

Grazing by the Antarctic fish *Notothenia coriiceps*: evidence for selective feeding on macroalgae

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Abstract: In Potter Cove, King George Island, Antarctica, macroalgae provide a significant food resource for herbivores. The demersal fish *Notothenia coriiceps* feeds on macroalgae. Eighteen algal species were identified in stomach contents: two chlorophytes, ten rhodophytes and six phaeophytes. Among these the rhodophyte *Palmaria decipiens*, the phaeophyte *Desmarestia menziesii* and the chlorophyte *Monostroma hartioides* comprised the greatest proportions of algal biomass. A food selection study showed four algae to be preferred (*P. decipiens*, *M. hartioides*, *D. menziesii*, *Iridaea cordata*) and two species to be avoided (*Desmarestia anceps* and *Himantothallus grandifolius*) by *N. coriiceps*. The present investigation indicates that this fish feeds not only intentionally, but also selectively, on macroalgae. Preference for particular algal species is not related to associated epifaunal biomass or to associated amphipod biomass.

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Introduction

The coastal waters along the west side of the Antarctic Peninsula and nearby islands are characterized by a rich and dense macroalgal flora composed of annual and perennial species (Skottsberg 1941, Neushul 1965, Moe & DeLaca 1976, Richardson 1979, Zielinski 1981, Etcheverry 1983, Heywood & Whitaker 1984, Picken 1985, Zielinski 1990, Chung *et al.* 1994, Klöser *et al.* 1994). Huge amounts of algae are degraded, until they are a suitable food resource for benthic organisms (Richardson 1979, Zielinski 1981, Brouwer 1996). Detached algae can be decomposed by biological and hydrodynamical processes (Reichardt & Dieckmann 1985, Rieper-Kirchner 1989, Rakusa-Suszczewski 1993) and some may drift into deeper waters to provide food for benthic deposit and suspension feeders (Fischer & Wiencke 1992, Lawson *et al.* 1993). The significance of living macroalgae as food for invertebrates and demersal fish in the Antarctic marine ecosystem, however, is less well understood (Richardson 1977, Brand 1980, Iken 1996).

Notothenia coriiceps Richardson (previously referred to as *N. neglecta* (Nybelin)) is the dominant inshore demersal fish in waters of the west Antarctic Peninsula, including the South Shetland Islands, Palmer Archipelago, and the South Orkney Islands (Fisher & Hureau 1985, Gon & Heemstra 1990, Barrera-Oro 1996). *N. coriiceps* remains nearshore once it becomes demersal after an early pelagic phase (White *et al.* 1982, Burchett *et al.* 1983, Casaux *et al.* 1990), although observations around Elephant Island indicate that it migrates to deeper waters for spawning (Kock 1989). Like other inshore demersal fish of the Southern Ocean, *N. coriiceps* is mainly abundant in areas of high macroalgal

density (Moreno & Zamorano 1980, Zukowski 1980, Casaux *et al.* 1990).

Macroalgae constitute a significant part of the diet of *N. coriiceps* from the South Shetland and the South Orkney regions (Richardson 1975, Moreno & Zamorano 1980, Linkowski *et al.* 1983, Barrera-Oro & Casaux 1990, Casaux *et al.* 1990). From the correlated occurrence of amphipods and algae in the stomachs of *N. coriiceps* at South Bay, Doumer Island, Moreno & Zamorano (1980) concluded that such algae were ingested accidentally while preying on invertebrates. Recent investigations in Potter Cove, however, revealed that algae were a major food item of *N. coriiceps* (Barrera-Oro & Casaux 1990) and that there was no correlation between amphipod and algal occurrence (Casaux *et al.* 1990). These results suggest deliberate grazing on macroalgae.

In this study we investigate

- i) whether *N. coriiceps* selects actively from among the algal species available, and
- ii) whether preference for algal species is related to the biomass of associated fauna.

