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Trophic relationships in the nearshore zone of Martel Inlet (King George Island, Antarctica): δ^{13}C stable-isotope analysis

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Abstract Carbon isotopic composition was used to assess the linkage between three different potential sources of energy and the community in the shallow coastal zone of Martel Inlet. Stable δ^{13}C ratios ranged from −28.7‰ for the zooplankton plus phytoplankton to −14.4‰ for the grazer *Nacella concinna*. Microphytobenthos (−16.7‰) was considerably more enriched in ^{13}C than were suspended particulate matter (SPM) (−25.6‰) and macroalgal fragments (−23.6‰ and −21.1‰), indicating that stable carbon isotope analysis might be used to discern the relative contribution of these sources of primary production. There is a benthic-pelagic coupling between plankton, benthic suspensivores, the ophiuroid *Ophionotus victoriae* and the icefish *Chaenocephalus aceratus*. Benthic grazers such as *N. concinna*, deposit feeders such as *Yoldia eightsi* and the nematodes showed a tight coupling with the microphytobenthos and the sediment. Some omnivorous/depositivorous polychaetes, echinoids, amphipods and the fish *Notothenia coriiceps* showed values close to the ratios of the macroalgal fragments. Benthic carnivores and/or scavengers were generally enriched over suspensivores and depleted in relation to microphytobenthos grazers, showing a considerable overlap in δ^{13}C values throughout the food web, without any clear coupling with the primary sources of organic matter. The trophic web in the shallow zone of high benthic production and under seasonal ice cover in the Antarctic is more complex than it is in shelf areas, where SPM is the main food source. The soft-bottom community in the shallow zone of Martel Inlet is enriched in ^{13}C due to the significant input of carbon from the microphytobenthos and macroalgal fragments.

Introduction

In high latitude ecosystems, the transfer of the water column's primary production to higher trophic levels appears more efficient than at lower latitudes (Petersen and Curtis 1980). A great proportion (30–96%) of the carbon fixed annually reaches the bottom ungrazed (Atkinson and Wacasey 1987; Wassman 1991), representing an important contribution to the benthos. The importance of the close benthic-pelagic coupling in shelf waters of highly seasonal primary productivity has already been established (Mills et al. 1984; Wada et al. 1987; Grebmeier et al. 1988; Dunton et al. 1989; Hobson et al. 1995).

In the Antarctic nearshore zone, where the ice cover varies throughout the year, there is a higher benthic standing stock than on continental shelves offshore, suggesting a close relationship between pelagic and benthic productivity, especially in some parts of the Antarctic Peninsula (Grebmeier and Barry 1991). Besides this source, in the polar nearshore environments other primary sources of food, such as the benthic microalgae, the ice-associated microalgae, and the macroalgae, can also contribute to those communities (Dayton et al. 1986; Gilbert 1991; Iken et al. 1998; Kaehler et al. 2000; Dunton 2001).

The benthic community of Martel Inlet has been the object of several ecological studies since 1988 (Wägele and Brito 1990; Nonato et al. 1992; Skowronski et al. 1998; Bromberg et al. 2000; Nonato et al. 2000; Skowronski and Corbisier 2002). These studies have presented high values for the density and biomass of the benthos in the nearshore zone. Nevertheless, there has been no investigation of trophic relationships for an assessment of the origin and pathways of organic matter in the community.

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Food and feeding habits of the Antarctic benthos have received considerable attention, because they may clarify the apparent paradox in the seasonally limited food resources and the existence of a rich benthic life (Arntz et al. 1994). Carbon stable-isotope ratio analysis is useful to elucidate the material flow in food webs, as the primary sources of organic matter, i.e., pelagic against benthic producers, may be isotopically distinct, thus providing information on the relative importance of each source and the direct relationships between the organisms and their diets (Michener and Schell 1994; France 1995; Hobson et al. 1995; Kaehler et al. 2000; Dunton 2001). Due to the high resistance of CO$_2$ to diffusion in water, autotrophs with well-defined boundary layers occupying regions of limited water motion will become enriched in ^{13}C relative to ^{12}C and thus benthic algae often display higher δ^{13}C values than do planktonic algae, which are exposed to turbulent conditions with consequently less resistance to diffusion (France et al. 1998). Close coupling of consumers with pelagic primary productivity results in less ^{13}C enrichment in consumer tissues than do these links in deposit feeders and detrital-based food webs (Hobson et al. 1995).

