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ORIGINAL PAPER

Feeding ecology of shallow water meiofauna: insights from a stable isotope tracer experiment in Potter Cove, King George Island, Antarctica

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Abstract Antarctic meiofauna is still strongly understudied, and so is its trophic position in the food web. Primary producers, such as phytoplankton, and bacteria may represent important food sources for shallow water metazoans, and the role of meiobenthos in the benthic-pelagic coupling represents an important brick for food web understanding. In a laboratory, feeding experiment ^{13}C-labeled freeze-dried diatoms (*Thalassiosira weissflogii*) and bacteria were added to retrieved cores from Potter Cove (15-m depth, November 2007) in order to investigate the uptake of 3 main meiofauna taxa: nematodes, copepods and cumaceans. In the surface sediment layers, nematodes showed no real difference in uptake of both food sources. This outcome was supported by the natural δ^{13}C values and the community genus composition. In the first centimeter layer, the dominant genus was *Daptonema* which is known to be opportunistic, feeding on both bacteria and diatoms. Copepods and cumaceans on the other hand appeared to feed more on diatoms than on bacteria. This may point at a better adaptation to input of primary production from the water column. On the other hand, the overall carbon uptake of the given food sources was quite low for all taxa, indicating that likely other food sources might be of relevance for these meiobenthic organisms. Further studies are needed in order to better quantify the carbon requirements of these organisms.

Keywords West Antarctic Peninsula · Feeding ecology · Meiobenthos · Stable isotopes

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Introduction

The recent global warming has increased the concern for the Southern Ocean since Antarctic ecosystems are experiencing strong changes (Turner et al. 2005; Vaughan et al. 2003; Schofield et al. 2010). In light of the relatively fast rate of these changes, it became of fundamental importance to investigate and quantify the biodiversity of Antarctica whose biota is still relatively poorly studied. Nevertheless, to understand an ecosystem and its resilience against changes, also a more functional approach is needed. Understanding the interactions between species and between the different functional components of an ecosystem is therefore of fundamental importance. In this context, tracer experiments (Middelburg et al. 2000; Moens et al. 2007; Maria et al. 2011) and natural stable isotope studies (Moens et al. 2007; Mincks et al. 2008; Nomaki et al. 2008) contribute to identify and/or to quantify the interactions between different trophic levels. In Potter Cove, and more specifically in Antarctic shallow waters ecosystems, this was the first time that such experimental approach was applied.

In this study, meiofauna (or meiobenthos) refers to the group of small-sized metazoan organisms that inhabit marine sediments and pass through a 1-mm mesh size sieve and are retained on a 32-μm sieve (Heip et al. 1985; Vincx 1996). Meiobenthos is often numerous and diverse. Past studies suggested that these metazoans are involved in the sediment organic matter remineralization (Coull 1999) and contribute to the overall benthic carbon flux (Szymelfenig et al. 1995), and they have been considered as an important link in marine food webs. More recent tracer experiments indicate microalgae and bacteria as possible meiofauna food sources (Urban-Malinga and Moens 2006; Evrard et al. 2010; Ingels et al. 2010). Nevertheless, the measured

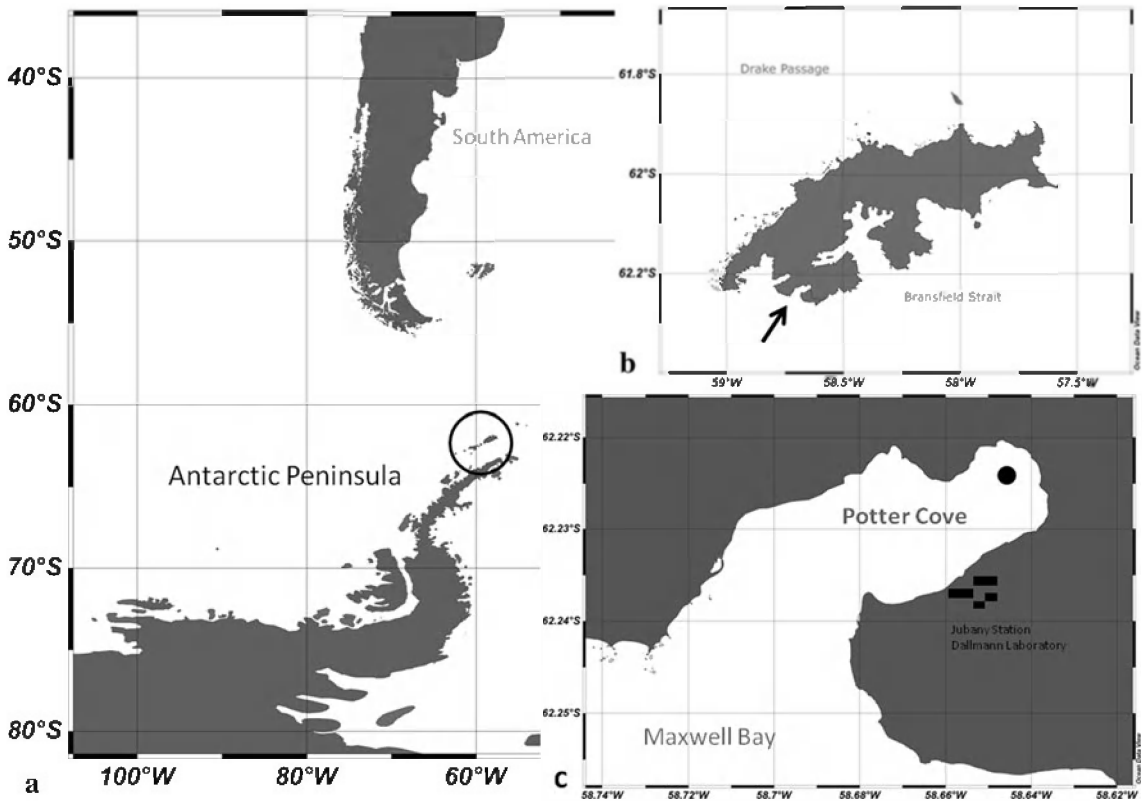

Fig. 1 Maps showing the location of the study site: **a** the map shows the area of the tip South America and the Antarctic Peninsula indicating in the circle King Gerge Island as part of the South Shetland Islands, Northern tip of the West Antarctic Peninsula; **b** the map shows King George Island (62°14′S, 58°40′W) indicating with the *arrow*, the location of Potter Cove; **c** the map shows Potter Cove and the black dot represents the study site

^{13}C uptakes often showed not to be enough to cover the expected carbon requirements of certain meiofauna taxa (e.g. for nematodes in Urban-Malinga and Moens 2006; Franco et al. 2008; Guilini et al. 2010; Ingels et al. 2010 and for copepods in De Troch et al. 2005), suggesting the importance of preference for food sources other than those provided in the experiments. On the other hand, other authors (Coull 1999; Nyssen et al. 2002) stated that meiofauna may play an important role in transferring carbon to the higher trophic levels being prey for many other organisms, mainly juvenile fishes. These conflicting results underline the numerous uncertainties in meiofauna feeding habits and their role in trophic food webs. Moreover, in extreme environments, such as Antarctica, there is an even bigger lack of relevant information to unravel the trophic position of meiofauna, which is one of the reasons this study was undertaken.

In this study, we focus on the feeding ecology of Potter Cove meiofauna. Potter Cove (62°14′S, 58°40′W, King George Island, West Antarctic Peninsula) is an Antarctic fjord-like small embayment (3 km^2) with a maximum depth of 50 m and influenced by the Fourcade Glacier (Fig. 1). Since the 1950s, the glacier has been actively retreating (Moll et al. 2006) in response to the air warming trends of the West Antarctic region (Schofield et al. 2010; Vaughan et al. 2003). So far, the meiobenthic community of this cove has been studied mainly in terms of densities, major taxonomic composition (Mayer 2000; Veit-Köhler et al. 2008), and abundances of copepods and their biovolumes in relation to environmental conditions (Veit-Köhler 2005). However, despite its high abundance, a more functional approach to unravel the trophic position and its possible contribution to the benthic food web is lacking so far. The present work would be the first such investigation in this remote environment.