Material and methods

Sampling was carried out in Potter Cove, King George Island, South Shetland Islands, near the Jubany Station & Dallmann Laboratory (62°14'S, 58°40'E) (Fig.1). Potter Cove is a small (6 km²) side bay of Maxwell Bay. The outer shores consist of rocky bottom covered by a dense algal community extending from the intertidal to about 40 m depth (Klöser *et al.* 1993). Sampling for fish and algae were carried

out at the northern coast of the outer Potter Cove (Fig. 1).

A total of 176 *Notothenia coriiceps* specimens were collected from November 1993–February 1994 by means of trammel nets. Fishing depth varied between 7 and 35 m. Total length and weight of all specimens were determined and stomachs were preserved in 96% ethanol for later identification of their content.

The stomach contents of each specimen were separated into the macroalgal and the animal fractions and weighed (g Wet Weight). Algal species were determined by light microscopy of cross-sections (Lamb & Zimmermann 1977). Frequency of occurrence and mean biomass (g WW) of all algal species were determined.

The species composition of the macroalgal community was determined by repeated transect sampling. Four transects were sampled from December 1993–February 1994 (Fig. 1). Along each transect, three replicates of 0.25 m² were sampled by SCUBA diving at four depths (5, 10, 15, 25 m). Average biomass of each algal species was computed by pooling the data of all transects for the particular species in order to minimize sampling errors due to patchy distribution. The chlorophyte *Monostroma hariotii* is very abundant above 5 m water depth, but did not occur within the depth range sampled. Based on quantitative data derived from Iken (unpublished data) and Klöser *et al.* (1996), the share of *M. hariotii* in total macroalgal biomass was estimated to be 2%.

To determine the amount of epifauna per algal species, one or more (depending on size) specimens of the most common 11 algal species and their associated epifauna were sampled with nets (mesh size <0.2mm) by SCUBA diving. The epifauna was sorted into major taxa and the algae and fauna were weighed (g WW).

To compare the availability of macroalgae in the benthos and their usage by *N. coriiceps*, we applied the “Linear Food Selection Index L_{ij} ” (Strauss 1979). The Linear Food Selection Index L_{ij} was calculated for each alga i ($i=1, \dots, N$; $N=20$, see results) and each fish j ($j=1, \dots, M$; $M=148$):

$$L_{ij} = \text{RBF} - \text{RBB} \quad [\text{RBF} = 100 \cdot B_{ij} / \Sigma B_{ij}; \text{RBB} = 100 \cdot B_i / \Sigma B_i]$$

where ΣB_{ij} is the total algal biomass in fish j and ΣB_i the total benthic algal biomass. This index is the difference between the relative biomass of the alga species i in the stomach of fish j (RBF) and the relative biomass of the same alga species i in the benthos (RBB). Positive or negative values of L_{ij} indicate preference or rejection of alga species i by the fish j , respectively.

RBF was derived from stomach content analysis. Only those stomachs ($N = 148$) which contained macroalgal species occurring also in the benthos samples were included in the selection study. Thus, overestimation of preference for those algae which were extremely rare or unrepresented in the transects due to the sampling profile (see above) was avoided. RBB was computed from the transect data.

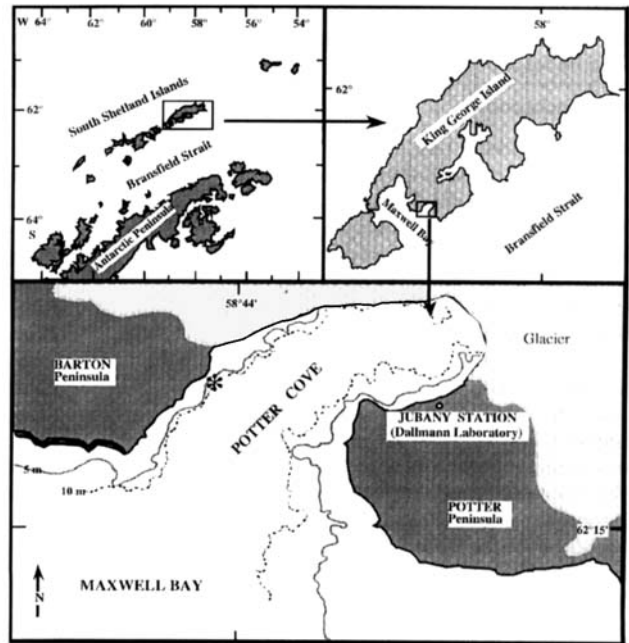


Fig. 1. General view of King George Island, South Shetland Islands and the location of Potter Cove. Sampling area is marked with an asterisk (*).

