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## Feeding strategies and diet composition of four Antarctic cnidarian species

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**Abstract** The diet of four species of Antarctic cnidarians, two hydroids and two anthozoans, was investigated. One hydroid, *Tubularia ralphii*, and one anthozoan, *Anthomastus bathyproctus*, seem to basically consume zooplankton whereas the other hydroid species, *Oswaldella antarctica*, has a diet mainly based on the fine fraction of seston. The last cnidarian investigated, the stoloniferan alcyonacean, *Clavularia* cf. *frankliniana*, feeds mainly on resuspended material. The wide range of diets of these Antarctic cnidarians indicates opportunistic behaviour by feeding on different sources and taking advantage of the available food sources. Data related to low C/N ratios in the sediment and high NO<sub>2</sub> concentrations in areas with dense communities of benthic suspension feeders, along with data on capture rates, lead us to hypothesize that these organisms play an important role in the recycling processes of organic matter in Antarctic benthic ecosystems.

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### Introduction

Cnidarians are one of the most conspicuous taxonomic groups on the Antarctic continental shelf, being part of the rich benthic communities which have been described from several locations around Antarctica (e.g. Arntz et al. 1994; Gutt and Starmans 1998; Starmans et al. 1999). Like other suspension feeders, cnidarians depend on the available food suspended in the water column and on the near-bottom currents for its renewal.

The Southern Ocean is principally an oligotrophic environment dominated by flagellates and other small organisms of the pelagic retention system, with short overlying outbursts of microalgae (bloom system) in spring and summer (Scharek and Nöthig 1995) which are, however, essential for larger zooplankton. For quite some time, these blooms were suspected of determining the feeding strategies of the benthic suspension feeders in Antarctica and the composition of their diet. These organisms were thought to feed heavily during a few weeks in summer and to be able to sustain long periods of starvation during most of the year. This would resemble overwintering as resting stages or the hibernation periods that have been described for other latitudes (Gili and Hughes 1995; Garrabou 1999). However, Barnes and Clarke (1995) demonstrated recently that certain species of Antarctic shallow-water benthic suspension feeders are able to feed throughout the year with only short periods of starvation. Phytoplankton (mainly microplankton) in these areas is also dominant in the water column and the sediment only during short periods of the year, but pico- and nanoplankton (between 0.2 and 20 µm) dominate the water column and the sediment during most of the year, and the suspension feeders take advantage of them (Cripps and Clarke 1998). From these findings, the question arose as to whether this situation might apply to deeper shelf communities as well.

In the Southern Ocean, vertical fluxes (Nöthig and von Bodungen 1989) are not the only source of food for the benthic suspension feeders, but zooplankton, seston,

elements of the microbial food web and resuspension processes could also contribute to the potential available food for this group. Although cnidarians have traditionally been considered mainly carnivorous (Hyman 1940), more recent studies have found evidence of herbivory (Elyakova et al. 1981; Fabricius et al. 1995a, b), which is supported by a study on an Antarctic hydroid, *Silicularia rosea*, which consumes mainly diatoms (Gili et al. 1996b). However, gorgonian diet varies from dissolved organic matter via plankton to benthic organisms, and is very well coupled with the dynamics of their potential prey (Ribes et al. 1998, 1999).