The aim of this study was to evaluate the assimilation of different potential sources of energy (phytoplankton, microphytobenthos and macroalgal fragments) by the shallow coastal zone sediment community of Martel Inlet, during an austral summer, and to establish a model of the trophic web in the area.

Materials and methods

Study area

King George is the largest of the South Shetland Islands (Fig. 1). Admiralty Bay, its largest embayment, covers an area of 122 km^2 and includes three inlets, Ezcurra in its western part, and Martel and Mackellar in the northern part, with the main part of the bay opening in the south into the Bransfield Strait. The bay's shoreline extends for 83.4 km, of which 44.5 km are ice-free (Rakusa-Suszczewski 1995).

Salinity and temperature are relatively homogeneous throughout the bay. In the period of this study they were within the range of the observations of Jazdzewski et al. (1986) in the austral summer, i.e, from 32.9‰ to 34.2‰ and from −0.2°C to 3.4°C, respectively, at the surface, and between 33.4‰ and 33.8‰ and −0.4°C and 0.9°C, respectively, at the bottom. The waters of Admiralty Bay are rich in oxygen (6.7–7.1 cm^3/dm^3 at the surface in the summer) and the concentrations of nutrients are high throughout the year (annual means for phosphates at all depths are 1.7×10^{-6}–1.84×10^{-6} µgram atom/dm^3; dissolved silicates are at 73×10^{-6}–90×10^{-6} µgram atom/dm^3 in surface waters; nitrites at 0.01×10^{-6}–0.60×10^{-6} µgram atom/dm^3; and nitrates at more than 30×10^{-6} µgram atom/dm^3 at the surface) and are not limiting for phytoplankton growth. Only nitrates decrease during algal blooms (Lipski 1987). The oceanographic, hydrochemical and hydrological conditions are typical of Antarctic shelf waters.

The study area, adjacent to the Brazilian Antarctic Station "Comandante Ferraz" (62° 04′ S, 58° 21′ W), is located in the shallow soft-bottom sublittoral zone of Martel Inlet. The bottom topography presents a steep slope down to 30 m, and ice scours were observed at around 18 m depth (Nonato et al. 1992). In general, the sediment comprises gravelly sand at 6 m, becoming muddy sand at 30 m (Nonato et al. 2000). Macroalgal fragments, mainly from *Desmarestia*, and a thick fluffy mat of microphytobenthos can accumulate on the sediment as well as at ice scours (Skowronski et al. 1998; Skowronski and Corbisier 2002).