Preference of *N. coriiceps* for algal species was statistically tested by analysis of variance (ANOVA) of the Box-Cox transformed (Sokal & Rohlf 1992) L_{ij} data and subsequent Post-Hoc-Test on differences among means. Some of the algal species occurring in the benthos were not found in the stomach contents at all, i.e. index values of these algae were always zero and hence lacking variances which made statistical comparison impossible. To overcome this problem, we added random statistical noise (normal distribution with mean = 0 and standard deviation = $2 \cdot 10^{-4}$) to all L_{ij} data prior to ANOVA.

To check for relations between preference for algal species and the associated epifauna, we grouped the 11 sampled algal species (see above) according to the results of the selection analysis into two groups (preferred, not preferred). The biomass of total epifauna and the biomass of amphipods (both log-transformed) as well as the percentage of amphipods (arcsin-transformed), which were assumed to be the main prey of *N. coriiceps* (Barrera-Oro & Casaux 1990, Casaux *et al.* 1990), were then compared by the Mann-Whitney test.

Results

From a total of 176 stomachs analysed, 97% contained food; only five stomachs were completely empty. Twenty five stomachs contained animal items only, and 10 stomachs only algal material. The mean proportion of animal components was 61.5% by weight, the mean proportion of algae was 38.5%. Frequency of occurrence of macroalgae in the stomachs was 85.8%.

Table I. Algal species investigated and their frequency of occurrence in the fish stomachs, and their relative biomass (%) in the stomachs (RBF) and in the benthos (RBB). (a) and (b) express preference and rejection by *N. coriiceps*, respectively; (1) species is rarely occurring below 5 m depth, (2) species is not occurring below 5 m depth.

Macroalgal species		frequency	RBF	RBB
<i>Monostroma hariotii</i> Gain (a)	(Chloroph.)	31.82	21.8 ± 34.0	2.0 (1)
<i>Urospora penicilliformis</i> (Roth) Areschoug	(Chloroph.)	0.57	<0.1 ± <0.1	0 (2)
<i>Desmarestia menziesii</i> J. Agardh. (a)	(Phaeoph.)	61.93	22.4 ± 34.3	8.7
<i>Desmarestia antarctica</i> Moe et Silva	(Phaeoph.)	10.80	4.7 ± 18.3	5.7
<i>Desmarestia anceps</i> Montagne (b)	(Phaeoph.)	3.98	1.1 ± 8.8	50.4
<i>Adenocystis utricularis</i> (Bory) Skottsberg	(Phaeoph.)	6.25	0.2 ± 1.6	0 (1)
<i>Ascoseira mirabilis</i> Skottsberg	(Phaeoph.)	1.71	0.1 ± 0.8	0.3
<i>Phaeurus antarcticus</i> Skottsberg	(Phaeoph.)	3.34	0.1 ± 0.6	<0.1
<i>Himantothallus grandifolius</i> (A. et E.S. Gepp) Zinova (b)	(Phaeoph.)	0	0	27.8
<i>Palmaria decipiens</i> (Reinsch.) R.W. Ricker (a)	(Rhodoph.)	60.23	28.3 ± 35.2	1.3
<i>Iridaea cordata</i> (Turner) Bory de Saint Vincent (a)	(Rhodoph.)	27.84	6.3 ± 18.0	0.2
<i>Gigartina skottsbergii</i> Setchell et Gardner	(Rhodoph.)	2.27	0.1 ± 0.9	1.5
<i>Neuroglossum ligulatum</i> (Reinsch) Kylin	(Rhodoph.)	8.52	2.6 ± 12.2	<0.1
<i>Plocamium cartilagineum</i> (Linn.) Dixon	(Rhodoph.)	6.25	1.2 ± 7.0	2.7
<i>Georgiella confluens</i> (Reinsch) Skottsberg	(Rhodoph.)	1.14	0.2 ± 2.6	0.7
<i>Curdiea racovitzae</i> Hariot in De Wildeman	(Rhodoph.)	0.57	<0.1 ± 0.2	0.1
<i>Gymnogongrus antarcticus</i> Skottsberg	(Rhodoph.)	0.57	<0.1 ± <0.1	<0.1
<i>Pantoneura plocamioides</i> Kylin	(Rhodoph.)	0.57	<0.1 ± 0.1	0
<i>Porphyra endivifolium</i> (Gepp et Gepp) Chamberlain	(Rhodoph.)	3.98	0.5 ± 2.8	0 (2)
<i>Kallymenia antarctica</i> Hariot	(Rhodoph.)	0	0	0.4
<i>Ballia callitricha</i> (Agardh) Kützing	(Rhodoph.)	0	0	0.1
<i>Myriogramme smithii</i> (Hooker fil. et Harvey) Kylin	(Rhodoph.)	0	0	<0.1
<i>Hymenocladopsis crustigena</i> Moe	(Rhodoph.)	0	0	0.1
<i>Phyllophora ahnfeltioides</i> Skottsberg	(Rhodoph.)	0	0	<0.1
<i>Sarcodia montagneana</i> (Hooker fil. et Harvey) Agardh	(Rhodoph.)	0	0	<0.1
undetermined plant substance		25.57	10.4 ± 24.2	

