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ORIGINAL PAPER

Carbon sources of Antarctic nematodes as revealed by natural carbon isotope ratios and a pulse-chase experiment

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Abstract $\delta^{13}C$ of nematode communities in 27 sites was analyzed, spanning a large depth range (from 130 to 2,021 m) in five Antarctic regions, and compared to isotopic signatures of sediment organic matter. Sediment organic matter $\delta^{13}C$ ranged from –24.4 to –21.9‰ without significant differences between regions, substrate types or depths. Nematode $\delta^{13}C$ showed a larger range, from –34.6 to –19.3‰, and was more depleted than sediment organic matter typically by 1‰ and by up to 3‰ in silty substrata. These, and the isotopically heavy meiofauna at some stations, suggest substantial selectivity of some meiofauna for specific components of the sedimenting plankton. However, ^{13}C-depletion in lipids and a potential contribution of chemoautotrophic carbon in the diet of the abundant genus *Sabatieria* may confound this interpretation. Carbon sources for Antarctic nematodes were also explored by means of an experiment in which the fate of a fresh pulse of labile carbon to the benthos was followed. This organic carbon was remineralized at a rate (11–20 mg C m^{-2} day^{-1}) comparable to mineralization rates in continental slope sediments. There was no lag between sedimentation and mineralization; uptake by nematodes, however, did show such a lag. Nematodes contributed negligibly to benthic carbon mineralization.

Keywords Antarctic · Nematodes · Meiobenthos · Carbon sources · Stable carbon isotopes · Pulse-chase experiment · Mineralization

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Introduction

Metazoan meiobenthic communities of the eastern Weddell Sea shelf attain high summer densities which are similar to those from comparable depths elsewhere (Vanhove et al. 1995; Soltwedel 2000). Nematodes are the most abundant taxon. Their distribution is patchy at small spatial scales (Vanhove et al. 1995, 1999), species diversity is usually high (Vermeeren et al. 2004; De Mesel et al. 2006; Ingels et al. 2006), and nematode abundances in deep Antarctic waters tend to be highest in the surface layer of the sediment, decreasing rapidly with sediment as well as with water depth (Vanhove et al. 1998). These elements suggest a strong dependence of Antarctic deep-water meiofauna on food availability (Vanhove et al. 1995, 2000).

While meiofauna at shallow and intertidal depths generally show rapid uptake of settling phytodetritus (a.o. Rudnick 1989; Graf 1992; Widbom and Frithsen 1995; Olafsson et al. 1999; Moens et al. 2002; Urban-Malinga and Moens 2006), deep-sea meiobenthos responses to sedimen-

tation pulses tend to be more variable. In particular, while foraminiferans often show a rapid uptake (Gooday 1988; Gooday et al. 1990; Linke et al. 1995; Moodley et al. 2002; Witte et al. 2003b), metazoan meiobenthos such as nematodes respond less uniformly (Gooday et al. 1996; Sommer and Pfannkuche 2000; Witte et al. 2003b).

Stable carbon isotope ratios of particulate organic matter (POM) and living marine organisms can provide insight into the various sources of energy within marine food webs (Peterson and Fry 1987). While Antarctic pelagic systems have already been well documented in this respect (a.o. Fontugne et al. 1991; Rau et al. 1991a, b, 1992; Kopczynska et al. 1995; Dehairs et al. 1997; Beaulieu 2002), benthic systems, which heavily depend on S(uspended)POM-inputs, have only recently been focused upon [see, e.g., Kaehler et al. (2000), Corbisier et al. (2004), and Pakhomov et al. (2004), in the SubAntarctic Islands, Nyssen et al. (2002), in the high-Antarctic Weddell Sea].

In this study, we use stable carbon isotopes as tracers of organic matter utilization by Antarctic meiofauna with emphasis on nematodes. In the frame of the EASIZ II and EASIZ III campaigns we sampled 27 sites, ranging in depth from 130 to 2,021 m, at Kapp Norvegia (KN), Vestkapp (VK), Halley Bay (HB) in the southeast Weddell Sea, and in the Drake Passage (DP) and Bransfield Strait (BS) near King George Island (in the north of the Antarctic Peninsula). We determined natural carbon isotopic signatures of nematode communities and compared those to isotopic signatures of bulk sedimentary organic matter and to published signatures of different organic matter sources. Our main aim was to assess whether the nematode communities in Antarctic marine sediments display any selectivity for specific sources from within the bulk sediment organic matter pool. During the EASIZ III campaign, we also performed an experiment in the Bransfield Strait in which a pulse of labile carbon to the benthos was mimicked with ^{13}C-labeled lyophilized cyanobacteria. The fate of this organic matter was followed in sediment cores recovered from a 227-m-deep station and incubated on board ship, with emphasis on its assimilation by nematodes and burial.

Materials and methods

Study site and sampling design

During the austral summer of 1998 (13 January–26 March), the RV "Polarstern" worked in the frame of EASIZ II in the South-East Weddell Sea (three regions: Kapp Norvegia, Vestkapp, Halley Bay) and in the north of the Antarctic Peninsula near King George Island (Drake Passage and Bransfield Strait) (Arntz and Gutt 1999). EASIZ III (18 March–11 May 2000) continued these efforts in the Bransfield Strait (Arntz and Brey 2001). During EASIZ II, we took sediment samples with a multiboxcorer (MG) or, occasionally, a multicorer (MUC—stations marked with * in Table 1), from 26 stations covering different substrates over a depth range of 130–2,021 m (Fig. 1; Table 1). Depths were unevenly spread over the above-mentioned regions. During EASIZ III, we additionally sampled one Bransfield Strait station (56/148) at a depth of 227 m using a MUC, and performed an on-board experiment with sediment from this station.

The samples were subsampled on board ship with perspex cores with internal diameters of 3.5 and 6.0 cm for analyses of meiofauna (mainly nematodes) and environmental variables (grain size, bulk organic carbon, C- and N-analysis, chl *a* and interstitial nutrients), respectively. Samples for the identification of nematodes were preserved in buffered formalin (4% final concentration); those for nematode stable isotope analyses and for environmental variables were stored frozen (–18°C) until further treatment. We focused on the upper 2 cm of the sediment column, since this depth stratum contains up to 80% of total depth-integrated nematode numbers (Vanhove et al. 1998). Processing of samples in formalin followed standard procedures of centrifugation-flotation with LUDOX TM 40, and sieving over 1,000- and 38-µm sieves (Heip et al. 1985; Vincx 1996). Nematodes 150–200 in number, per station, were assigned to feeding groups; in the absence of empirical data on feeding behavior of most genera concerned, we used the mouth-morphology based scheme of Wieser (1953). Information on nematode community composition (at species or genus level) is available from 11 of the current stations (4 in Drake Passage, 4 in Kapp Norvegia, 2 in Vestkapp and 1 in Bransfield Strait; these correspond to the stations marked with + in Table 1) and from sampling sites adjacent to another 11 of our stations (Vanhove and Lee unpublished data).

