Feeding ecology of three inshore fish species at Marion Island (Southern Ocean)

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The diets, morphological features and habitats of 258 specimens of the three inshore fish species *Notothenia coriiceps, N. macrocephala* and *Harpagifer georgianus* from Marion Island are described and compared. Correspondence analysis of the three diets shows the existence of three clearly defined feeding niches despite the occurrence of some common prey species. Inter- and intraspecific similarities and differences in the diets of small and large size classes of each species are also displayed by correspondence analysis. Size-limited predation by *N. coriiceps* of the limpet *Nacella delesserti* is described. Differences in the habitats occupied by the fish appear to be important in determining the species composition of their diets.

S. Afr. J. Zool. 1982, 17: 164 – 170

Die diëte, morfologiese kenmerke en habitat van 258 eksemplare van die drie vis-spesies, *Notothenia coriiceps, N. macrocephala* en *Harpagifer georgianus*, wat naby die kus van Marion-eiland voorkom, word beskryf en vergelyk. Vergelykende analise van die drie diëte toon die bestaan van drie duidelik gedefinieerde voedingsgebiede ten spyte van die voorkoms van sommige algemene roofspesies. Inter- en intraspesifieke ooreenkomste en verskille in die diëte van klein en groot klasmonsters van elke spesie is ook aangetoon deur vergelykende analise. Grootte-beperkte roof deur *N. coriiceps* op die klipmossel *Nacella delesserti* word beskryf. Verskille in die habitat van die verskillende spesies blyk belangrik te wees in die vasstelling van die spesiesamestelling van hulle diëte.

S.-Afr. Tydskr. Dierk. 1982, 17: 164 – 170

Three species of fish occur in the shallow inshore waters of Marion Island. *Notothenia macrocephala* Günther 1860 and a subspecies of *N. coriiceps* Richardson 1844 are Antarctic cods of the family Nototheniidae. The third species, *Harpagifer georgianus* subsp. *georgianus* Nybelin 1947, which was previously described as *Harpagifer bispinis* subsp. *marionensis*, is a member of the plunderfish family Harpagiferidae.

While there are many studies on Antarctic fish (Holloway 1969; Everson 1970; Meier 1971; Permitin & Tarverdieva 1972; Richardson 1975; Targett 1981), few detailed reports on the feeding of sub-Antarctic fish exist except that of Hureau (1966) who examined the diet of *Notothenia macrocephala* and two other species of Nototheniidae at Kerguelen Island. De Villiers (1976) described the major prey of the three species of fish at Marion Island without providing any quantitative data. The aim of the present study was to provide baseline quantitative data on the diets and interrelationships of the three species mentioned above.

Materials and Methods

Specimens were obtained through numerous collections between May 1979 and May 1980, made at various sites in Transvaal Cove, a relatively sheltered bay close to the research station on the north-east coast of Marion Island. *Notothenia macrocephala* was captured on hook and line at depths ranging from 20 cm in the intertidal zone to 20 m at the base of the offshore *Macrocystis* belt. *Notothenia coriiceps* was caught mainly at depths of 1 – 4 m by using a hand-net whilst snorkelling, although a few specimens were obtained on hook and line in the shallow subtidal zone. *Harpagifer georgianus* was found under boulders and amongst rubble or algal turf in the intertidal and in shallow subtidal zones, and all specimens were caught by hand.

Specimens were examined and dissected in the laboratory. The standard length of each fish was recorded to the nearest millimetre and mass measured to the nearest 0,1 or 1,0 g. Stomachs were removed and the wet mass of contents recorded. Prey from each stomach were sorted to species level and then counted and weighed to the nearest 0,01 g. Lengths of selected prey species from each stomach were also recorded. Ingested seaweeds were classified as rhodophytes, chlorophytes or phaeophytes and wet mass recorded. Intestinal contents were examined although they were not used in the final analysis. All gut

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Received 15 December 1981; accepted 15 April 1982

contents were preserved in 10% formalin. Stomach content data were pooled for each fish species and the contribution of each prey species compared by four methods:

(i) as a percentage of the total wet mass of stomach contents (% mass);
(ii) as the percentage of stomachs in which it appeared (% occ.);
(iii) the number of prey specimens (*N*);
(iv) the ranking index method recommended by Hobson (1974).