Krill (*Euphausia superba* Dana) was the most important animal prey (c. 80% by weight), followed by amphipods, gastropods and isopods. The algal diet consisted of 18 species – 2 Chlorophyta, 10 Rhodophyta, 6 Phaeophyta (Table I), with *Palmaria decipiens*, *Monostroma hariotii*, and *Desmarestia menziesii* comprising the greatest portion of algal biomass.

Fish length varied between 16–45 cm, and fish weight between 48–1288 g WW; no significant correlation was found between fish size and the amount of algae in the stomach.

Benthic transect samples of algae consisted of 21 species, 1 chlorophyte, 6 phaeophytes, and 14 rhodophytes. The mean relative biomass of each algal species found in the transects and in the fish stomachs is shown in Table I. Among the algal species ingested, *P. decipiens*, *M. hariotii*, *D. menziesii*, and *Iridaea cordata* were significantly preferred ($P < 0.001$), whereas *Himantothallus grandifolius* and *Desmarestia anceps* were significantly avoided ($P < 0.001$). For the remaining 15 species, neither significant preference nor rejection was detected, i.e. *N. coriiceps* is indifferent with respect to those species (Fig. 2).

Algal species, their total associated epifaunal biomass, the biomass of associated amphipods, and the percentage of amphipods in the epifauna, are listed in Table II. The Mann-Whitney test could not detect any relationship between the two algal categories (preferred, not preferred) and total

biomass of epifauna ($P = 0.8774$), amphipod biomass ($P = 0.5371$), or the percentage of amphipods in the epifauna ($P = 0.6434$).

Discussion

Feeding on macroalgae is common among fishes, mainly in tropical marine ecosystems (Horn 1989). In the Antarctic, grazing has been observed in a number of Nototheniids (Richardson 1975, Moreno & Zamorano 1980, Burchett 1983, Burchett *et al.* 1983, Linkowski *et al.* 1983, Barrera-Oro & Casaux 1990, Casaux *et al.* 1990, Coggan 1993, Gröhsler 1994). Among Antarctic studies, however, there is still a debate whether fish intentionally consume macroalgae (Daniels 1982, Barrera-Oro & Casaux 1990, Casaux *et al.* 1990) or accidentally ingest plant material while predating epifauna associated with macroalgae (Moreno & Zamorano 1980). With respect to *Notothenia coriiceps*, our results confirm the conclusion of Barrera-Oro & Casaux (1990) and Casaux *et al.* (1990) that this species deliberately ingests macroalgae. We found macroalgae to occur with high frequency (c. 86%) in the stomachs of *N. coriiceps*, as also reported by Barrera-Oro & Casaux (1990) (80%, Potter Cove) and by Moreno & Zamorano (1980) (88%, South Bay, Doumer Island), but more frequently than around Signy Island (40%, Richardson 1975, c. 5% in juveniles, Coggan 1993). The mean algal proportion of the stomach content

