A seasonally varying biotope at Signy Island, Antarctic: implications for meiofaunal structure

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ABSTRACT: Under the typical high-latitude conditions of temperature, productivity and settlement of chlorophyll and phaeophytin to the sediment, many benthic organisms in the Antarctic show strong seasonal variation. Although meiofauna comprise an important component of the southpolar benthic ecosystem, our knowledge of them is limited. The metazoan meiofauna and the surrounding sediments were studied fortnightly for 18 mo in a shallow bay at Signy Island (Factory Cove, South Orkneys, Antarctica) to test whether and how the temporal variability of the environment influenced meiobenthos dynamics. By examination of the distribution of the abundance and biomass of the total community, the density of higher taxonomic groups, and of individual dominant nematode genera and feeding categories, we assessed changes in faunal structure. Short-term variations were often effective, and several correlations were observed between temperature and food availability (chlorophyll and its derivatives and bulk organic matter, C and N, in both sediment and water column). However, complex temporal patterns characterised the otherwise fairly predictable seasonal variations of the Antarctic ecosystem. The results suggest that variations in meiobenthic population density and structure were primarily regulated by the input and availability of organic matter and less so by water temperature, which was constantly low. The virtual lack of a 'winter stop' also leads to the conclusion that food was not limiting in the Antarctic coastal sediment.

KEY WORDS: Signy Island · Trophic relationships · Free-living marine nematodes · Bentho-pelagic coupling

INTRODUCTION

Shallow marine meiobenthos are known to vary seasonally with the physico-chemical regime (Ansari & Parulekar 1993, Guidi-Guilvard & Buscail 1995), temperature (Juario 1975), and trophic dynamics of the environment (Rudnick et al. 1985, Danovaro 1996, Grémare et al. 1997, Ólafsson & Elmgren 1997). However, parameters regulating their standing stocks within a given site are often poorly described, and it is difficult to separate the effects of, for example, temperature and food availability (Warwick & Buchanan 1971, Bouvy & Soyer 1989, Fleeger et al. 1989) or temperature and salinity (Santos et al. 1996), since these variables are generally closely linked. This is not the case for the Southern Ocean: the combination of low but stable temperature and a markedly seasonal pattern of primary production characterise an environment where annual variations in temperature and production are uncoupled (Clarke 1988). In this study, we have tried to distinguish the relative effect of these 2 factors.

While there is much literature on the meiofauna as a group, investigations on the natural fluctuations within a particular taxon (e.g. nematodes and copepods) are comparatively scarce, and are limited to estuarine (Eskin & Coull 1987, Ansari & Parulekar 1993), intertidal (Alongi 1987, Bouvy & Soyer 1989, Schizas & Shirley 1996), or temperate subtidal (Juario 1975, Boucher 1980, 1983, Rudnick et al. 1985, Vincx 1989, Ólafsson & Elmgren 1997, Steyaert et al. 1999) regions.

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To our knowledge, there is only one study on the seasonal dynamics of a single meiofauna taxon in a polar subtidal ecosystem (i.e. copepods: Ólafsson & Elmgren 1997). The present study places special attention on the temporal variability of the most abundant taxon, the nematodes.

The work reported here represents a year-round study on the ecology of meiofauna in the Antarctic, covering 2 austral winters and the intervening summer, and designed to evaluate how assemblages react to the extreme properties of the Antarctic ecosystem (e.g. low temperature and strong temporal changes in food input). Previous work on meiofaunal structure from the same site demonstrated that very high standing stock, low diversity, and shallow depth penetration in the sediment column may have occurred because of the highly nutritive and reductive character of the benthic environment (Vanhove et al. 1998). Here an attempt is made to discover how the community responds to low temperatures and the markedly seasonal variation in food supply. This has been done by analysing the temporal variability of meiofaunal density, biomass and composition (generic and trophic).

Questions central to this research can be summarised as follows: How do meiofaunal populations fluctuate in the extreme environment of Antarctica? How tightly are they coupled to temperature and temporal changes in primary production?

We hypothesise that, because of the extreme conditions in the Southern Ocean, metazoan meiofauna may, like many macrobenthic organisms (Knox 1994), experience temporal changes tightly coupled to the changing environmental conditions. We expect a sharp increase in standing stock shortly after bloom events, followed by impoverishment due to acute resource limitation mediated by the winter sea-ice cover. If so, this would be accompanied by shifts in taxon composition and feeding guilds.

MATERIALS AND METHODS

Area and period of investigation. Metazoan meiofauna and the surrounding sediments were studied as part of an integrated British research programme (i.e. Antarctica 2000, Ecological and Physiological adaptations, NERC) at Signy Island, South Orkney Islands, Antarctica (60° 43′ S, 45° 38′ W; Fig. 1). The pelagic environment off this site has been extensively monitored, producing a long-term dataset of seawater temperature, ice cover, macronutrients and chlorophyll standing crop (Whitaker 1982, Clarke et al. 1988, Leakey et al. 1994, Clarke & Leaky 1996). The data for the period of investigation are presented in Fig. 2. They show an intense summer period of open-water phytoplankton productivity alternating with a period of low temperature and the presence of winter fast-ice.