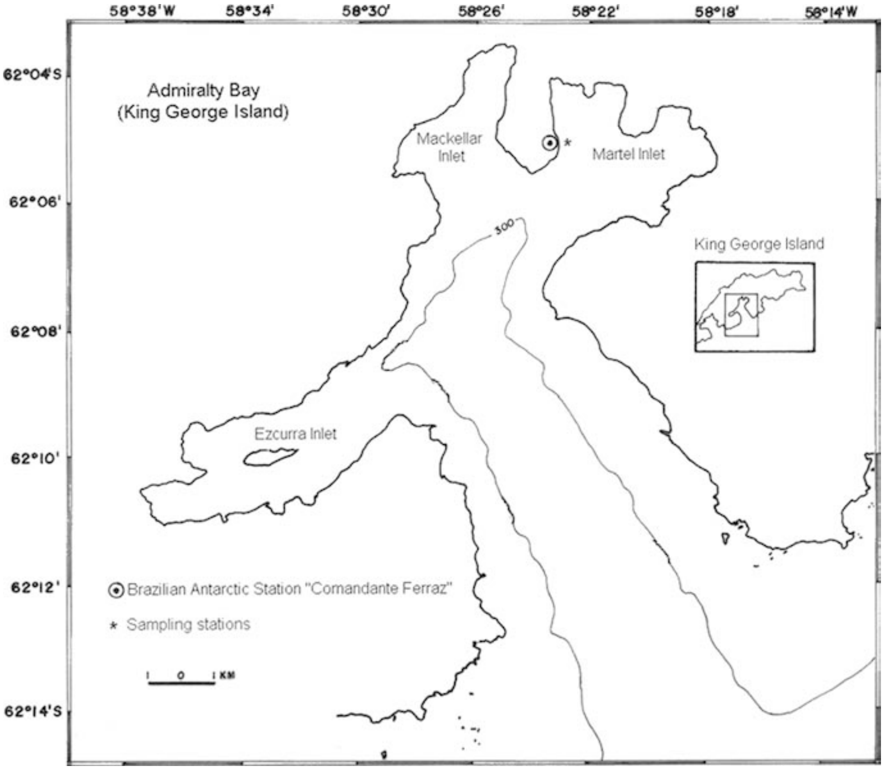

Fig. 1 Map of the study area

Sampling and isotope analysis

Samples were collected off the Brazilian Antarctic Station, at between 10 m and 20 m depth, during December 1996 and January 1997 (Fig. 1).

Phytoplankton and suspended particulate matter (SPM) were obtained by filtering surface seawater, large plankton being removed by filtration with a 62-μm mesh net, and then with precombusted (500°C, for 2 h) GF/F glass fibre filters (47-mm diameter, nominal pore size 0.7 μm) and stored frozen. Plankton samples were collected by two vertical tows (0–15 m) with 150-μm and 225-μm meshes, kept in seawater overnight to allow the evacuation of gut contents, then filtered through precombusted glass fibre filters and stored frozen.

Macrobenthic infaunal invertebrates were collected with a van Veen grab, washed on a 1-mm screen and sorted alive. Polychaetes and small crustaceans were kept in filtered seawater overnight to allow gut clearance. Molluscs were removed from shells and their muscle tissue dissected, and small crustaceans were treated with 1 N HCl to remove carbonates. Small individuals of the same species were pooled to obtain sufficient material for analysis. Some polychaetes, although unidentified, were pooled by morphological characteristics.

Surface sediment samples were obtained by SCUBA divers using a mini-dredge with a 125-μm screen net to collect nematodes, the most abundant meiobenthic group. Around 10,000 nematodes were sorted alive, left in Petri dishes in seawater overnight and stored frozen. Microphytobenthos was obtained by collecting the fluffy thick mat from the sediment with small black flasks. These samples were filtered out in precombusted glass fibre filters and stored frozen. Fragments of two macroalgae (*Desmarestia* sp. and one unidentified green alga) were sorted from the sediment samples.

Some common megafaunal invertebrates were hand-collected by SCUBA divers. Echinoderms and crustaceans were treated with 1 N HCl to remove carbonates before ^{13}C analysis. Muscle tissue samples were dissected from the fishes *Notothenia coriiceps* and *Chaenocephalus aceratus* and from some megabenthic species, such as *Laternula elliptica*. All samples were freeze-dried and crushed into powder with mortar and pestle. The lipids were not extracted from the tissues.

Samples were composites of many organisms whether from grab or hand collection. The number of replicates is indicated in Table 1.