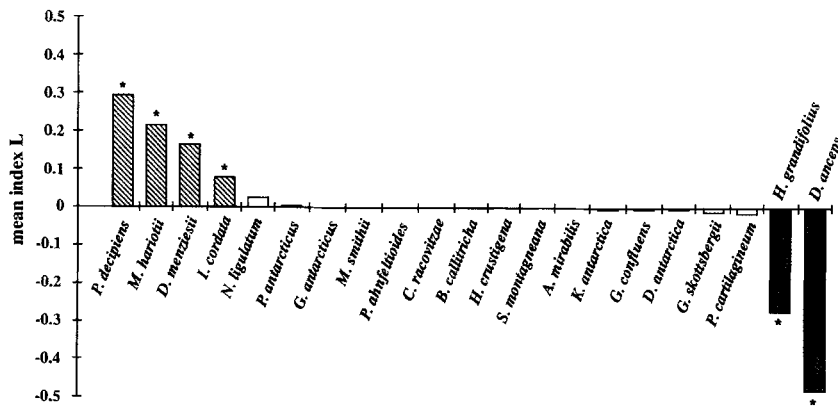


Fig. 2. Linear Food Selection Index L of algal species ingested by *N. coriiceps*. Significant differences ($P < 0.001$) are marked (*).

was high (38.5% by weight) compared with the results of Casaux *et al.* 1990 (c. 5%).

Our identification of 18 algal species in the diet of *N. coriiceps* greatly exceeds the numbers recorded in previous investigations, which either did not distinguish between species at all (Richardson 1975, Barrera-Oro & Casaux 1990, Coggan 1993) or identified a few species only (Moreno & Zamorano 1980). It is likely that, due to the lack of hard structures, macroalgae are often not recognized and therefore underestimated in stomach content analyses. Algal species with the highest portion of biomass in the stomach contents were the red alga *Palmaria decipiens*, the brown alga *Desmarestia menziesii*, and the green alga *Monostroma hartiotti* (Table I). The red and the green algal species have not been recorded previously as food items of *N. coriiceps*.

None of the previous studies of *N. coriiceps* analysed feeding selectivity with respect to macroalgae in detail. Barrera-Oro & Casaux (1990) found macroalgae to be one of seven preferred food items of *N. coriiceps* in Potter Cove, while for juvenile fish at Signy Island algae were classified as tertiary (summer) or incidental (other seasons) prey only (Coggan 1993). Our study, however, shows a distinct selection of certain algal species from those available: Four species, *Palmaria decipiens*, *Monostroma hartiotti*, *Desmarestia menziesii*, *Iridaea cordata*, were significantly preferred and two species, *Desmarestia anceps*, *Himantothallus grandifolius*, were significantly avoided (Fig.2). The latter are abundant key species of the algal community below 10 m depth in Potter Cove (Klöser *et al.* 1996). Obviously, the selection strategy of *N. coriiceps* is independent of the availability (in terms of abundance or biomass) of algal species.

Further investigations are required to evaluate the overall significance of distinct macroalgal species to the diet of *N. coriiceps*, since little is known about their calorific values, and the energy intake in general is presumably low while feeding on algae (Coggan 1993). Chlorophytes and Rhodophytes are considered easily digestible, while brown algal constituents are mainly assimilable after microbial fermentation only (Montgomery & Gerking 1980).