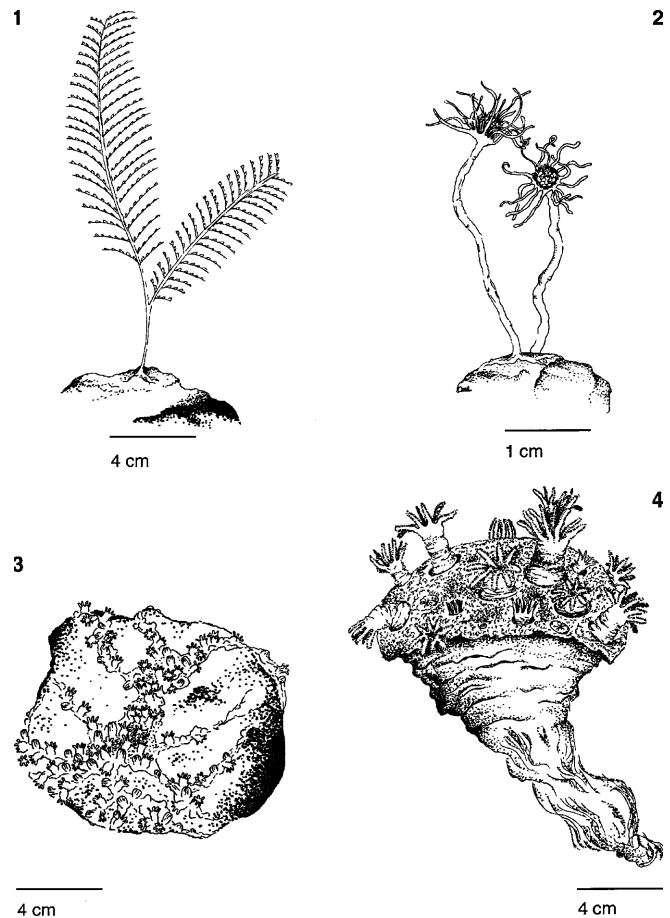
Considering the various potential food sources for benthic suspension feeders, the goal of the present study was to determine the diet of four species of Antarctic cnidarians: *Oswaldella antarctica* (Hydrozoa), *Tubularia ralphii* (Hydrozoa), *Clavularia cf. frankliniana* (Anthozoa) and *Anthomastus bathyproctus* (Anthozoa). We also consider the relation between their feeding strategies, the Antarctic environment and the factors which regulate the availability of food at the sea floor. We present new insights into the significance of plankton production, resuspension processes and nekton migration for the feeding strategies of these organisms, and on the role of the group in the trophic food web of the Southern Ocean.

## Materials and methods

Four benthic cnidarian species were studied (Fig. 1). *O. antarctica* (Jäderholm 1904) is a benthic hydroid found on hard substrates in a depth range between 50 and 200 m, approximately, forming arborescent colonies and presenting very small polyps (200–375 µm diameter). *T. ralphii* Bale 1884 is a common Antarctic hydroid, which forms creeping colonies on stones and is mainly distributed in shallow areas (Stepanjants 1979). *T. ralphii* presents large hydranths with long aboral tentacles, and the hydrocaulus is usually more than 2 cm above the substratum. The stoloniferous alcyonacean, *C. cf. frankliniana* Roule, 1902 was one of the most common species collected in shallow waters during the second EASIZ (Ecology of the Antarctic Sea Ice Zone) cruise. This species forms encrusting colonies covering, in some cases, great parts of the stones. *A. bathyproctus* Bayer, 1993 is a common alcyonacean in the waters of the Antarctic Peninsula area. Their colonies live mainly on sandy substrates. They were caught between 400 and 450 m depth; however, off the South Shetland Islands, specimens have been found at 1,153 m depth (Bayer 1993).

Sampling, experimental design and analysis of gastrovascular contents

Sampling on board RV "Polarstern" was carried out during the second EASIZ cruise between January and March 1998 at two



**Fig. 1** Studied species: 1 *Oswaldella antarctica*, 2 *Tubularia ralphii*, 3 *Clavularia cf. frankliniana*, 4 *Anthomastus bathyproctus*

sites: for *O. antarctica*, *T. ralphii* and *C. cf. frankliniana* in the eastern Weddell Sea, and for *A. bathyproctus* off the Antarctic Peninsula (Table 1). Sampling was conducted with an Agassiz trawl, a bottom trawl and a large TV grab of 1.82 m<sup>2</sup> sampled area.