Ranking index (R.I.) values for each prey species were calculated from the formula:

$$\text{R.I.} = \%\ \text{mass} \times \frac{\%\ \text{occ.}}{100}$$

and then expressed as a percentage of the sum of all R.I. values for each species of fish.

Diets of the three species were compared by correspondence analysis, a relatively recent technique developed by French statisticians. An early review of the technique is given by Benzécri *et al.* (1973). Greenacre (1978) provides a more recent description and Underhill (1981) describes the computer program used. Correspondence analysis was used for inter- and intraspecific comparisons of the species composition of diets of small and large fish (which were defined as those fish less than, or more than, the median standard length for each species, respectively). The lengths of all shells of the limpet *Nacella delesserti* retrieved from the stomachs or intestines of *Notothenia coriiceps* were measured with vernier calipers to the nearest 0,1 mm.

Results

Size, morphology and habitats

Notothenia coriiceps was the largest of the three fish and the 31 specimens studied had a mean standard length and standard deviation of 304 ± 60 mm. Maximum length and mass were 444 and 1800 g. Colour was always dark blue-black with a yellow to white ventral surface. Notable features were the squat head, wide mouth and fleshy pelvic fins (Figure 1A). Solitary individuals were always seen lying on the bottom, between boulders or on rocky ledges, usually in association with the abundant limpet *Nacella delesserti.* Swimming was poorly developed and specimens usually attempted to escape capture by moving into gaps between boulders rather than swimming away.

The 129 specimens of *Notothenia macrocephala* (Figure 1B) had a mean standard length and standard deviation of 166 ± 60 mm. Maximum length and mass recorded were 294 mm and 546 g. Colouration patterns were varied, and younger specimens were usually dark red with white to orange bellies, whilst larger ones were dark brown dorsally, with orange and white ventral markings. Small specimens of *N. macrocephala* were regularly sighted under water at depths of 1 – 4 m, either singly or in loose aggregations of up to 30 fish. Large specimens inhabit deeper water and were mostly caught in water 10 – 30 m deep.

The 98 *Harpagifer georgianus* (Figure 1C) had a mean standard length and standard deviation of 48 ± 8 mm. Maximum length and mass were 69 mm and 6,5 g. Colours were cryptic and specimens were usually mottled brown and red with pale ochre undersurfaces. Notable features were the two pairs of defensive opercular spines, forward directed eyes and sharply pointed jaw. The species was abundant in the intertidal zone and many specimens were found in residual pools of water under boulders at low tide. A few individuals were encountered amongst algal turf at depths of 2 – 3 m. Like *N. coriiceps,* this species also spends much of its time lying motionless on the bottom. Up to three *H. georgianus* could be found in close proximity to one another although most specimens were found singly.

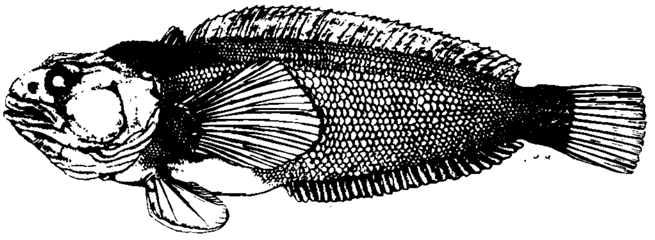

Figure 1A *Notothenia coriiceps* (length = 260 mm)

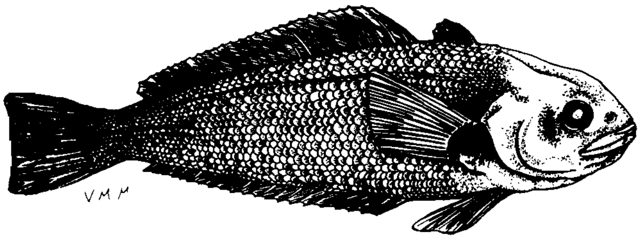

Figure 1B *Notothenia macrocephala* (length = 166 mm)

