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Meiofauna towards the South Sandwich Trench (750–6300 m), focus on nematodes

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Abstract

Meiobenthos (excluding foraminifers) from the South Sandwich Trench was studied in sediment samples collected by multiple core (MUC) or multiple grab (MG). Sampling stations were chosen along a depth transect that covered the continental slope and abyssal plain towards the trench (water depths from 747 to 6319 m). Total abundance and biomass of meiobenthos ranged between 354 and 1675 ind. 10 cm^{-2} , and between 16.3 and 80.8 $\mu\text{g C } 10\text{ cm}^{-2}$, respectively. Standing stock decreased, though not linearly, with increasing water depth. Biomasses and densities were situated above the world ocean's regression line of meiobenthic stocks against water depth, and higher on the trench floor (354–930 ind 10 cm^{-2} , 18.7 $\mu\text{g C } 10\text{ cm}^{-2}$ at 6300 m) compared to most other oceans' trench regions. This observation confirms earlier results from the Antarctic continental margins that Antarctic meiofauna is characterised by dense populations in which nematodes predominate over the other taxonomic groups (87–98% of total abundance). Taxonomic investigations at genus level revealed that Chromadoridae, Monhysteridae, Desmodoridae, Desmoscolocidae, Xyalidae and Cyatholaimidae were dominant. Most of the nematode genera (in total 94) occurred in all depths, with only a slight distinction between the “shallow” (*Daptonema*, *Dichromadora* and *Molgolaimus* preferentially at 750–2300 m) and “deep” (with *Tricoma* preferentially from 3000 m on). The “shallow” communities were comparable to those from the Weddell Sea continental margin; the sediments at 2300–6300 m harboured in big lines similar compositions as abyssal and trench communities worldwide. Two main morph clusters were distinguished among the South Sandwich Trench nematodes: plump nematodes, with average $L : W = 9$, belonging to the taxonomic similar selective deposit-feeding genera of the Desmoscolocida, and comparable slender nematodes ($L : W = 26$; biomass size class -4 to -2) such as *Monhystera*, *Acantholaimus*, *Daptonema*, *Dichromadora*, *Molgolaimus*, *Microlaimus* and some species from *Paracanthochus*, mixed among mainly selective and epistratum feeding modes. They formed the bulk of the trench community. The results did not fit well with the general decrease in standing stock with increasing water depth and distance from the continental shelf. Similarly, nematode size (length from 124 to 2991 μm , biomass from 0.023 to 0.042 $\mu\text{g dwt}$) did not show clear bathymetric trends. The lack of the usual deep-sea trends of structural characteristics of meiofauna in general (density, total biomass, taxon composition) and functional attributes of

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nematodes (morphometrics, biomass, trophic guild structure, and maturity index) is explained by the particularly complexity of the sedimentary environment of the South Sandwich Trench, which was the result of physical processes (turbidites), bioturbation activity by invertebrate taxa and food supply along the depth transect.

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1. Introduction

There is a large number of studies that show the prime importance of sediment properties and trophic sources on meiofauna communities, particularly nematodes (see Heip et al., 1985; Giere, 1993, for reviews). Besides structural aspects of standing stock and community composition (family, genus, species), functional approaches based on feeding type, size and biomass, and maturity may give alternative insights on the impact of these parameters. Specifically for nematodes there is a suit of ecologically useful characteristics.

The feeding ecology can be inferred from the morphology of their buccal cavity. Many species feed on bacteria, algae or both; they eat detritus and possibly dissolved organic matter, and a considerable number are predators, feeding on other nematodes, oligochaetes, polychaetes, etc. (Wieser, 1953). Different proportions of different feeding modes may point towards different types of food available. Nematode communities in the deep sea are generally looked upon as detritivore grazers of nanobiota like fungi and bacteria. Epistratum feeders are also present, though in often in lower proportions as to the virtual absence of fresh organic sources. Scavengers and facultative predators are relatively unimportant (Tietjen, 1984; Jensen, 1988; Goering et al., 1990; Soetaert and Heip, 1995; Vanaverbeke et al., 1997a; Vanreusel et al., 2000; Iken et al., 2001).

The size of animals can determine various physiological characteristics (growth rate, metabolic rate, rate of reproduction) (Peters, 1983). On first sight nematode worms look very similar; they are structurally simple, basically consisting of two concentric tubes. However, looking more carefully, it becomes clear that also this benthic group of small-sized animals is determined by habitus-dependent ecological roles. A general factor is geometry, and especially the different exponents

relating surfaces and volumes, which provide powerful and inescapable constraints of growth. It was suggested that the nematode morphotype reflects the quality of exploited food and that nematode behaviour is a direct consequence of sediment texture (Soetaert and Heip, 1989; Tita et al., 1999; Soetaert et al., 2002).

Biomass within the meiofaunal the benthic spectrum is often dominated by nematodes. This group of animals has a minimum contribution of 46% to the total biomass in weight class 0.5–1 μgC , but in all other weight classes (<0.5 μgC), almost 100% of the biomass is attributed to nematodes (Duplisea and Hargrave, 1996; Drgas et al., 1998). Therefore, constructing nematode biomass spectra (NBS) would reveal a similar picture as if all animals in the meiobenthic sample were measured. Furthermore, biomass spectra are useful tools in assessing functional changes in nematode communities as a result of a changing environment (Vanaverbeke et al., 2003).

Based on life-history syndromes, genera of nematodes can be ordered on a “coloniser-persister” (cp) scale. The scale ranges from one (early coloniser of new resources) to five (persisters in undisturbed habitats). The maturity index (MI) for a site is the weighed mean of “cp” value of the individuals in a representative sample. In practice, MI values for sediments subjected to varying levels of disturbance range from less than 2.0 in nutrient-enriched and/or disturbed systems to over 4.0 in undisturbed, pristine environments (Bongers et al., 1991). Although the MI was originally constructed to implement terrestrial nematode studies, it has shown possibilities to monitor the deep-sea environment as well (Bongers et al., 1991; Lee et al., 2001; Gambi et al., 2003).

Nematodes are ubiquitous in all kinds of biotopes that provide available organic carbon sources. Their rapid response to any change (for example, disturbance and food enrichment) in the

environment make them as good bio-indicators (Heip et al., 1985) and useful for setting management priorities in unique and valuable habitats (Bongers and Ferris, 1999). Life-strategy-based parameters such as trophic status, morphometrics, biomass spectra, and maturity index may thus be helpful in describing the trench ecosystem.

Previous work on meiofaunal and nematode structure from the continental margin (Vanhove et al., 1995, 1999; De Broyer et al., 2001) demonstrated that at the higher phylum level, Antarctic meiofauna is characterised by dense (biomass- and specimen-rich) populations in which nematodes dominate. Although the broad geographical distribution of predominant nematode genera is identical to major bathyal assemblages, a striking high abundance of atypical deep-water genera attracts the attention to the Antarctic nematofauna.

Ocean trenches have a suite of characters that make them unique. Their seismic activity results in a relatively unstable and unpredictable habitat in comparison with the great environmental stability of the abyssal plains. Due to their close vicinity to island arcs and continental land-masses, primary production and sedimentation rates tend to be high (Menzies et al., 1973; Jumars and Hessler, 1976). The dominant sources of these sediments are of terrigenous origin and consist of inert mineral particles. Several trenches underlie upwelling zones, or zones of high productivity that stimulate intense blooms of phytoplankton, which in turn support pelagic population growth. As a significant proportion descends to the bottom, this provides important food source for the trench (or 'hadal') communities (Angel, 1982). However, because of the relative difficulty of oceanographic surveys in the area, the marine science has heretofore rested on poorly investigated hypotheses about hadal and trench faunas (Soltwedel et al., 2003; Danovaro et al., 2002). In 2002, two international cruises of PFS *Polarstern* (ANDEEP and LAMPOS) provided the opportunity to investigate faunas and habitat topography in the tectonically active deeps of the South Sandwich Trench nearby the Scotia Arc in Antarctica. The trench is, apart from being controlled by a combination of an infinite ocean and tectonism,

characterised by continental glaciation (Holdgate and Baker, 1979). Since no other place on earth has these parameters in common for comparison, the *Polarstern* campaigns have led many benthic researchers to describe a unique set of material available from a region difficult and expensive to explore (e.g., due to extreme weather conditions and ice-coverage). Antarctic meiobenthos deeper than 2000 m has never been studied before.

This paper is designed to evaluate meiofauna parameters and their relationships with environmental properties of grain size and food properties in the sediments in and along the South Sandwich Trench. Morphometric analyses, biomass spectra, trophic status and maturity will offer additional information on functional aspects of the deep-sea nematodes. Questions central to this research can be summarised as follows:

- Are meiofauna and specifically nematodes from the South Sandwich Trench different from other trenches worldwide and from other deep-water areas elsewhere in Antarctica?
- How do the meiobenthos and specifically the nematode fauna vary with bathymetry?

This work aims to support the basic hypotheses stated by ANDEEP and LAMPOS (Brandt and Hilbig, 2001; Fütterer and Arntz, 2001) that, because of the extreme environment and isolation of the tectonically active deep-sea trench, a typical benthos inhabit the sediments.