Environmental variables

Sediment granulometric analysis of the 4- to 800-µm fraction was performed using a Coulter LS Particle Size Analyzer. Bulk organic matter content was determined after sediment combustion at 550°C. Total sedimentary nitrogen and organic carbon were determined using a Carlo Erba elemental analyzer on dried sediment samples after acidification with dilute HCl. Chl *a* concentration was determined photometrically after dark extraction in acetone and separation using reverse phase HPLC (Mantoura and Llewellyn 1983). Concentrations of interstitial nutrients (NO_3^-, NO_2^-, NH_4^+, PO_4^{3-}) were assessed on an automatic chain (SAN^{plus} segmented flow analyzer, SKALAR) after pore water extraction and filtration over Whatman GF/C filters.

Table 1 Location, depth, median grain size, % organic carbon and nitrogen, chl *a* content (in ng per g sediment dry weight) and sediment type [silt, sand, biotic (sponge spicule or bryozoan mats) and iceberg disturbed] of the sampling stations

	Site	Depth (m)	Chl*a* (ng/g)	Carbon (%)	Nitrogen (%)	Median (μm)	"Type"	Nematode community data
48/326	BS	606	117.25	0.31	0.03	27.44	Silt	–
48/325	BS	805	47.45	0.55	0.06	12.98	Silt	–
48/356	DP	130	52.62	0.36	0.05	46.06	Silt	–
48/345	DP	218	207.06	0.25	0.02	39.91	Silt	+
48/341	DP	429	14.30	0.30	0.03	45.25	Silt	+
48/334	DP	1028	62.53	0.36	0.04	140.50	Silt	+
48/330	DP	2009	8.61	0.56	0.06	7.92	Silt	+
48/146	HB	1021	–	0.40	–	290.00	Sand	–
* 48/143	HB	1528	13.10	0.75	–	232.75	Sand	–
48/136	HB	2012	119.90	0.35	–	82.87	Sand	–
* 48/135	HB	2021	14.00	0.40	–	83.48	Sand	–
48/230	KN	220	20.55	0.55	0.01	100.57	Biotic	–
48/064	KN	231	–	0.75	0.06	137.30	Biotic	–
48/063	KN	234	–	0.70	0.03	163.50	Iceberg	–
48/047	KN	244	56.81	0.20	0.02	104.10	Biotic	+
48/048	KN	245	63.91	0.70	0.03	64.59	Biotic	–
48/187	KN	255	107.50	0.55	0.06	81.50	Iceberg	+
48/224	KN	273	7.25	0.30	–	102.80	Iceberg	–
48/228	KN	298	9.90	0.33	0.06	57.30	Biotic	+
48/067	KN	311	8.00	2.55	0.06	57.66	Biotic	–
48/227	KN	332	26.09	1.43	0.10	49.02	Biotic	+
48/092	VK	994	–	0.40	0.04	106.55	Sand	+
48/091	VK	1510	–	0.30	0.04	68.81	Sand	–
* 48/090	VK	1557	36.20	0.65	–	66.37	Sand	–
48/131	VK	1985	–	0.25	0.03	36.53	Sand	+
48/093	VK	1988	–	0.95	–	31.91	Sand	–
* 56/148	BS	227	–	0.43	0.09	96.76	Silt	+

Data are from the upper 2 cm of sediment, except for station 56/148 (upper 3 cm). All samples were obtained during the EASIZ II cruise, except for station 56/148 which was sampled during EASIZ III. All stations were sampled with a multicorer, except those marked with *, which were sampled using a multiboxcorer. Nematode community data of stations marked with + have been used for the nMDS in Fig. 3

HB Halley bay, *VK* Vestkapp, *KN* Kapp Norvegia, *DP* Drake passage side of King George Island, *BS* Bransfield Strait side of King George Island

Carbon isotopic composition of bulk sediment organic matter and nematodes

Aliquots (30–40 mg) of carefully dried, ground and homogenized sediment were weighed in preglown (4 h at 550°C) Ag cups (12.5 × 5 mm, Elemental Microanalysis Ltd). Samples were acidified in situ with dilute HCl till complete elimination of carbonates (Nieuwenhuize et al. 1994) and thoroughly dried again. Cups were then folded and stored under dry atmosphere until analysis.

Nematodes were elutriated from thawed sediment samples using colloidal silica (Ludox HS-40, Du Pont) at a specific density of 1.18 and sieved over 1,000- and 38-μm meshes. This procedure was repeated three times. The fraction retained on the sieves was thoroughly rinsed with tap water. Preliminary tests showed no measurable influence of this elutriation protocol on nematode carbon isotope ratios (see also Moens et al. 2002). Nematodes were sorted under a stereoscopic microscope using a fine Tungsten wire needle. They were rinsed twice by transfer through distilled water to remove adhering sediment particles, and finally put in a drop of distilled water in preglown (4 h at 550°C) aluminum pans (2.5 × 6 mm, Elemental Microanalysis Ltd). At least 100 individuals were pooled per sample, except when nematode densities were too low. We aimed at a total carbon biomass of more than 5 μg. Nematodes retained on the 1-mm mesh were omitted because their comparatively large biomass could otherwise have a dominant effect on the community carbon isotope analysis. After elutriation, the nematode samples were dried at 60°C,