δ^{13}C values of sediment and krill, which had not been included in our sampling, were obtained from a later analysis of the material

Table 1 Values of δ^{13}C for selected components of the marine food web in the nearshore zone of Martel Inlet. The trophic categories of consumers were compiled from several authors

	δ^{13}C ± SD (‰)[a]	Authors for trophic categories
Primary producers		
Phytoplankton (suspended particulate matter) (<62 μm)	−25.6 ± 1.9 (23)	
Macroalgal fragments		
Desmarestia sp.	−23.6 (1)	
Green algae	−21.1 ± 1.8 (2)	
Microphytobenthos	−16.7 ± 2.1 (4)	
Sediment[b]	−16.7 (1)	
Suspension feeders		
Plankton (phytoplankton and zooplankton) (>150 μm)	−28.7 (1)	
Sabellidae polychaetes	−28.7 ± 0.4 (2)	Gambi et al. (1997)
Polychaetes	−27.8 ± 1.9 (4)	
Euphausia superba[b]	−27.2 (1)	Perissinotto et al. (1997)
Laternula elliptica	−26.7 ± 0.1 (3)	Ahn (1993)
Anemone	−26.5 (1)	
Zooplankton (>225 μm)	−25.5 (1)	
Planktivore/euryphage fish		
Chaenocephalus aceratus	−26.5 ± 0.1 (2)	Kozlov et al. (1988)
Opportunistic generalist feeder		
Ophionotus victoriae	−25.1 (1)	Fratt and Dearborn (1984)
Omnivore/opportunist fish		
Notothenia coriiceps	−22.5 ± 0.7 (2)	Linkowski et al. (1983); Barrera-Oro and Casaux (1990); Casaux et al. (2003)
Benthic omnivores/depositivores		
Terebellidae polychaetes	−23.3 ± 0.8 (3)	Gambi et al. (1997)
Polychaetes	−21.4 ± 0.5 (2)	
Holothurians	−20.3 (1)	Gutt and Starmans (1998)
Sterechinus neumayeri	−19.1 ± 0.4 (2)	Dayton et al. (1986)
Gondogeneia antarctica	−18.8 ± 0.2 (2)	Iken et al. (2001)
Uristes georgianus	−18.1 ± 2.1 (8)	De Broyer (personal communication)
Yoldia eightsi	−18.0 ± 2.9 (3)	Davenport (1988); Peck and Bullough (1993)
Benthic carnivores/scavengers		
Neobuccinum eatoni	−20.7 ± 0.4 (2)	Presler (1986)
Serolis polita	−20.1 ± 1.2 (3)	Presler (1986)
Aglaophamus ornatus	−19.6 ± 0.7 (3)	Gambi et al. (1997)
Barrukia cristata	−18.9 (1)	Gambi et al. (1997)
Odontaster validus	−18.2 (1)	Presler (1986)
Glyptonotus antarcticus	−18.1 ± 0.2 (3)	Presler (1986)
Parborlasia corrugatus	−17.8 ± 0.3 (2)	Presler (1986)
Epistrate feeders/depositivores		
Nematodes	−15.6 ± 0.7 (11)	Skowronski (2002)
Benthic grazers		
Nacella concinna	−14.4 (1)	Iken et al. (1998), Picken (1980)

[a] Numbers in parentheses are numbers of replicates

[b] From S. Bromberg, personal communication

collected in the same area in December 2000 (S. Bromberg, personal communication).

The analysis of carbon stable-isotope ratios was made using a Finnigan MAT 251 mass spectrometer coupled to a CHN analyser at the Horn Point Environment Laboratory, University of Maryland, USA. Stable-isotope ratios were expressed in δ notation as parts per thousand (‰) according to the following relationship:

$$\delta(‰) = \left[\left(R_{sample}/R_{standard}\right) - 1\right] \times 1000 \quad \text{where} \quad R = {}^{13}C/{}^{12}C$$

The standard for ^{13}C was Pee Dee Belemnite (Boutton 1991).