2. Material and methods

2.1. Morphology and geophysical structure of the area

The South Sandwich Islands lie between 57°35.28'–58°50.85'S and 23°58.26'–26°27.57'W (Fig. 1) within the maritime Antarctic zone. They form a curving chain extending about 386 km from north to south on the eastern side of the Scotia Arc (i.e. land-bridge between South America and the Antarctic Peninsula) presenting the eastern boundary of the Scotia Sea. Between the small volcanic islands, which are separated on average about

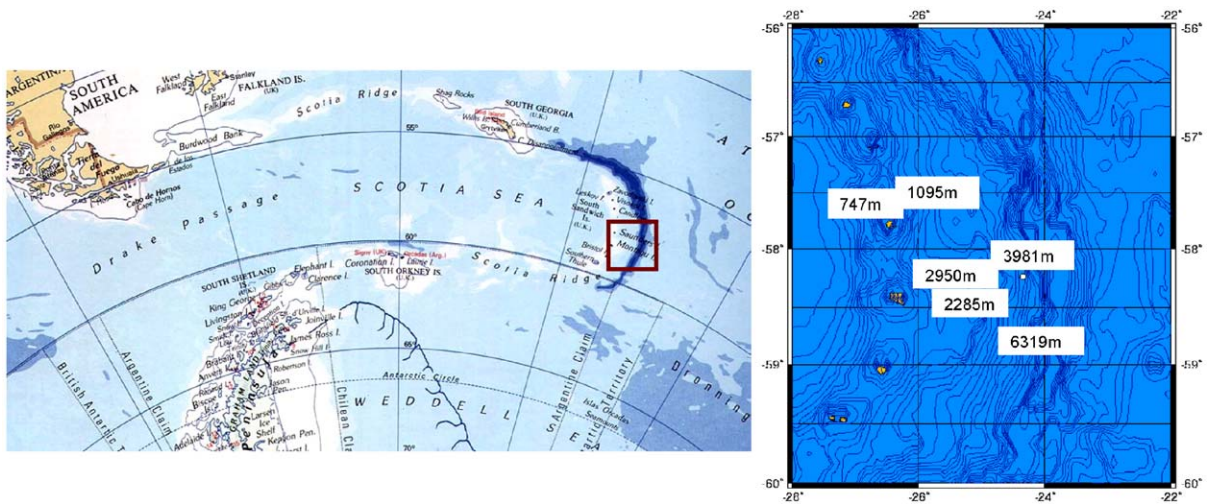


Fig. 1. Sampling area and station locations.

42 km from each other, the water usually reaches a depth of about 2300 m (Holdgate and Baker, 1979). At the eastern side of the arc, the seafloor has a steep slope bounded by the South Sandwich Trench at a distance of ~ 150 km east and axis NW–SE parallel of the island arc. The seismically highly active trench is formed by the subduction of the South American Plate under the small South Sandwich Plate to the east of the trench, at a continuous rate of $67\text{--}81\text{ mm yr}^{-1}$ since for at least 15 Myr (Larter et al., 2003, and references therein). The resulting volcanism has produced the island arc of the South Sandwich Islands. The trench can be divided into three sections: the northern section, which is the widest and the deepest; the central section, which is characterised by a broad shelf between the islands and the trench; and the southern section, which is characterised by the end of the trench against the Scotia ridge. The entire trench shows an asymmetric profile: on its western side the slope descends with an angle up to 7° to over 8000 m (Vanneste and Larter, 2002; Vanneste et al., 2002; Larter et al., 2003). The eastern slope exhibits an almost vertical wall, which connects to abyssal depths (4000–5000 m) of the Indian/Atlantic Basin. The hydrography of the region is mainly determined by the Weddell Sea Deep Water (WSDW), flowing from the Weddell Sea to the Scotia Sea and along the South

Sandwich Trench into the deep abyssal plains to the east with potential temperatures between -0.7 and 0°C (Heywood et al., 2002). Along with the wind-driven Antarctic Circumpolar Current (ACC), the WSDW provides the main component of deep, bottom-current circulation (oceanography summarised by Howe et al., 2004).

2.2. Sampling

Meiofauna samples were taken during the complementary ANDEEP (ANTarctic DEEP sea study: 28.02.2001–01.04.2002) and LAMPOS (Latin American POLarstern Study: 03.04.2002–05.05.2002) expeditions in the South Sandwich archipelago (Brandt and Hilbig, 2001; Fütterer and Arntz, 2001). Sampling sites are shown in Fig. 1; station data and sediment characteristics are given in Table 1. Sediment samples were taken at bathyal and abyssal depths east off Saunders Island (747 m, 1095 m) and on the steep narrow slope ($7\text{--}12^\circ$ inclination) east off Montague Island (2285, 2950, 3933 m) and at hadal depths (6300 m) SE off Montague Island, at the western side of the central section of the South Sandwich Trench (60°S , $25^\circ\text{W}\text{--}58^\circ\text{S}$, 20°W) (Tectonic Map of the Scotia Arc, 1985).

The sediments were collected with a multiple corer (MUC) equipped with 12 core tubes of

Table 1

Sampling stations of ANDEEP2 (South Sandwich Trench, east of Montague Island) and LAMPOS (slope off Saunders Island) campaigns

Station	Gear	Deployment no.	Sampling dates	Coordinates	Depth (m)
<i>ANDEEP 2</i>					
139	MUC	4	19.03.02	S58°14,75 W24°20,22	3933
		8	20.03.02	S58°14,26 W24°20,62	3974
		9	20.03.02	S58°14,14 W24°20,51	3982
140	MUC	3	21.03.02	S58°15,99 W24°53,62	2950
		5	21.03.02	S58°16,02 W24°53,75	2949
		6	21.03.02	S58°16,07 W24°54,12	2942
141	MUC	4	22.03.02	S58°24,96 W25°00,84	2293
		6	22.03.02	S58°24,96 W25°01,07	2277
		8	22.03.02	S58°24,98 W25°01,00	2286
142	MUC	4	24.03.02	S58°50,85 W23°58,26	6319
		5	24.03.02	S58°50,83 W23°50,73	6316
<i>LAMPOS</i>					
199	MG	1	15.04.02	S57°37,92 W26°27,46	747
211	MUC	1	16.04.02	S57°35,58 W26°23,68	1095

Notes: MG deployment at 550 m station was unsuccessful because of washing out of fine material. Other boxes of MG at Sta. 199 were not available due to sample sharing and failure of boxes (e.g. the second box of the MG contained no upper water layer anymore and was therefore considered to be disturbed; other deployments (both MG and MUC) failed at this station because of stony substrates.

57 mm internal diameter, equivalent to 25.5 cm² surface area (Barnett et al., 1984). From every station water from above the sediment surface was checked for meiofaunal presence and three to four complete cores were sliced (0–1, 1–3, 3–5, 5–10, 10–15 cm). The samples were a combination of true replicates (different drops) and pseudo-replicates (different cores from the same drop). Where the sediments contained abundant volcanic debris and ice-rafted drop stones that could harm the fragile MUC cores (e.g., this occurs in all stations above the 1000 m line in the region under study, e.g., Sta. 199), the multiple box corer (multigrab, MG: nine individual boxes; 240 cm² each) was deployed (Gerdes, 1990). Due to sample sharing of the only successful MG drop and very few successful MG boxes, three pseudo replicate subsamples (=three samples from 1 box taken with hand cores, internal diameters 3.5 cm) were considered and sliced as described above. The samples were preserved in buffered 4% formalin solution. Additional environmental variable samples (granulometry, pigment content and organic carbon/nitrogen content) (1–2 cores per station)

were sliced; each slice was divided over two petridishes and stored at –30 °C for further analysis. Temperatures of the water above the cores, measured after core recovery on board, ranged between –1.1 and +1.9 °C.

2.3. Environmental parameters and potential food sources

Grain size analyses were carried out using a Coulter LS&100 Particle Size Analyser, after sieving the coarse fraction (boulders, pebbles) on a 1000 µm screen. Sediment fractions from 0.4 to 900 µm are expressed as volume percentages and classified according to the Wentworth system (0–4 µm-clay, 4–63 µm-silt, 63–125 µm-very fine sand, 125–250 µm-fine sand, 250–500 µm-medium sand, 500–800 µm-coarse sand) (Wentworth, 1922), while fractions >1000 µm were termed grits and stones. Total sedimentary nitrogen and organic carbon were determined on dried and acidified (with 10 N HCl) sediment samples using a Carlo Erba elemental analyser (combusted at 1000 °C). Sediment-bound pigments were determined photometrically after

dark extraction in acetone and separation using reversed phase HPLC (Mantoura and Llewellyn, 1983).

2.4. Meiofauna parameters

For meiofaunal extraction, sediment samples were passed through 1000- μm mesh, and a standard deep-sea 32- μm mesh was used to retain the smallest organisms. The fraction remaining on the latter sieve was resuspended and centrifuged three to four times (at 1800g for 10 min) with LUDOX HS 40 (density 1.15 g cm⁻³), as described by Vincx (1996). All metazoan meiobenthic animals were counted and classified at higher taxon level under a stereomicroscope after staining with Rose Bengal (0.5 g l⁻¹).

Fifty specimens from the top 0–1 cm slices per replicate (for a total of 150 specimens per station) were transferred to glycerol, mounted, measured (body length, L , and width, W) using a Quantimet 500+ image analysis system on a microscope (Leitz Dialux, 20), and identified using a Leica DMLS microscope and pictorial keys and relevant taxonomic literature (e.g., Platt, 1985; Soetaert, 1989; Bussau, 1993; Muthumbi, 1998; Platt and Warwick, 1998; Chen, 1999). Biomass was calculated with the adjusted formula of Andrassy (Andrassy, 1956; Soetaert, 1989): WWT nematode (mg) = [largest body width (mm)² × body length (mm)] × 1.13 g cm⁻³ / 1.9, where an empirical value of 1.9 was used to calculate nematode volumes, and a specific gravity of an average marine nematode of 1.13 (*i.c.* based on measurements for *Enoplus communis*, Wieser, 1960) was used to calculate biomass values from the volume data. This method calculates volume from different widths along the nematode habitus. Conversion to dry weight usually assumes a dry:wet weight ratio of 0.25 (Wieser, 1960). Resulting calculations give dry weight measures in mg. Carbon content was considered to be 40% of the dry weight (Feller and Warwick, 1988). Both length and dry weight measures were expressed with harmonic (mean by averaging) and geometric (mean after log-transformation); the first for comparative purposes with literature data; the second as it is less sensitive to the presence or

absence of extremely large individual (Soetaert and Heip, 1989). The nematodes were classified into four feeding groups suggested by Wieser (1953) linked to buccal morphology, distinguishing selective (1A) and non-selective deposit feeders (1B), epistratum feeders (2A) and predators/omnivores (2B).