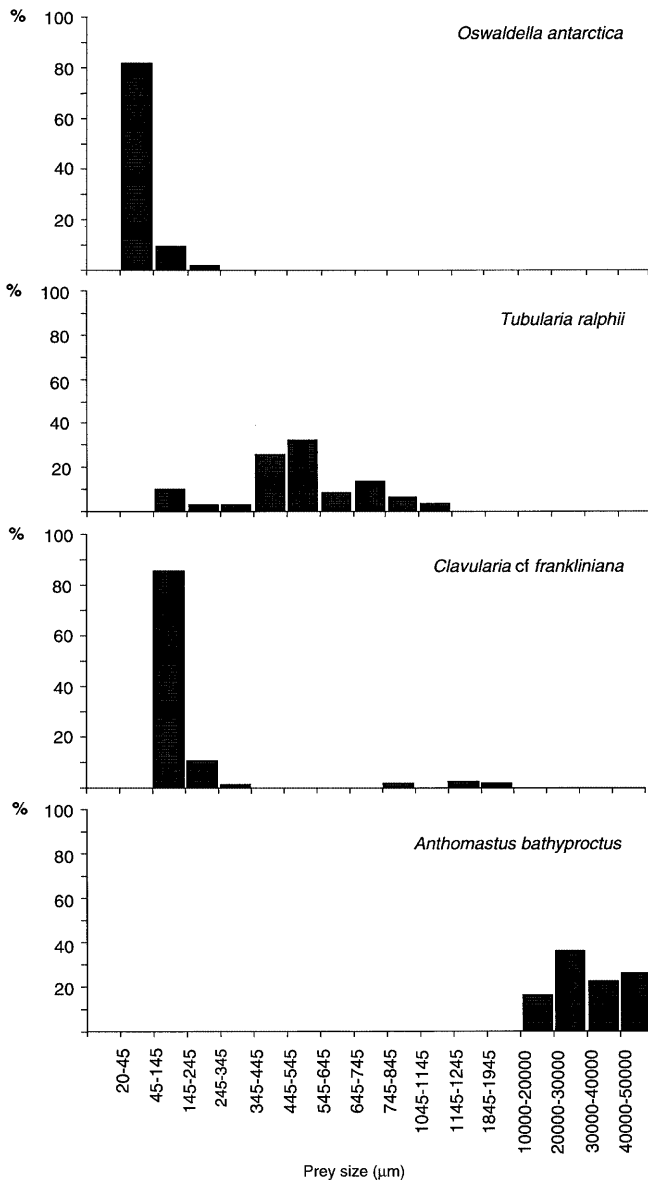
In order to determine the trophic role of the seston (also of its fine fraction) for suspension feeders, data are derived from analyses of cnidarian gastrovascular contents and from feeding experiments. Polyps of all four species were dissected to analyse the gastrovascular contents under a binocular and a light microscope. The number of dissected polyps was between 110 and 148, depending on the species, because of their varying abundance in the samples and in the studied area.

Feeding experiments were done only with the hydrozoan species, *O. antarctica*. A modified prototype of incubator developed by the Instituto de Ciencias del Mar (Ribes et al. 1998) was used to study the diet of benthic suspension feeders. The incubator consists of a chamber in which the colony is placed, and an empty control chamber. Each closed chamber was connected to a pump that

**Table 1** Sampling stations for the four studied species (KG King George Island; KN Kapp Norvegia; N/KN north of Kapp Norvegia; AGT Agassiz trawl; BT bottom trawl; TV grab bottom grab 1.82 m<sup>2</sup> with video camera)

	Area	Station	Gear	Latitude (S)	Longitude (W)	Depth (m)
<i>Oswaldella antarctica</i>	N/KN	71	BT	70°49.3'	10°28.6'	281
	KN	210	TVgrab	71°07.2'	11°28.4'	67
<i>Tubularia ralphii</i>	KN	210	TVgrab	71°07.2'	11°28.4'	67
<i>Clavularia cf. frankliniana</i>	KN	210	TVgrab	71°07.2'	11°28.4'	67
<i>Anthomastus bathyproctus</i>	KG	303	AGT	62°16.5'	58°43.1'	430
	KG	304	AGT	62°16.4'	58°43.9'	447