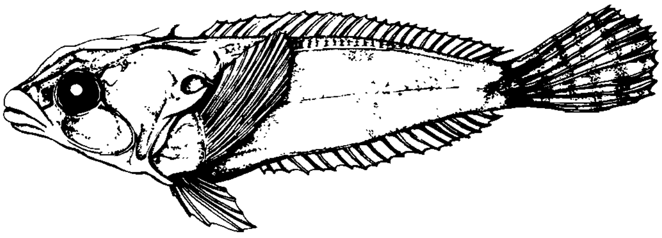

Figure 1C *Harpagifer georgianus* (length = 57 mm)

Diets

Notothenia macrocephala stomachs contained the widest range of prey types of which *Dynamenella huttoni, Platynereis australis,* and rhodophyte algae had the highest percentage R.I. values of 27,8%, 20,3% and 17,9% respectively (Table 1). Algae, isopods, polychaetes and amphipods formed the bulk of the diet. *Notothenia coriiceps* stomachs contained mostly rhodophytes (53,1%) and the limpet *Nacella delesserti* (32,2%). Chlorophyte algae, isopods and other fish were also eaten (Table 1). *Harpagifer georgianus,* the smallest of the three fish, was the most carnivorous species and algae had a low percentage R.I. value of 0,7%. The three amphipods *Shakeltonia* sp., *Hyale hirtipalma* and *Jassa falcata* formed 76,8% of the diet but isopods and polychaetes were also preyed on.

Table 1 shows that only a few prey species were consumed in significant numbers by all three species of fish

Table 1 Analysis of stomach contents of *Harpagifer georgianus*, *Notothenia macrocephala* and *N. coriiceps*

	H. georgianus				*N. macrocephala*				*N. coriiceps*			
Prey species	% mass	% occ.	*N*	% R.I.	% mass	% occ.	*N*	% R.I.	% mass	% occ.	*N*	% R.I.
Algae												
Chlorophyta												
small pieces (1 – 10 mm)	00,5	4,1	–	–								
leafy pieces (up to 150 mm long)					8,7	15,5	–	6,6	12,5	32,3	–	9,2
Rhodophyta												
leafy pieces					16,1	22,5	–	16,0	41,9	54,8	–	52,9
filamentous species	1,9	16,3	–	0,7	4,4	9,3	–	1,9	0,8	16,1	–	0,2
Phaeophyta												
Durvillaea antarctica					0,2	1,6	–	–				
Macrocystis pyrifera					3,2	1,6	–	0,5	1,4	6,5	–	0,2
Desmarestia rossii					3,7	1,6	–	0,5				
Totals				0,7				25,5				62,5
Invertebrata												
Cnidaria												
Hydroida (unid.)	0,3	1,0	–	–	0,1	3,1	–	–				
Annelida												
Polychaeta												
Platynereis australis	10,4	20,4	36	5,1	13,3	32,0	122	20,3	1,0	9,7	16	0,2
Romanchella perreiri	0,1	1,0	1	–	–	0,8	3	–				
Unidentified species									0,2	6,5	7	–
Oligochaeta												
Lumbricillus spp	0,7	1,0	3	–	0,1	0,8	4	–				
Totals				5,1				20,3				0,2
Mollusca												
Gastropoda												
Nacella delesserti	0,5	1,0	1	–	3,1	7,0	11	1,0	27,1	51,6	56	32,2
Laevilitorina caliginosa	–	2,0	2	–	0,1	7,0	14	–	–	9,7	4	–
Polyplacophora												
Hemiarthrum setulosum					0,1	3,9	8	–				
Bivalvia												
Lasaea consanguinea	1,6	10,2	30	0,5	0,3	14,1	78	0,2				
Kidderia bicolor	–	1,0	1	–								
Gaimardia trapesina	0,1	1,0	1	–	4,6	12,5	103	2,7	0,3	6,5	18	0,1
Cephalopoda												
Unidentified squid					0,8	0,8	1	–	0,1	3,2	1	–
Totals				0,5				3,9				32,3
Crustacea												
Copepoda												
Trigriopus angulatus	0,4	6,1	30	0,1								
Tanaidacea												
Anatanais gracilis	0,4	4,1	5	0,1	–	3,9	7	–				
Isopoda												
Antias bicornis	9,7	45,9	180	11,0								
Munna instructa					0,1	5,5	20	–				
Jaeropsis curvicornis					–	1,6	2	–				
Dynamenella huttoni	4,4	18,4	34	2,0	12,8	46,1	338	27,8	1,1	45,2	112	1,2
Exosphaeroma gigas					0,9	4,7	14	0,2	1,7	25,8	17	0,9
Unidentified					–	0,8	1	–				
Amphipoda												
Jassa falcata	13,6	35,7	187	12,0	4,6	57,8	1336	12,3	0,3	41,9	114	0,2
Eophiliantidae (unid.)	2,6	22,5	41	1,5	0,1	14,0	61	–				
?*Shakeltonia* sp	28,6	65,3	415	45,7								