With the present study, we wanted to investigate the uptake of 3 chosen meiofauna taxa when provided with phytoplanktonic algae or benthic bacteria as potential food sources. Phytoplankton has been highly studied in Potter Cove. In fact, the cove is characterized by frequent high turbulence and high water column turbidity which lead to relatively low primary production (PP) in the water column (Schloss and Ferreyra 2002; Schloss et al. 2002). Anyhow, in light of the strong warming of the average air temperatures occurring in Potter Cove during the last 50 years, the cove ecosystem is facing visible changes. Melt water flow

is a constant phenomenon during summer months (Eraso and Domínguez 2007), and the Fourcade glacier is actively retreating (Domínguez and Eraso 2007). On the local scale, water column stabilization and more intense phytoplankton blooms are expected to represent part of the effects that are likely to occur because of these climate-related changes (Smith and Nelson 1985; Dierssen et al. 2001; Schloss et al. 2002; Turner et al. 2005), leading to an increasing importance of the phytoplankton contribution to these sediments' food input.

In addition to sinking phytoplankton cells, also microphytobenthic diatoms, sea-ice algae and macroalgal fragments are potential constituents of the sediment's organic matter pool on which the detritus pathway is based. Bacteria can play an important role in the detritus pathway, especially in the winter months when the summer production is accumulated in the sediments and is likely to be transferred to higher trophic levels (e.g. meiofauna organisms and other detritivores) via microbial reworking (Nedwell et al. 1993). In this study, we therefore focused on both phytoplanktonic diatoms and benthic bacteria as possible food sources for the meiobenthos.

The main questions of this tracer study can be resumed as follows: (1) is there a different uptake of bacteria and phytoplanktonic diatoms by meiofauna over time? and (2) do the main taxa differ in terms of uptake of the given food sources?

Materials and methods

Sampling site and experimental design

The sampling site was located in Potter Cove in front of the Fourcade Glacier (see black dot in Fig. 1), at a depth of about 15 m, where fine sand soft bottoms were suitable for scuba diving sampling. A total of 18 sediment push cores (5.6 cm inner diameter, 24.62 cm^2 surface) were retrieved at the beginning of the austral summer (November 2007) in the same day over an area of about 5 m^2. As control (natural carbon isotopic signature of metazoans), 3 replicate cores were sliced (0–1, 1–2 cm) and stored frozen (−80 °C); 3 extra replicates were sliced (0–1, 1–2, 2–3, 3–4, 4–5 cm) and stored in 4 % formaldehyde for meiofauna community analysis. In addition, 12 cores were collected to serve as experimental units in the laboratory experiment.

Prior to the sampling campaign, diatoms and bacteria were grown and ^{13}C pre-labeled to be used as food sources in a tracer experiment. The planktonic diatom species *Thalassiosira weissflogii* (strain CCMP1587, 14–18 µm length, 8–10 µm width) was selected for this experiment. The diatoms were reared in 2L erlenmeyers with f/2 culture medium (Guillard 1975, 30 psu) where 5 ml of a $NaH^{13}CO_3$ solution (336 mg in 100 ml milliQ H_2O) was added per 100 ml of the culture medium. After 3 weeks of growing at 20 °C and on a 12-h:12-h light/dark light regime, the algae passed from an initial $\delta^{13}C$ signature of −15.9 ‰ (Atm% 1.1) to an enriched value of 47491.9 ‰ (average Atm% 35.3) for untreated and enriched cultures, respectively. Bacteria from Schelde estuary's sediments (at the Belgium,the Netherlands border) were initially grown on marine agar for 4 days at 15–16 °C. In order to maximize the bacterial diversity in the inoculum, a dilution series was setup. The liquid growth medium consisted of autoclaved artificial seawater (24.5 PSU, Instant Ocean synthetic salt), Beef extract (DIFCO, 3 g L^{-1}) and Bactopeptone (DIFCO, 5 g L^{-1}). Two erlenmeyers were inoculated with the bacterial mix scraped from the agar plates and placed on a shaking table at room temperature. After 3 days of growth, new growth medium was prepared as stated above but diluted by a factor 20, and 0.5 g L^{-1} ^{13}C glucose (D-glucose, U-$^{13}C6$, 99 %, Cambridge Isotope Laboratories, Inc.) was added to label the bacteria. After 24 h of growth, this labeling technique yielded an increase in $\delta^{13}C$ from −15.2 ‰ (Atm% 1.1) to 70268.9 ‰ (average Atm% 44.5), for untreated and ^{13}C enriched cultures, respectively. After sufficient growth, both cultures were washed with autoclaved filtered natural seawater and freeze dried.

A total of 12 single-food source experimental units were incubated including triplicates of two treatments (food source) for two time intervals: Diatoms 5 days, Diatoms 10 days, Bacteria 5 days and Bacteria 10 days. One aliquot of freeze-dried food source (diatoms or bacteria) was added to each core, and the water surface was gently stirred until all food settled on the sediment surface. Each core was provided with 30 mg of freeze-dried material which corresponded to about 8–9 mg C per core. All cores were left open at the top and were oxygenated with an air pump. This experiment was carried out in the dark to avoid primary production. After the incubation period, the first two centimeters (0–1, 1–2 cm) of the sediment were sliced, collected into Petri dishes and stored frozen (−80 °C), pending further analysis. Here, we report only the uptake results for the first two centimeters for the nematodes since they contain the majority (>50 %) of the total meiofauna community and because in absence of sediment stirring the label may not have penetrated deeper than that. Moreover, harpacticoid copepods and cumaceans were only found in the upper layer in sufficient biomass to conduct reliable stable isotope analyses.

Meiofauna processing and statistical analyses

Extraction of meiofauna from the 4 % formaldehyde preserved samples followed standard procedures of centrifugation–flotation with LUDOX HS40, and sieving over 1,000

and 32 μm sieves (Heip et al. 1985; Vincx 1996). Meiofauna taxa identification was based on Higgins and Thiel (1988). We identified the nematodes at the genus level. The identification was carried out by collecting 100 individuals randomly from each replicate of each layer of sediment and then mounting them on glass slides. The online identification key for free-living marine nematodes (NeMysKey©) developed within Nemys (http://nemys.ugent.be/), and the identification key by Warwick et al. (1998) were used. For the nematode biomass determination, standard methods were used by the estimation of body volume using Andrassy's formula (Andrassy 1956): $V = L \times W^2/16x \times 10^5$, where V is the volume in nanoliters, L is the length in μm (excluding filiform tails, if present) and W is maximal width in μm. Body volume was converted to biomass (μg wet weight 10 cm^{-2}) assuming a specific gravity of 1.13 (Wieser 1960) and a dry/wet weight (DW/WW) ratio of 0.25. Biomass was then converted to carbon assuming a dry weight/μg C ratio of 0.124 (Jensen 1984). In this way, nematode biomass could be measured for all depth layers. Biomass (μg C 10 cm^{-2}) of copepods and cumaceans was estimated based on the stable isotope μg C values (see further) by multiplying the individual average biomass with the total number of individuals per 10 cm^2 of the 0–1 cm layer of natural community samples.

Possible dissimilarities in terms of meiofauna densities and nematode biomasses between sediment depth layers were investigated through ANalysis Of SIMilarities and the ANalysis of SIMilarities PERcentages (ANOSIM and SIMPER, Primer-E, ltd, version 6.1.6).

Stable isotope analysis

The frozen sediment of both control and experimental cores was thawed, and meiofauna was elutriated via Ludox HS40 and sieved as for the community analysis (Heip et al. 1985; Vincx 1996). The use of Ludox was not expected to have any effects on the stable isotopic signatures of the organisms as demonstrated in previous studies (Moens et al. 2002). The extracted meiofauna was transferred into milliQ (MQ) water in sterile Petri dishes and directly processed in order to avoid potential leakage of label (see Mourelatos et al. 1992; Moens et al. 1999). About 150 nematodes, 15 cumaceans and 30 harpacticoid copepods have been separately handpicked with a fine sterile needle, rinsed twice in MQ water to remove adhering particles and finally transferred to a drop of MQ water in 2.5 × 6 mm Al cups. The cups had been preheated at 550 °C to remove any contaminating organic carbon. The Al cups with the animals were then oven-dried overnight at 60 °C, pinched closed and stored in air-tight multi-well microtiter plates. The carbon isotopic composition of the samples was determined with a PDZ Europa ANCA-GSL elemental analyzer 230 interfaced to a PDZ Europa 20–20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK; UC Davis Stable Isotope Facility, http://stableisotopefacility.ucdavis.edu/).