2.5. Statistical analysis and ecological indexes

A Kruskal-Wallis ANOVA by ranks was performed to delineate significant differences in meiofauna composition between the (pseudo) replicated stations along the South Sandwich Trench transect. A Spearman-Rank correlation analysis was carried out to test the correlations among densities (nematodes, harpacticoid copepods, total meiofauna) and environmental parameters (water depth, sediment properties). The spatial analysis was carried out on mean station values; vertical analysis on separate sediment slices averaged over the (pseudo) replicates.

To define nematode communities spatially, the genus percentages were used as input for the Two-Way INDicator SPecies ANALysis-TWINSpan (Hill, 1979). First, as rare genera can be informative on the state of the community, the non-reduced percentage matrix was used for total analysis. Second, a reduced dataset for assessing the impact of more frequently occurring genera (*i.e.* those with only 1 or 2 occurrences over the entire dataset were omitted) was subjected to classification with cut levels 0, 0.020, 0.375, 0.070, 0.120. In a third step, multivariate ordination techniques were used to identify spatial pattern relationships within the nematode assemblages across the bathymetric station set hereby assessing the consistency of the TWINSpan results. A Correspondence Analysis (CA-option from the package PC-ORD; McCune and Meford, 1999) on the arcsine transformed data matrix was done to explore the ordination length (SD, standard deviation of species turnover). DCA is particularly chosen with SD > 3 and presents unimodal relationship between samples in terms of their similarity of species abundance; PCA is to be used when SD < 1.5 and presents linear relationships.

The maturity index (MI) was calculated according to the weighted mean of the individual genus scores: $MI = \sum v(i)f(i)$, where v is the “cp” value (“colonisers-persisters”) of genus i as given in the Appendix of Bongers et al. (1991) and $f(i)$ is the frequency of that genus. This index proposes a classification for nematodes into ‘colonisers’ (comparable to r -strategists, characterised by short life-cycle, high colonisation ability and tolerance to disturbance, eutrophication and anoxibiosis) and ‘persisters’ (with opposite characteristics, K -strategists with low reproduction rate, long life-cycle, low colonisation ability and tolerance to disturbance).

Nematode morphometrics of lengths and widths were analysed with scatter plot and histograms as introduced by Soetaert et al. (2002). NBS were constructed using \log_2 groupings of nematode dry weight (μg) on the x -axis and total biomass per size class (dry weight, μg) on the y -axis. The \log_2 weight-class represents the organism weight within the class; e.g., the biomass in Size Class 0 represents the sum of the biomass of all organisms in the dry weight range $\geq 2^0 - < 2^1$ (i.e. $\geq 1 - < 2 \mu\text{g}$).

3. Results

3.1. Environmental parameters and food availability at the seafloor

All sediments showed left-skewed (fine-grained) profiles and contained on average 79% silt. Mean and mode particle sizes as average per station ranged from 16 to 56 μm and 18 to 58 μm , respectively. Sands and clays were found in lower proportions (11% and 10%, respectively) (Fig. 2). All sediments were intensively perturbed and large, intact faecal traces of holothurians were abundant. Biogenic material (average of 20%, containing siliceous diatoms, radiolarians, sponge spicules and silicoflagellates) was heavily mixed with stone debris (volcanic and ice-rafted in origin) making the sediments completely different from adjacent deep-sea floors in Weddell/Scotia (Antarctic) and Atlantic abyssal plains (Diaz and Carpenter, 2004) (Table 2).

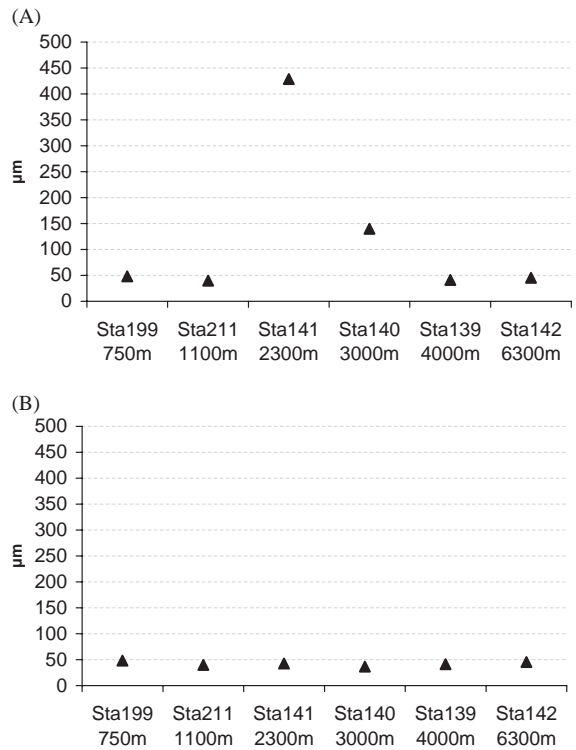


Fig. 2. Sediment texture over all stations along the South Sandwich Trench. Average Sediment texture per station given as mode: (a) burrows included, (b) burrows excluded.

The shallowest stations off Saunders Island, Sta. 199 (747 m) and 211 (1095 m), showed a unimodal sediment profile (not presented) with a clear finer fraction than the deeper sites in the trench. A thin fluff layer was found on the moderately sorted silts mixed with volcanic stone debris ($> 1000 \mu\text{m}$). Mean, median and mode were rather conservative along the sediment profile (up to 10 cm into the sediment). At 2300 m water depth, sediments were coarser. A refining tendency with further increasing water depth was observed (Fig. 2). Burrows, pockets and bioturbation were frequent among the sandy silts/silty sands mixed with volcanic glass. The sediments became thus poorly sorted and had two modes in grain size distributions. Again a fluffy layer of biogenic phytodetritus was observed on top of the sediments. The sediments were hemipelagic (i.e. low energy settling of suspended material, under 30% biogenic; high levels of bioturbation), pelagic (i.e. low energy settling of

Table 2
Sediment properties

Sta ^a	Boardship observations	Sediment sorting	Observations of seabed photography, video sequencing and sediment profiling by Howe et al. (2004) and Diaz and Carpenter (2004) ^b
141 (2300 m)	Many lumps of phyto-detritus, fluffy layer of loose material	Poorly sorted	Hemipelagic and turbiditic Dark greyish brown silty sand with gravel pockets High energy downslope depositional environment Bioturbated pockets of pelagic biogenic material (diatomaceous <i>Chaetoceras</i> frustules, discoid <i>Actinocyclus</i> fragments) and sponge spicules, sand filled burrows throughout the cores, well sorted sand at 8–15 cm, traces of high surface biogenic productivity; volcanic origin and exotic ice rafted debris
140 (3000 m)	Many lumps of phyto-detritus, fluffy layer of loose material	Poorly sorted	Hemipelagic and turbiditic Dark greenish grey silty sand Moderate energy depositional environment Siliceous biogenic (radiolarian and diatomaceous) material and volcanic glass, bioturbated, sand filled burrows throughout the cores Below 20 cm diatom <i>Chaetoceras</i> , <i>Actinocyclus</i> and sponge spicule layer
139 (4000 m)	Silt, many stones and coarse basalt grit, fluffy layer of loose material	Poorly sorted	Turbiditic and hemipelagic Dark greenish grey sandy silt, with clay Very low-moderate energy depositional environment Much siliceous biogenic (radiolarian and diatomaceous) material and volcanic glass, intensely bioturbated, holothurian (?) fecal traces, common sand filled burrows
142 (6300 m)	No green fluff; some faecal pellets, surface mat-like deposit	Moderately sorted	Hemipelagic and pelagic Dark greyish brown sandy silt Very low-energy depositional environment with much radiolarians, diatomaceous <i>Chaetoceras</i> frustules and discoid <i>Actinocyclus</i> fragments; intensely bioturbated, abundant fecal traces and sand filled burrows throughout the cores, rare-Mn covered dropstones
199 (750 m)	Very thin fluff layer with volcanic stone debris	Moderately sorted silts with grits	
211 (1100 m)	Very thin fluff layer with volcanic stone debris	Moderately sorted silts with grits	

^aRound figures for water depths.

^bMean particle size in 0.4–2000 µm range.

suspended material from productive surface waters, over 30% biogenic; high levels of bioturbation), and turbid (i.e. high energy downslope reworking of sediments) in varying combination from high (Sta. 141, 2300 m) to moderately low (Sta. 139, 4000 m) energy deposition. The replicates of Sta. 141 (2300 m) deviated from each other depending on whether a burrow was present in the core (mode in silt and coarse sand fraction, at 1–3 and 3–5 cm) or missing (mode in the silt fraction,

at 1–3 and 3–5 cm). Sta. 141 was, in general, more sandy than any other station (Fig. 2). The upper cm of the only available replicate of Sta. 140 (3000 m) had an important modus in the medium to coarse sand fraction, in contrast to all silt-moded deeper sediment layers. Similarly, Sta. 139 (4000 m) had an upper cm high sand concentration of 22%, though sand became no important mode in particle size distribution. It may be interpreted as an old burrow or bioturbation pocket as deeper

layers (from 2 cm on) contain more biogenic material (40% and in mostly diatoms frustules and sponge spicules) (Diaz and Carpenter, 2004). In contrast to the slope and abyssal stations (2000–4000 m), sediments at the trench floor (Sta. 142; 6300 m) again showed a unimodal platykurtic pattern (broad range of particle sizes in modus, kurtosis -0.253 to -0.508 , graph not depicted) of clearly finer constitution: mean particle size $14\text{--}20\ \mu\text{m}$, up to 97% silt and 18% clay, disappearance of medium and coarse sand. No burrows and no fluff were recognised, and the vertical profile showed only minute changes with depth.