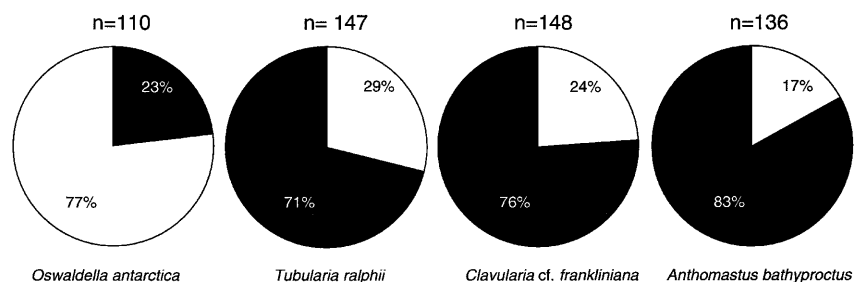




**Fig. 3** Percentage (by number) of prey items of different size range found in the dissected polyps for the four studied species

*thompsoni* were found in 113 (83%) of them whereas 23 (17%) were empty (Fig. 4). The size of the salps was between 10 and 50 mm (Fig. 3). Many polyps contained other items (mainly diatoms of the genus *Corethron*, and

**Fig. 4** Percentage (by number) of prey items in the dissected polyps for each studied species. Black colour shows coelenteron with prey items; white colour without prey items



also centric diatoms and fecal pellets of small size). It seems, however, that these items came from prey gut contents, which was confirmed by dissecting the prey guts. No statistically significant differences were found between number and size of prey items and polyp diameter, or between number of prey items and capitulum diameter. However, there were significant differences between number of prey items and height of the capitulum (ANOVA,  $F=10.649$ ,  $N=8$ ;  $P<0.01$ ), and between prey size and height of the capitulum (ANOVA,  $F=6.087$ ,  $N=8$ ;  $P<0.05$ ). The number of polyps/capitulum in relation to height of the capitulum and also with capitulum diameter showed significant differences (ANOVA,  $F=61.898$ ,  $N=8$ ;  $P<0.001$ ; ANOVA,  $F=139.033$ ,  $N=8$ ;  $P<0.001$ , respectively).

### Feeding experiments

Net prey growth rates were calculated for the potential prey items of *O. antarctica* working at the level of taxonomic group: bacteria, nanoflagellates, dinoflagellates, ciliates and diatoms; POC and DOC values were also calculated. Sizes of the prey items were also taken into account (excluding in this case values of bacteria). Statistically significant differences ( $P<0.01$ ) were found for nanoflagellates (Wilcoxon test). Results are shown in Fig. 5. However, a pattern could also be observed for the other groups: dinoflagellates showed a clear decrease in the experimental chamber, as did *Chaetoceros* species and other phytoplankton groups. Different types of diatoms were lumped because of the low number of specimens found in the samples.

### Nutrients and C/N ratio

The concentration of nutrients  $\text{NO}_2$ ,  $\text{NO}_3$  and  $\text{PO}_4$  varied between 0.02 and 0.20  $\mu\text{mol/l}$ , 15.94 and 40.35  $\mu\text{mol/l}$  and 0.77 and 1.49  $\mu\text{mol/l}$ , respectively. C/N values in the sediment varied between 6 and 293, showing a clear pattern in relation to the distribution of benthic suspension-feeder communities: areas which showed a high presence of benthic suspension feeders presented the highest values (Fig. 6). Conversely, the areas with higher nitrogen values correspond to areas with a low density of benthic suspension feeders. The same pattern was observed for nutrient values, with