A fixed station at 10 m depth near Outer Mooring in Factory Cove was chosen; here the sediment consisted of moderately sorted, very fine sand (medium grain-size range = 73 to 95 μm; SD = 0.71 to 1.00 μm). Sampling was carried out fortnightly from 27 April 1991 to 10 November 1992, covering 2 austral winters and the intervening summer. Duplicate cores were taken for meiofauna counting and identificatios, and 1 core for analysis of particulate organic matter (carbon, nitrogen). A 4th core for pigment (chlorophyll *a*, chlorophyll *c*, fucoxanthin, β-carotene) and dissolved organic carbon (DOC) content of the pore water was taken during the first 11 mo of the time series. The cores were sampled within close proximity of each other. In open-water periods (summer) samples were taken by SCUBA diving from an inflatable boat at the buoy-marked site; in winter sampling was carried out through a hole cut in the fast-ice.
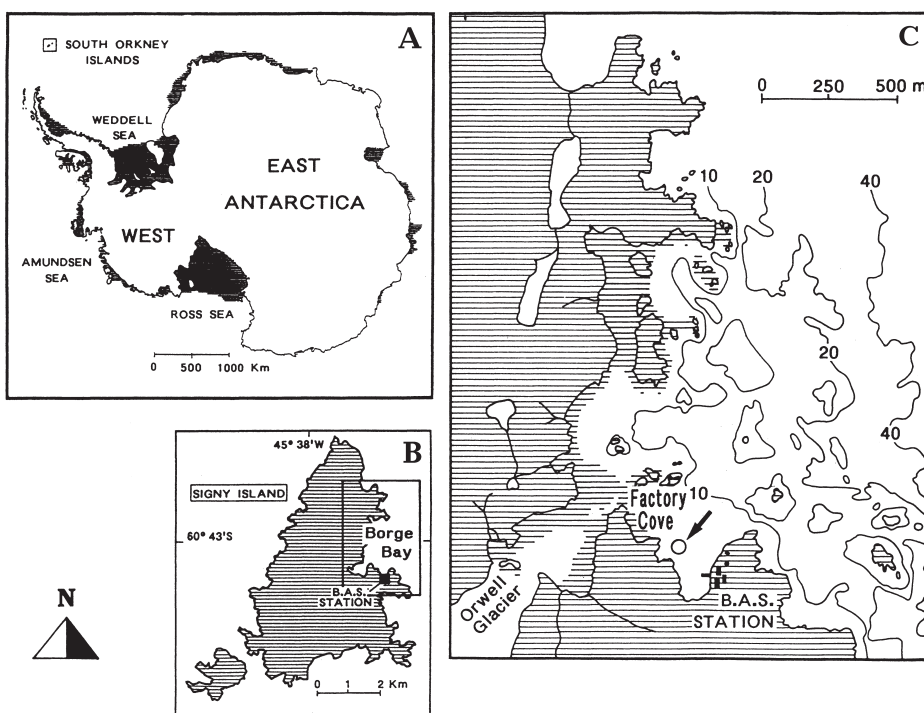

Fig. 1. South Orkney Islands (A), Signy Island (B) and (C) arrow indicates sampling site at Outer Mooring Point, Factory Cove

Meiofauna and nematodes. Meiofauna were extracted from the formalin (buffered with $LiCO_3$; 70°C; 4% final concentration) and preserved. Bulk sediment samples were obtained by decantation, centrifugation, passing through a 1 mm sieve, and retention on a 38 μm screen, according to Higgins & Thiel (1988). The metazoan meiofauna were counted after staining with Rose Bengal. Because of restrictions imposed by time and manpower, subsampling was made from samples with very high meiofauna abundances. This was done by pipetting 3 aliquots of 25 ml from slurry of a 250 ml sediment/water sample (see Table 2). To test the validity of the subsampling method, the adequacy of estimating abundances from subsamples was evaluated by comparing the meiofauna counts from randomly chosen complete cores and the results obtained from 3 recalculated subsamples. No significant differences were found between the 2 methods (the counts agreed within 10%), but a bias attributable to subsampling can be expected to occur more frequently in taxa with low abundances. From each entire sample, approximately 200 randomly chosen specimens were picked out and mounted on glycerine slides (cf. Seinhorst 1959). The weights were determined from length and width, using the adjusted method of Andrassy (Soetaert 1989), i.e.

$$\text{dry weight} = (W^2 \cdot L \cdot 1.13 \cdot 0.25)/1.9$$

where W = maximum body width, L = body length, 1.9 is an empirical value, 1.13 = specific gravity, and 0.25 = dry/wet weight ratio.

Identifications were done based on the pictorial keys to the higher meiofauna taxa of Higgins & Thiel (1988) and nematode genera of Platt & Warwick (1988). The nematodes were classified in 4 feeding groups according to Wieser (1953), distinguishing selective (Category 1A) and non-selective (1B) deposit-feeders, epistratum feeders (2A) and predator/omnivores (2B).

Sediment analysis. Samples for the analysis of elemental total carbon and nitrogen were vertically sliced into 0 to 2, 2 to 5 and 5 to 10 cm layers, oven-dried for 10 h at 60°C before storage, and redried for 24 h at 60°C prior to measurement on a Carlo Erba NA-1500 analyser.