Organic matter showed extremely low signals, often below detection level (N: 0% and C: 0.9–1.0%). Pigments were extremely low at the shallowest station 199 (750 m) (total pigments: 467 and $1585\ \text{ng g}^{-1}$ sediment) with mainly Chl-*a* (36 and $521\ \text{ng g}^{-1}$ sediment) and Chl-*c* (293 and $655\ \text{ng g}^{-1}$ sediment). Only a thin fluff layer was observed on top of the cores. At 1100 m pigments (total pigments: 1308 and $1598\ \text{ng g}^{-1}$ sediment) were mainly composed of diatoxanthin (occurring in brown and unicellular algae like diatoms, 387 and $277\ \text{ng g}^{-1}$ sediment) and β -carotene (in all algae, 444 and $649\ \text{ng g}^{-1}$ sediment). Extremely low figures characterised the trench floor (total pigments: 163 and $123\ \text{ng g}^{-1}$ sediment), without any fluff layer. As the pigment and organic matter readings were extremely low and often differing a lot between the two replicates of each station analysis was restricted to the ends of the bathymetric profile (e.g., Sta. 199 and 211 against Sta. 142).

3.2. Meiofauna standing crop

Highest densities were observed at 1100 m depth (average for 1100 m: $1675 \pm 273\ \text{ind } 10\ \text{cm}^{-2}$; replica C with $1900\ \text{ind } 10\ \text{cm}^{-2}$) (Fig. 3). From this point on the meiofauna decreased with decreasing and increasing water depth from this point on. The densities at the shallowest station (750 m: $932 \pm 172\ \text{ind } 10\ \text{cm}^{-2}$) were in the same range as at 3000 m; those on the trench floor still exceeded 600 individuals $10\ \text{cm}^{-2}$ (with in replica 142–5: $930\ \text{ind } 10\ \text{cm}^{-2}$). Between replicate variability was high, and extremely high at Sta. 141 (2300 m)

where minimum data (312 and $375\ \text{ind } 10\ \text{cm}^{-2}$) were at least 4 times lower than the highest figure of $1358\ \text{ind } 10\ \text{cm}^{-2}$. Nevertheless, the differences between the stations were significant (Kruskal-Wallis, $p=0.05$) and total density covaried significantly with water depth (Spearman Rank, $p=0.04$). In total 7–11 meiobenthic taxa were found over all replicates. Free-living nematodes were by far the dominant taxon with 85–97%, followed by harpacticoid copepods with 1–6%. The latter were in highest abundances at the uppermost stations (750 m, $38\ \text{ind } 10\ \text{cm}^{-2}$ and 1095 m, $40\ \text{ind } 10\ \text{cm}^{-2}$) and lowest on the trench floor with only $5\ \text{ind } 10\ \text{cm}^{-2}$. Trace numbers of 20 other taxa were observed in a range between 0.002% and 1.5% (“rest” in Fig. 3). Among the most frequent were Ostracoda, Halacarida, Cumacea, Kinorhyncha and Bivalvia. Sta. 139 (4000 m) showed highest taxon diversity (although nematodes still take 87% of total densities). Sta. 142 (6300 m) contained almost exclusively nematodes. Vertical distribution showed a classical decreasing density with sediment depth (graphs not presented). Both harpacticoid copepods (nauplii included), nematodes and total numbers correlated negatively (Spearman Rank, $p=0.0006$) with clay percentages in the sediment, whereas other sediment parameters (sand, silt, mean, mode, variance) showed no correlation at the 5% significance level. Food parameters were too few to relate with meiofaunal parameters.

3.3. Nematode composition

Ninety-four nematode genera (belonging to 30 families) were found in the present study (996 specimens were identified). Chromadoridae (17.2%), Monhysteridae (16.4%), Desmodoridae (9.9%), Desmoscolecidae (7.1%), Xyalidae (6.5%) and Oxystominidae (5.6%) were most abundant (>5%). Comesomatidae and Cyatholaimidae were present in relatively high proportions in the upper stations down to 2300 m. Relative abundances of Desmodoridae decreased with depth, whereas Desmoscolecidae were more frequently found at deeper sites. Monhysteridae and Diplopeltidae occurred everywhere in high proportions, except for the shallowest site. Chromadoridae,

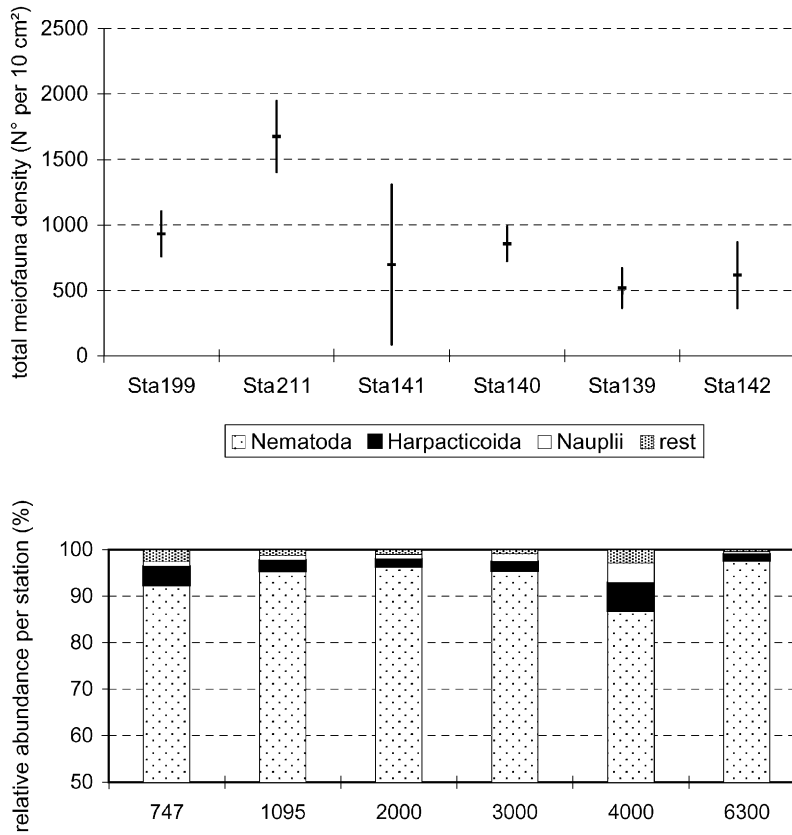


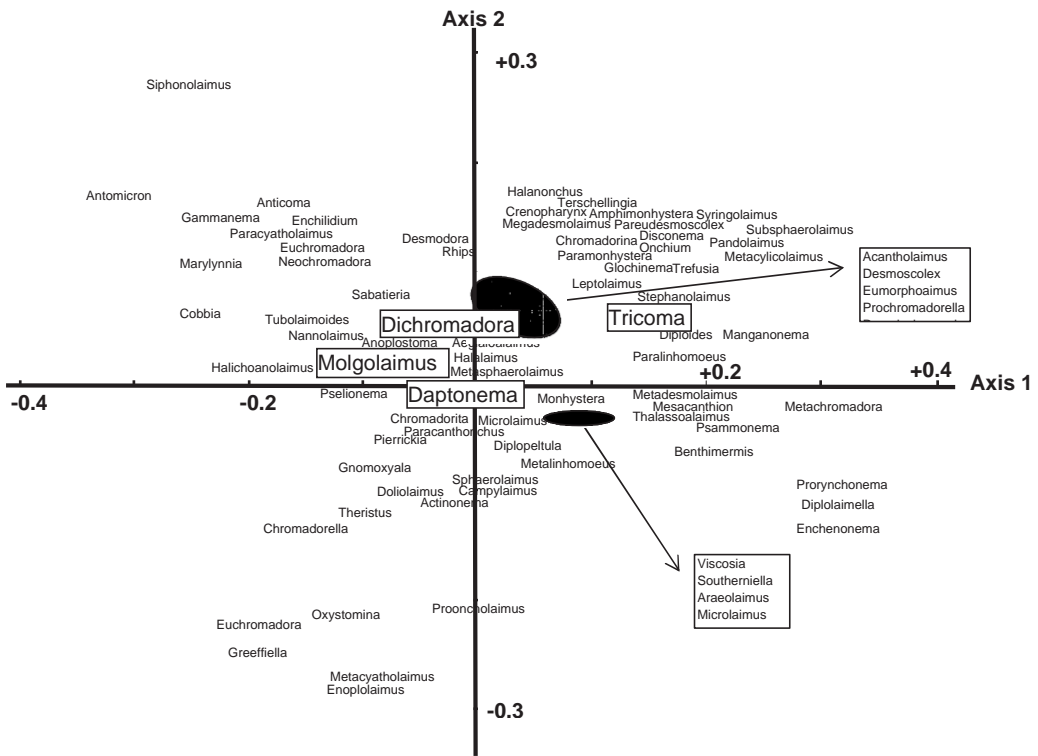
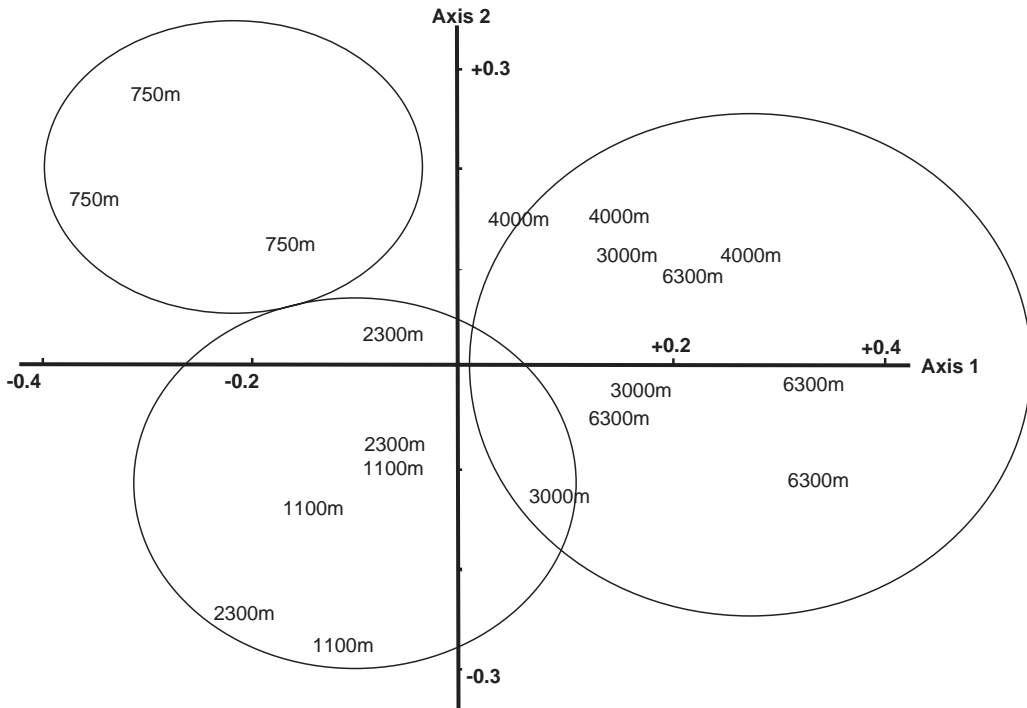
Fig. 3. Total meiofauna density (average $10\text{ cm}^{-2} \pm$ standard deviation) and relative abundance.