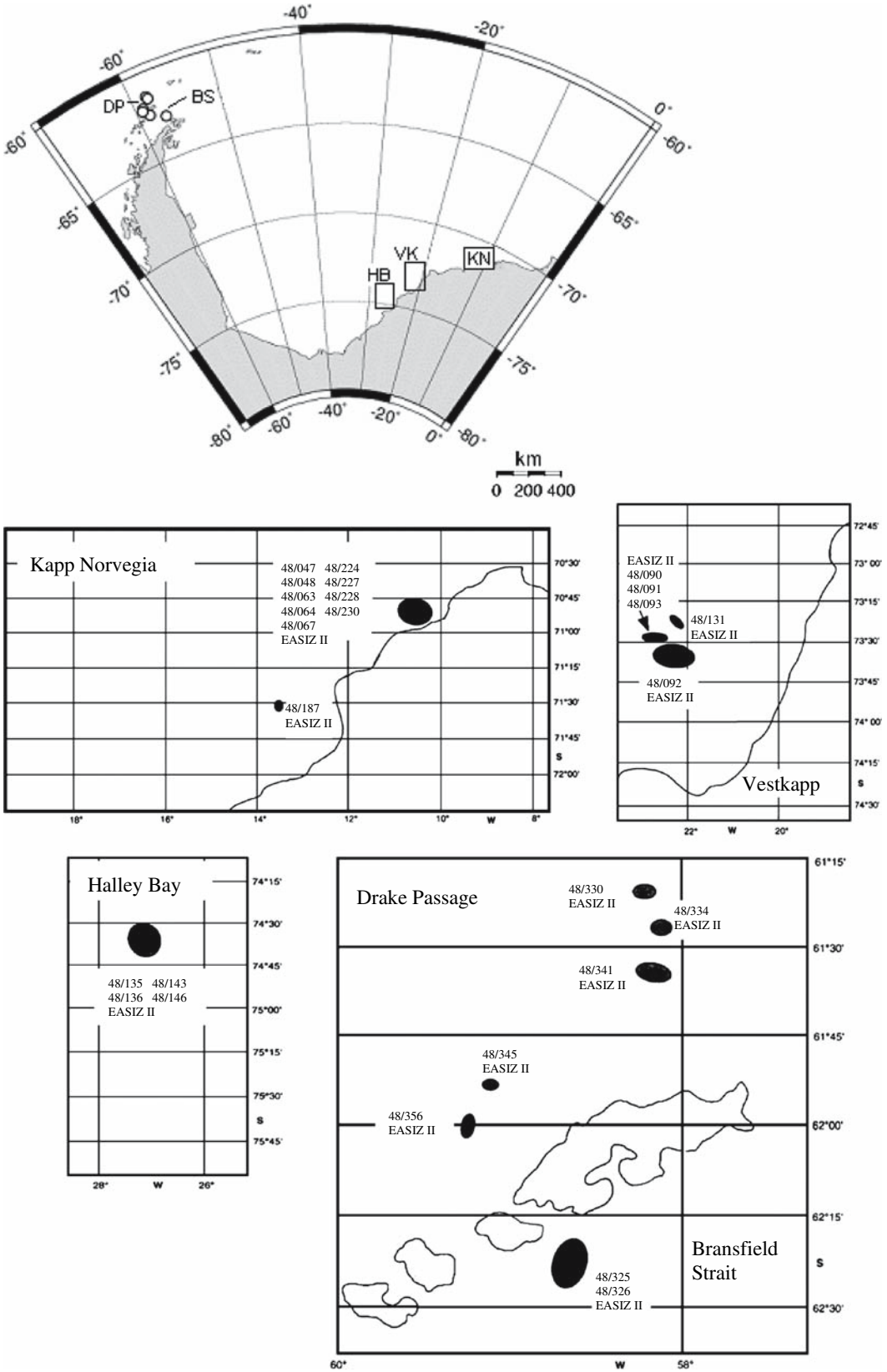

Fig. 1 Map of sampling locations in the northern Peninsula area near King George Island (**a**) and south-eastern Weddell Sea near Kapp Norvegia (**b**), Vestkapp (**c**) and Halley Bay (**d**)

pinched close and stored in screw-capped glass tubes until analysis. A few sediment samples contained sufficient biomass of other invertebrate taxa (harpacticoid copepods, polychaetes and/or amphipods) and those were then also sorted and analyzed as described for nematodes.

Carbon isotopic composition of sedimentary organic matter was determined with a ThermoFinnigan Flash 1112 elemental analyzer coupled online via a conflo 2 interface to a Finnigan Delta + XL mass spectrometer. Carbon isotopic analysis of nematodes used a C–N–S elemental analyzer (Carlo Erba, Italy) coupled to a continuous flow isotope ratio mass spectrometer (Optima, Micromass, UK). Results are reported in the δ notation with Vienna PDB as the reference standard, and expressed in units of ‰, according to the standard formula: $\delta^{13}C = [(R_{sample}/R_{standard}) - 1] \times 10^3‰$, where R is the ratio of $^{13}C/^{12}C$. Analytical precision is typically better than 0.2‰.

Pulse-chase experiment

Fifteen 30.2 cm^2 surface area cores, down to a depth of at least 12 cm, were collected in three consecutive MUC deployments and incubated in the dark at –1°C, close to natural temperature conditions. Each core was topped with a 20-cm deep column of bottom water. Four-mg portions of freeze-dried, lyophilized ^{13}C-labeled cyanobacterial cells (>98% ^{13}C, Cambridge Isotope Laboratories) were suspended in a little ambient water and frozen so as to form ice cubes. At time zero (T_0), one such ice cube was added to each of the 15 sediment cores, thus improving homogeneous distribution of settling organic matter while at the same time minimizing sediment disturbance. The amount of C added per core was 1.04 ± 0.03 mg, i.e. 344.4 ± 10 mg C m^{-2}. Three randomly chosen cores were processed after each of the following incubation periods: 5, 9, 13 and 16 days. Cores were sectioned into four depth horizons: 0–1, 1–2, 2–5 and 5–10 cm. Each sample was stored frozen until further treatment. Samples were split in equal halves, one of which was used for elutriation of nematodes (as described above) and the other for stable carbon isotope analysis of the bulk organic matter fraction of the sediment.

Results of the pulse-chase experiment are expressed as mg ^{13}C recovered in the sediment or in nematodes. This was calculated as the product of excess ^{13}C (E) and sediment organic mass or nematode biomass for each depth layer (Moens et al. 2002). Excess ^{13}C is the difference between the fraction ^{13}C (F) of unenriched sediment/nematodes (T_0) and sample, i.e.

$$E = F_{sample} - F_{unenriched}$$

$$\text{with:} \quad F = {}^{13}C/({}^{13}C + {}^{12}C) = R/(R + 1), \text{ and:}$$

$$R = (\delta^{13}C/1000 + 1) \times R_{VPDB}$$

where $R_{VPDB} = 0.0112372$ = the carbon isotope ratio of the reference material (Vienna PDB).

Nematode biomass in each MUC was obtained from the product of nematode density and mean individual biomass. Individual volume was determined from measurements of length (L) and body width (W) on at least 50 individuals per MUC and per depth layer, using a Quantimet 500+ image analysis system on a Leitz Dialux 20 microscope. Biomass was calculated with the formula (modified after Andrassy 1956):

$$\text{WWTnematode (mg)} = [\text{largest body width (mm)}^2 \times \text{body length (mm)}] \times 1.13/1.7$$

where 1.13 is the specific gravity of a nematode. Carbon was estimated at 11.5% of wet weight (Somerfield et al. 2005).