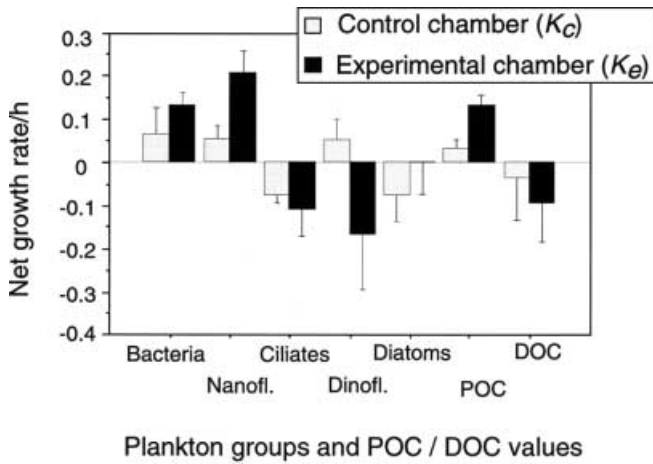


Fig. 5 Net growth rate in control ( $K_c$ ) and experimental ( $K_e$ ) chambers of the different groups of plankton and POC/DOC

higher values in areas where benthic suspension feeder communities were abundant.

#### Zooplankton abundance

Data of zooplankton densities (focusing on copepod data because of their abundance) were extracted from preliminary results of the second EASIZ cruise. Near-bottom copepod abundances, obtained by epibenthic sledge, were registered by Brandt et al. (1999) on the Weddell Sea shelf, reaching summer values between 232 and 702 individuals/1,000 m<sup>2</sup> at 400 m depth. Copepod abundance (calanoids) was also measured by Schiel (personal communication) in the upper 200 m of the water column in the same area. The values ranged between 1,000 and 4,500 ind./1,000 m<sup>3</sup> during the Antarctic summer.

#### Discussion

Anthozoans and hydrozoans are groups which have received great attention in tropical and temperate waters, and substantial data on their natural diet are available (anthozoans, e.g. Coma et al. 1994; Ribes et al. 1998; hydrozoans, e.g. Gili et al. 1998). Scarce information exists, however, for Antarctic and Arctic species (Gili et al. 1996b; Slattery et al. 1997). Benthic zooplanktivorous species, which feed on substratum-associated organisms or larvae, also consume a few holoplanktonic animals such as calanoid copepods (Sebens and Koehl 1984). We name these species "macrophagous" but introduce a new food item, the fine fraction of seston, calling the species which feed on this fraction, "microphagous". The four studied species reflect this whole spectrum of prey items (Fig. 2).

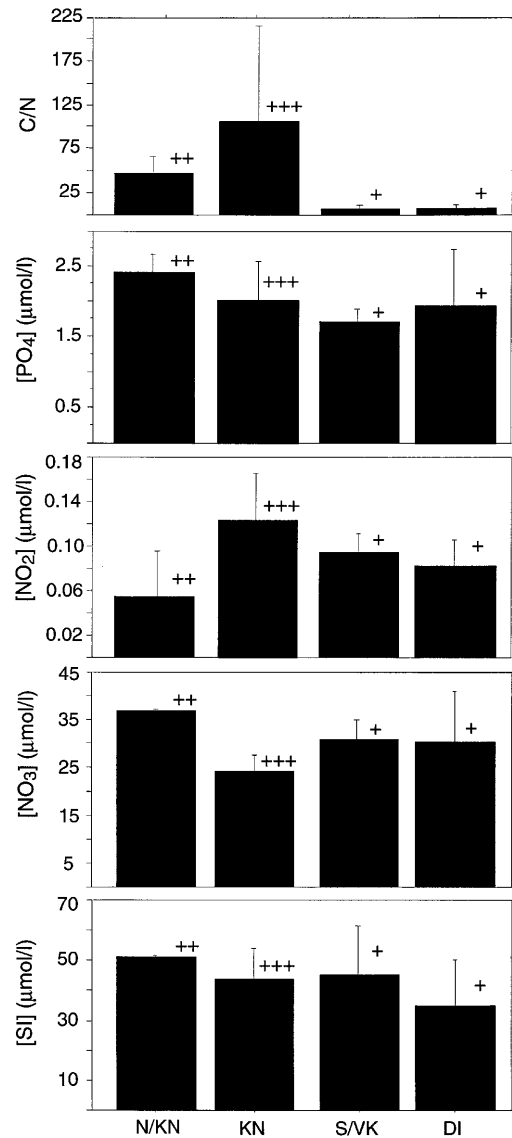


Fig. 6 Values of C/N rate and nutrients for the areas north of Kapp Norvegia (N/KN), Kapp Norvegia (KN), south of Vestkapp (S/VK) and Drescher Inlet (DI) (+++ high dominance of benthic suspension feeders; ++ regular abundance of benthic suspension feeders; + occasional presence of benthic suspension feeders)