Oxystominidae, Xyalidae, Leptolaimidae, Aegialoalaimidae and Microlaimidae showed no bathymetric trend. Chromadoridae were negatively correlated with clay (Spearman Rank, $p=0.04$), in contrast to Monhysteridae (Spearman Rank, $p=0.005$, with positive sign). This latter family was further inversely correlated to sand percentage and mean particle size.

At the shallower stations 199 and 211 there were 47 genera, in contrast to 2300 m (Sta. 141) to 4000 m (Sta. 139) with 63 genera. Only 34 genera were found at the trench floor. TWINSPLANs (graphs not depicted) on the total and reduced nematode genus matrices united stations according to depth. TWINSPLAN groups were 750–2000 m

(respectively, Sta. 199, Sta. 211 and Sta. 141) on one side and 4000–6000 m (respectively, Sta. 139 and Sta. 142) on the other side. 3000 m was scattered over these two groups. Within the first TWINSPLAN group the three 750-m replicates separated in a second step from both the 1100- and 2300-m replica's. PCA ordination results confirmed the big lines (Fig. 4). Most of the nematode genera did not differentiate much between depths; they were grouped in the center of the ordination plane. The resulting ordination explained thus only a small variation between the nematode communities of the different sites (axis 1 and 2, respectively, 19% and 12% of total variation). A strongly reduced nematode dataset (restricted to

Fig. 4. Output of ordination (PCA) with indication of the major clusters identified by TWINSPLAN on total datamatrix at nematode genus level of organization (gradient length of the DCA = 1.5) (Eigenvalue of axis 1: 0.65, 19.2%, eigenvalue of axis 2: 0.40, 11.8%). The TWINSPLAN indicator species are in enlarged.



relative abundances >5%) against depth, however, clearly distinguished between the shallow (Sta. 199 and 211) and deep (Sta. 139 and 142), with the intermediate stations showing overlap between both extremes. The genus *Tricoma* showed preference for the abyssal and hadal sites (from 4000 m on), whereas the genera *Daptonema*, *Dichromadora* and *Molgolaimus* had with some exceptions a slight preference for depths shallower than 3000 m. They corresponded with the indicator species in the TWINSPAN. Other dominant genera (*Paracanthochus*, *Halalaimus*, *Monhystera*, *Microlaimus* and *Acantholaimus*) were proportionally equally present over all sites (Table 3). They showed no correlations with sediment properties (Spearman Rank, $p > 0.05$). In general, similar genera were found all over the sites, though with changing relative abundances (Table 3).

3.4. Functional aspects of the nematode communities along the South Sandwich Trench

Nematodes along the South Sandwich Trench were mainly selective deposit-feeders (1A: 36%), epistratum grazers (2A: 33%) and non-selective deposit feeders (1B: 27%). Predators/omnivores were well below 10%. There was no significant change in this composition with depth. Predators/omnivores were, however, extremely few at 2300 and 6300 m (Fig. 5). The 1A group was negatively correlated with the mean particle size and sand fraction of the sediment in the burrows (Spearman Rank, $p = 0.0004$) and outside burrows (Spearman Rank, $p = 0.0006$). Conversely, 1B was positively correlated with these parameters (Spearman Rank, $p = 0.005$) and negatively with clay and silt (Spearman Rank, $p = 0.0005$). So were the 2A. No correlation was found with food in the sediment.

The maturity index (MI) differed only slightly between the stations. The shallowest site had the highest (MI=2.4), pointing towards a higher abundance of nematodes with *K*-strategies. Sta. 140 and 142 had lowest MIs (both MI=1.6). MIs were negatively correlated with the modulus of grain size distribution (Spearman Rank, $p = 0.02$).

Nematode length over 940 single measurements varied from 124 to 2991 μm (average 631, geometric mean 537 μm) within the assembly of all

measurements. Body width versus length (Fig. 6) showed two demarcated oval clusters representing two distinct morphological groups: comparably plump nematodes (L : 124–400 μm , W : 17–53 μm ; *Tricoma*) and mostly slender nematodes (L : >200 μm , W : mostly about 20–25 μm ; *Monhystera*, *Acantholaimus*, *Daptonema*, *Dichromadora*, *Molgolaimus*, *Paracanthochus*, *Microlaimus*). At the right side of this cluster a third less clear group was set off, combining very slender nematodes (*Halalaimus*; L : 500–2000 μm ; W : 10–20 μm) and the few very big nematode specimens from subdominant genera *Mesacanthion*, *Diplopeltula*, *Sabatieria*, *Viscosia* and some species of *Paracanthochus* (L : 1600–3000 μm ; W : 60–90 μm). The clusters were visible as two modes (e.g., at ratios of 9 and 26, respectively) and a long tail in the $L : W$ ratio frequency distribution towards the very slender nematode genera with $L : W$ varying between 50 and 100. The $L : W$ ratios of the above mentioned dominant genera are given in Table 4. The frequency distributions of nematode $L : W$ did not express a clear relationship with water depth (figures not depicted). Only Sta. 139 and was clearly different in that it harboured much higher abundances (up to 20%) of plump nematodes (with $L : W$ ratios of 11). The nematodes from Sta. 142 (6300 m) had a higher average length (both harmonic and geometric) than those from Sta. 140 (3000 m) and Sta. 139 (4000 m) (Fig. 7). $L : W$ morphometrics were negatively correlated with sand and positively with silt (Spearman Rank, $p = 0.02$). There was no relation with food.

Average nematode biomass displayed values between 0.076 and 0.140 $\mu\text{g dwt}$ (harmonic mean) and 0.023–0.042 $\mu\text{g dwt}$ (geometric mean), with a decreasing trend with depth for harmonic, but not for geometric mean (Fig. 7). The nematodes from Sta. 141 and Sta. 142, in particular, deviated from a linear decrease. NBS (Fig. 8) illustrated big differences between the stations, thus showing a highly different morphological nematode structure with depth. Differences were more pronounced in the higher biomass values of the spectrum. At the stations 199, 211 and 141, a peak appeared in the higher size class 0 or 1, meaning that the few big nematodes at these sites (for example, *Paracanthochus*, Table 5) had a high impact on total

Table 3

Check list of the dominant nematode genera (mean relative abundance $\geq 1\%$ of the total number of individuals) encountered along the South Sandwich Trench with TWINSpan indicator species in bold

Sta199(750 m)		Sta211 (1100 m)		Sta141 (2300 m)	
Molgolaimus	20.9	<i>Monhystera</i>	22.2	Molgolaimus	11.8
<i>Acantholaimus</i>	8.6	Molgolaimus	13.0	<i>Microlaimus</i>	11.1
Dichromadora	8.1	Daptonema	8.5	<i>Monhystera</i>	8.5
<i>Halalaimus</i>	7.9	<i>Halalaimus</i>	8.0	<i>Paracanthochus</i>	8.4
Daptonema	5.2	<i>Paracanthochus</i>	5.2	Dichromadora	7.4
<i>Procamacolaimus</i>	4.6	<i>Diplopeltula</i>	3.5	<i>Halalaimus</i>	4.6
<i>Rhyps</i>	4.5	Dichromadora	2.8	Daptonema	4.2
<i>Sabatieria</i>	3.9	<i>Pselionema</i>	2.2	<i>Chromadorita</i>	4.2
Tricoma	3.4	<i>Sphaerolaimus</i>	2.1	<i>Aegialoalaimus</i>	3.4
<i>Desmodora</i>	2.6	<i>Aegialoalaimus</i>	2.1	<i>Acantholaimus</i>	3.4
<i>Aegialoalaimus</i>	2.0	<i>Acantholaimus</i>	2.1	<i>Diplopeltula</i>	3.1
<i>Pselionema</i>	2.0	<i>Actinonema</i>	1.5	<i>Prochromadorella</i>	2.6
<i>Anticoma</i>	2.0	<i>Campylaimus</i>	1.5	<i>Procamacolaimus</i>	2.2
<i>Monhystera</i>	1.9	<i>Metaacyatholaimus</i>	1.5	<i>Southerniella</i>	1.9
<i>Cobbia</i>	1.4	<i>Pierrickia</i>	1.5	<i>Desmoscolex</i>	1.6
<i>Paracyatholaimus</i>	1.4	<i>Desmoscolex</i>	1.5	<i>Campylaimus</i>	1.3
<i>Siphonolaimus</i>	1.4	<i>Halichoanolaimus</i>	1.4	Tricoma	1.1
<i>Metasphaerolaimus</i>	1.3	<i>Oxystomina</i>	1.4	<i>Actinonema</i>	1.0
<i>Gammanema</i>	1.3	<i>Microlaimus</i>	1.4	<i>Cygnonema</i>	1.0
<i>Pierrickia</i>	1.3	<i>Theristus</i>	1.4	<i>Eumorpholaimus</i>	1.0
<i>Araeolaimus</i>	1.3				
<i>Chromadorita</i>	1.3				
<i>Paralongicyatholaimus</i>	1.3				
<i>Southerniella</i>	1.3				
Sta140 (3000 m)		Sta139 (4000 m)		Sta142 (6300 m)	
<i>Monhystera</i>	13.4	<i>Monhystera</i>	14.6	<i>Monhystera</i>	25.4
<i>Acantholaimus</i>	13.1	Tricoma	10.1	<i>Acantholaimus</i>	9.1
<i>Microlaimus</i>	8.7	<i>Acantholaimus</i>	8.2	<i>Microlaimus</i>	8.8
Tricoma	5.1	<i>Pareudesmoscolex</i>	5.1	Tricoma	5.6
<i>Halalaimus</i>	5.0	<i>Desmoscolex</i>	4.5	Daptonema	4.5
Dichromadora	4.5	<i>Halalaimus</i>	4.4	<i>Procamacolaimus</i>	4.1
<i>Diplopeltula</i>	3.5	<i>Microlaimus</i>	4.0	<i>Araeolaimus</i>	3.6
Daptonema	3.2	Molgolaimus	2.6	<i>Aegialoalaimus</i>	3.1
<i>Pseudochromadora</i>	2.2	<i>Subsphaerolaimus</i>	2.5	<i>Diplopeltula</i>	2.0
<i>Paracanthochus</i>	1.9	<i>Syringolaimus</i>	2.4	<i>Diplopeltoides</i>	1.7
<i>Southerniella</i>	1.9	<i>Rhyps</i>	2.2	<i>Diplolaimella</i>	1.6
<i>Desmoscolex</i>	1.7	<i>Procamacolaimus</i>	2.0	<i>Southerniella</i>	1.6
<i>Araeolaimus</i>	1.5	Daptonema	2.0	<i>Paralinhomoeus</i>	1.5
<i>Metasphaerolaimus</i>	1.4	<i>Chromadorita</i>	1.8	<i>Manganonema</i>	1.1
<i>Aegialoalaimus</i>	1.2	<i>Dichromadora</i>	1.5	<i>Thalasoalaimus</i>	1.0
<i>Metalinhomoeus</i>	1.2	<i>Leptolaimus</i>	1.4	<i>Desmodora</i>	1.0
<i>Procamacolaimus</i>	1.2	<i>Pandolaimus</i>	1.4	<i>Leptolaimus</i>	1.0
<i>Campylaimus</i>	1.1	<i>Diplopeltula</i>	1.3	<i>Paralongicyatholaimus</i>	1.0
		<i>Disconema</i>	1.3	<i>Pseudochromadora</i>	1.0
		<i>Araeolaimus</i>	1.2		
		<i>Manganonema</i>	1.2		