Data analysis

Environmental data were analyzed using PCA (PC-ORD™ software (McCune and Mefford 1999). Data were transformed using the formula: [(value – average)/stdev] – minimum value in order to standardize variables with different dimensions (%, µm, ng, etc.). The relationships between the different environmental variables and the first two ordination axes were calculated with Pearson's r correlation analysis.

Differences in nematode community structure between the 11 stations from which both nematode community composition and stable carbon isotope data are available (those marked with + in Table 1) were analyzed by non-metric MultiDimensional Scaling (nMDS) using the Bray-Curtis similarity coefficient (Clarke and Warwick 1994). Nematode abundance data were fourthroot-transformed prior to analysis.

As the requirements for parametric statistics were not met, nematode densities (total densities and feeding types) and isotopic abundances between stations were compared using non-parametric Kruskal–Wallis ANOVA by ranks (STATISTICA™ software, Microsoft, StatSoft, 2000) with subsequent pairwise comparisons following Conover's procedure (1971).

Results

Characterization of the environment

Sediments ranged from fine silts (median grain size down to 8 µm, Sta 330) to fine/medium sands (median grain size up to 290 µm, Sta 146) (Table 1). Organic carbon content spanned a range between 0.2 and 1.0%C for most stations,

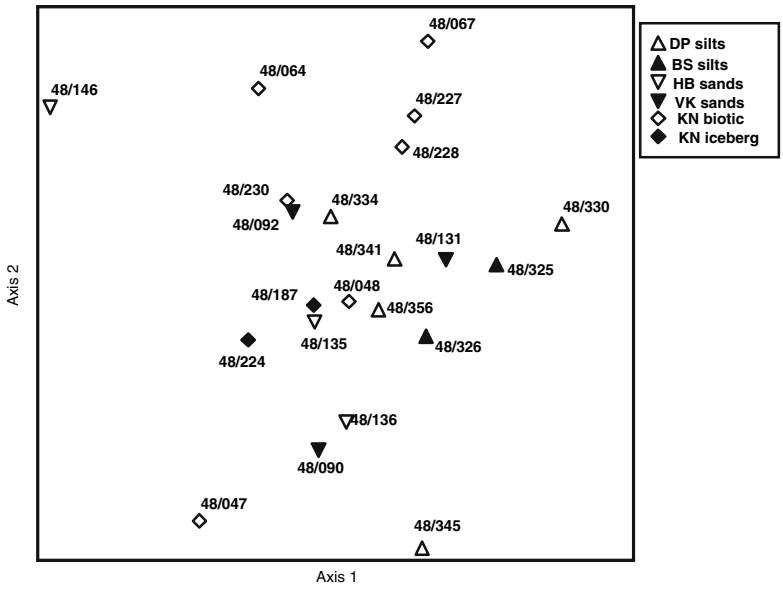

Fig. 2 PCA analysis on environmental properties of the sediments (axis 1: 38.4 % of total variance; axis 2: 15.3% of total variance). The parametric linear Pearson's *r* correlations between the different environmental variables and ordination axes are given. Chl *a* was not included in the analysis because of missing data. Axis 1 and 2 explain 54% of the total variance

		Nutrients					Organic matter		Sediment texture					Depth
		NO2	NO2+NO3	NH4	PO4	Si	C	N	38	63	800	median	stdev	
		µg/l	µg/l	µg/l	µg/l	µg/l	%	%	µm	µm	µm			m
axis1	r =	-0.72	-0.05	-0.16	-0.44	0.04	0.14	0.49	-0.88	-0.92	-0.80	-0.93	-0.93	0.18
axis2	r =	-0.09	-0.47	-0.43	-0.49	-0.61	0.55	0.58	-0.03	0.04	0.29	0.03	0.26	-0.37

with highest values of 1.43 and 2.55% at Sta 227 and Sta 067, respectively. Chl *a* concentrations varied strongly among stations (between 7 and 207 ng per g sediment dry weight), indicating that organic matter quality shows substantial among-site variability. A PCA-analysis on environmental characteristics largely linked variability among the silty sediments of BS and DP (exception made for Sta 48/345, DP) to axis 1, which is correlated with sediment texture (Fig. 2). Sandy stations (except for Sta 48/146, HB) and biotic substrates (undisturbed sediments covered with a thick biogenic layer of sponge spicules and/or bryozoan debris) were mainly structured along axis 2, which is correlated with organic matter. Samples from iceberg-disturbed stations clustered together. There was only a very weak relation with water depth (Pearson's $r = 0.18$ and –0.37 for axis 1 and 2, respectively).

Nematode communities

Total nematode densities differed significantly ($P < 0.05$, Kruskal–Wallis ANOVA) among stations as well as regions, and averaged, respectively, 3,470 ± 1107 (BS), 2,174 ± 1,210.9 (DP), 1,498 ± 795.8 (VK) and 1,416 ± 393.1 (KN) ind. 10 cm^{-2} in the different regions. Nonselective deposit feeders (feeding type 1B) were the predominant trophic group over all stations combined (mean ± SD: 38 ± 13.2%, range: 20–67%), followed by epistrate feeders (2A) (29 ± 12.3%, 6–51%) and selective deposit feeders (1A) (29 ± 9.2%, 18–46%). Predators/omnivores (2B) were relatively scarce (3 ± 1.8 %, 1–7%). Feeding-type composition did not differ significantly with depth, between regions or between substrate types (data not shown).

In an nMDS of nematode community structure of the 11 stations from which both nematode community composition and stable carbon isotope data are available (those marked with + in Table 1), stations did not cluster well per region. Only the single station from Bransfield Strait (sta 56/148) and one station from Drake Passage (sta 48/341) were clearly separated from the rest (Fig. 3). The latter station was characterized by a very high relative abundance of the genus *Sabatieria* (49.8%) (Table 2). Caution is, however, due when comparing sta 56/148 with the other stations, since sta 56/148 was sampled with a different and more efficient sampling gear. The deviant position of this station in the nMDS is partly a result of the high abundance of *Minolaimus*. This genus was most abundant in the upper 2 cm at sta 56/148, and it is the upper sediment stratum which is typically most affected by the down-wash effect of box corers (Bett et al. 1994), so this nematode could have been undersampled in the other stations where it was rare or absent. However, unless it is specifically associated with flocculent detritus, it is very doubtful that its abundances could have been so selectively biased by box coring.