As a measure of microalgal biomass, the concentrations of sediment-bound pigments (i.e. chlorophylls *a* and *c*, β-carotene and fucoxanthin) were determined using the upper 0.5 cm from vertical sliced sediment cores (frozen at −80°C, stored at −20°C). Measurements were done on thawed aliquots filtered onto
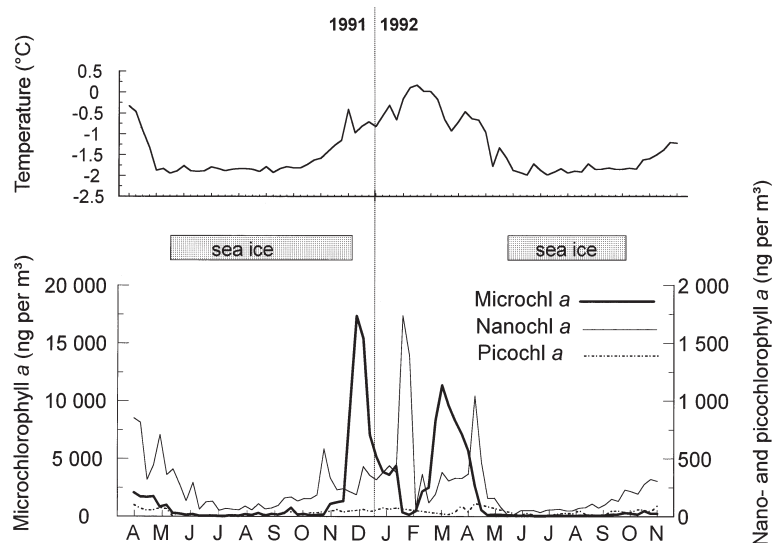

Fig. 2. Variation in sea-ice cover (indicated by shaded bars), temperature and phytoplankton biomass (microchlorophyll *a*, nanochorophyll *a* and picochlorophyll *a*) from April 1991 to November 1992 at Signy Island (data from British Antarctic Survey)

Whatman glass-fibre filters and extracted in 90% acetone on a Gilson HPLC-chain (fluorometrical and UV-visible detection) according to the method of Mantoura & Llewellyn (1983). DOC was measured in pore waters extracted under an N_2 atmosphere of thawed sediment cores, and measured on a SKALAR (SK-12) DOC/TOC-analyser.

Data analysis. Nonparametric statistics were chosen, as the assumptions for parametric analysis were not met (e.g. replication). The matrices of taxon densities (amphipods, bivalves, harpacticoid copepods, nematodes, ostracods and turbellarians), total density, total biomass, and the percentages of the dominant genera were analysed by a Kruskal-Wallis test to determine whether there were significant differences among sampling dates (Siegel 1956). Spearman rank correlations (Sokal & Rohlf 1981) were computed between meiofaunal variables on the one hand and sediment features and water-column variables on the other hand. The water-column variables were obtained from the British Antarctic Survey (A. Clarke pers. comm.) and are presented in Fig. 2. For the respective methods see Clarke & Leaky (1996); fractionating of water-column plankton followed Sieburth (1979), with micro-plankton-cells retained by a 20 μm nylon mesh, nano-plankton-cells passing the 20 μm mesh but retained by a 2 μm Nuclepore membrane, and picoplankton-cells passing the 2 μm membrane but retained by a 0.2 μm Nuclepore membrane.

For all statistical analyses, the 0.05 significance level was used as the conventional rejection value.

RESULTS

Environment

The organic carbon and nitrogen data were highly variable as a function of time in all depth layers, with a mean organic loading of 0.5 % C and 0.03 % N (Fig. 3). DOC varied between ~340 and ~1040 mg l^{-1} (Table 1). Although the minimum value was recorded in September, no clear seasonal trend was observed. Benthic pigments gradually increased from lowest readings in the second half of the winter (September value of 3 µg chlorophyll a g^{-1} sediment) to a maximum in summer (January values of 58 µg chlorophyll a g^{-1} sediment: Table 1).

Total meiofaunal density and biomass

Total meiofaunal density fluctuated between 700 and 18 800 ind. per 10 cm^2 (average 6200 ind. per 10 cm^2). Overall variation between the replicates (i.e. within-sample variance) was significantly lower than between sampling dates (i.e. between-sample variance). The numbers differed significantly between dates (Kruskal-Wallis, p < 0.001). A temporal pattern of high values at the start of the sampling period (>10 000 ind. per 10 cm^2) and much lower numbers in the winter (<5000 ind. per 10 cm^2) was observed during the 1st year (Fig. 4A). Meiofaunal densities peaked in February 1992 (>10 000 ind. per 10 cm^2). In 1992, total density varied greatly, masking any seasonal pattern.

The average total biomass was 1400 µg dry wt per 10 cm^2 (= 0.6 g C m^{-2}) (Fig. 4B). Early winter (May/June) recordings in 1991 were very high (13 290 µg dry wt per 10 cm^2 and differed from all other readings (Kruskal-Wallis, p < 0.001). Biomass declined sharply

to a minimum of 200 µg dry wt per 10 cm^2 in September. A similar but less pronounced temporal variation characterised the 1992 readings with higher values in June (1200 µg dry wt per 10 cm^2), followed by a decline to a minimum in August (200 µg dry wt per 10 cm^2) and a rise at the start of the summer.