Results and discussion

There was considerable variation in δ ^{13}C values in Martel Inlet (Table 1), greater than that previously reported for Southern Ocean pelagic invertebrates [from −32.3‰ for netted plankton to −20.5‰ for sediment in Wada et al. (1987) and from −30.3‰ to −23.0‰ for particulate organic matter (POM) in Rau et al. (1991a)], but within the range of those found on the south-western side of Anvers Island on the Antarctic peninsula costal zone [from −29.8‰ for krill to −16.8‰ for benthic herbivores in Dunton (2001)] and on the nearshore of sub-Antarctic Marion Island [from −27.0‰ for planktonic grazers to −14.38‰ for kelp in Kaehler et al. (2000)]. The values ranged from −28.7‰ for plankton greater than 150 µm (probably a mixing of phytoplankton and zooplankton) to −14.4‰ for the gastropod *Nacella concinna*. Three major primary producers were identified: phytoplankton, macroalgae and microphytobenthos, which exhibited different δ^{13}C signatures.

Microphytobenthos (−16.7‰) was considerably richer in ^{13}C than were SPM (−25.6‰) and macroalgal fragments (−23.6% and −21.1‰), indicating that stable carbon isotope analysis might be used to discern the relative contribution of these three primary sources of carbon (Fig. 2).

The average δ^{13}C value for SPM was −25.6‰, considerably lower than values previously recorded for other regions but within the Antarctic range [−27.4‰ and −26.4‰ (Wada et al. 1987; Fischer 1991)] and the Arctic values [−28.4‰ and −27.9‰ (Hobson et al. 1995)]. Polar SPM is in general depleted in ^{13}C as compared with predominantly temperate SPM (−22 ± 3‰) (reviews in Rau et al. 1982; Fischer 1991; France 1995). Low temperature (below 2°C), low light intensity and high water [CO_2 (aq)] values lead to very low ^{13}C content in the phytoplankton (Rau et al. 1989, 1991a). Thompson and Calvert (1994) also suggest a substantial role for irradiance rather than for [CO_2 (aq)] in the physiology of ^{13}C incorporation in a marine diatom.

There was no enrichment in δ^{13}C between SPM and SPM grazers, although the carbon isotopic compositions of animals reflect those of the diet within about 1‰ (Michener and Schell 1994). Wada et al. (1987) observed that the greater part of zooplankton, and also euphausiids, in Antarctica showed lower values of δ^{13}C than does suspended particulate organic matter (SPOM). One possible reason for this fact is the high lipid content (rich in ^{12}C, depleted in ^{13}C) in zooplankton that may deplete the ^{13}C content (Wada et al. 1987; Rau et al. 1991b). High lipid content would result in a lowering of the total plankton δ^{13}C (Sackett et al. 1974).