Natural isotopic composition of sediment detritus and meiobenthos

The $\delta^{13}C$ of sediment organic matter ($\delta^{13}Cs$) spanned a fairly narrow range (–24.4 to –21.9‰) and did not show

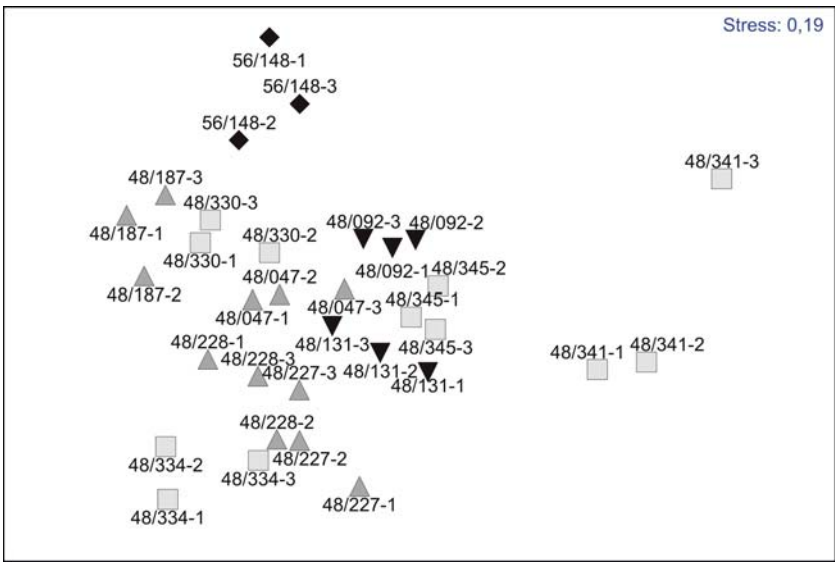

Fig. 3 nMDS ordination based on nematode community composition of the 11 sampling stations for which both nematode community composition and nematode $\delta^{13}C$ data are available. For details on the sampling locations, see Table 1. *Grey squares*, Drake Passage stations; *grey triangles*, Kapp Norvegia stations; *black diamonds*, Bransfield Strait stations; *black inverted triangles*, Vestkapp stations

Table 2 Relative abundances of the five most dominant nematode genera per station (g1 = group 1)

Drake passage							
sta 48/345 (218 m)		sta 48/341 (429 m)		sta 48/334 (1028 m)		sta 48/330 (2009 m)	
Sabatieria	26.77	*Sabatieria*	49.81	*Monhystera*	15.45	*Sabatieria*	16.21
Leptolaimus	6.14	*Leptolaimus*	9.48	*Acantholaimus*	9.01	*Neochromadora*	12.32
Xyalidae g1	5.86	*Monhystrella*	6.90	*Desmoscolex*	8.31	*Monhystera*	10.16
Molgolaimus	4.68	*Xyalidae g1*	4.89	*Tricoma*	8.24	*Daptonema*	6.83
Acantholaimus	3.94	*Acantholaimus*	2.93	*Xyalidae g1*	5.43	*Theristus*	6.04
Kapp Norvegia							
sta 48/047 (244 m)		sta 48/187 (255 m)		sta 48/228 (298 m)		sta 48/227 (332 m)	
Monhystera	14.40	*Neochromadora*	17.86	*Monhystera*	16.90	*Desmoscolex*	13.68
Desmoscolex	10.56	*Sabatieria*	16.78	*Desmoscolex*	12.24	*Monhystera*	13.45
Molgolaimus	9.54	*Monhystera*	16.24	*Leptolaimus*	10.36	*Greeffiella*	7.39
Sabatieria	8.10	*Daptonema*	9.77	*Sabatieria*	8.98	*Acantholaimus*	5.23
Xyalidae g1	7.39	*Halalaimus*	4.35	*Acantholaimus*	7.11	*Molgolaimus*	4.50
Vestkapp				Bransfield Strait			
sta 48/092 (994 m)		sta 48/131 (1994 m)		sta 56/148 (230 m)			
Molgolaimus	13.30	*Monhystera*	25.77	*Molgolaimus*	19.98		
Sabatieria	11.68	*Acantholaimus*	7.81	*Minolaimus*	5.47		
Microlaimus	10.41	*Sabatieria*	6.95	*Desmoscolex*	5.39		
Monhystera	10.05	*Xyalidae g1*	4.63	*Sabatieria*	5.32		
Aegialoalaimus	5.46	*Halalaimus*	4.44	*Halalaimus*	4.92		

any statistically significant differences between regions (Fig. 4a) or substrate types (Fig. 4b) or with depth (data not shown) (all $P > 0.1$). Nematode $\delta^{13}C$ ($\delta^{13}Cn$), by contrast, showed a much larger range, from –34.6 to –19.3‰ , although $\delta^{13}Cn$ and $\delta^{13}Cs$ were positively correlated ($r = 0.512$, $P = 0.03$). The lowermost $\delta^{13}Cn$ value concerned a single measurement on a subgroup of the non-selective deposit-feeders (in contrast to all others which were total community samples), i.e., comesomatid nematodes comprising the genus *Sabatieria* and, to a lesser

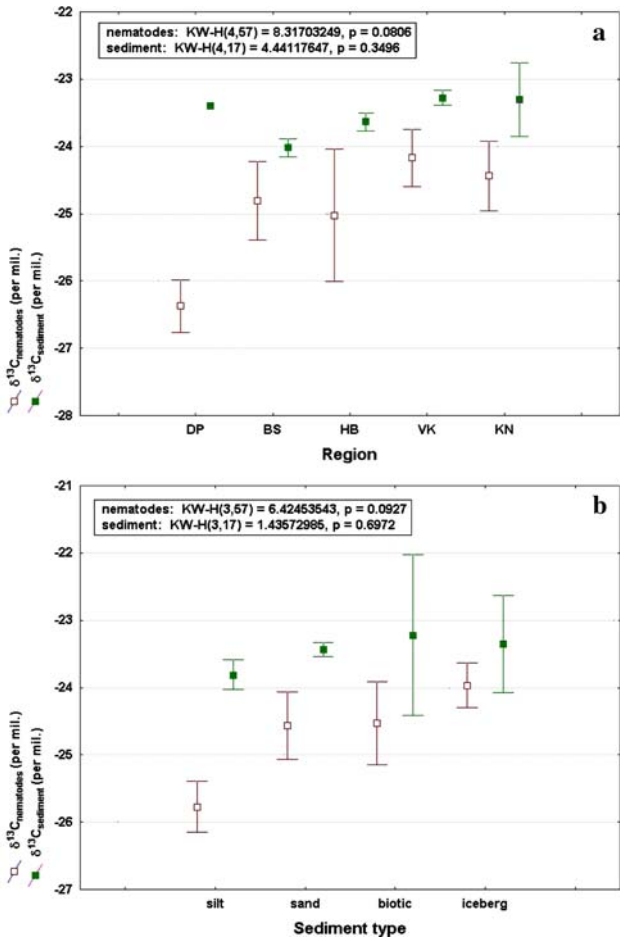

Fig. 4 Isotopic ratios (in ‰) of sediment organic matter and nematodes (**a**) in the five geographic regions, and (**b**) in the four substrate types sampled. *DP*, Drake Passage; *BS*, Bransfield Strait; *HB*, Halley Bay; *VK*, Vestkapp, *KN*, Kapp Norvegia. The data present average δ^{13}C ± 1 standard error. Kruskal–Wallis *H* values (+degrees of freedom, number of samples) and corresponding *P*-levels are added

