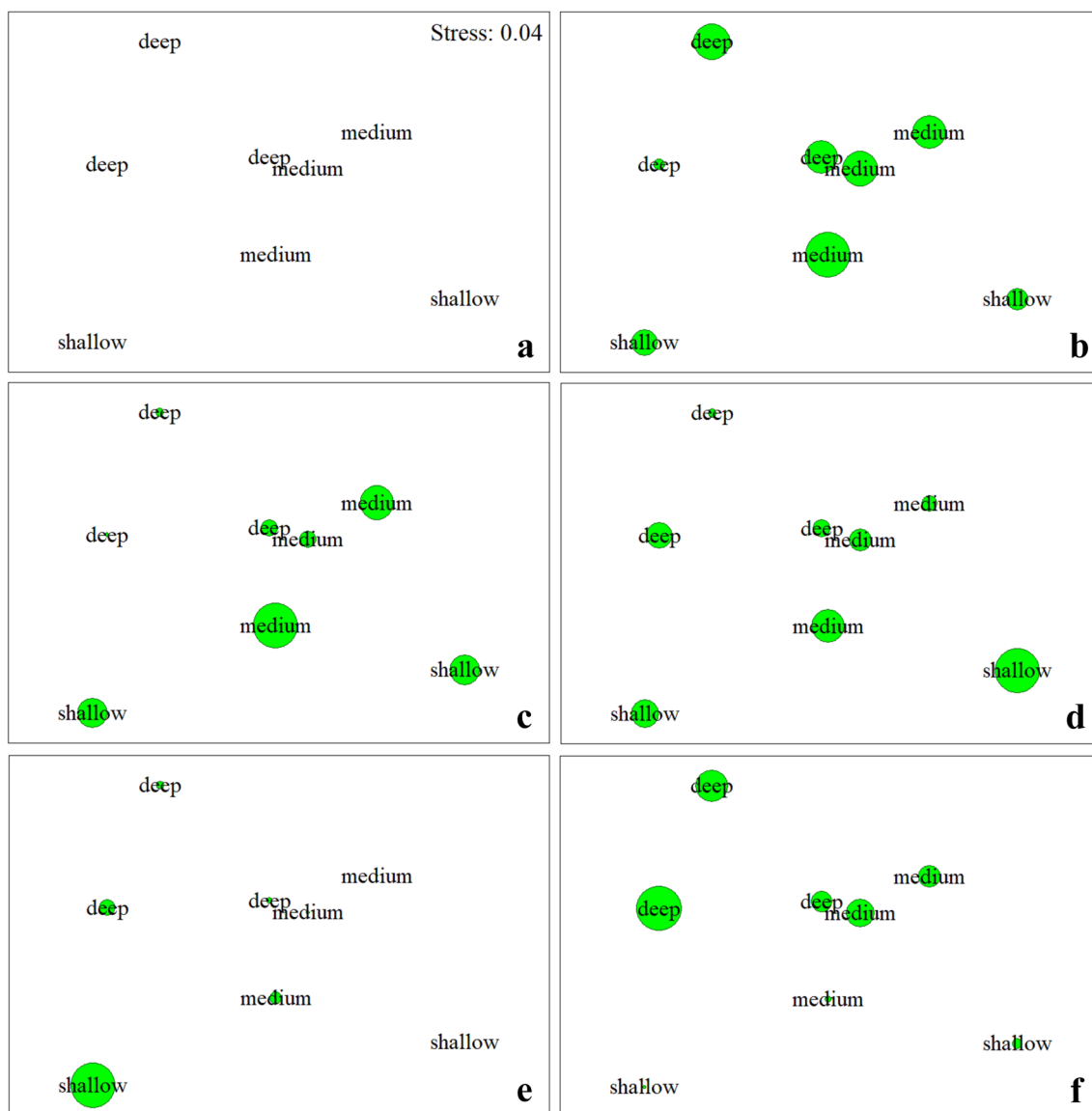
Within the family Nototheniidae, the black rockcod is by far the dominant fish species in shallow waters along the western Antarctic Peninsula and associated islands (DeWitt et al. 1990). According to Daniels (1982), this species exhibits a variety of feeding strategies, often varying seasonally. Being a visual hunter (Zamzow et al. 2010), the black rockcod is primarily an ambush feeder pursuing benthic motile organisms, although occasionally it feeds in the water column on pelagic prey, such as euphausiids, amphipods and other fishes (North 1996). Grazing becomes the most important foraging mode in spring and summer, when macroalgae are dominant food (Daniels 1982). It has been demonstrated that algae are not eaten accidentally, but they are actively selected and consumed by this species and not related to associate epifaunal biomass, like amphipods (Barrera-Oro and Casaux 1990; Casaux et al. 1990; Iken et al. 1997).