Meiofauna taxa

Nematodes (82 % of the meiofauna), followed by harpacticoid copepods, ostracods and turbellarians were the most abundant taxa (Table 2). Others were bivalves and amphipods, which occurred in low proportions, and the remainder consisted of polychaetes, gastrotrichs and halacarids, with only a few specimens per 10 cm^2. As a result of their high relative contribution to total numbers, nematodes strongly structured the pattern of total density (Fig. 5A). The total numbers of nematodes and copepods differed significantly among dates (Kruskal-Wallis, p < 0.001). Maxima in the density of copepods were in April 1991, June 1991, February 1991 and June 1992 (Fig. 5B). The patterns were very similar between the 1st and 2nd year (apart from the aberrant reading in June 1992). No clear annual pattern was visible in ostracod density (Fig. 5C), and a high coefficient of variation (between 2 and 106 %) illustrates high variability between the replicate counts of this taxon. Despite a similar high replicate variation in turbellarian density, clear minima were visible during mid-winter 1991 (Fig. 5D). The 1992 counts were extremely low.

Nematodes

A low number (28) of nematode genera were identified from 15 000 specimens (Table 3). Only 6 genera (*Daptonema*, *Aponema*, *Neochromadora*, *Sabatieria*, *Microlaimus* and *Chromadorita*) were abundant (>2 %), comprising 97 % of the total nematode population. The relative-dominance structure prevailed during the entire study period (Fig. 6). *Sabatieria*, and to a lesser degree *Neochromadora* and *Daptonema*, showed a temporal pattern starting with maximum densities in May/June 1991, gradually decreasing to minima in September/October 1991 and then increasing again towards the next summer (January/February 1992) (Fig. 7). The temporal pattern of the 2nd Antarctic season was more complicated. The distribution patterns of *Aponema*, *Microlaimus* and *Chromadorita* were sporadic. Epistrate and non-selective deposit-feeders dominated
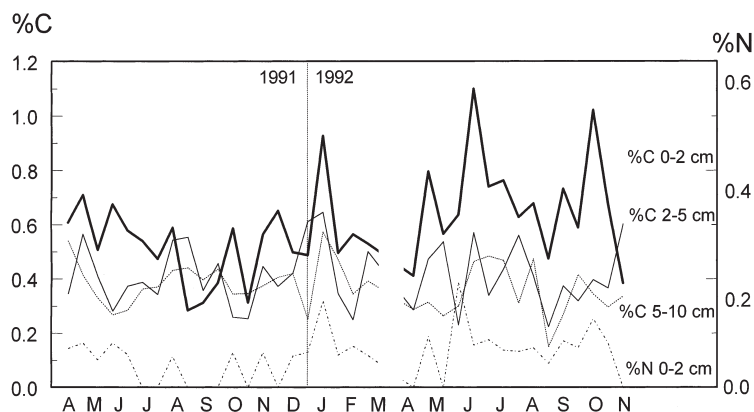

Fig. 3. Variation in organic carbon (mass %) in 0 to 2, 2 to 5 and 5 to 10 cm core sections and organic nitrogen (mass %) in 0 to 2 cm horizon from April 1991 to November 1992 at Signy Island

Table 1. Dissolved organic carbon (DOC, mg l^{-1}) and chloropigment concentrations (µg g^{-1}) in sediments of Factory Cove; mean of 2 replicates (SD)

Sampling date	DOC Mean	SD	Chlorophyll *a* Mean	SD	Fucoxanthin Mean	SD	Chlorophyll *c* Mean	SD	β-carotene Mean	SD
1991										
27 Apr	1037	(571)								
14 May			26	(2.6)	13	(2.6)	7	(1.1)	9	(1.7)
28 May	528	(118.2)								
11 Jun			31	(13.3)	14	(5.1)	10	(8.3)	10	(3.4)
26 Jun	630	(365.4)								
12 Jul			18	(4.5)	7	(1.4)	4	(4.2)	5	(1.0)
28 Jul	938	(1048)								
10 Aug			28	(2.6)	13	(1.2)	7	(0.7)	9	(0.8)
23 Aug	639	(248.6)								
05 Sep			3	(0.3)	2	(0.0)	1	(0.1)	1	(0.0)
20 Sep	342	(182.7)								
04 Oct			14	(14.1)	6	(5.8)	4	(3.5)	4	(3.9)
17 Oct	851	(768.5)								
14 Nov	594	(56.4)								
28 Nov			27	(6.1)	12	(2.5)	8	(2.0)	8	(1.7)
13 Dec	919	(591.2)								
27 Dec			23	(20.4)	13	(6.3)	8	(4.2)	9	(4.2)
1992										
10 Jan	598	(663.7)								
22 Jan			58	(16.2)	28	(7.8)	16	(3.4)	19	(5.2)
09 Feb	786	(693.3)								
26 Feb			49	(33.5)	26	(11.6)	13	(6.5)	18	(7.8)