extent, *Cervonema* and *Pierrickia*. This was the single sample where sufficient biomass of this group was obtainable for separate measurement, and it explains the large standard deviation on δ^{13}Cn at Halley Bay. Omitting this value narrows the range of δ^{13}Cn to –27.9 to –19.3‰. δ^{13}Cn was almost always more depleted than sediment organic matter, with an offset of typically ca. 1‰, but of up to 3‰ for Drake Passage stations and for silty substrata in general.

The δ^{13}C of other meiofaunal taxa were in the same range as for nematodes: amphipods, –26.5 to –22.9‰; harpacticoid copepods, –29.4 to –20.8‰; polychaetes, –28.1 to –23.9‰; and single values for halacarid mites of –21.5‰ and for cumaceans of –21.2‰.

Nematodes from Drake Passage were on average more depleted in ^{13}C than nematodes from other regions (Fig. 4a); similarly, nematodes from silty sediments tended to be more depleted than nematodes from sandy, "biotic" and iceberg-impacted substrata (Fig. 4b). However, these differences between regions and sediment types were not significant at the $P < 0.05$ level (both $P < 0.1$). The regional difference becomes more obvious when comparing the offset between δ^{13}Cs and δ^{13}Cn. This offset, then, was typically larger for Drake Passage (nematodes being depleted compared to sediment organic matter) than for the other regions ($P < 0.01$); differences in this offset between substrate types again lacked statistical support ($0.05 < P < 0.1$). Depth differences in nematode δ^{13}Cn did not follow any clear trend when all regions were considered together (data not shown). However, in Drake Passage comparatively depleted δ^{13}Cn in shelf communities contrasted with more enriched δ^{13}Cn of slope communities. δ^{13}Cn was not correlated with feeding type composition, i.e., differences in δ^{13}Cn were not linked to proportional abundances of specific feeding types (data not shown).

Enrichment experiment

The inventory of ^{13}C in the sediment showed very little vertical label penetration, even after 16 days (Table 3). High variability between cores hampered a reliable calculation of the rate of disappearance of ^{13}C (through respiration) from the sediment. If we assume that mineralization was a linear function of time (supported by the data at days 0, 5 and 13, or by the data at days 0, 9 and 16 (both $R^2 > 0.94$), but not by the total dataset), then the ^{13}C inventories at the end of the experiment (after 16 days) imply a mineralization rate of 11.5 mg ^{13}C m^{-2} day^{-1}. If, by contrast, we use the mean ^{13}C inventory after 13 days, which was on average lower than that after 16 days due to the above-mentioned high variability among replicates, the estimated mineralization rate becomes 19.8 mg ^{13}C m^{-2} d^{-1}. These values may provide slight overestimates, since there were no controls allowing accounting for mineralization and leaching of organic matter in the water column. From visual inspection it appeared that settlement of this organic matter was relatively rapid and was complete after less than 10 h, but we have no means of estimating the magnitude of the decomposition during settlement through the water column.

The inventory of ^{13}C in nematode biomass was again highly variable between replicates. This variability can be attributed to within-core—resulting from an uneven distribution of label over the core surface, only half of each sediment slice having been used for nematode stable isotope analysis—and, yet more importantly, between-MUC. Hence, different cores and, especially, different MUCs could not be considered proper replicates. However, inspite of this high variability, some important trends emerged.

First, carbon uptake, expressed as a percentage of the total amount of ^{13}C added at the start of the experiment,

Table 3 $\Delta\delta^{13}C$ (in ‰) of sediment organic matter at different sediment depth layers in the pulse-chase experiment

Depth (cm)	5 days Mean ± stdev	9 days Mean ± stdev	13 days Mean ± stdev	16 days Mean ± stdev
0–1	404.03 ± 247.86	583.47 ± 259.75	129.73 ± 88.94	316.48 ± 317.45
1–2	3.27 ± 0.82	4.72 ± 1.65	16.9 ± 19.04	6.63 ± 6.16
2–5	0.9 ± 0.35	42.07 ± 58.29	7.44 ± 4.34	2.06 ± 0.59
5–10	0.77 ± 0.40	0.82 ± 0.30	1.34 ± 0.54	1.66 ± 0.91

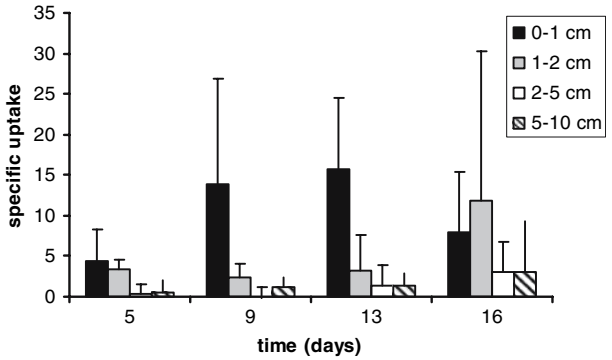

Fig. 5 Specific uptake ($\Delta\delta^{13}C$, in ‰) in nematodes from different depth layers in the pulse-chase experiment

was extremely low. At the shortest time scales (5 and 9 days), 0.0007 (MUC 1) to 0.0053 (MUC 2)% of the added label was recovered in nematode biomass, with little difference between the 5- and 9-day results. In cores originating from MUC 3, this percentage subsequently decreased, but in cores from MUCs 1 and 2 it increased toward the end of the experiment, with a range from 0.0028 to 0.0231% of the ^{13}C initially added present in nematode biomass after 16 days.

Specific uptake ($\Delta\delta^{13}C$) by nematodes was much higher in the upper 1 cm than deeper down, consistent with the observation that most of the added label remained on the sediment surface. By the end of the experiment, nematodes from the second cm in some cores also showed measurable label uptake; in one core, nematode $\delta^{13}C$ was elevated down to the 5–10 cm depth stratum (Fig. 5).