Uptake of ^{13}C is reflected as excess (above natural abundance) ^{13}C and is expressed as total uptake in the sample (I) in μg C (quantitative) and as specific uptake $\Delta\delta^{13}C$ ($\Delta\delta^{13}C = \delta^{13}C_{sample} - \delta^{13}C_{control}$) in parts per thousands (‰) (qualitative), according to Middelburg et al. (2000). $\delta^{13}C_{sample}$ is calculated as $[(R_{sample} - R_{VPDB})/R_{VPDB}] \times 10^3$ with $R_{VPDB} = 0.0112372$ = the carbon isotope ratio of the Vienna Pee Dee Belemnite standard, and $R_{sample} = [(\delta^{13}C_{sample}/1000) + 1] \times R_{VPDB}$ (Craig 1957; Middelburg et al. 2000). Fractional abundance of ^{13}C (F) equals $R/(R + 1)$ and is used to calculate the excess ^{13}C (E) in the samples, which is the difference between the ^{13}C fraction of the sample (F_{sample}) and the ^{13}C fraction of the control ($F_{control}$): $E = F_{sample} - F_{control}$. I is here calculated as the product of E and C weight (μg) of each sample (as measured in the isotope analysis results). Since we added 2 different food sources, uptake values (I) have been corrected according to their initial level of label incorporation. The uptake has been reported as (1) individual uptake (*I per ind.*, *μg ^{13}C ind^{-1}*), which can show differences between the taxa due to their individual biomass, (2) a standardized uptake expressed per unit of biomass (*I per unit C*, *μg ^{13}C C^{-1}*) and the (3) *I per total number of ind. core^{-1}* which was calculated by multiplying *I per ind.* values with the average total abundances in the corresponding first cm depth layer (Fig. 5).

Significant differences in $\Delta\delta^{13}C$ and the biomass specific uptake (*I per unit C*) were investigated by means of a three-way analysis of variance (3-way ANOVA) on the rank values with the Statistica [version 7.0] software (StatSoft Inc., 2001). Results are reported indicating p values and F values. The values for each factor's degrees of freedom are 1 for food, 2 for taxa and 1 for time. N depends on the combination of factors. In case of the 3-way ANOVA, N = (3 replicates × 3 taxa × 2 food sources × 2 incubation periods) = 36. A posteriori comparisons were carried out with the Tukey's HSD test using 95 % of confidence limits. Prior to the ANOVA, the Levene's test was used to check the assumptions on homogeneity of variances only in case raw data were used.

Results

Meiobenthic community

The meiobenthic community was characterized by total abundances ranging from 3,671 to 10,873 ind. 10 cm^{-2}. The dominant taxon was nematodes (91 %), followed by nauplii (and copepodites) (5.4 %) and harpacticoid

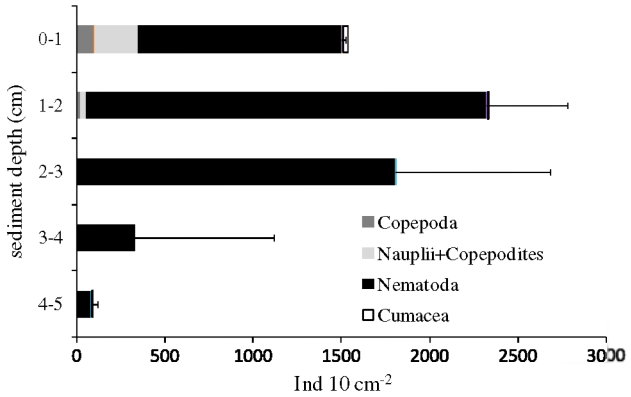

Fig. 2 Vertical density profiles of meiofauna taxa (mean ± standard error)

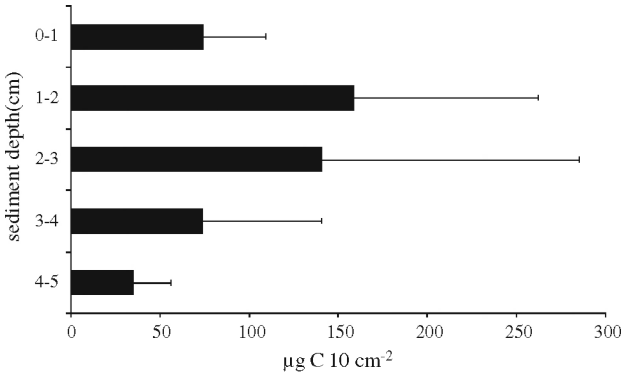

Fig. 3 Vertical distribution of average nematode biomasses in µg C 10 cm^{-2} (mean ± standard deviation)

copepods (2.1 %). Nematode abundances (0–5 cm) showed a high variability between the three replicates ranging from 3,339 to 10,409 ind. 10 cm^{-2}, with an average value of 6,010 ind. 10 cm^{-2}. In the upper layers, nematodes were found in average densities of 2,643 and 5,186 ind. 10 cm^{-2}, in the 0–1 and 1–2 cm layer, respectively (Fig. 2).

The average abundance of copepods was 115 ± 16 ind. 10 cm^{-2} (mean ± SD). Among the other metazoans, cumaceans were the most important (0.6 % of total abundance), showing relatively high abundances with an average value of 29 ± 11 ind. 10 cm^{-2} (mean ± SD). Up to 41 specimens per replica have been counted, and 90 % of them were confined in the upper centimeter. Polychaetes (0.3 % of total abundance) were important too and were present in almost all sediment layers analyzed. Other meiofauna groups present were Hydrozoa, Amphipoda, Isopoda, Ostracoda and Bivalvia, representing together on average 0.23 % of the total meiobenthic abundance over the 5-cm depths analyzed (but the taxa were present only in the 0–2 cm layer).

In general, the total nematodes' biomass in the top layers (0–5 cm) (Fig. 3) showed an average value of 482.98 ± 350.84 µg C 10 cm^{-2} (mean ± SD). In the 0–1 and 1–2 cm sediment layer, nematodes showed average biomass values of 74.45 ± 34.63 and 158.91 ± 102.79 µg C 10 cm^{-2} (mean ± SD), respectively. Increasing mean individual body sizes toward the deeper layers indicated the presence of higher relative abundances of large nematodes (i.e. *Metasphaerolaimus*, *Sabatieria*, *Metalinhomoeus*). Copepods' biomass in the first layer of the sediment was 93.37 ± 117.55 µg C 10 cm^{-2} (mean ± SD), and cumaceans accounted for 127.07 ± 50.50 µg C 10 cm^{-2} (mean ± SD).

The nematode assemblage consisted of 44 genera in total. Table 1 shows the most abundant genera and their corresponding trophic guilds. The genera *Daptonema*, *Aponema*, *Amphymonhystrella* and *Halalaimus* were most abundant accounting together for >60 % of the total nematode community. Vertical distribution of the various nematode genera illustrated a gradual depth gradient in terms of genus presence/absence and relative abundances, with the intermediate layers forming a transition zone in terms of community structure between the surface (0–2 cm) and the deeper layers (3–5 cm) (Table 2). The ANOSIM results confirm these findings (factor = cm depth; $R = 1$) with a significance level of $p < 0.002$. The nematode genera *Daptonema*, *Dichromadora* and *Anticoma* were abundant in the upper layer (0–1 cm) and showed a clear drop in densities toward the deeper sediment layers. *Amphimonhystrella*, *Retrotheristus* and *Aponema* increased in importance in the intermediate sediment layers which coincides with peaks in total nematode abundances. *Sabatieria* and *Metalinhomoeus* were characteristic for the deeper layers (3–5 cm).

Stable isotope signatures

Background $\delta^{13}C$ average values (natural stable ^{13}C ratios) for the studied meiobenthic taxa were as follows: nematodes −19.35 ± 1.37 ‰, copepods −17.89 ± 0.53 ‰ and cumaceans −14.57 ± 0.32 ‰. The natural stable isotopic signatures point at some trophic differentiation between the 3 chosen taxa (1-way ANOVA $p < 0.05$).