It has been hypothesized that benthic organisms just feed during favourable periods, remaining in hibernation or in resting stages during cold seasons and under unfavourable environmental conditions (for review see Gili and Hughes 1995). This is true for the "macrophytoplankton system" (Smetacek et al. 1990; Scharek and Nöthig 1995) which occurs in summer, and most zooplanktonic (hence macrophagous) species profit from these summer blooms to grow and reproduce. However, the "flagellate system" (Smetacek et al. 1990; Scharek and Nöthig 1995), consisting mainly of nanoplankton and members of the microbial food web, is also active during winter (Clarke 1988; Ahn 1993). This system might be capable of sustaining communities of

benthic suspension feeders during the whole year, as has been observed by Barnes and Clarke (1995) at Signy Island.

Cnidarian diet: macrophagous and microphagous suspension feeders

*Macrophagous species: Tubularia ralphii, Clavularia cf. frankliniana, Anthomastus bathyproctus*

*T. ralphii* showed a diet highly dependent on the water column; 85% of their diet were copepods, some of which have been identified as pelagic harpacticoids, indicating a dependence on the planktonic community. The lack of relation between polyp size and prey size suggests an opportunistic strategy contrasting with that observed in a congeneric species from the North Atlantic, *T. larynx* (Gili et al. 1996a).

The feeding strategy of the stoloniferan *C. cf. frankliniana* could be linked with resuspension processes at the sea floor. Its polyps are located very close to the substrate and they capture prey moving around their tentacle crown. This kind of feeding is quite frequent in massive and encrusting anthozoans such as alcyonaceans and actinarians (Sebens and Koehl 1984). Sediment might be continually resuspended by the effect of currents, but also by various animals such as bivalves (e.g. Stockton 1984; Alexander and DeLaca 1987), echinoderms and demersal fish.

The diet of *A. bathyproctus* is probably related to the patchiness of plankton. They might profit from episodes of high availability of food, as occurs during the salps' downward migration. The occurrence of gelatinous zooplankton close to the sea floor has been shown in some cases (Gili et al., in press). Vertical migration of Antarctic zooplankton to the sea bed has been documented for salps (Weibe et al. 1979; Casareto and Nemoto 1986) and krill (Gutt and Siegel 1994). In gorgonians (Coma et al. 1994), plankton patches can cause events of high prey capture rates. The presence of large, although occasional, prey in the stomachs of the studied species may be quite significant for their energetic balance (Coma et al. 1998). In the guts of the *A. bathyproctus* specimens, we also found diatoms (mainly *Corethron* spp.) which seem, however, to come from prey gut contents, as has been described for other prey items in other cases (Sebens and Koehl 1984).

Two possible strategies might be applied by *A. bathyproctus*: (1) they might feed on zooplankton, i.e. prey that occasionally passes by, in an opportunistic way, but feed on the fine fraction of seston too, using a "sieving" mechanism; (2) they might feed episodically only on large prey items. This latter possibility does not appear to be realistic because they would depend completely on Antarctic summer production to survive. A more realistic scenario is that they use, in different proportions, both resources. In any case, *A. bathyproctus* is neither a deposit nor a sediment feeder. Its ana-

tomical characteristics show the animal to be capable of doubling its size by way of hydrostatic mechanisms. Thus it can take better advantage of the water column, the food composition of which can vary greatly from the bottom to some centimetres above it (Schloss et al. 1999).