Table 1 (continued)

	H. georgianus				*N. macrocephala*				*N. coriiceps*			
Prey species	% mass	% occ.	*N*	% R.I.	% mass	% occ.	*N*	% R.I.	% mass	% occ.	*N*	% R.I.
Hyale spp.	19,0	40,8	146	19,1	1,4	24,2	202	1,6	0,1	9,7	13	–
Eusiridae (unid.)	4,6	20,4	41	2,2	3,5	37,5	312	6,1	1,2	35,5	292	0,9
Pontogeniella brevicornis					0,3	7,0	62	0,1	1,1	16,1	61	0,5
Unidentified					0,1	1,6	17	–				
Euphausiacea												
Unidentified					0,1	2,3	3	–				
Natantia												
Nauticavis marionis					4,2	4,7	59	0,9				
Brachyura												
Unidentified					1,5	3,9	5	0,3				
Totals				93,7				49,3				3,7
Chelicerata												
Acarina												
Halozetes sp.	0,2	3,1	3	–								
Pycnogonida												
Tanystylum cavidorsum					–	2,3	3	–				
Insecta												
Ectemnorrhinis similis	0,2	1,0	1	–	–	3,1	6	–				
Echinodermata												
Anasterias rupicola					–	0,8	1	–				
Chordata												
Pisces												
Harpagifer georgianus					5,4	3,1	9	0,8	0,9	9,7	3	0,2
Notothenia macrocephala					2,4	0,8	1	0,1	6,6	6,5	2	1,0
Unidentified					3,3	0,8	3	0,1	1,0	3,2	3	0,1
Totals								1,0				1,3
Unidentified objects					–	2,3	14	–				
Inorganic matter												
Gravel	0,1	4,1	5	–	0,3	9,4	12	0,1	–	3,2	2	–

(e.g. *Dynamenella huttoni, Jassa falcata* and *Platynereis australis*) but that there are overlaps in the diets of any two species compared against one another. Correspondence analysis was a useful technique for displaying these feeding relationships graphically. As shown in Figure 2, the computer-generated plot of each prey species graphically places it closest to the fish that consumes it. A prey that is consumed almost exclusively by one species of fish will be furthest from the origin. A prey that is shared by two species of fish will be drawn towards both fish species and consequently will lie between them. A prey shared by all three species would lie close to the origin. Figure 2 reveals that the most exclusive prey of *N. coriiceps* is the fish *N. macrocephala* and the limpet *Nacella delesserti*, while *N. coriiceps* and *N. macrocephala* both consume chlorophytes and *N. macrocephala* and *H. georgianus* share *Jassa falcata*. The equal distribution of the three fish around the origin indicates that the species composition of their diets is very different so that competition for common prey species is unlikely. *Notothenia coriiceps* and *N. macrocephala* lie closest together because of their common consumption of algae (mostly *Ulva, Porphyra* and *Rhodymenia*) whilst the distance between *N. coriiceps* and *H. georgianus* is largest since amphipods contribute little to the diet of *N. coriiceps* compared to *H. georgianus*.

Size relationships

The three fish differed widely in size and shape yet managed to share a few common prey species. However, these common prey usually had different mean sizes for the three species of fish. Thus the mean wet mass of *Platynereis* consumed by *H. georgianus* was 0,02 g compared to 0,21 and 0,29 g for *N. macrocephala* and *N. coriiceps* respectively. Similarly the mean mass of *Nacella* consumed by *N. macrocephala* was 0,54 g compared to 2,25 g for *N. coriiceps*, and the mean mass of *Dynamenella* taken by *H. georgianus* was 0,008 g compared to 0,073 g for *N. macrocephala*. The mean mass of the 1 163 animals in the stomachs of *H. georgianus* was 0,005 g compared to 0,04 g for the 2 850 found in *N. macrocephala* and 0,28 g for the 721 recovered from *N. coriiceps*.