Discussion

Sediment organic matter $\delta^{13}C$ in the high-latitude Southern Ocean span a broad range from –32.3 to –16.7‰. Differences in phytoplankton biomass and/or growth rates, variable nutrient and/or pCO_2 regimes, differences in species composition of planktonic assemblages, and presence/absence of ice algae are all factors that contribute to this large range in organic matter $\delta^{13}C$ signatures in the Southern Ocean (Fontugne et al. 1991; Rau et al. 1991a, b, 1992; Kopczynska et al. 1995; Dehairs et al. 1997; Beaulieu 2002). By contrast, the sediments sampled in the present study exhibited a fairly narrow range of bulk organic matter $\delta^{13}C$, without significant regional differences. For instance, we found no reflection of a North–South latitudinal gradient in carbon isotopic signatures (Kopczynska et al. 1995).

The Drake Passage stations near King George Island generally had the most depleted nematode $\delta^{13}C$ signals (–26.4 ± 1.1‰). This area is characterized by high-standing stocks of grazing zooplankton and a concomitant large production of faecal pellets comprising organic matter and fragmented diatom valves. Such particulate matter settles rapidly and is typically depleted in $\delta^{13}C$ (Abelmann and Gersonde 1991). For example, $\delta^{13}C$ values of –31.9 to –29.7‰ have been reported for flagellates (Kopczyńska et al. 1995) and *Corethron*-bearing faecal pellets (Bathmann et al. 1991). While Drake Passage stations in our study had much heavier sediment organic matter $\delta^{13}C$ signals (–23.4 ± 1.4‰), they also exhibited the highest offset between $\delta^{13}Cn$ and $\delta^{13}Cs$. In fact, the strongly depleted $\delta^{13}Cn$ suggest that faecal pellets, phytodetrital aggregates and their associated microflora are important carbon sources for the metazoan meiobenthos in the Drake Passage area and are consumed selectively from within the bulk sedimentary organic matter pool.

By contrast, nematode $\delta^{13}C$ in the Bransfield Strait area were comparatively heavier (–24.8 ± 1.3‰), inspite of the fact that surface water plankton communities in this area are similarly characterized by strongly depleted $\delta^{13}C$ signatures (Leventer 1991). Analysis of sediment traps in this region has indicated potentially significant lateral and near-bottom transport of isotopically heavier organic matter resuspended from the slopes of the surrounding islands and from nearby shelf areas (Abelmann and Gersonde 1991). This is supported by the observation of strong bottom currents during the sampling for the present study. Hence, in the Bransfield Strait area advected organic matter may contribute more to the nematodes' nutrition than the local phytoplankton production.

At Kapp Norvegia, organic matter sedimentation pulses are highly dependent on biological processes associated with the receding ice edge and with advective processes. Early summer sedimentation pulses in this region, for instance, consist mainly of neritic diatoms and rapidly settling krill faecal strings with an average $\delta^{13}C$ of

ca. –24‰ (Bathmann et al. 1991), very similar to our δ^{13}Cs (–23.3 ± 1.2‰) and δ^{13}Cn (–24.4 ± 2.2‰) values. These faecal strings often contain phytoplankton cells that are undigested or have undergone only limited biochemical degradation (Bathmann et al. 1991), and that constitute a potential food source for certain nematode species and/or feeding types. Sea-ice algae, on the other hand, are typically characterized by heavier carbon isotopic signatures (–18 to –20‰) (Wada et al. 1987; Fischer et al. 1988; Bathmann et al. 1991), and may be an important food source for several Southern Ocean invertebrates (Nyssen et al. 2002). In our study, heavy δ^{13}C signatures (–21.5 to –19.3‰) of nematodes at two Kapp Norvegia, two Vestkapp and one Halley Bay station, and of some of the samples of other meiobenthos (particularly harpacticoid copepods), are also indicative that rapidly sedimenting sea-ice algae may be a significant food source for metazoan meiobenthos. However, during austral summer organic particle fluxes may vary considerably over even short time scales, and it is therefore likely that carbon sources available to, and utilized by, the meiobenthos in this area are temporally variable.

Regional variability in δ^{13}Cs and δ^{13}Cn signatures may be partly blurred by the large heterogeneity in substrate types sampled here. The study areas off King George Island and in the Weddell Sea clearly differed in seabed characteristics. A considerable part in the Weddell Sea shelf along Kapp Norvegia was covered by coarse biogenic debris or was iceberg disturbed (Gutt et al. 1998). Bryozoan debris and sponge spicule mats form a very loosely woven substrate that may effectively trap sedimenting particles, thus, for instance, enhancing the availability of the above-mentioned isotopically heavier sea-ice algae or particles associated with krill faeces. While sediment organic matter δ^{13}C in our study did not differ among substrate types, nematode δ^{13}C was typically more depleted in the fine-grained sediments off King George Island (Bransfield and Drake Passage silts).

Regional variability in sediment organic matter and nematode δ^{13}C signatures may further be obscured by depth-dependent patterns. The degradation of organic matter during transport to the seabed typically causes a decrease in energy content of sedimenting organic matter with water depth (Graf 1992), which is often parallelled by an increase in POM δ^{13}C through the selective respiration of ^{12}C (Rau et al. 1991b). Although we did not find clear depth-related trends in either sediment or nematode δ^{13}C over all stations sampled, we did observe heavier meiobenthic δ^{13}C with depth along the continental margin of Drake Passage, with depleted nematode δ^{13}C signatures on the shelf and comparatively heavy nematode δ^{13}C on the slope.

Based on stable isotope data, deep-sea nematodes have been suggested to feed on nannobiotic fungi and bacteria, which links them closely to the detrital food web (Goering et al. 1990; Iken et al. 2001). The carbon isotopic abundances of Antarctic nematodes in this study (–24.8 ± 2.3‰) were also close to those of bulk sediment organic matter (–23.5 ± 0.7‰). However, in a majority of stations nematode δ^{13}C was depleted compared to that of bulk particulate organic matter, a trend, which was particularly pronounced in the Drake Passage area (see above). These, and the isotopically heavy nematode and harpacticoid communities at some stations, suggest a substantial selectivity of the metazoan meiobenthos for specific components of the sedimenting plankton, such as ice algae and flagellates.

Caution is, however, warranted when interpreting the ^{13}C-depletion of Antarctic nematodes relative to bulk sediment organic matter. First of all, Danovaro et al. (1999) demonstrated lipid levels twice those of coastal nematodes in a deep-sea (950 m depth) assemblage in the Cretan Sea. Lipids are typically depleted in ^{13}C compared to whole animal tissues (Wada et al. 1987). Because of limited available biomass, samples for the present study were not defatted. We suggest that lipids may have contributed to the ^{13}C-depletion in our nematode samples; however, in view of the clear regional differences in offset between nematode and bulk organic matter δ^{13}C, it is unlikely that this phenomenon alone could explain the observed ^{13}C-depletion.