The results of a 3-way ANOVA analysis based on the $\Delta\delta^{13}C$ ranked values for the experimental results are summarized in Table 3. All factors of interest (time, taxon and food) had a significant effect on the specific uptake values. Based on the $\Delta\delta^{13}C$ values (Fig. 4a), copepods and cumaceans showed at each time interval a higher uptake of diatoms in comparison with bacteria (Fig. 4a, Tukey's HSD test: $p < 0.01$). Nematodes, however, did not show any significant difference in $\Delta\delta^{13}C$ values for both food sources (Tukey's HSD test: $p > 0.05$). Nematodes also showed a slower response to the enrichment with both food sources since only after 10 days of incubation their uptake was appreciable.

Table 1 Relative abundances (%) of nematode genera in the first two centimeters layer (left part of the table) and in the total community (0–5 cm) (right part of the table)

Genus	0–1 cm	Genus	1–2 cm	Genus	0–5 cm	Trophic guild
Daptonema	45.09	*Aponema*	31.55	*Aponema*	31.06	*2A*
Halalaimus	13.03	*Halalaimus*	17.12	*Daptonema*	13.82	*1B*
Dichromadora	6.91	*Daptonema*	9.16	*Amphimonhystrella*	12.67	*1B*
Aponema	5.40	*Desmolaimus*	8.97	*Halalaimus*	12.02	*1A*
Anticoma	4.58	*Amphimonhystrella*	7.12	*Desmolaimus*	4.37	*1B*
Prochromadorella	3.56	*Trichotheristus*	4.53	*Dichromadora*	3.31	*2A*
Acantholaimus	2.66	*Chromadorita*	3.86	*Metasphaerolaimus*	2.68	*2B*
Metasphaerolaimus	2.66	*Retrotheristus*	3.32	*Trichotheristus*	2.66	*1B*
Desmolaimus	1.88	*Dichromadora*	3.15	*Metalinhomoeus*	2.66	*1B*
Paramonhystera	1.68	*Acantholaimus*	2.10	*Chromadorita*	1.79	*2A*
Amphimonhystrella	1.19	*Metasphaerolaimus*	1.37	*Retrotheristus*	1.76	*1B*
Trichotheristus	1.19	Aegialoalaimus	0.89	*Acantholaimus*	1.43	*2A*
Chromadorina	1.13	*Wieseria*	0.74	*Anticoma*	1.33	*1B*
Metalinhomoeus	1.04	*Leptolaimus*	0.71	*Prochromadorella*	1.01	*2A*
Chromadorita	0.97	*Anticoma*	0.56	*Sabatieria*	0.87	*1B*
Neochromadora	0.97	*Linhomoeus*	0.56	*Linhomoeus*	0.70	*1B*
Mesacanthion	0.85	*Oxystomina*	0.52	*Oxystomina*	0.65	*1A*
Microlaimus	0.69	*Gnomoxyala*	0.40	*Paramonhystera*	0.59	*1B*
Retrotheristus	0.69	*Prochromadorella*	0.40	*Aegialoalaimus*	0.54	*1A*
Halomonhystera	0.63	*Chromadorina*	0.37	*Neochromadora*	0.51	*2A*

Trophic groups (Wieser 1953) legend: 1A = selective deposit feeders, 1B = non-selective deposit feeders, 2A = epistratum feeders, 2B = predators/omnivores

Table 2 Relative abundances (%) of the most important genera showing the vertical zonation of these genera

Genus	0–1 cm	1–2 cm	2–3 cm	3–4 cm	4–5 cm	Trophic guild
Daptonema	**45.09**	9.16	3.02	1.76	1.76	*1B*
Dichromadora	6.91	3.15	1.9	0.37	0.4	*2A*
Anticoma	4.57	0.55	0.31	0	0	*1B*
Halalaimus	13.03	17.12	8.4	3.25	8.71	*1A*
Aponema	5.4	**31.55**	**41.62**	**56.5**	17.28	*2A*
Retrotheristus	0.69	3.31	1.35	0	0	*1B*
Amphimonhystrella	1.19	**7.12**	**26.34**	**13.51**	4.08	*1B*
Metalinhomoeus	1.03	0	4.27	**9.82**	**15.79**	*1B*
Sabatieria	0	0.18	1.08	**2.42**	**24.81**	*1B*
Desmolaimus	1.88	8.97	1.8	2.42	1.66	*1B*
Metasphaerolaimus	2.66	1.37	3.9	2.5	8.46	*2B*
Acantholaimus	2.66	2.1	0.31	0	0	*2B*

ANOSIM showed the following groups: upper layer zone (0–2 cm), an intermediate zone (1–4 cm) and a deep zone (3–5 cm). The genera contributing most to this dissimilarity and to the similarity within each group, as indicated by SIMPER, are highlighted

Standardization toward individual uptake values (*I per ind.*) yielded a statistically significant difference between both food sources with a higher consumption of the diatom *Thalassiosira weissflogii* by all tested taxa (Fig. 4b). Uptake of bacteria has been recorded as well for all groups but was lower than that of the phytoplankton food source for each taxon. In the first sediment layer (0–1 cm), there was a clear difference in terms of individual uptake between the different taxa, with Cumacea showing higher values for both food sources when compared to nematodes at each time interval (Tukey's HSD: $p < 0.01$). In comparison to copepods, cumaceans showed a higher individual uptake just after 5 days and only when feeding on bacteria (Tukey's HSD: $p < 0.01$). Further, standardization toward *I per unit C* (Fig. 4c) aimed

Table 3 Results of a 3-way ANOVA analysis performed on the ranked values of the $\Delta\delta^{13}C$, *I per ind.* and *I per unit C*

Factors	$\Delta\delta^{13}C$		*I per ind.*		*I per unit C*	
	F	*p*	**F**	*p*	**F**	*p*
Food	41.6395	**0.000001**	147.505	**0.000000**	20.3774	**0.000143**
Taxon	10.5764	**0.000509**	226.514	**0.000000**	24.6566	**0.000045**
Time	12.8517	**0.001493**	17.143	**0.000369**	7.5792	**0.002809**
Food*taxon	0.8487	0.440430	9.505	**0.000912**	0.2057	0.815529
Food*time	1.3627	0.275061	0.171	0.682522	0.0906	0.766051
Taxon*time	0.3681	0.549760	2.057	0.149765	0.2057	0.815529
Food*taxon*time	0.9612	0.396667	0.514	0.604369	1.4283	0.259371

F values and *p* values are reported for food (bacteria and diatoms), taxon (nematodes, copepods and cumaceans) and time (5 and 10 days) and for all the combinations of these three factors. Significant *p* values ($p < 0.05$) are highlighted in bold font

at illustrating possible differences in the C assimilation from the ^{13}C-labeled sources by the different taxa. However, despite the significant level of variance of the 3-way ANOVA for *I per unit C* (Fig. 4c), the post hoc analysis did not show any significant difference in the assimilation of the two different food sources or in the assimilation between the different groups (Tukey's HSD $p > 0.05$).

Based on the contribution of each taxon to the uptake of the food sources (see Fig. 5), it was observed that after 10 days the three dominant taxa together consumed a total of ~4.2 µg C from ^{13}C-labeled source per 10 cm^{-2} or 9.3 µg C from ^{13}C-labeled diatoms core^{-1} and a total of 0.72 µg C from ^{13}C-labeled source per 10 cm^{-2} or 1.68 µg C from ^{13}C-labeled bacteria core^{-1}. These values mean that after 10 days the nematodes, copepods and cumaceans together took up 0.39 and 0.04 % of the total ^{13}C carbon from diatoms and bacteria, respectively. After 5 days, nematodes alone took up 0.01 and 0.002 % of diatoms and bacteria, respectively, while at the end of the experiment they showed a total uptake of about 0.09 and 0.01 % of the C present in the ^{13}C-labeled diatoms and bacteria standing stock.

Comparing nematodes of both sediment layers (0–1 cm versus 1–2 cm) (see Fig. 6), it was clear that the labeled food sources were not very accessible in the subsurface layer since a delayed response can be noticed and higher overall uptakes were shown in the upper centimeter layer community. Again, the nematodes did not show a significant (1-way ANOVA $p > 0.05$) preference for any of the two given food sources.