the samples (Fig. 8). They switched in ranking over the annual cycle, with the epistrate feeders (Category 2A) generally prevailing over the non-selective deposit-feeders (1B). The abundances of both trophic guilds showed very strong oscillations during the entire period of investigation. Selective deposit-feeders (Category 1A) and predators/omnivores (2B) were very scarce in our samples.
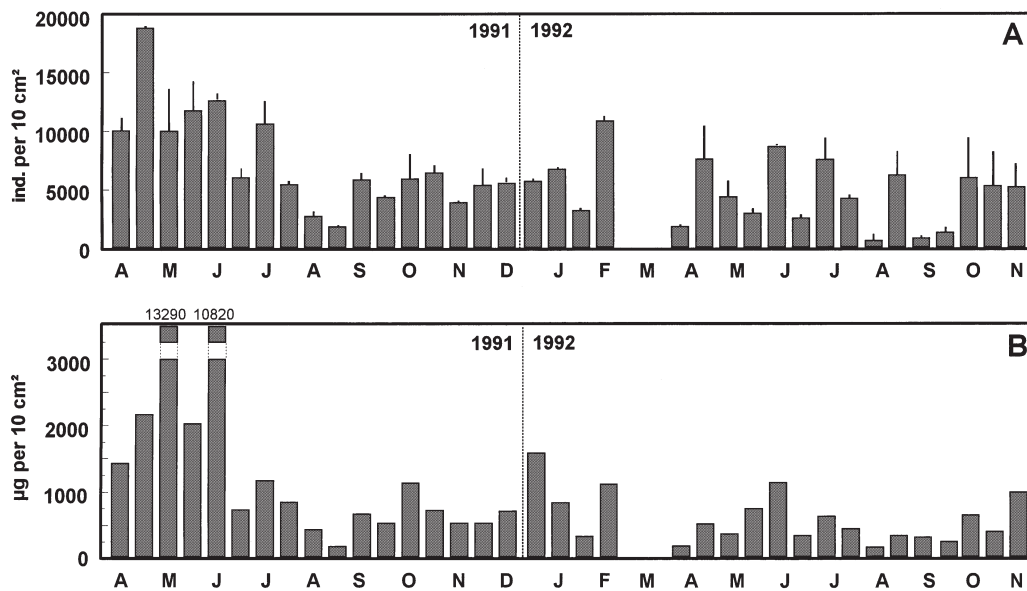

Fig. 4. (A) Total density (ind. per 10 cm^2 ± 1 SD, n = 2) and (B) total biomass (µg per 10 cm^2) from April 1991 to November 1992 at Signy Island

Correlations between meiofaunal taxa and environmental variables

Correlation analysis (Table 4) showed that meiofaunal taxa were positively related to the temperature of the seawater. The same taxa were also correlated with nanochlorophyll concentrations in the water column. Turbellarians and nematodes were positively correlated with the bigger microchlorophyll fraction and its derivates. Harpacticoid copepods were positively correlated with the sediment-bound pigments and organic nitrogen in the sediments. Some scattered relationships were observed between the nematode genera and trophic types on the one hand and environmental variables on the other.

More significant correlations were obtained between meiofaunal and water-column variables when only the 1st year of the time series was used (Table 5A). All of them were positive. Densities of bivalves, adult harpacticoids, ostracods, turbellarians and nematodes were correlated with the food available in the water column.
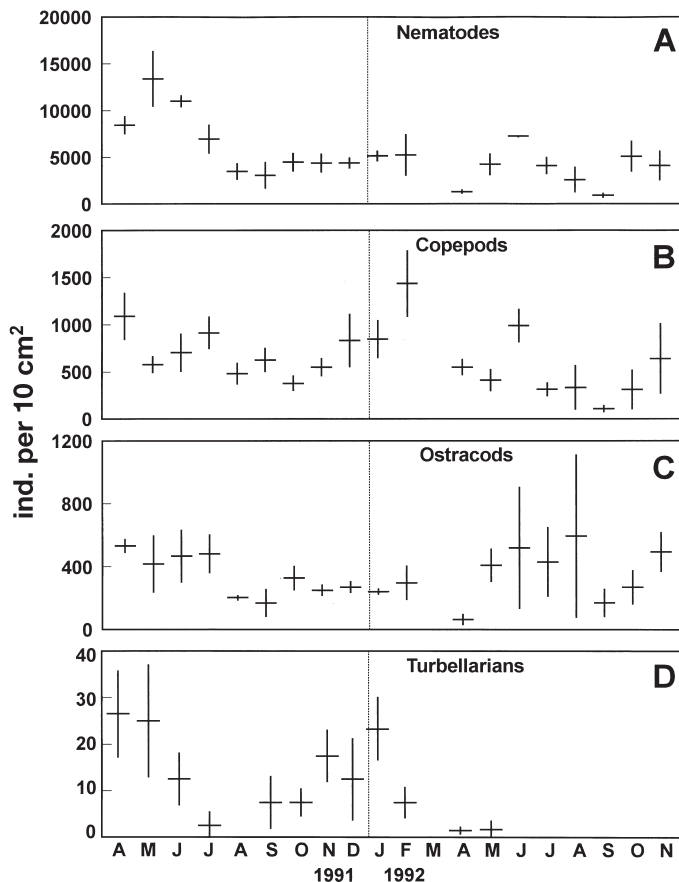
Table 2. Relative proportion of nematodes, harpacticoids + nauplii, ostracods and turbellarians during the sampling period. Values averaged over 2 replicates. Asterisks indicate subsampling