Secondly, the most depleted nematode δ^{13}C in our study (–34.6‰, Halley Bay station 135) was recorded in a sample in which we only included comesomatid nematodes (the genera *Sabatieria* and to a lesser extent *Pierrickia* and *Cervonema*). Although we have to be cautious not to overinterpret this single measurement, such a low δ^{13}C suggests a contribution of chemosynthetic production (Levin and Michener 2002; MacAvoy et al. 2003) to the diet of these comesomatids, either via grazing on chemosynthetic bacteria or through the presence of chemosynthetic symbionts. *Sabatieria* and some other comesomatids are enigmatic taxa because they are found in a wide range of environments, including anoxic sediments (Jensen 1981; Hendelberg and Jensen 1993; Dando et al. 1993; Thiermann et al. 1997), and their feeding biology remains unknown. These comesomatid nematodes were prominently present in almost half of the stations studied here, and if their depleted carbon isotopic signatures were a more general phenomenon, this would obviously affect whole-community δ^{13}C. Indeed, the lowermost δ^{13}Cn were found in two shelf stations at Drake Passage with the highest relative abundances of *Sabatieria* (49.8 and 26.8%, respectively, at 429 and 218 m depth) of all stations. At the 429 m station (sta 48/341), *Sabatieria* was five times more abundant than the second-ranked genus, and at the 218 m station (sta 48/345) it was four times more abundant. This

high dominance of *Sabatieria* also explains the deviant position of station 48/341 in an nMDS of nematode community data of different stations and regions (Fig. 3). Several other stations in our study had *Sabatieria* as the most abundant, or among the five most abundant genera, but with relative abundances always <17% and never exceeding that of the second-ranked genus by more than half. In any case, the very low δ^{13}C for comesomatid nematodes at Halley Bay station 135 needs further investigation to assess whether this is a local phenomenon or not, and to what extent it may have contributed to the depletion of δ^{13}Cn compared to δ^{13}Cs.

Pulse-chase experiment

We added a pulse of fresh, labile organic matter to sediment cores withdrawn from a 227-m deep station at Bransfield Strait. This organic carbon was remineralized at a rate (11–20 mg C m^{-2} day^{-1}) comparable to mineralization rates observed in deeper (1,265 and 2,170 m) sediments in the temperate NE Atlantic (9–25 mg C m^{-2} over 1.5 days, Moodley et al. 2002; Witte et al. 2003a). There was no apparent lag between sedimentation and mineralization as sometimes observed in deep-sea sediments (Pfannkuche 1993; Smith et al. 2002). Specific uptake in nematodes, however, did show such a lag, with a clear increase in uptake during the second half of the incubation, but only in cores originating from MUC 1 and 2 (not MUC 3). Similar uptake kinetics were observed for nematodes and foraminiferans in abyssal sediments, where benthic macrofauna dominated initial organic matter uptake (Witte et al. 2003b). Macrofauna were, however, extremely scarce at sta 56/148, which is reflected in the limited and slow ^{13}C-penetration into subsurface layers, a consequence of both low sediment porosity and lack of bioturbation.

In the absence of macrofauna, benthic mineralization in our experimental cores can be attributed to bacteria, foraminiferans and metazoan meiobenthos, dominated by nematodes. We have no measurements in support of the role of bacteria and foraminifera, but both groups have been shown to be key players in short-term deep-sea benthic responses to phytodetritus deposition (Moodley et al. 2002). Nematodes contributed negligibly to benthic carbon mineralization in our study, with considerably less than 0.1% of the processed ^{13}C showing up in nematode biomass at any given time, in agreement with Moodley et al. (2002). Even if we take into account that this represents assimilation rather than uptake, and that assimilation is underestimated because of (1) leakage of low-molecular weight material from frozen and thawed specimens (Moens et al. 1999), and (2) (unknown) carbon turnover times in nematode tissues, nematodes contributed less than 1% to the recorded benthic carbon mineralization. While several authors have suggested a quantitative importance of meiofauna in benthic carbon and energy flows (a.o. Kuipers et al. 1981; Coull 1999), the current results group with other recent stable-carbon-isotope tracer experiments in intertidal (Moens et al. 2002; Urban-Malinga and Moens 2006) and deep-sea sediments (Moodley et al. 2002; Witte et al. 2003b), which all indicate a limited direct contribution of the metazoan meiobenthos to the short-term processing of fresh organic matter. This phenomenon may, however, be very context-specific and there is currently insufficient evidence for generalizations to be made.

The extremely low specific uptake ($\Delta\delta^{13}$C, i.e. $\delta^{13}C_{sample} - \delta^{13}C_{background}$) by nematodes may indicate that the organic matter source we used—lyophilized cyanobacteria—was unsuitable as a food source for a majority of the nematodes in this Bransfield Strait station, even though cyanobacteria are important players in mineralization processes in the deep-sea pelagial and benthos (Lochte and Turley 1988; Pfannkuche and Lochte 1993). The retarded uptake also suggests that most of the cyanobacterial carbon eventually entered nematodes indirectly, e.g., through feeding on bacteria that in turn had utilized the cyanobacterial carbon (see also Moens et al. 2002). It is therefore unclear whether the low specific uptake by nematodes reflects comparatively slower response times in this Antarctic sediment, a selection against the organic matter source utilized, or a combination of both.

Conclusions

The general observation that nematode δ^{13}C in Southern Ocean sediments is depleted in ^{13}C by—on average—1 to 3‰ compared to bulk sediment organic matter, and that this depletion is comparatively higher in the Drake Passage region, suggests that nematodes selectively utilize specific components of the sedimenting plankton and their associated microorganisms. ^{13}C-depletion in lipids may also contribute to the ^{13}C-depletion in nematodes. Furthermore, the data presented in this study only provide community-averaged isotopic signatures. Future studies will have to achieve genus-level resolution, and incorporate temporal changes in organic matter inputs to the seabed, in order to provide a more dynamic understanding of carbon utilization by the meiobenthos in Antarctic sediments.

The preferential utilization of specific components of sedimenting detritus does not necessarily imply that nematode communities can either respond rapidly to (seasonal) pulses of detritus to the seabed, or that they play an important role in the mineralization of detritus. The results of our pulse-chase experiment show a lagged response in nematodes, indicating that their uptake largely channels through bacteria or other microheterotrophs. At the same time, uptake was very low, suggesting a very

limited contribution of nematodes to the mineralization of the organic matter pulse.

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