*Microphagous species: Oswaldella antarctica*

Little information exists on the role of types of prey other than zooplankton in hydroid feeding (Gili and Hughes 1995). Several studies reported that dinoflagellates, diatoms, tintinnids and bacteria are sparse in hydroid gut contents (Gili et al. 1996a). However, nanoplankton, mainly of plant origin, is the most abundant food source in the Southern Ocean, and Coma et al. (1995) demonstrated that detritus from plant matter or particles of unspecified origin represent more than 90% of prey captured in a Mediterranean hydroid. Diatoms have been also reported to be an important food source for the Antarctic hydroid *Silicularia rosea* (Gili et al. 1996b).

Recently it has been observed that the fine fraction of seston (pico- and nanoplankton) may represent an important part of the diet of benthic suspension feeders (Pile et al. 1996; Ribes et al. 1999). The studies by Bröckel (1981) showed that nanoplankton cells are also a very important component of the planktonic community in nearshore Antarctic waters. The case of *O. antarctica* is the first where the importance of this fraction has been shown for hydroids. Our feeding experiments show that components from the fine fraction of seston contribute to the diet of the hydroid (Fig. 5). This is not surprising taking into account that particles smaller than 2 µm and between 2 and 20 µm diameter dominate the pelagic planktonic community in terms of biomass and production (Platt et al. 1983). It has also been demonstrated that suspension feeders can remove very effectively particles of these sizes, and that active filtration is not the only method by which suspension feeders efficiently extract small particles from the water (Rubinstein and Koehl 1977; Okamura 1990). The importance of small prey in the diet of hydroids indicates that other mechanisms of capture may also occur, e.g. inertial impact or gravitational deposition, and creation of currents (Koehl 1977a, b; LaBarbera 1984; Harris 1990).

A wide variety of diets in benthic cnidarians has recently been shown also for two gorgonian species: *Plexaura flexuosa* (Ribes et al. 1998) in the Caribbean, and *Paramuricea clavata* (Ribes et al. 1999) in the Mediterranean Sea, with prey items comprising bacteria to zooplankton. Apparently, feeding strategies and diets in this group are not very different in Antarctica compared with other latitudes. An example is the capture rates of *T. ralphii*, which are in the same order of magnitude as for related species in temperate waters (Gili et al. 1998).

## Role of the suspension-feeder communities in the Antarctic benthic communities

Particle composition in the water column in Antarctica may be very different during the year (Clarke and Leakey 1996). In the Southern Ocean, a strong vertical flux of organic matter occurs during a short time, but due to the low decomposition rate of the sediments, they keep their nutritional value longer (Bathmann et al. 1991). The data of Palanques et al. (in press) show high values of nitrogen even in winter. Benthic communities may respond to sedimentation events, increasing their activity and production (e.g. Grémare et al. 1997).

The high values of C/N ratio observed (Fig. 6) in places where the benthic suspension feeders are very abundant might reflect their feeding activity consuming the sediment organic component (POC or small organisms). Benthic cnidarians might be able to use sediment material due to resuspension processes. A similar set of sediment C/N values has been observed in the Bransfield Street (Palanques et al., in press) and the authors hypothesize that this organic sediment decomposition could be related to the activity of benthic organisms, and not to the different organic composition of material sedimenting from the water column. Parallel to these near-bottom feeding processes, high nutrient values such as the observed nitrite values may be expected (Fig. 6). Below the depth limit of photosynthetic activity, nitrite cycling is controlled by microbial nitrification, as well as denitrification in the water layer close to the bottom, but benthic filter feeders can increase nitrite cycling by ammonium from their excretion processes. The role of nitrite as an obligatory intermediate in nitrification processes and the high values found during our experimental work point to the possible role of benthic suspension feeders in the recycling and remineralization of the organic matter and their role as very active organisms in the dynamics of benthic boundary layers.

In summary, cnidarians exploit both patch food and seasonally available food. This information on the natural diet of Antarctic benthic cnidarians supports the hypothesis that they are adapted to perform a wide spectrum of prey capture, which enhances their survival in a stochastic environment. Furthermore, it indicates that the activity and production of Antarctic benthos does not stop during winter. The role of benthic suspension feeders in such communities is still far from being clear, but they must play a principal role both in the benthic pelagic coupling processes and in organic matter recycling.

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