biomass. Below 4000m big nematodes disappeared and were substituted by nematodes in the size class -4 to -2 (*Tricoma*, *Acantholaimus*, *Dichromadora*, *Halalaimus*, *Daptonema*, *Microlaimus*, *Molgolaimus*). At 6300m bigger nematodes were completely absent. Meiofaunal total biomasses were obtained from the product of nematode density and mean individual biomass (Table 6), and ranged between 16 and 80 $\mu\text{gC } 10\text{cm}^{-2}$ (for harmonic mean), and between 5 and 19 $\mu\text{gC } 10\text{cm}^{-2}$ (for geometric mean). Juveniles dominated at all stations, ranging between 38% (Sta.142, 6300m) and 55% (Sta. 140, 3000m) (Table 7). Females were approximate as abundant (between 27% and 40%); males much less abundant (between 13% and 25%). The male to female ratio ranged between 1.1 and 3.0, the juvenile to adult ratio between 0.6 and 1.2

(Table 7). There was no relation of sex ratio to depth, sediment texture and food content.

4. Discussion

4.1. Sampling device

The use of a MUC is now widespread in deep-sea meiofaunal research. Unlike the USNEL box corer, this device recovers samples in which the sediment–water interface is virtually intact. It therefore retains much more loose, surficial deposits of phytodetritus, and consequently may recover a much higher proportion of the meiofauna than box corers (where over 50% of specimens may be lost) (Bett et al., 1994; Horton and Bett,

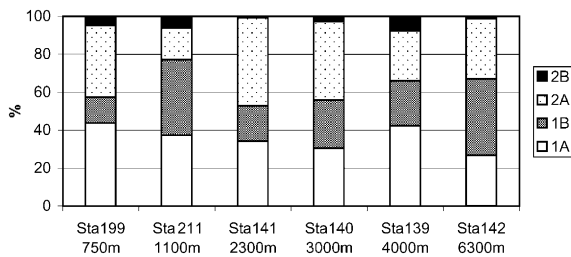


Fig. 5. Trophic composition of the nematodes along the South Sandwich Trench: 2B: predators/omnivores; 2A: epistratum grazers; 1B: non-selective deposit feeders; 1A: selective deposit feeders.

Table 4

Average *L : W* ratios of the dominant nematode genera (> 5%) (juveniles and adults together)

	<i>L : W</i>
<i>Tricoma</i>	9.1
<i>Microlaimus</i>	22.7
<i>Paracanthochus</i>	24.5
<i>Molgolaimus</i>	24.7
<i>Dichromadora</i>	26.0
<i>Daptonema</i>	32.0
<i>Acantholaimus</i>	33.2
<i>Monhystera</i>	39.4
<i>Halalaimus</i>	58.8

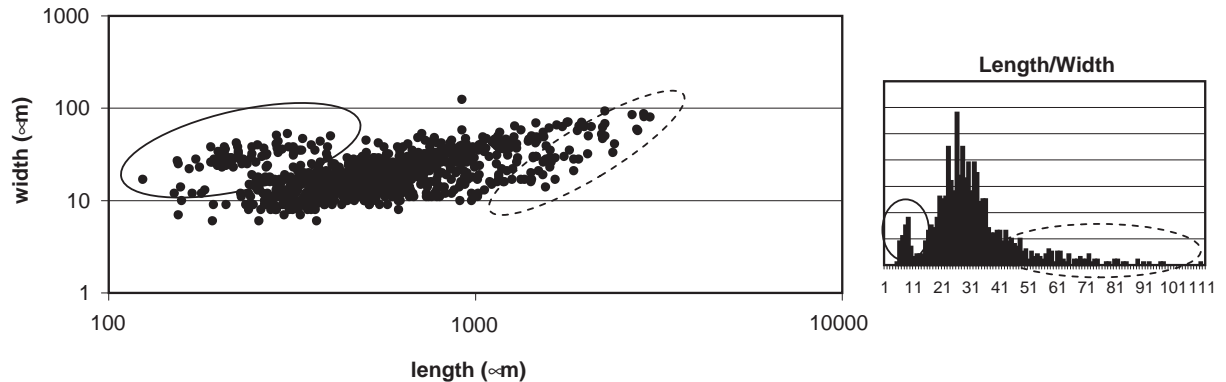


Fig. 6. Morphological landscape of nematodes in the upper sediment layers of the South Sandwich Trench ($n = 940$): body width against body length on log scale (left); length/width ratio on linear scale (right).

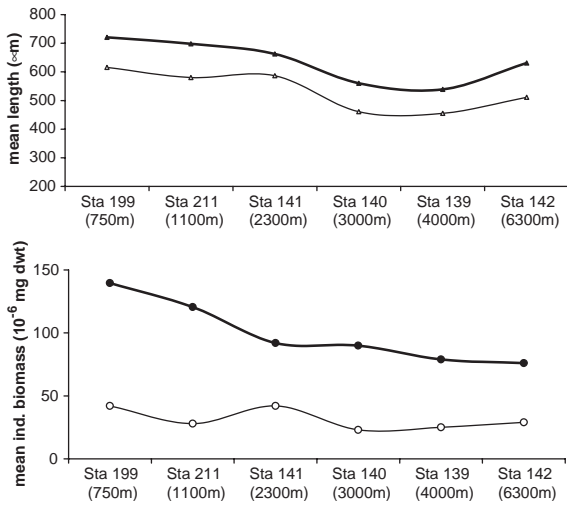


Fig. 7. Nematode length and biomass versus water depth in the upper sediment layers along the South Sandwich Trench: harmonic mean (upper thick lines); geometric mean (lower thin lines).

2003). In many Antarctic shelf and slope regions sediments containing high mud and gravel fractions, ice-rafted debris and/or boulders (drop stones from icebergs) sampling with the MUC is almost impossible. The multi-box corer overcomes these difficulties (Gerdes, 1990). Combined with a TC camera it provides a method for semi-targeted

Table 5

Average weight characteristics of the dominant nematode genera (>5%) (juveniles and adults together): individual dry weight and weight class to which the genera belong

	Weight ($\mu\text{g dwt}$)	Weight class
<i>Paracanthocheilus</i>	0.537	-1
<i>Tricoma</i>	0.101	-3
<i>Acantholaimus</i>	0.090	-3
<i>Dichromadora</i>	0.072	-3
<i>Halalaimus</i>	0.066	-4
<i>Daptonema</i>	0.059	-4
<i>Microlaimus</i>	0.032	-4
<i>Molgolaimus</i>	0.030	-4
<i>Monhystera</i>	0.024	-4

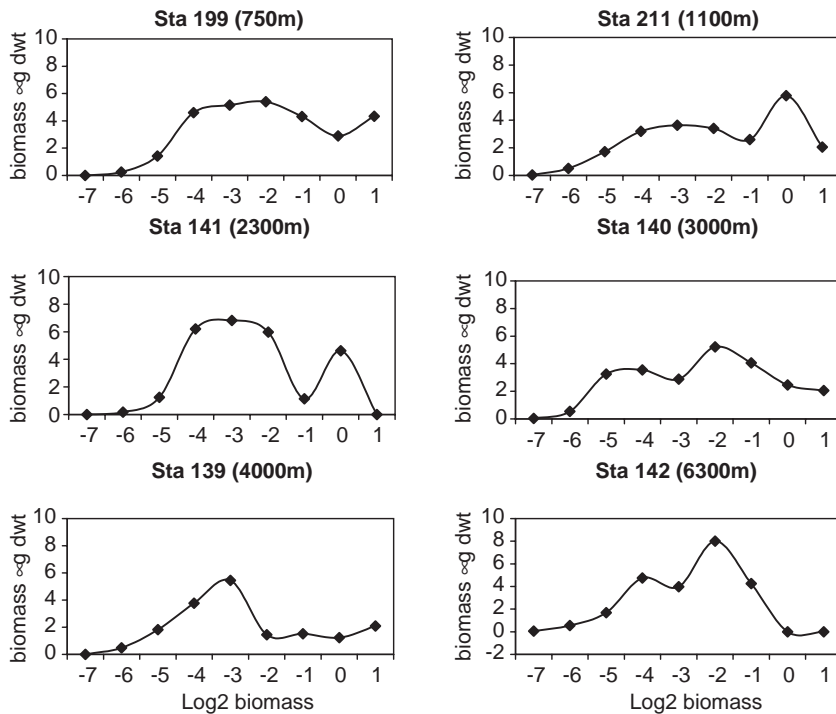


Fig. 8. Nematode biomass spectra in the different stations of the South Sandwich Trench.