Discussion

Meiofauna community standing stocks

The total meiofauna abundances of this site were high compared to temperate shallow water ecosystems (Vanhove et al. 1998 and comparisons therein; Le Duc and Probert 2010). Veit-Köhler et al. (2008) found similarly high densities between 10 and 20 m water depth (up to 16,835 ind. 10 cm^{-2}) in Potter Cove. In agreement with our results, nematodes were the most abundant taxon followed by copepods (including nauplii), cumaceans and annelids. The first meiofauna study in Potter Cove by Mayer (2000), however, showed much lower meiobenthos densities (maximum densities of 485.5 ind. 10 cm^{-2} at a depth of 10 m) in comparison with Veit-Köhler et al. (2008) and the present study. However, similar high abundances (and high between replicate variances) have been recorded in other Antarctic areas by Vanhove et al. (1998, 2000) (Factory Cove South Orkney Islands, Antarctica, average 6,200 ind. per 10 cm^{-2}) and in Martel Inlet (Admirality bay, KGI, by de Skowronski et al. 1998) (Siciński et al. 2011) (densities between 3,523 and 8,216 ind. 10 cm^{-2}) (and by de Skowronski and Corbisier 2002) (densities between 1,953 and 6,310 ind. 10 cm^{-2}). It is important to state that abundance data are also dependent on the mesh size range used during the investigation, and unfortunately not always the same mesh size sieve are widely used (e.g. de Skowronski et al. 1998 used 500 and 68 µm sieve). This can make comparisons more difficult. Anyhow, the high abundances suggest that food is not limiting in shallow water Antarctic bottoms, and microscale differences in the sediment characteristics, such as primary production (microphytobenthos and macroalgae), secondary (bacteria and protozoans) production processes and sediment granulometry (Vanhove et al. 2000; de Skowronski and Corbisier 2002; Veit-Köhler et al. 2008; de Skowronski et al. 2009) may lead to high spatial heterogeneity.

Nematode community, diversity and structure

The dominant nematode genera in the investigated Potter Cove station were *Daptonema* and *Aponema*. Both genera were also reported by Vanhove et al. (1998, 2000) representing more than 60 % of the nematodes assemblage at Factory Cove. In general, the assemblage found in the

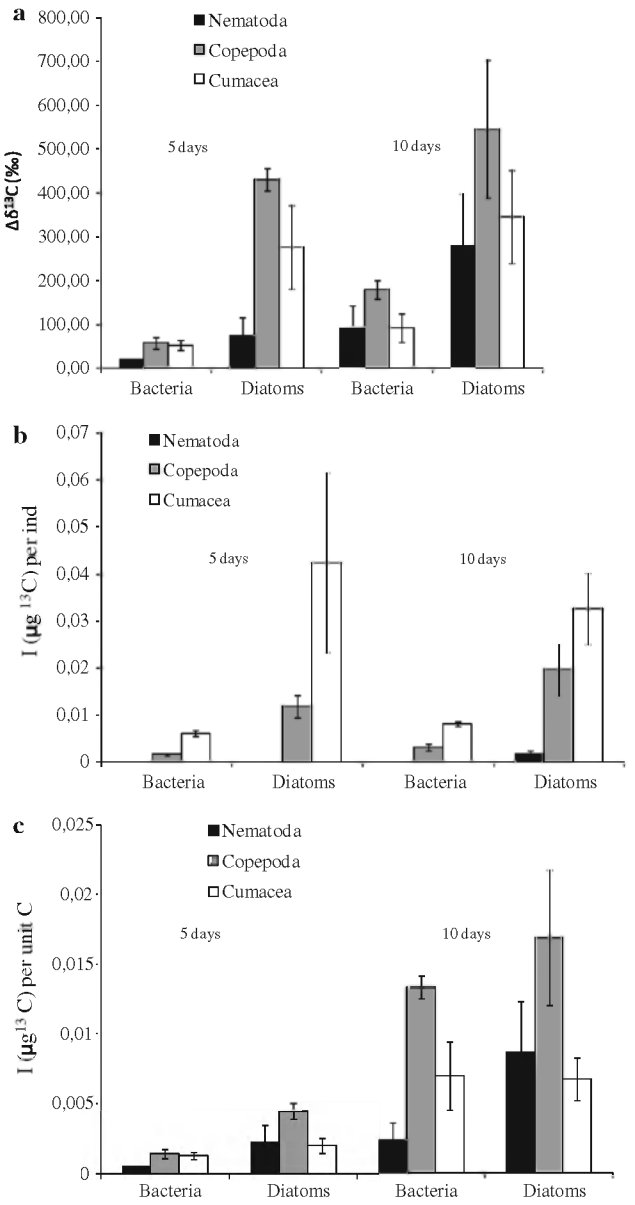

Fig. 4 **a** $\Delta\delta^{13}C$ (in ‰), **b** *I per ind.* (µg ^{13}C ind^{-1}) and **c** *I per unit carbon* (µg ^{13}C µg C^{-1}) for 3 meiofauna taxa in the 0–1 cm depth (mean ± standard error)

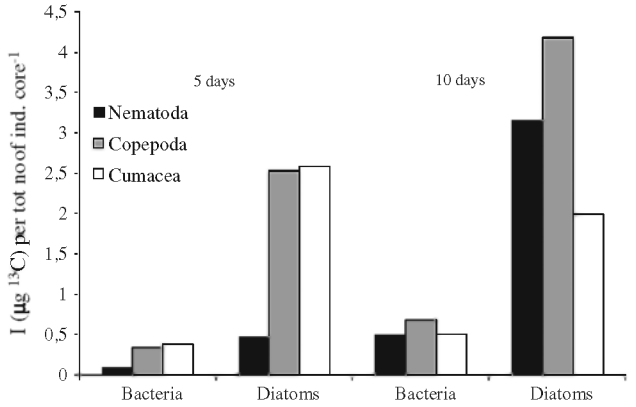

Fig. 5 Total uptake *I* (µg ^{13}C) of bacteria and diatoms by nematodes, copepods and cumaceans (total number of individuals per core) in the 0–1 cm layer (mean ± standard error)

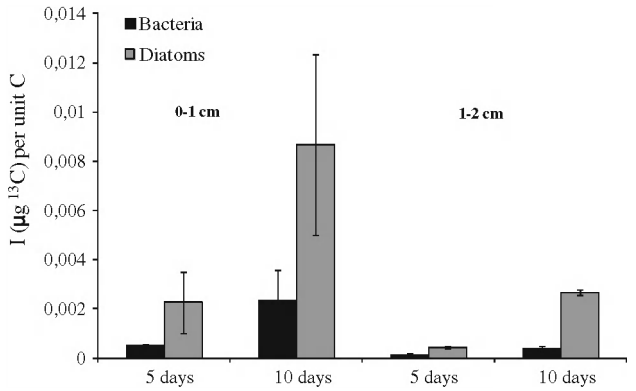

Fig. 6 *I per unit carbon* (µg ^{13}C µg C^{-1}) of the nematode community in two different layers (0–1 cm and 1–2 cm depth) (mean ± standard error)

present study appears to be similar, at genus level, to those found in other shallow meiobenthic communities in subtidal fine sands worldwide (Juario 1975; Heip et al. 1985; Vanreusel 1990).

In the surface layer, *Daptonema*, which is classified as a non-selective deposit feeder (group 1B), dominates the community representing almost half of it in terms of abundances. It is well known as an "opportunistic genus" (Vanhove et al. 2000) because it shows a particular preference for diatoms as food source but can easily switch to bacteria. *Daptonema* can be stated to be a very flexible genus having been positively correlated with the pico- and nano-fraction of water pigments (so to say phytoplankton, Vanhove et al. 2000) and with microphytobenthos (Moens et al. 2005), and moreover, it has been observed to feed on small ciliates (Moens and Vincx 1997). As a result, an opportunistic genus that is capable to feed on different food sources seems to be successful, also in Antarctic shallow waters. Moreover, Schratzberger et al. (2000) reported for two North Sea species of *Daptonema* a high resistance to the temporal absence of food, which may indicate that beside the feeding plasticity this genus may have evolved the capacity to survive in conditions of starvation. *Aponema* (an epistrate feeder) became more dominant in the 1–4 cm layer. It is possible that being capable of fast vertical migrations (Schratzberger et al. 2000), this genus could still benefit in the subsurface layer of the presence of food on top of the sediment, and at the same time avoid surface predation.