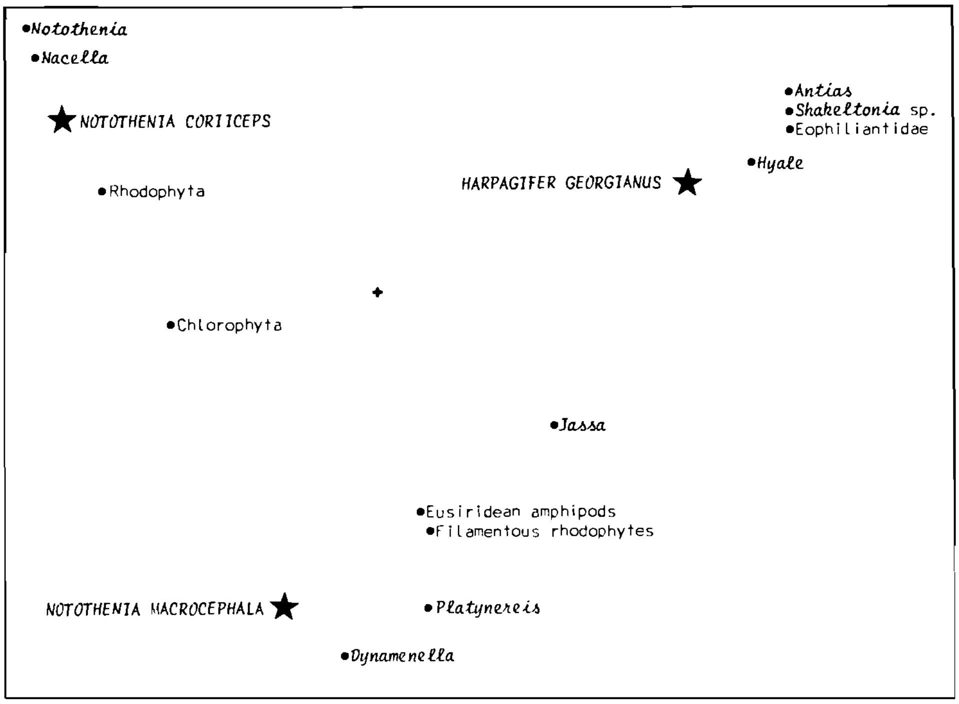

Figure 2 Correspondence analysis of the diets of the three fish. Data for the analysis were percentage R.I. values. ★ = fish species; ● = prey species; + = origin.