Sampling date		Nema-todes	Harpacticoid copedods	Ostracods	Turbel-larians
1991					
27 Apr	*	84	11	5	0.3
14 May	*	92	4	4	0.1
28 May	*	93	5	2	0.3
11 Jun	*	90	5	4	0.0
26 Jun	*	90	6	3	0.2
12 Jul	*	80	11	8	0.0
28 Jul	*	84	11	4	0.0
10 Aug	*	85	12	4	0.0
23 Aug	*	81	11	7	0.0
05 Sep		58	38	4	0.0
20 Sep	*	85	9	4	0.3
04 Oct	*	82	7	10	0.2
17 Oct	*	87	8	4	0.1
14 Nov	*	89	7	4	0.2
28 Nov	*	75	17	7	0.5
13 Dec		86	8	6	0.0
27 Dec	*	73	22	4	0.5
1992					
10 Jan	*	77	17	4	0.5
22 Jan	*	85	10	4	0.2
09 Feb		62	31	6	0.3
26 Feb	*	78	18	4	0.0
16 Apr		68	29	3	0.1
04 May	*	90	4	7	0.0
15 May	*	87	8	4	0.1
29 May	*	65	18	16	0.0
13 Jun	*	83	11	6	0.0
01 Jul	*	84	12	4	0.0
16 Jul	*	83	5	12	0.0
28 Jul	*	90	5	5	0.0
15 Aug		91	3	6	0.0
27 Aug	*	73	10	17	0.0
11 Sep		86	6	7	0.1
28 Sep	*	67	11	22	0.0
07 Oct	*	96	1	3	0.0
27 Oct	*	76	14	9	0.0
10 Nov	*	78	12	10	0.0

Fig. 5. Abundance (ind. per 10 cm^2 ± 1 SD, n = pooled number of replicates per month) of the 4 major taxa from April 1991 to November 1992 at Signy Island. Ordinate scale varies with taxon

The nematodes and bivalves were also positively correlated with the temperature of the seawater. *Daptonema* and *Sabatieria*, members of the non-selective deposit-feeders (Group 1B), and *Chromadorita* and *Neochromadora*, members of the epistrate feeders (Category 2A) were all positively correlated with the quantity of food in the water column. The relations differed however with size fraction of the pigments. The same genera were also positively correlated to the temperature of the water. When restricting the analysis to the 2nd year of the time series (Table 5B), the only significant correlations were between harpacticoid density (adults, nauplii and total) and all size fractions of the water pigments (positive relation), and between *Daptonema* and the nano- and pico-fraction of the water pigments (positive relation).

DISCUSSION

The meiofaunal community structure at Signy Island resembled that of communities in other shallow, subtidal, fine sediments (Heip et al. 1985), but an extremely high meiofauna standing stock was found throughout the sampling period (average density = 6.2×10^6 ind. m^{-2} and average biomass = 1.4 g dry wt m^{-2}). The peak density in May 1991 (18.8×10^6 ind. m^{-2} and 13.3 g dry wt m^{-2}) was higher than reported for any other sediment (see comparison in Vanhove et al. 1998). Based on annual P:B values for temperate nematodes, annual production is estimated to be between 2.2 and 38.4 g C m^{-2} for P:B ratios between 4 and 69 (Vranken & Heip 1986), and 5.0 g C m^{-2} for a P:B of 9 (Gerlach 1971). These values greatly exceed those calculated for nematodes (average 1.2 g C m^{-2} yr^{-1}: Heip et al. 1982; max. 2.6 g C m^{-2} yr^{-1} in the North Sea: Vincx 1989).

The relationship linking meiofauna and primary producers has been underlined by many authors (Montagna et al. 1983, Romeyn & Bouwman 1983). In the present study, correlations between meiofaunal and environmental variables pointed often towards food sources in the water column. Almost all relationships were positive, indicating that planktonic food was indeed a very important structuring force for the temporal distribution of the meiobenthic communities. For example, harpacticoid copepod numbers followed patterns of water-column productivity, with high densities in productive periods and low numbers in late winter. They showed immediate responses to the nanochloro-

phyll fraction (cf. Fig. 5B with Fig. 2, bottom graphs), and were related with a time-lag to all other food components in the water column and to pigments in the sediments. This is consistent with the results of other studies, which report that copepod densities are strongly associated with fresh inputs of food into the system, often with a time-lag of ~2 mo (Montagna et al. 1983, Shirley et al. 1987, Decho & Fleeger 1988, Rudnick 1989).

While temporal fluctuations were evident for harpacticoid copepods, other taxonomic groups, individual nematode genera and trophic groups sometimes showed more complicated patterns. Fluctuations in densities were often very large, and inter-annual variability was also large. There was very little or no agreement with the traditional seasonal picture of Antarctic production (i.e. varying between a summer maximum of >15 and a negligible winter minimum of <1 mg m^{-3} microchlorophyll a). Why do most of the meiofauna communities at Signy Island display so poor seasonality despite their many correlations with the seemingly highly seasonal trophic environment?