The black rockcod population sampled in inshore waters off the Argentine Islands consisted exclusively of subadults and a few adult specimens of relatively small size. Body growth of females was slightly higher than in males, in agreement with previous data obtained from a neighbouring black rockcod population off the Danco Coast (Casaux et al. 2003). On the other hand, the condition factor did not differ between sexes, suggesting a comparable fitness and food intake between them. The feeding intensity over the entire sample of the black rockcod was relatively high (26.5% of empty stomachs), but lower in comparison to other populations sampled elsewhere, where the proportion of empty stomachs ranged from 3% in smaller individuals (Moreira et al. 2014) to 14% in fish

of comparable size (Casaux et al. 2003). It should be noted that, different from previous studies and due to logistic constraints in the harsh Antarctic environment, we had to collect fish almost exclusively by hook and line, a sampling methodology inherently biased in selecting hungry individuals, in some cases with empty stomachs. In addition, the lack of weight data of each prey item may have introduced some biases in the results, leading to an overestimation of the importance of small prey (e.g. amphipods and gastropods) and/or an underestimation of large prey (e.g. fish).

Diet composition of the black rockcod off the Argentine Islands closely resembled those reported in inshore waters from other sites along the western Antarctic Peninsula (Moreno and Zamorano 1980; Casaux et al. 2003; Zamzov et al. 2011; Casaux and Barrera-Oro 2013) and off the King George Island (Linkowski et al. 1983; Fanta et al. 2003; Moreira et al. 2014; Raga et al. 2015; Barrera-Oro et al. 2019). As observed elsewhere, this species can be defined as a generalist and opportunistic feeder with indications of foraging plasticity. Off the Argentine Islands, the intraspecific trophic competition is mitigated by an ontogenetic shift of food preferences, with small fish consuming primarily amphipods and krill and large specimens relying on fishes. Grazing is still one of the most widespread feeding mode, as macroalgae represented a common shared food resource throughout the year. In this case, however, there was an increasing trend of algal consumption with fish size, consistent with an ontogenetic increase of intestine length reported for this species in previous studies (Moreira et al. 2020).

In summary, the sampled population of black rockcod consisted of individual fish that appeared to specialize on a few food items with different individuals sometimes specialized on different prey items, resulting a generalized feeding at the population level. Diet composition did not differ significantly during the sampling period, as indicated by constant local prey availability throughout the year. Conversely, the food composition varied with sampling depth, probably reflecting a different spatial distribution in prey availability. Dietary differences are therefore driven by two main factors: one intrinsic, due to individual food preference, and another linked to the different microhabitats that characterize the inshore waters of the Argentine Islands, with a consistent reduction in home range and mobility especially during the autumn and winter (Campbell et al. 2008).



**Fig. 5** Multi-dimensional scaling (MDS) and SIMPER analyses performed on the mean numerical abundance of prey taxa in each sampling depth strata. **a** MDS ordination plot of sampling depth strata (8) with labels corresponding to three depth groups arbitrarily defined as

shallow, medium and deep; bubble plots show mean numerical abundance (increasing with bubble diameter) pattern of these main contributing prey taxa (superimposed to the relevant MDS plot): **b** algae, **c** gastropods, **d** amphipods, **e** euphausiids and **f** fishes

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**Author contributions** VT conceived the study, MLAM wrote the manuscript and AZ and ID conducted field and lab work. All authors effectively contributed to the interpretation of the findings and revision and editing of the final draft of the article.

## Declarations

**Conflict of interest and ethics approval** All authors declare they have no conflicts or competing interest and that the study was conducted in accordance with the ethical standards of their national research committee. The dataset is available from the corresponding author on request.

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