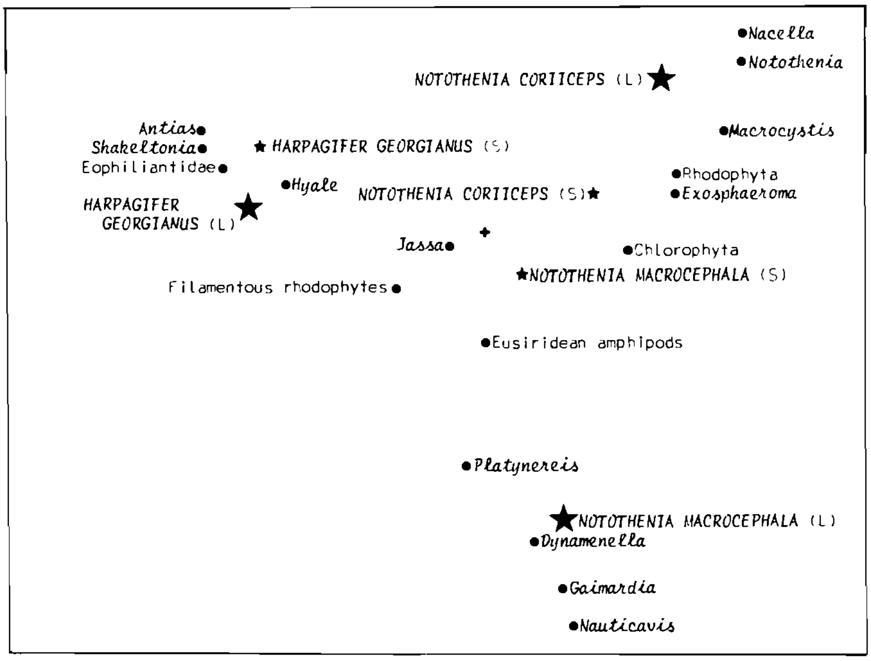

Figure 3 Correspondence analysis of diets of small and large size classes of the three species of fish. ★ = large size classes; ★ = small size classes; ● = prey species; + = origin.

The correspondence analysis of feeding relationships between small and large size classes of the three species of fish is shown in Figure 3. The relatively short distance between the small and large classes of *H. georgianus* indicates that size makes little difference to diet in this species. Small and large *N. macrocephala* showed the greatest difference in prey species composition because smaller individuals consumed more *Jassa falcata* and seaweeds than larger specimens which fed more on *Platynereis* and *Dynamenella*. Larger *N. coriiceps* ate more *Nacella* than smaller ones. Small *N. macrocephala* and small *N. coriiceps* showed the greatest interspecific similarity in diet, based on their corresponding reliance on rhodophytes, chlorophytes and *Jassa falcata*. The diet of large *H. georgianus* showed a far closer similarity to the diets of the small classes of the other two fish species than to the large size classes.

Predation of *Nacella* by *Notothenia coriiceps*

A total of 136 *Nacella* shells were recovered from the stomachs and intestines of 22 of the 31 *N. coriiceps* specimens examined. The majority of limpet shells was found far back in the intestine so that it seems likely that shells are voided with faeces although they were not encased in mucoid capsules as reported by Stobbs (1980) for the giant clingfish *Chorisochismus dentex* which feeds on patellid limpets. Even the largest *Nacella* were easily removed from rocks by hand and did not appear to cling to surfaces with the great force recorded by Branch & Marsh (1978) for some South African limpets, so that *N. coriiceps* is easily able to dislodge *Nacella* with its strong mouth while the limpets are moving around with their shells elevated. This was seen on two occasions whilst snorkelling. Figure 4 shows that there is a wide variation in the sizes of *Nacella* preyed on (9,0 – 55,0 mm), particularly by large fish. Nevertheless a significant correlation ($r = 0{,}6$; $p < 0{,}01$) exists between the standard lengths of the individual fish and the lengths of *Nacella* shells found in their guts. Figure 4 shows that larger *N. coriiceps* were able to consume larger limpets but data are insufficient to conclude whether they prefer larger to smaller limpets or whether they simply feed randomly on limpets up to the size they can handle. Relatively few limpets with shell lengths greater than 45 mm were preyed on by the fish, so that *Nacella*, which has a maximum size of 68 mm, has a refuge in size from predation by *N. coriiceps*.

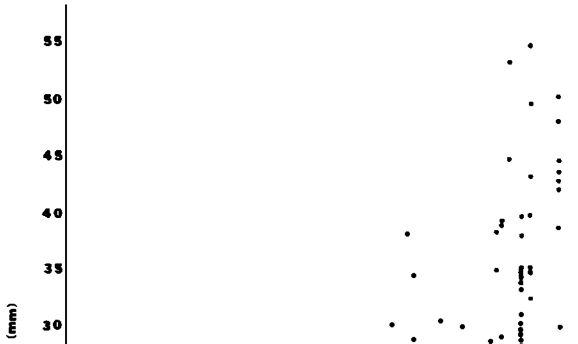

Figure 4 *Notothenia coriiceps* predation of *Nacella delesserti*; lengths of shells from fish guts compared to the size of the fish predator.

Discussion

Antarctic fish communities are comparatively simple and the level of interspecific competition for food resources is low compared to that in temperate and tropical regions (Targett 1981). The presence of only three inshore species of fish at Marion Island reflects the low diversity of the isolated and relatively youthful marine community to which they belong. The oldest Marion Island lavas are less than 300 000 years old (McDougall 1971). The results of this study show that the three species have distinct differences in morphological characteristics, life habits and diet, and hence competition for food resources is virtually non-existent.