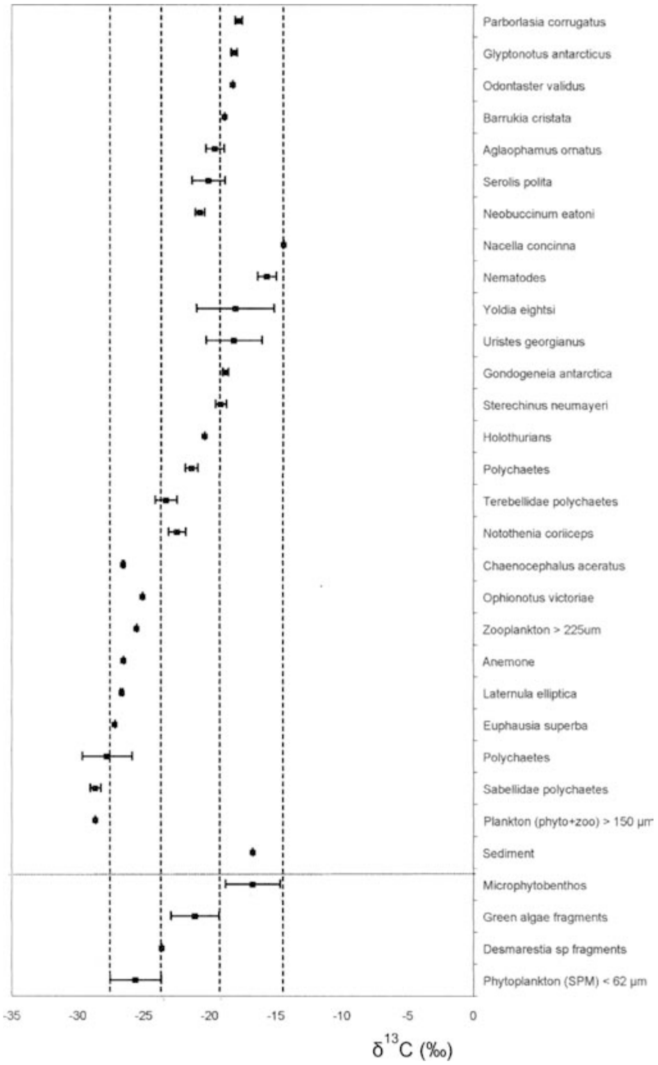

Fig. 2 δ^{13}C values of the organisms, suspended particulate matter and sediment collected in the nearshore zone of Martel Inlet, Antarctica

Benthic suspensivorous organisms showed δ^{13}C values similar to those of SPM and zooplankton (>225 µm). Amongst these, suspensivorous polychaetes presented low values of δ^{13}C, close to SPM values (between −28.7‰ and −27.8‰). The suspensivorous bivalve *L. elliptica* (−26.7‰) as well as an anemone (−26.5‰) also presented a close relationship with SPM and zooplankton. Suspensivorous invertebrates, such as bivalves, ascidians, and some cnidarians showed ratios close to those of zooplankton and SPOM, in the Arctic and sub-Arctic region (Dunton et al. 1989) and Antarctica (Dunton 2001).

Stomach content data and laboratory studies indicated that *Ophionotus victoriae* is extremely opportunistic, utilising a variety of feeding methods but not suspension feeding. The δ^{13}C value found for this species (−25.1‰), close to that of suspension feeders, could be due to the ingestion of euphausiids, one of the most important items of its stomach contents, captured when they are moribund moving on the substrate surface or even in the water column (Fratt and Dearborn 1984). Adults of *Euphausia superba* in Antarctica had δ^{13}C values between −29.3‰ and −25.0‰ (Wada et al. 1987; Rau et al. 1991b; Hodum and Hobson 2000), and −27.2‰ in Martel Inlet (Table 1), while larval krill had values around −24.5‰ (Frazer 1996). The icefish *C. aceratus* also showed a δ^{13}C value close to that of the suspensivores. This species is known to feed on fish and planktonic organisms, mainly euphausiids and mysids (Kozlov et al. 1988).

The microphytobenthos showed a mean value of −16.7‰, enriched around 10‰ in relation to SPM. Similar values were observed in temperate regions (Currin et al. 1995; Riera et al. 1996). The enrichment of microphytobenthos in relation to SPM can be explained as due to several mechanisms. It is highly probable that the extent of ^{13}C enrichment is to be attributed to the intensity and/or mode of benthic respiration (Fischer 1991). Another possible reason is the greater diffusion resistance of benthic algae, as a possible consequence of reduced water turbulence, and subsequent assimilation of otherwise normally discriminated ^{13}C (France 1995). Ice algae are also believed to be one of the probable candidates for the source of the organic matter in the sediment (Wada et al. 1987; Rau et al. 1991b), as they are also enriched in relation to phytoplankton (France et al. 1998), but this implies rapid sedimentation of the ice algae after their release from the sea ice. The samples in the present study were collected a long time after the ice algae's release from sea ice during the spring.

Benthic grazers such as the limpet *N. concinna* (Picken 1980; Iken et al. 1998), and the meiobenthos, represented by the nematodes, were considerably enriched in δ^{13}C, showing values very close to those of the microphytobenthos (between −15.6‰ and −14.4‰), and representing a tight coupling with this primary source of food. As regards to nematodes, δ^{13}C values similar to those of the microphytobenthos have been observed in other areas (Couch 1989; Riera et al. 1996). In the study area, epistrate-feeder nematodes are as important as the deposit-feeder nematodes (Skowronski 2002). The sediment also showed a ^{13}C signature similar to that of the microphytobenthos (Table 1). Carbon isotopic ratios higher than those of the nematodes and *Nacella* were not found among the benthic invertebrates, but some small depositivore polychaetes, such as apistobranchids, spionids, cirratulids and orbiniids, very common in the area (Bromberg et al. 2000), were not analysed in this study.