Trophic ecology

The natural carbon signature of the 3 meiofauna taxa analyzed in the present study was compared with data on the

food sources taken from Corbisier et al. (2004), Kaehler et al. (2000) in view of the similarities in terms of biota and environmental characteristics of these Antarctic sites. The natural carbon signatures of the possible food sources ranged from the more depleted values of phytoplankton (around −25 ‰) to those of microphytobenthos and macroalgae (from around −16 ‰ to around −23 ‰).

Cumaceans showed the highest $\delta^{13}C$ values, with an average value of −14.57 ‰. There is still not much known about the feeding ecology of cumaceans. This taxonomic group includes families with large differences in morphological characteristics which in turn create a wide range of feeding strategies within the order. Cumaceans of shallow water environments in the Antarctic are primarily known as deposit feeders (feeding for instance on organic matter and microorganisms) but able to graze on epipelic algae growing on sand grains (Blazewicz-Paszkowyczi and Ligowski 2002). However, there are also examples of predatory behavior among members of few families (e.g. Nannastacidae and Gynodiastylidae), which have piercing mandibles and may prey on polychaetes and foraminiferans (Kozloff 1990; Blazewicz-Paszkowyczi and Ligowski 2002; Brusca and Brusca 2003). Comparing these values with the results of our feeding experiment (where cumaceans showed they feed more on diatoms than bacteria), we could support the idea that this taxon feeds on detritus (e.g. algal material with associated diatoms) both in a direct (selectively) and in an indirect (e.g. feeding on bacteria that degrade detritus) way, although additional food sources may play a role too.

Copepods showed an average $\delta^{13}C$ value of −17.89 ‰. Copepods are known to feed on both microalgae (benthic and planktonic) and bacteria (directly or from a biofilm), which can lead to different species-specific isotopic signatures (De Troch et al. 2005; Urban-Malinga and Moens 2006; Nascimento et al. 2008). On the other hand, the tracer experiment showed a higher uptake of planktonic diatoms with values (both *I per ind.* and *I per unit C*) laying within the range of those measured during various experiments performed on different temperate copepods' species under laboratory conditions (De Troch et al. 2005, 2006b; Wyckmans et al. 2007). Anyhow, copepods from our study showed a much lower *I per unit C* compared to their temperate counterparts, as reported by Maria et al. (2011). In this study, the authors found uptake as high as 0.7 µg c µg C^{-1} when the small crustaceans were given benthic-labeled diatoms. The use of benthic diatoms was not planned in our experiment, but future studies in Potter Cove should focus also on this component of the benthic primary producer biota. In terms of food quality, diatoms are known to synthesize polyunsaturated fatty acids (PUFA) that are important metabolic compounds that animals cannot synthesize de novo (Tocher 2003). Bacteria can contain a large variety of fatty acids but normally produce very small amounts of ω-3 and ω-6 PUFA (Brett et al. 2009 and references therein). So far, it remains unclear whether grazers' selectivity is based on food quality or on other factors such as particle size (De Troch et al. 2006a) and food concentration (De Troch et al. 2007). The fact that labeled diatoms uptake remained anyhow low can be possibly explained by the fact that (1) other non-labeled diatoms were also present in the experimental cores and (2) the studied taxa feed more specifically on benthic diatoms than on phytoplanktonic species.

Nematodes showed an average stable $\delta^{13}C$ signal of −19.35 ‰, which appears to be more depleted than the $\delta^{13}C$ values reported for the nematode community in Martel Inlet ($\delta^{13}C = -15.6 \pm 0.7$ ‰) by Corbisier et al. (2004) but heavier than the values ($\delta^{13}C = -24.8 \pm 1.3$ ‰) found for Bransfield Strait shelf (230-m depth) communities (Moens et al. 2007). These natural stable isotope values seem to point to a predominance of pelagic carbon sources in the nematodes diet in Potter Cove, which is, however, in contrast to the results of our feeding experiment. These may be related to a delayed response of nematodes (uptake of already reworked labeled food sources) or to the use of other food sources. From the literature, nematodes are known to potentially feed on bacteria that may degrade sedimentary detritus (e.g. macroalgae) and also on microphytobenthos. Accordingly, nematodes' responses to our feeding experiment confirm these previous findings: they feed similarly on both given food sources, bacteria and microalgae. The nematode community in our study was dominated by *Daptonema* in the first cm layer, which can exploit the diverse available food sources (bacteria and/or benthic/phytoplanktonic diatoms and/or ciliates) present in the cove sediments, supporting all year around relatively high nematodes' densities as observed in a temporal study on Signy Island in similar conditions (Vanhove et al. 2000). In Corbisier et al. (2004), nematodes were significantly linked to microphytobenthos as food source. Microphytobenthos may be an important food source also in Potter Cove, but up to now, a lack of information about its abundance and biomass within the cove is avoiding possible inferences on its role as food for benthic organisms analyzed in the present study.

The delayed response of nematodes observed in the experiment has been reported before also for deep-sea (Witte et al. 2003; Ingels et al. 2010) and the Antarctic shelf (Moens et al. 2007) communities. However, this result is in contrast to what Moens et al. (2002) found in a temperate estuarine tidal flat, where nematodes have been seen consuming labeled microalgae already in the first 3 h of the experiment. Our result may indicate that, as mentioned before, (1) the labeled carbon entered the animals indirectly (e.g. feeding on bacteria that already had grown on the labeled diatoms or on protozoans that fed on them)

or (2) the nematodes of these Antarctic shallow water sediments have a slower response to the input of new carbon. If we compare our surface nematode community with that of a temperate sandy beach (Maria et al. 2011), it was noticed that interestingly the *I per unit C* values from our experiment are in the same order of magnitude of those that Maria et al. (2011) found for the 1B community group, in this case, feeding on labeled benthic diatoms. On the contrary, our community total uptake per unit of organism is much lower than that that Maria et al. (2011) reported for the 2A feeding group (epistratum feeders) community. In fact, our community in the first cm layer showed to be dominated for 45 % by *Daptonema*, a genus belonging to the 1B group. The dominance of a detritus feeder community may lead to lower direct uptake of microalgae which may on the other hand be taken up via detritus after reworking by other organisms (see also Moens et al. 2002). In general, after 10 days, the nematode community still did only incorporate about 0.09 % of the ^{13}C-label in the diatom food source. This is a relatively small amount (2 orders smaller) in comparison with a shallow water North Sea nematodes community where after 2 weeks 1.29 % of the given labeled *Skeletonema costatum* inoculum was taken up (as recalculated from Franco et al. 2008). Antarctic shelf nematodes collected at 230 m water depth and fed with cyanobacteria, only took up ~0.03 % of ^{13}C in the bacterial food after 10 days (Moens et al. 2007). This illustrates that the nematodes from Potter Cove respond similar as the Antarctic shelf community, at least in terms of uptake, responding in the same order of magnitude (i.e. <0.1 %) to the given food sources (bacteria in Moens et al. 2007 or diatoms in this study). Up to now, most of the experiments aimed at tracing the uptake of labeled food sources in meiofauna taxa, found that these animals do not seem to fulfill the expectations on carbon cycling and benthic mineralization, despite the fact that they are given the food sources they supposedly consume. These findings may point at difference plausible reasons: (1) the food sources given in the experiments are not in a state that is appetible for the animals (fresh cells vs freeze-dried ones, Cnudde et al. 2011); (2) the competition for food with other organisms, not taken into account during the analyses (e.g. macrofauna) may be underestimated; (3) technical biases during the analysis may be the cause of an underestimate of the real uptake of the given food sources. The lower nematodes' uptake in the deeper sediment layer may indicate that the food needed more time to reach these strata; however, due to the high variances between replicates, no statistically significant difference was found. The scarce penetration of added labeled food to deeper layers in laboratory sediment cores has been reported already by other authors (Middelburg et al. 2000; Moens et al. 2007; Ingels et al. 2010). Additional factors in the experimental setup that may interact with the food uptake that was actually measured include the presence of organic matter in the test sediment, the presence of other organisms and the use of freeze-dried food sources.