Our comparison of the amount of epifauna associated with the two algal groups identified (preferred, not preferred) shows clearly that the preference for certain algal species is not related to total epifauna or to epifaunal amphipods (Table II). On the contrary, some algae with few epifauna, such as *P. decipiens*, are preferred whereas *N. coriiceps* is indifferent to some algae which harbour a rich epifauna. The contradictory findings of Moreno & Zamorano (1980) may have resulted from their limited approach, i.e. analysis of the stomach contents without a concurrent study of the epifaunal communities associated with distinct macroalgal species.

It should be noted, however, that sampling of algal epifauna was carried out by day and that the proportions of epifauna with nocturnal activity might be slightly different by night. Feeding activity of *N. coriiceps* is supposed to be higher in darkness (Richardson 1975, Moreno & Zamorano 1980),

Table II. Algal species and the total biomass of associated epifauna as well as the biomass and percentage of amphipods. Weights in g WW. Preference for algal species by *N. coriiceps* is characterized as + (preferred) and - (not preferred).

sample no	algal species	total epifauna (g 100 g ⁻¹ algae)	amphipods (g 100 g ⁻¹ algae)	amphipods (%)	preference
1	<i>M. hartiotti</i>	0.5838	0.0118	1.34	+
2	<i>M. hartiotti</i>	4.7576	2.7113	56.98	+
3	<i>I. cordata</i>	12.1079	4.0230	33.23	+
4	<i>I. cordata</i>	3.9794	3.1467	79.08	+
5	<i>I. cordata</i>	6.4809	0.1724	2.66	+
6	<i>P. decipiens</i>	0.0671	0.0000	0.00	+
7	<i>D. menziesii</i>	15.0633	3.8964	25.87	+
8	<i>D. menziesii</i>	9.1922	5.1376	55.89	+
9	<i>G. skottsbergii</i>	3.8277	0.8195	21.41	-
10	<i>G. confluens</i>	95.9185	3.3143	3.46	-
11	<i>G. confluens</i>	24.1214	3.5769	14.83	-
12	<i>P. cartilagineum</i>	14.9182	9.0034	60.35	-
13	<i>P. cartilagineum</i>	28.4211	2.4385	8.58	-
14	<i>P. antarcticus</i>	1.0569	0.4053	38.35	-
15	<i>A. mirabilis</i>	9.7294	0.0973	1.00	-
16	<i>A. mirabilis</i>	3.4226	0.1328	3.88	-
17	<i>D. anceps</i>	1.2386	0.6177	49.87	-
18	<i>H. grandifolius</i>	0.0322	0.0307	95.27	-
19	<i>H. grandifolius</i>	0.0757	0.0269	35.46	-
20	<i>H. grandifolius</i>	0.0344	0.0283	82.13	-

although recent investigations of Casaux *et al.* (1990) showed an activity peak of the fish during daytime.

While stomach content analyses provide information about the relative importance of single food items and about feeding strategies (e.g. generalist or specialist), food selection studies deliver a more detailed picture of feeding habits and strategies. Hence, they may contribute to the understanding of trophic interactions between algae and grazers and their impact on the structure of algal communities. Klöser *et al.* (1994) suggested that selective grazing of *N. coriiceps* on *Desmarestia anceps* may cause the replacement of this alga by *Himantothallus grandifolius* in the deep sublittoral algal community of Potter Cove. Although stomach content analyses showed *D. anceps* to be part of the diet of *N. coriiceps*, the food preference study showed this alga to be significantly rejected compared to its availability in the benthos (Fig. 2). Hence, grazing of *N. coriiceps* on *D. anceps* is unlikely to affect the competition between *D. anceps* and *H. grandifolius* significantly. However, grazing of *N. coriiceps* on *Desmarestia menziesii* and its avoidance of *D. anceps* may play a role in the spatial competition of these two algal species (Klöser *et al.* 1996).

Our results indicate that living macroalgae may be a more important food source for the Antarctic shallow water benthic fauna than previously assumed. The extended usage of macroalgae by shallow water demersal fish indicates strong food limitation and a tendency towards wider trophic niches to minimize food competition.

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