A variety of factors may account for the difficulty to interpret the temporal variations of the meiofauna community in terms of seasonality. One factor is the uncommon character of the pelagic environment during the seasons under study. Usually, an annual cycle in pelagic activity at Signy Island occurs throughout a summer bloom (December and January) of diatoms, superimposed on a less intense but longer nanoflagellate bloom. In the middle of winter, nanoplankton chlo-
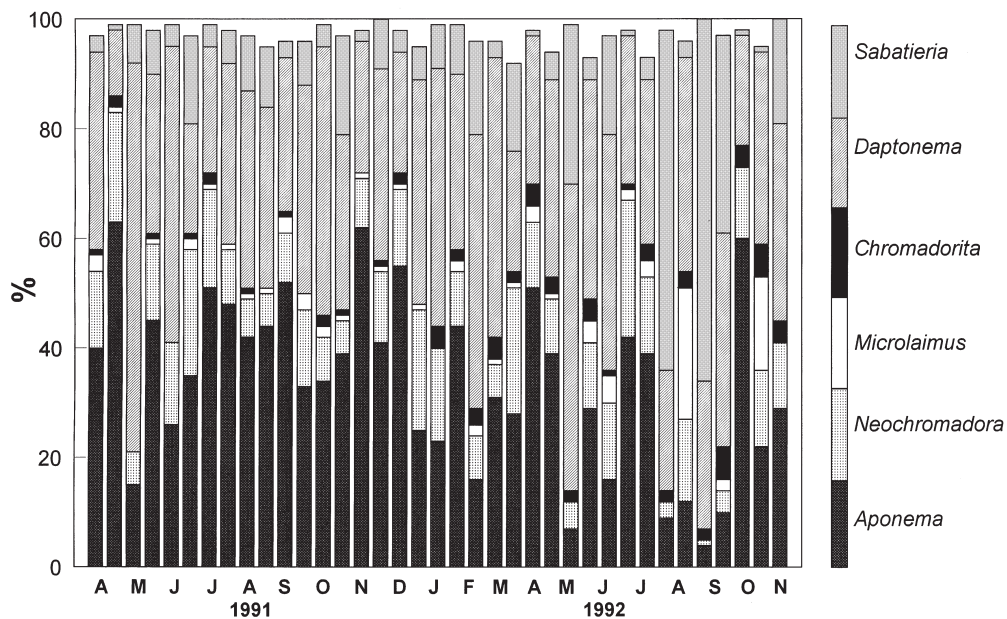

Fig. 6. Comparison of relative composition (mean % of 2 cores) of the 6 predominant nematode genera in sediments of Signy Island during the course of study
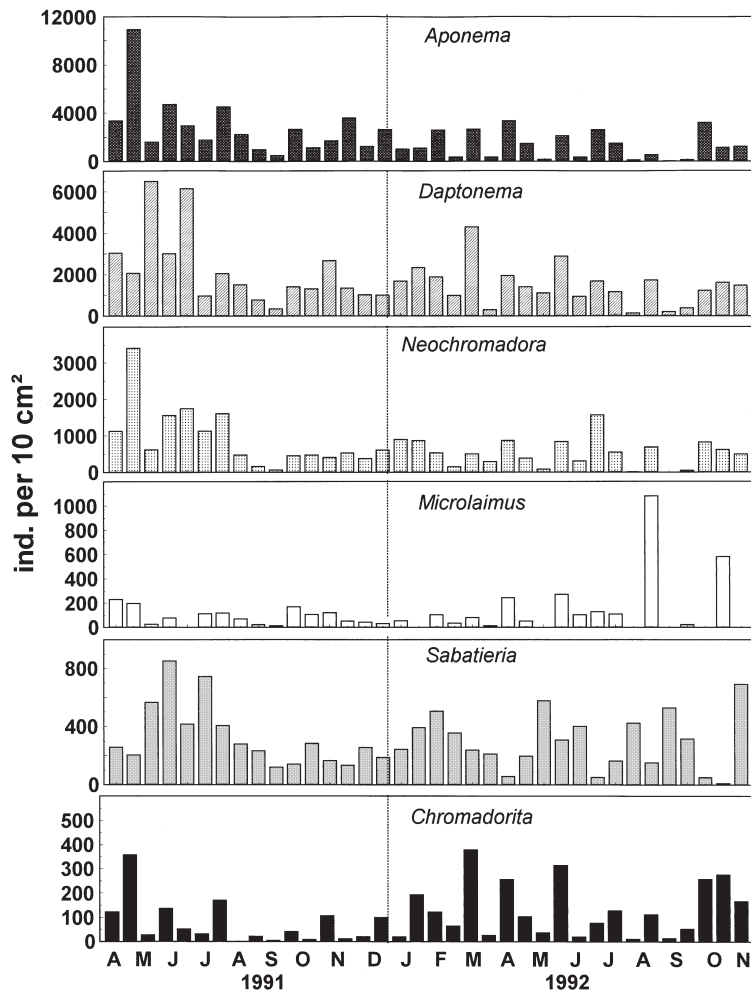
Fig. 7. Temporal variability of density (mean ind. in two 10 cm^2 cores) of the 6 predominant genera in sediments of Signy Island

Generally, strong benthic-pelagic coupling may be expected in high-latitude areas because these are often characterised by high levels of 'new primary production' attributed to large phytoplankters, especially diatoms, which have high sinking rates (Smetacek 1980, 1984). This was underlined by our observations: positive correlations between the sediment-bound pigments from our study and water column variables from the study of Clarke & Leaky (1996) indicate that production and deposition events can be tracked in the sediments, with some weeks of delay for diatom blooms, and no visible delay for flagellate blooms. This is also supported by the fact that peaks of benthic pigments followed maximum settlement rates of chlorophyll and phaeophytin in sediment traps (Nedwell et al. 1993).