Sediment-living microflora has been recognised as the major food source for deposit feeders like the bivalve *Yoldia eightsi* (Davenport 1988; Peck and Bullough 1993), but it is possible that macroalgal fragments also contribute to its diet, as shown by its δ^{13}C value and its range of variation (Fig. 2), as observed by Dunton (2001). The algal fragments showed ratios of −23.6‰ (*Desmarestia* sp.) and 21.1‰ (the green alga). There is a great range of stable carbon isotope composition for macroalgae (Fisher and Wiencke 1992; Dunton 2001). In the nearby shelf areas of the King George Basin most of the brown macroalgae show a carbon isotope ratio around −20‰ (Fisher 1991; Fisher and Wiencke 1992) and in the Anvers Island coastal zone the isotopic ratio for *Desmarestia menziesii* and *D. anceps* was −25‰ (Dunton 2001). The enrichment in the ^{13}C of *Desmarestia* fragments in the Martel Inlet may be explained by the process of bacterial decomposition at the bottom.

Benthic depositivores or omnivores (Table 1) were generally enriched more than SPM and suspension feeders, and overlapped considerably in δ^{13}C values throughout the food web (between −23.3‰ and −18.0‰). Their diets must be a mixture of macroalgal fragments and organic matter from the sediment, including a small part of microphytobenthos and/or meiobenthos. Some omnivorous/depositivorous polychaetes showed values close to the macroalgal ratios, such as the terebellids (−23.3‰) and other unidentified polychaete species (−21.4‰). The large variation in δ^{13}C of *Uristes georgianus* indicates a wider dietary spectrum, suggesting the ability of many amphipod species to take advantage of different food resources (Dauby et al. 2001). The benthic and kelp-associated communities from the vicinity of Marion Island exhibited no discrete trophic levels, also suggesting a higher degree of omnivory (Kaehler et al. 2000).

The larger part of the benthic carnivores/scavengers, such as the isopods *Serolis polita* and *Glyptonotus antarcticus*, the seastar *Odontaster validus*, the nemertean *Parborlasia corrugatus*, the gastropod *Neobuccinum eatoni* (Presler 1986), and the polychaetes *Aglaophamus ornatus* and *Barrukia cristata* (Table 1) had δ^{13}C values enriched slightly above that of the omnivores/depositivores (between −20.7‰ and −17.8‰), and without a clear coupling with the sources of organic matter. Probably their diets consisted of a wide variety of prey, including small invertebrates, not considered in our sampling, that feed on microphytobenthos, sediments and meiobenthos, besides the depositivores/omnivores analysed.

In contrast to *C. aceratus*, the fish *Notothenia coriiceps* is enriched in ^{13}C values. *N. coriiceps* is omnivorous, feeding on a varied range of food, composed of both benthic (amphipods, polychaetes, gastropods, small bivalves and algae) and pelagic (salps and krill) organisms (Linkowski et al. 1983; Barrera-Oro and Casaux 1990; Casaux et al. 2003). Domaneschi et al. (2002) also discovered large quantities of the small suspensivorous bivalve *Mysella charcoti* in the gut of *N. coriiceps*. The lower ^{13}C values of *Notothenia* muscles (−22.5‰) comparable to *N. coriiceps* from Anvers Island (−20.5‰) (Dunton 2001) could be explained by the food availability in the area, since their feeding