Conclusions

Despite the fact that the natural stable isotopic signatures pointed at some trophic differentiation between the 3 dominant taxa of the Potter cove meiofauna, no striking differences in assimilation were shown between these taxa by means of laboratory enrichment experiments in which selected pre-labeled bacteria and pelagic diatoms were used. However, copepods and cumaceans showed at each time interval a higher uptake of diatoms in comparison with bacteria, whereas nematodes did not show any significant difference in uptake for both food sources.

The relatively high dominance of an opportunistic genus such as *Daptonema* (which can feed on many different food sources) supports this less selective feeding behavior of the nematode community.

Nematodes also showed a slower response to the enrichment with both food sources since only after 10 days of incubation their uptake was appreciable. Possibly, there is a lower direct uptake of microalgae which may on the other hand be taken up via detritus after reworking by other organisms.

However, overall, our experiments showed that after 10 days the nematodes, copepods and cumaceans together took up only 0.4 and 0.04 % of the total ^{13}C carbon from diatoms and bacteria, respectively. This observation can have different causes but may point to the fact that other food sources play a significant role.

The overall contribution of nematodes to the remineralization of phytoplanktonic carbon in Potter Cove appears to be limited compared to other temperate regions, but it is higher than showed for Antarctic deep-sea environments. On the contrary, the uptake of bacteria is similar to that of deep-sea communities, and again it shows how nematodes feed on this food source to a very limited extent.

In conclusion, we can state these three shallow water sub-Antarctic meiofauna taxa may depend on the overlying water column, but still their low uptake does not seem to mirror their putative carbon requirements. Their contribution to the reworking of the given food sources appeared too low to be considered essential to the potential overall sediment carbon flux. Whether other food sources are more important for their diet or the given food sources were not in a state that was appetizing for the animals, or whether the presence of other organisms (e.g. macrofauna organisms) in the experimental unit did have an influence on the selected meiobenthic taxa uptake needs further investigations.

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References

Andrassy I (1956) Die Rauminhalts und Gewichtsbestimmung der Fadenwurmer (Nematodes). Acta Zool Hung 2:1–15

Blazewicz-Paszkowyczi M, Ligowski R (2002) Diatoms as food source indicator for some Antarctic Cumacea and Tanaidacea (Crustacea). Antarct Sci 14:11–15

Brett MT, Kainzb MJ, Taipalea SJ, Seshan H (2009) Phytoplankton not allochthonous carbon sustains herbivorous zooplankton production. PNAS 10:21197–21201

Brusca RC, Brusca GJ (2003) Invertebrates. Sinauer Associates Inc., Sunderland

Cnudde C, Willems A, Van Hoorde K, Vyverman W, Moens T, De Troch M (2011) Effect of food preservation on the grazing behaviour and on the gut flora of the harpacticoid copepod *Paramphiascella fulvofasciata*. J Exp Mar Biol Ecol 407:63–69

Corbisier T, Petti M, Skowronski R, Brito T (2004) Trophic relationships in the nearshore zone of Martel Inlet (King George Island, Antarctica): $d^{13}C$ stable-isotope analysis. Polar Biol 27:75–82

Coull BC (1999) Role of meiofauna in estuarine soft-bottom habitats. Aust J Ecol 24:327–343

Craig H (1957) Isotopic standards for carbon and oxygen and correction factors for mass spectrometric analysis of carbon dioxide. Geochim Cosmochim Acta 12:133–149

de Skowronski RSP, Corbisier T (2002) Meiofauna distribution in Martel Inlet, King George Island (Antarctica): sediment features versus food availability. Polar Biol 25:126–134

de Skowronski RSP, Corbisier T, Robles FR (1998) Meiofauna along a coastal transect in Admirality bay, King George Island (Antarctica). Pesqui Antàr Bras 3:117–131

de Skowronski RSP, Gheller PF, Bromberg S, David JC, Petti MAV, Corbisier TN (2009) Distribution of microphytobenthic biomass in Martel Inlet, King George Island (Antarctica). Pol Biol 32:839–851

De Troch M, Steinarsdóttir MB, Chepurnov V, Ólafsson E (2005) Grazing on diatoms by harpacticoid copepods: species-specific density-dependent uptake and microbial gardening. Aquat Microb Ecol 39:135–144

De Troch M, Chepurnov V, Gheerardyn H, Vanreusel A, Ólafsson E (2006a) Is diatom size selection by harpacticoid copepods related to grazer body size? J Exp Mar Biol Ecol 332:1–11

De Troch M, Houthoofd L, Chepurnov V, Vanreusel A (2006b) Does sediment grain size affect diatom grazing by harpacticoid copepods? Mar Environ Res 61:265–277

De Troch M, Grego M, Chepurnov VA, Vincx M (2007) Food patch size, food concentration and grazing efficiency of the harpacticoid *Paramphiascella fulvofasciata* (Crustacea, Copepoda). J Exp Mar Biol Ecol 343:210–216

Dierssen HM, Smith RC, Vernet M (2001) Glacial meltwater dynamics in coastal waters West of the Antarctic Peninsula. In: Kennett JP (ed) University of California, Santa Barbara

Domínguez MC, Eraso A (2007) Substantial changes happened during the last years in the icecap of King George, Insular Antactica. In: Tyk A, Stefaniak K (eds) Karst and cryokarst, studies of the faculty of earth sciences. University of Silesia 45:87–110

Eraso A, Domínguez MA (2007): Physicochemical characteristics of the subglacier discharge in Potter Cove, King George Island, Antarctica. In: Tyk A, Stefaniak K (eds) Karst and cryokarst, studies of the faculty of earth sciences, University of Silesia 45: 111–122

Evrard V, Soetaert K, Heip CHR, Huettel M, Xenopoulos MA, Middelburg JJ (2010) Carbon and nitrogen flows through the benthic food web of a photic subtidal sandy sediment. Mar Ecol Prog Ser 416:1–16

Franco MA, Soetaert K, Van Oevelen D, Van Gansbeke D, Costa MJ, Vincx M, Vanaverbeke J (2008) Density, vertical distribution and trophic responses of metazoan meiobenthos to phytoplankton deposition in contrasting sediment types. Mar Ecol Prog Ser 358:51–62

Guilini K, Van Oevelen D, Soetaert K, Middelburg JJ, Vanreusel A (2010) Nutritional importance of benthic bacteria for deep-sea nematodes from the Arctic ice margin. Results of an isotope tracer experiment. Limnol Oceanogr 55:1977–1989

Guillard RRL (1975) Culture of phytoplankton for feeding marine invertebrates. In: Smith WL, Chanley MH (eds) Culture of marine invertebrate animals. Plenum Press, New York, pp 108–132

Heip C, Vincx M, Vranken G (1985) The ecology of marine nematodes. Oceanogr Mar Biol 23:399–489

Higgins RP, Thiel H (1988) Introduction to the study of Meiofauna. Smithsonian Institution Press, Washington

Ingels J, Van den Driessche P, De Mesel I, Vanhove S, Moens T, Vanreusel A (2010) Evidence for preferred utilisation of bacteria over phytoplankton by deep-sea nematodes in Polar Regions. Mar Ecol Prog Ser 406:121–133

Jensen P (1984) Measuring carbon content in nematodes. Helgol Meeresunters 38:83–86

Juario JV (1975) Nematode species composition and seasonal fluctuation of a sub littoral meiofauna community in the German Bight. Veröff Inst Meeresforsch Bremerhav 15:283–337

Kaehler S, Pakhomov EA, McQuaid CD (2000) Trophic structure of the marine food web at the Prince Edward Islands (Southern Ocean) determined by $d^{13}C$ and $d^{15}N$ analysis. Mar Ecol Prog Ser 208:13–20

Kozloff EN (1990) Invertebrates. Sinauer Associates Inc, Sunderland

Le Duc D, Probert PK (2010) Small-scale effect of intertidal seagrass (*Zostera muelleri*) on meiofaunal abundance, biomass, and nematode community structure. J Mar Biol Ass U K 91:579–591