Table 6
Weight characteristics of nematode assemblages along the transect

	Sta199 (750 m)	Sta 211 (1100 m)	Sta141 (2300 m)	Sta140 (3000 m)	Sta139 (4000 m)	Sta142 (6300 m)
<i>Harmonic mean</i>						
Individual biomass ($\mu\text{g C}$)	0.056	0.048	0.037	0.036	0.032	0.030
Total biomass ($\mu\text{g C } 10\text{ cm}^{-2}$)	52.0	80.8	25.6	30.8	16.3	18.7
<i>Geometric mean</i>						
Individual biomass ($\mu\text{g C}$)	0.017	0.011	0.017	0.009	0.010	0.011
Total biomass ($\mu\text{g C } 10\text{ cm}^{-2}$)	15.7	18.8	11.7	7.9	5.2	6.9

sampling. The MG is a relatively “open” device that enables the gentle lowering of the gear to the sea floor, i.e. without ‘bow wave’ effects of the kind described and criticised for most other grabs and corers (such as the bigger USNEL type). Unfortunately, no study has been performed, at present, on the meiofauna sampling efficiency of the MUC and MG specifically used in Antarctica (e.g., the MG has been deployed only in the volcanic sediments of the shallowest station). We cannot rule out any sampler bias, but it might have been relevant in samples recovered at the shallowest station (although sub-samples from the inner part of the MG boxes showed a perfectly undisturbed sediment surface under clear overlying water resulting in classical vertical distribution patterns of meiofauna in the sediment column).

4.2. Meiofauna standing crop

In the deep sea, the presence and persistence of life can be primarily seen as a response to input of detrital pulses from the surface layers (Beaulieu, 2002). The degradation of this organic matter during transport, combined with the offshore gradients in phytoplankton productivity, causes the well-documented decrease in energy content of sedimenting organic matter with water depth (Graf, 1989). The pelagic silts of the South Sandwich Trench are low in organic matter. With signals below 1% carbon and $0.1\text{--}1.6\text{ ng g}^{-1}$ pigments, they are 20–450 times lower than those in the Atacama Trench at similar depths (Danovaro et al., 2002). Accordingly, one should expect a highly depauperate fauna. However, bathyal and

abyssal meiobenthic densities and biomasses from the South Sandwich Trench (down to 4000 m: $932\text{--}1675\text{ ind } 10\text{ cm}^{-2}$ and $1.4\text{--}5.2\text{ }\mu\text{g dwt } 10\text{ cm}^{-2}$) are situated above world ocean’s regression line of meiobenthic stocks against water depth (Vanhove, unpublished results based upon Soltwedel, 2000), and confirm earlier results from the Antarctic continental margins (Vanhove et al., 1995). Abundances and biomasses on the trench floor ($354\text{--}930\text{ ind } 10\text{ cm}^{-2}$, $18.7\text{ }\mu\text{g C } 10\text{ cm}^{-2}$ at 6300 m) are also higher than at similar depths in other oceans’ trench regions (summarised in Soltwedel et al., 2003; Danovaro et al., 2002). Exceptions are the Atacama Trench, which presents very high concentrations of nutritionally rich organic matter (Danovaro et al., 2002), and the Barbados Trench, where meiofaunal abundances are indirectly linked to highly enhanced biological production (particularly due to bacterial activity) from the mud volcanoes (Olu et al., 1997).

The discrepancy between high meiofaunal stocks and seemingly low food markers in the sediments cannot directly be explained with the current data (e.g., Spearman Rank did not show a correlation), but the Antarctic trench meiofauna likely utilises incoming food very efficiently so that no clear traces of organic sources are left behind (thus explaining the low food content of the sediments). Primary production in the area is high and controlled by the position of the Polar Front and spring-time sea-ice edges (Angel, 1982; Vinogradova et al., 1974, 1993; Howe et al., 2004). Water-column sedimentation in the Southern Ocean is often in the form of fecal pellets originating from zooplankton feeding activities (in the Scotia Sea mainly from Euphausiidae.

(Vinogradova et al., 1993), which may sink at fast rates of $>200 \text{ m d}^{-1}$. Often these pellets enclose fresh diatoms as decomposition rates in the cold waters are low enough to keep the organic material rather free of bacterial degradation or scavenging by mid-water organisms¹ (Bathman et al., 1991; Beaulieu, 2002). Such fresh food may rapidly be consumed by an opportunistic behaviour of the meiobenthos, which normally has to rely on older matter during most of the time. Further evidence for a strong and efficient response to the inputs of fresh organic matter from above is given by the vertical density profiles. Abundances were highest in the surface layer of the sediment, decreasing rapidly with layer depth, despite sometimes aberrant vertical distribution patterns of sediment granulometry where deeper layers contain often more sands than upper layers.

4.3. Nematode community composition and morphology

Bathyal nematode communities have very little affinity to hadal sites (Gambi et al., 2003; Tietjen, 1989). This is not due to the presence or absence of certain families/genera, but rather to the different composition of nematode assemblages at bathyal and hadal depths, respectively. Our study generally revealed nematode assemblages containing similar compositions all over the bathymetric line (e.g., most of the genera were clustered in the centre of the PCA plane), though dominance distribution differs considerably between the “shallow” (750–1100 m, with preferentially genera *Daptonema*, *Dichromadora* and *Molgolaimus* and Comesomatid, Cyatholaimid and Desmodorid

families) and “deep” (4000–6300 m, with preferentially the Desmoscolecid *Tricoma*). The intermediate stations (especially 3000 m) form a transit with changing overlap with both extremes. The “shallow” communities resemble those from the Weddell Sea continental margin (Vanhove et al., 1999). The sediments at 2300–6300 m harbour similar compositions as abyssal nematode communities worldwide. These assemblages are consistently dominated by a few genera with abundances over 5% leading to a clustering of all abyssal sites with depths varying from 2000 to as much as 8000 m (Soetaert and Heip, 1995) rather than grouping them on a geographical basis due to the ‘homogeneity’ of deep-sea settings. The abyssal genera are *Daptonema*+*Theristus*, Monhysterids, *Acantholaimus*+*Spiliphera*, *Halalaimus*, *Leptolaimus*, *Desmoscolex*, *Tricoma*+*Quadricoma*, *Dichromadora*, *Prochromadorella*, *Microlaimus*, *Bolbolaimus*, *Syringolaimus*, *Eleutherolaimus*, *Paralongicyatholaimus*, and *Metalinhomoeus* (N. Atlantic Scotian Rise, 4626 m, Thistle and Sherman, 1985; Puerto Rico Trench and Hatteras Abyssal Plain, 2217–8380 m, Tietjen, 1989; NE Atlantic Goban Spur, 2182 and 2760 m, Vanaverbeke et al., 1997a; Arctic Laptev Sea, 2621 and 3237 m, Vanaverbeke et al., 1997b, Antarctic Weddell Sea, 2080 m, Vanhove et al., 1999; Atacama Trench, 7800 m, Gambi et al., 2003). However, a few additional genera such as *Molgolaimus*, *Paracanthonchus*, *Dichromadora*, and *Paruedesmoscolex*, which are generally situated higher in the water column of the slope, shelf break and shelf (Vanaverbeke et al., 1997b; Vanhove et al., 1999; Gambi et al., 2003) are observed in high proportions deeper than 2000 m. This shallowing

Table 7
Sex ratio of the nematode assemblages along the transect

%	Sta199 (750 m)	Sta211 (1100 m)	Sta141 (2300 m)	Sta140 (3000 m)	Sta139 (4000 m)	Sta142 (6300 m)
Juveniles (<i>J</i>)	41	48	37	55	48	38
Females (<i>F</i>)	37	27	40	31	39	40
Males (<i>M</i>)	22	25	23	14	13	22
<i>Ratio's</i>						
<i>J</i> : <i>A</i> (<i>A</i> = Adults)	0.7	0.9	0.6	1.2	0.9	0.6
<i>F</i> : <i>M</i>	1.7	1.1	1.7	2.2	3.0	1.8

the consequence of a much more heterogeneous sediment texture (and higher food input?) along the South Sandwich Trench compared to the usual homogeneous nutrient poor silts and clays of the world abyss. Finally, the deepest assemblages at the South Sandwich Trench are very alike to those from the Puerto Rico (Tietjen, 1984) and Atacama Trench (Gambi et al., 2003). Depth is clearly important in dominance distribution at genus and family level, though forms no barrier for presence of most taxa. Downward and subsequent horizontal movement of nematode genera and families, despite strong geographic separation of sites, is seemingly no problem. The wide distribution of families and genera suggests that radiation of nematodes in abyssal depths occurred relatively long ago, or modern-day dispersal of nematodes over vast distances has been quite efficient. Current radiation of deep-sea nematodes probably occurs at species level (Tietjen, 1989).