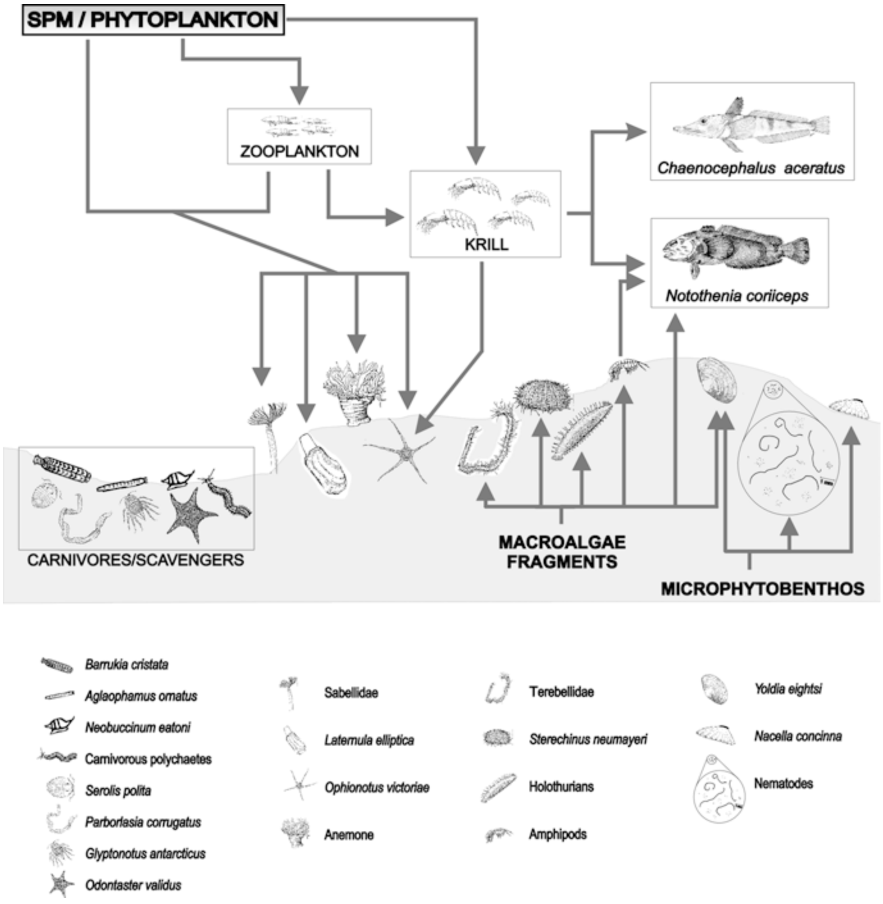

Fig. 3 Representation of the nearshore-zone food web in front of the Brazilian Antarctic Station (Martel Inlet), based on the isotopic carbon values. The depth zonation of the benthic megafauna is found in Nonato et al. (2000)

habits indicate that their diet may differ considerably even within the same study region (Linkowski et al. 1983).

In general the isotopic values and the knowledge of the feeding habits of the great majority of animals are in agreement. The trophic structure of the nearshore zone of Martel Inlet, based on the isotopic carbon values, is set out in Fig. 3. Part of the benthic fauna is less directly coupled to the pelagic primary production, assimilating carbon derived from other carbon sources, mainly benthic microalgae as well as macroalgal fragments and is more complex with respect to the contribution of more than one source of carbon from benthic primary producers besides pelagic producers.

The range in mean carbon isotope ratios was greater in the shallow coastal zone community of Martel Inlet than in shelf areas. Comparing our results with those of other nearshore Antarctic or sub-Antarctic areas, it may be observed that the benthic feeders collected in front of the Brazilian Station (Martel Inlet) were more enriched than the others. Kaehler et al. (2000) studied an area close to kelp beds and their samples were collected in deeper waters (more than 45 m). On the other hand, Dunton (2001) analysed benthic samples collected on rocky shores from different islands where macroalgae form extensive beds. Our study was undertaken on a sheltered soft bottom with a dense microphytobenthic layer and where the macroalgae are present mainly as fragments. The abundance of these two sources of carbon in the study area might explain the differences observed.

Further isotopic measurements, including δ^{15}N, may prove useful in elucidating the sources of primary production, the diets and the trophic positions of nearshore coastal zone organisms in Antarctica.

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