Maria TF, De Troch M, Vanaverbeke J, Esteves AM, Vanreusel A (2011) Use of benthic vs planktonic organic matter by sandy-beach organisms: a food tracing experiment with ^{13}C labelled diatoms. J Exp Mar Biol Ecol 407:309–314

Mayer M (2000) Zur Ökologie der Benthos-Foraminiferen der Potter Cove (King George Island, Antarktis) = Ecology of benthic foraminifera in the Potter Cove (King George Island, Antarctica). Berichte zur Polarforschung 353:1–126

Middelburg JJ, Barranguet C, Boschker HTS, Herman PMJ, Moens T, Heip CHR (2000) The fate of intertidal microphytobenthos carbon: an in situ ^{13}C-labeling study. Limnol Oceanogr 45:1224–1234

Mincks SL, Smith CR, Jeffreys RM, Sumida PYG (2008) Trophic structure on the West Antarctic Peninsula shelf: detritivory and benthic inertia revealed by $d^{13}C$ and $d^{15}N$ analysis. Deep-Sea Res II 55:2502–2514

Moens T, Vincx M (1997) Observations on the feeding ecology of estuarine nematodes. J Mar Biol Ass U K 77:211–227
Moens T, Verbeek L, Vincx M (1999) Preservation and incubation time-induced bias in tracer-aided grazing studies on meiofauna. Mar Biol 133:69–77
Moens T, Luyten C, Middelburg JJ, Herman PMJ, Vincx M (2002) Tracing organic matter sources of estuarine tidal flat nematodes with stable carbon isotopes. Mar Ecol Prog Ser 234:127–137
Moens T, Bouillon S, Gallucci F (2005) Dual stable isotope abundances unravel trophic position of estuarine nematodes. J Mar Biol Ass U K 8:1401–1407
Moens T, Vanhove S, De Mesel I, Kelemen B, Janssens T, Dewicke A, Vanreusel A (2007) Carbon sources of Antarctic nematodes as revealed by natural carbon isotope ratios and a pulse-chase experiment. Polar Biol 31:1–13
Moll A, Braun M, Lluberas A (2006) Determination of glacier velocities on King George Island (Antarctica) by DInSAR geoscience and remote sensing symposium 2006. IGARSS (2006) IEEE international conference
Mourelatos S, Rougier C, Lacroix G (1992) Radiotracers losses due to freezing in formalin carbon-14-labelled cladocerans. Arch Biol 126:239–253
Nascimento FJA, Karlson AML, Elmgren R (2008) Settling blooms of filamentous cyanobacteria as food for meiofauna assemblages. Limnol Oceanogr 53:2636–2643
Nedwell DB, Walker TR, Ellis-Evans JC, Clarke A (1993) Measurements of seasonal rates and annual budgets of organic carbon fluxes in an antarctic coastal environment at Signy Island, South Orkney Islands, suggest a broad balance between production and decomposition. Appl Environ Microbiol 59:3989–3995
Nomaki H, Ogawa NO, Ohkouchi N, Suga H, Toyofuku T, Shimanaga M, Nakatsuka T, Kitazato H (2008) Benthic foraminifera as trophic links between phytodetritus and benthic metazoans: carbon and nitrogen isotopic evidence. Mar Ecol Prog Ser 357:153–164
Nyssen F, Brey T, Lepoint G, Bouquegneau JM, Broyer C, Dauby P (2002) A stable isotope approach to the eastern Weddell Sea trophic web: focus on benthic amphipods. Polar Biol 25:280–287
Schloss I, Ferreyra GA (2002) Primary production light and vertical mixing in Potter Cove a shallow bay in the maritime Antarctic. Polar Biol 25:42–48
Schloss I, Ferreyra GA, Ruiz-Pino D (2002) Phytoplankton biomass in Antarctic shelf zones: a conceptual model based on Potter Cove, King George Island. J Mar Syst 36:129–143
Schofield O, Ducklow HW, Martinson DG, Meredith MP, Moline MA, Fraser WR (2010) How do polar marine ecosystems respond to rapid climate change? Science 328:1520–1523
Schratzberger M, Rees HL, Boyd SE (2000) Effects of simulated deposition of dredged material on structure of nematode assemblages–the role of burial. Mar Biol 136:519–530
Siciński J, Jażdżewski K, DeBroyer C, Presler P, Ligowski R, Nonato EF, Corbisier TN, Petti MAV, Brito TAS, Lavrado HP, Błażewicz-Paszkowycz M, Pabis K, Jażdżewska A, Campos LS (2011) Admiralty Bay benthos diversity: a census of a complex polar ecosystem. Deep-Sea Res II 59:30–48
Smith RC, Nelson DM (1985) Phytoplankton bloom produced by a receding ice edge in the Ross Sea: spatial coherence with the density field. Science 227:163–166
Szymelfenig M, Kwaśniewski S, Węsławski JM (1995) Intertidal zone of Svalbard 2. Meiobenthos density and occurrence. Polar Biol 15:137–141
Tocher DR (2003) Metabolism and functions of lipids and fatty acids in teleost fishes. Rev Fish Sci 11:107–184
Turner J, Colwell SR, Marshall GJ, Lachlan-Cope TA, Carleton AM, Jones PD, Lagun V, Reid P, Iagovkina S (2005) Antarctic climate change during the last 50 years. Int J Climatol 25:279–294
Urban-Malinga B, Moens T (2006) Fate of organic matter in Arctic intertidal sediments: is utilization by meiofauna important? J Sea Res 56:239–248
Vanhove S, Lee HJ, Beghyw M, Van Gansbeke D, Brockington S, Vincx M (1998) The metazoan meiofauna and its biogeochemical environment the case of an Antarctic shallow water environment. J Mar Biol Ass U K 78:411–434
Vanhove S, Beghyn M, Van Gansbeke D, Bullough LW, Vincx M (2000) A seasonally varying biotope at Signy Island, Antarctic: implications for meiofaunal structure. Mar Ecol Prog Ser 202:13–25
Vanreusel A (1990) Ecology of the free-living marine nematodes from the Voordelta (Southern Bight of the North Sea) 1 Species composition and structure of the nematode communities. Cah Biol Mar 31:439–462
Vaughan DG, Marshall GJ, Connolley WM, Parkinson C, Mulvaney R, Hodgson DA, King JC, Pudsey CJ, Turner J (2003) Recent Rapid Regional climate warming on the Antarctic Peninsula. Clim Chang 60:243–274
Veit-Köhler G (2005) Influence of biotic and abiotic sediment factors on abundance and biomass of harpacticoid copepods in a shallow Antarctic bay. Sci Mar 69:135–145
Veit-Köhler G, Antacli JC, Rose A (2008) Metazoan meiofauna in Potter Cove, King George Island. In: Wiencke C, Ferreyra GA, Abele D, Marenssi S [Hrsg.] The Antarctic ecosystem of Potter Cove, King-George Island (Isla 25 de Mayo). Ber Polarforsch Meeresforsch 571:135–140
Vincx M (1996) Meiofauna in marine and freshwater sediments. In: Hall GS (ed) Methods for the examination of organism's diversity in soils and sediments. CAB international Wallingford, pp 187–195
Warwick RM, Platt HM, Somerfield PJ (1998) Free-living marine nematodes: part III Monhysterids: pictorial key to world genera and notes for the identification of British species. Synopses of the British fauna (new series) 53. Field Studies Council: Shrewsbury, UK ISBN 1-85153-260-9 III volumes
Wieser W (1953) Die Beziehung zwischen Mundhöhlengestald, Ernahrungsweise und Vorkommen bei freilebenden marinen Nematoden. Arkiv Zool 4:439–484
Wieser W (1960) Benthic studies in Buzzards bay. II. The meiofauna. Limnol Oceanogr 5:121–137
Witte U, Wenzhöfer F, Sommer S, Boetius A, Heinz P, Aberle N, Sand M, Cremer A, Abraham W-R, Jørgensen BB, Pfannkuche O (2003) In situ experimental evidence of the fate of a phytodetritus pulse at the abyssal seafloor. Nature 424:763–766
Wyckmans M, Chepurnov V, Vanreusel A, De Troch M (2007) Effect of food diversity on diatom selection by harpacticoid copepods. J Exp Mar Biol Ecol 345:119–128