The carnivorous plunder fish, *Harpagifer georgianus*, has the most specialized diet of the three species with five species of amphipods and two isopod species forming 93,5% of its food, so that it is clearly dependent on small crustaceans as its prey. *Harpagifer* is preyed on by the other two species of fish and heavy predation by the imperial cormorant *Phalocrocorax atriceps* and occasional predation by the gull *Larus dominicanus* also occurs (Blankley 1981). *Harpagifer georgianus* thus forms an important link in the marine food web of Marion Island. Other studies confirm the reliance of *H. georgianus* on crustaceans as food, and Meier (1971), Richardson (1975), Duarte & Moreno (1981) and Targett (1981) all found that amphipods formed more than 95% of the diet of *Harpagifer* species.

The diet of *Notothenia macrocephala* is likely to be far more complex than described here since this species has pelagic and not demersal eggs, as found in the other two species (unpublished data), and is therefore likely to spend part of the year at sea. *N. macrocephala* is omnivorous and feeds mostly on seaweeds and its major prey (isopods, amphipods and polychaetes) are species found associated with algal turf. Hureau (1966) found that *N. macrocephala* at Kerguelen Island mainly ate the isopod *Glyptonotus antarcticus*, the bivalve *Hiatella antarctica*, amphipods, small fish and algae. The mean mass of animal prey eaten by *N. macrocephala* at Kerguelen Island can be derived from Hureau's (1966) data as 0,25 g which is close to the figure of 0,28 g recorded in the present study. However, Hureau (1966) found that algae formed only 20% of the total mass of *N. macrocephala* stomach contents compared to 36% in this study. Further studies on the distribution and life habits of this species would be useful.

Notothenia coriiceps is a widely distributed species found around most of the Antarctic continent and at most sub-Antarctic islands (Biomass Scientific Series, 1977). Shabika (1971) recorded that *N. coriiceps* consumes the limpet *Patinigera polaris* at Palmer Station, Antarctica. Richardson (1975) found that the stomach contents of *N. coriiceps neglecta* at Signey Island, South Orkney Islands, consisted mostly of algae, amphipods, anthozoans and molluscs, of which the limpet *Nacella concinna* was found in 35% of the stomachs examined. Targett (1981) found that *N. coriiceps* at South Sandwich Islands fed mostly on amphipods and some isopods, but his samples were taken 3,5 km offshore at depths of 15 – 70 m. In the present study *N. coriiceps* was found to be mostly herbivorous, although the limpet *Nacella delesserti* is likely to provide it with more energy since seaweeds were voided in a fairly undigested state.

Each of the three species appeared to occupy a clearly defined feeding niche in this study, although some similarities in the diets of *H. georgianus* and the smaller size classes of *N. macrocephala* and *N. coriiceps* are shown in Figure 3. These similarities are likely to be the result of overlap in habitat occupation since the smaller *N. macrocephala* and *N. coriiceps* were caught close inshore only a metre or two deeper than the sites where most of the *Harpagifer* were found in the intertidal zone: as Targett (1981) has stated 'habitat separation is important more often than either within-habitat prey separation or temporal separation in avoiding food resource overlap' based on Schoener's (1974) findings. Thus large *N. macrocephala* which inhabited deep (5 – 20 m) water and large *N. coriiceps* which were found on the bottom in water 2 – 5 m deep showed clear-cut differences in diet between one another and the intertidal population of *H. georgianus*, because the habitats they occupy offer different species as prey. Targett (1981) attributes the success of the Nototheniidae in the Antarctic to their evolution of 'niche differences allowing the exploitation of prey in different habitats', and this certainly rings true for the inshore fish community at Marion Island.

Acknowledgements

This study forms part of a research programme on the intertidal ecology of Marion Island directed by Prof. J.R. Grindley. I would like to thank Prof. G.M. Branch for valuable criticisms of the manuscript and Dr L.G. Underhill for doing the correspondence analysis for me. Thanks also to Vanessa Moore for her fish illustrations and to Dr C.L. Griffiths for identifications of some of the amphipods. Research was funded by the Department of Transport on the advice of S.A.S.C.A.R.

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