Over evolutionary timescales, selection in deep-sea sediments has also led to two nematode morphologies within the smaller size range (<500 µm length). (1) Short and corpulent “plump” nematodes (with small $L : W$ ratios) are less susceptible to predation, but have a reduced mobility. Such nematodes are generally restricted to the most oligotrophic deep sea or to coarse sediments (Soetaert et al., 2002). In our study, plump nematodes occur predominantly (20%) at Sta. 139. This site is characterised by sediments with many stones and coarse basalt grit and intensely bioturbated. As in all stations the sediments are oligotrophic. These plump nematodes ($L : W = 9$) belong to the taxonomic similar selective deposit-feeding genera of the order Desmoscolecida (*Tricoma*, *Desmoscolex*, and *Par-eudesmoscolex*). Predation is avoided by the presence of protective desmen and cuticular protrusions. Selective deposit-feeding is needed for distinguishing between particles in different stages of decomposition (Vanhove et al., 1999).

(2) “Slender” nematodes ($L : W = 26$; biomass size class -4 to -2) such as *Monhystera*, *Acantholaimus*, *Daptonema*, *Dichromadora*, *Molgolaimus*, *Microlaimus* and some species from *Paracanthonchus*, mixed among mainly selective and epistratum feeding modes, show no preference

for certain sites thus forming the bulk of the trench community. As discussed by Soetaert et al. (2002) these long and slender nematodes are able to move swiftly through the fine sediment common for ocean margins. Apart from the stony station 139, they occur together in abundances between 43% (Sta. 140) and 50% (Sta. 211). The presence of sand burrows in some stations along the bathymetric profile seems not to have affected the presence of this morph type.

A third less clear group of nematodes combines “very slender” taxa (*Halalaimus*; L : 500–2000 µm; W : 10–20 µm; $L : W = 60$) and a few “very big” nematode specimens from subdominant genera *Mesacanthion*, *Diplopeltula*, *Sabatieria*, *Viscosia* and *Paracanthonchus* (L : 1600–3000 µm; W : 60–90 µm; in the higher size class 0 or 1). The very slender nematodes belong to the selective deposit-feeders with minute buccal cavity, presumably feeding on bacteria. They are observed in highest proportions in the two shallowest stations with moderately sorted silts with thin fluff layer on top. The very big nematodes belong to non-selective deposit (with big mouth cavity) and predatory/scavenging (with big teeth) feeding modes. They appear more at the shallow (Sta. 199, 211) and burrow rich (Sta. 141) sites. Both feeding types are, generally, related to high-energy labile organic matter levels: non-selectivity prevails over selectivity in circumstances of excess labile detritus (Vanhove et al., 1999) and higher trophic complexity (with relatively more abundant higher trophic levels) is to be expected where food is trapped (Soetaert and Heip, 1995).

4.4. Bathymetric features of meiobenthic deep-sea organisms

A unique feature of meiobenthic deep-sea organisms seems to be the decrease in standing stock with increasing water depth and distance from the continental shelf. The controlling mechanism is, as described above, the productivity in the euphotic zone of the water column and the sedimentation regime determining the availability of food for the benthos (Thiel, 1983; Shirayama, 1984; Pfannkuche, 1985; DeBovée et al., 1990; Soltwedel, 2000). Our results do not fit well with

this hypothesis: highest meiobenthic abundances are observed at 1100 m depth (4272 ± 696 ind 10 cm^{-2}) and not at the shallowest station; densities are greater at 6300 m than at 4000 m.

A second feature is the decreasing trend in meiofauna sizes with depth. Average nematode biomass along the South Sandwich Trench displays values between 0.076 and $0.1396 \mu\text{g dwt}$, with a decreasing trend with depth. However, this is not substantiated with geometric mean (where the effect of bigger nematodes is reduced due to logarithmation), neither by nematode size spectra, length measures or $L:W$ ratios. It implies that there is not a general miniaturisation tendency with depth, as introduced by Thiel (1975). Confirmed by later studies (Shirayama, 1983; Pfannkuche, 1985; Jensen, 1988; Shirayama and Horikoshi, 1989; Soetaert and Heip, 1989; DeBovée et al., 1990; Vanreusel et al., 1995; Soltwedel et al., 1996; Schewe and Soltwedel, 1999; Soetaert et al., 2002; Gambi et al., 2003), there is rather a decreasing abundance of bigger nematodes at greater depth. This, in turn, suggests a lower abundance of, for example, predating taxa (from the Enoplid, Leptosomatid, Oncholaimid, Hali-choanolaimid families). The age-structure does not affect this trend as the percentage of juveniles is not a function of water depth.

4.5. Relation with the specific environment of the South Sandwich Trench

From what has been described so far, it can be concluded that there is an absence of a clear (linear) bathymetric gradient in both structural and functional parameters of South Sandwich Trench meiofaunal assemblages. This can only be explained by the combination of several factors. Sediments of the South Sandwich Trench, instead of being uniformly fine silts (as is the case in most deep-sea settings), are particularly complex and poorly sorted. They originate from three different sources: *tectonic*, (Goodell, 1964; Vanneste and Larter, 2002), *pelagic and turbiditic sources* (i.e. Sta. 141 and 142 give indication of a high energy downslope depositional environment with high surface biogenic productivity and sediment supply leading to localised downslope mass-movements

on the trench slope (Vanneste and Larter, 2002; Howe et al., 2004)), and by the *lateral transport from northwest Weddell Abyssal Plain* (debris ice rafted by the Antarctic Circumpolar Current (Goodell, 1964) and by the general water circulation pattern of Weddell Sea Bottom Water (Vanneste and Larter, 2002; Heywood et al., 2002; Howe et al., 2004)).

Whereas physical processes deliver sediments to the sea floor, it is the activity of benthic organisms (bioturbation) that may alter the physical structure of the sediments. Stations 139 and 141 in the South Sandwich Trench show intensely bioturbated fine-grained sediments and many sand-filled burrows (Diaz and Carpenter, 2004). The effect of bioturbation is evident by a significant change in the mode of the grain-size distribution. The literature has emphasised how increased surface area of the oxic/anoxic boundary caused by invertebrate burrows change grain-size distribution and enhance solute fluxes, reaction rates, and bulk microbial process rates, and hence influence faunal distribution, in favour or disadvantageous for the meiofauna (Yingst and Aller, 1982; Aller and Aller, 1986, 1992; Clough et al., 1997). The presence of old burrows at Sta. 139 give a community with lowest total abundances, more harpacticoids despite the general reduction of copepods with depth, relatively more predators and a higher proportion of smaller, plumper organisms (such as *Tricoma*). High between-core variability at Sta. 141 may be explained by the presence or absence of burrows in single replicates.

In the South Sandwich Trench the physical setting differs from that typically found in the deep sea. Rather than being a part of the tranquil abyss, this region is characterised by a relatively high mean near-bottom current velocity in excess of $5\text{--}10 \text{ cm s}^{-1}$ of Weddell Sea Bottom Water (WSBW) flowing into the South Sandwich Trench and exiting the Scotia Sea in the north adjacent to South Georgia (Hollister and Elder, 1969; Barber and Crame, 1995; Pudsey and Howe, 1998; Heywood et al., 2002; Matano et al., 2002). Strong near-bottom currents can reduce the abundance of meiofauna in the deep sea significantly (Aller, 1997; Thistle and Levin, 1998; Thistle et al., 1999), and may also have resulted (in addition to the

above described bioturbation) in low densities at Sta. 141 (2300 m). Disturbance by bioturbation and high-energy hydrography has, however, no real impact on the community composition, and thus the maturity index at this station. On the contrary, the maturity index (MI) of all sites along the Sandwich Trench is on average 1.98 (range 1.6–2.4), lower than the MI's from the Atacama Slope and Trench (range 2.4–2.7; Gambi et al., 2003), and much lower than the MI's from the 'stable' deep-sea fauna of the Hatteras Abyssal Plain (range 2.8–2.9; Bongers et al., 1991). Lower values indicate that nematode assemblages in the South Sandwich Trench are dominated by opportunistic "colonisers", with small sizes (in the same range as those from the Atacama Trench, Gambi et al., 2003). As such, nematodes (usually with short life-cycles and high colonisation ability) are tolerant to environmental disturbance (Bongers et al., 1991); this might indicate that the trench is still an instable habitat for deep-sea nematodes. Seismic activity, resulting in episodic turbidity, might be an example of such environmental disturbance.

The trophic sources do not decrease linearly with depth: the 750 m station contain 2–3-times less pigments than at 1100 m, and in contrast to the upper stations many lumps of phytodetritus are observed at 2300–4000 m. Further down, the trench floor contains extremely low amounts of organic material. The nearest source of primary production for this station is 6 km or more above. So the trench-floor is remote from the primary supplies of energy, and descending particles are likely to be utilised by pelagic microorganisms before the particles reach the sea-bed. Nevertheless, the sediments at 6300 m contain high Ba/Li (500 ppm) levels, reflecting some limited enhanced productivity and thus food availability (Howe et al., 2004). Elevated stocks, higher average individual nematode length and biomass and high proportions of epistratum feeders at the deepest station may be an indication of increased food supply. The study of food and feeding habits of Antarctic meiobenthos has already received some attention in former deep-water surveys, since they may explain part of the discrepancy between low organic carbon content of the sediments, despite

important sedimentation pulses during summer (Vanhove et al., 1995, 1999). These studies conclude that, although there is no straightforward evidence about how the proposed feeding groups of Wieser (1953) manifest under the extreme natural conditions of the Antarctic Ocean and deep sea, a surprisingly high proportion of epistratum feeders are found, even at 2000 m depth. This is explained by a functional adaptation of nematodes to short-term events of food supply. On the other hand genus numbers are lowest on the trench floor (half of those at 3000 and 4000 m). In many cases nematode diversity is positively related to primary production and food supply in the deep sea (Boucher and Lamshead, 1995), contradicting our observation. Similar reduction in nematode diversity was observed in the Atacama Trench and explained as being a consequence of extreme pressure conditions at these hadal depths (Gambi et al., 2003).

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