It is possible that the community of bottom-dwelling organisms was fuelled to a large extent by labile organic matter from the pelagic system. For example, during the 1st year, total density and biomass were very high in early winter, shortly after the post-summer minibloom (Fig. 9) and high carbon availability in the sediments (Nedwell et al. 1993). During the 2nd year, higher total biomass values in late summer were recorded after the first diatom bloom, and elevated biomass in early winter lagged the 2nd autumn bloom, confirming again the response of meiofaunal standing stock to food input into the system.

Stock sizes dropped significantly (to almost 50%) within 2 wk and depauperation occurred until only 10% of initial peak density and 1% of initial total biomass remained. This minimum occurred around the period of extreme low primary production. The winter, rather than being a severe period with low densities, was confined to a short interval around August, and even when stocks were drastically depressed, the minimum values (1.9×10^6 ind. m^{-2} and 0.2 g dry wt m^{-2}: 5 September 1991) were still comparable to average values in many shallow soft-bottom communities (see review by Rudnick et al. 1985). Nanoplankton, occurring throughout much of the year, might be sufficient to maintain the deposit-feeding meiobenthic groups at reasonable high densities during winter. This suggests that pelagic food was not the limiting factor for the meiofauna at Signy Island during the study period.

However, pelagic production is probably not the only factor influencing temporal patterns in the meiofauna.

rophyll concentrations often exceed microplankton chlorophyll concentrations, which are generally very low (0.05 mg m^{-3}) (Fig. 9). However, the summer season of 1990/1991 was not as predictable as in other years. Apart from the normal diatom bloom of 16 mg m^{-3}, a second small bloom of microchlorophyll (<5 mg m^{-3}) was observed. This mini-bloom peaked in the period preceding our sampling (March 1991: arrowed in Fig. 9). Superimposed upon this was a more intense nanoplankton production compared to other seasons, which prevailed from early summer to early winter 1991 (Figs. 2 & 9). The 1991/1992 summer season had 2 consecutive microchlorophyll blooms, with peaks of 17.5 and 11.5 mg m^{-3} in early summer (November/December) and autumn (March/April), respectively. Furthermore, 2 nanoplankton peaks (1.75 and 1 mg m^{-3}) before the appearance of sea-ice mirrored the 2 blooms in the microplankton size fraction (Clarke & Leaky 1996).
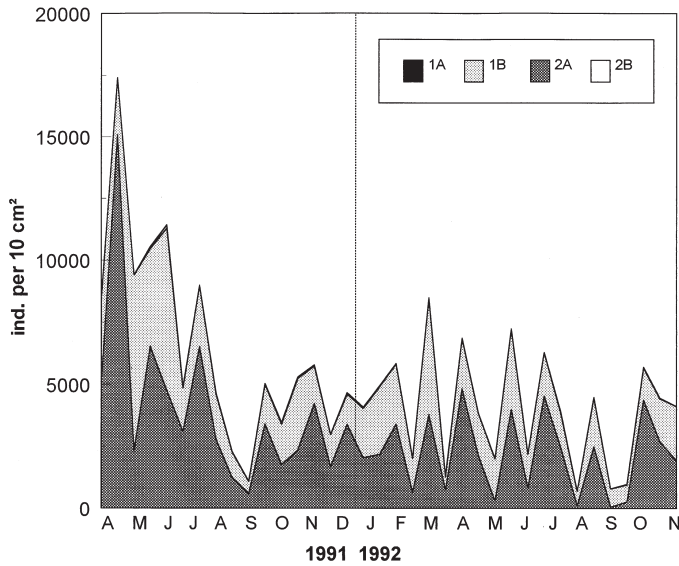
Fig. 8. Variation in trophic composition of nematode communities during time course of study. Category 2A: epistrate feeder, 1B: non-selective deposit-feeder, 1A: selective deposit-feeder, 2B: predator/omnivore. Data are mean numbers of two 10 cm² sediment cores

Table 3. Ranking in feeding categories of nematode genera retrieved from sediments of Factory Cove during the sampling period. 1A: selective deposit-feeder; 1B: non-selective deposit-feeder; 2A: epistrate-feeder; 2B: predator/omnivore

Genus	Trophic type	%
Daptonema	1B	34.96
Aponema	2A	34.12
Neochromadora	2A	12.05
Sabatieria	1B	11.55
Microlaimus	2A	2.49
Chromadorita	2A	2.08
Sphaerolaimus	2B	0.62
Dichromadora	2A	0.61
Prochromadorella	2A	0.50
Promonhystera	1B	0.44
Eleutherolaimus	1B	0.29
Calomicrolaimus	2A	0.05
Desmodora	2A	0.05
Leptolaimus	1A	0.04
Desmoscolex	1A	0.02
Molgolaimus	2A	0.02
Camacolaimus	2A	0.02
Odontophora	1B	0.02
Southerniella	1A	0.01
Oxystomina	1A	0.01
Ascolaimus	1B	0.01
Marylynnia	2A	0.01
Terschellingia	1A	0.01
Epsilonematodae sp.	1A	0.01
Paramesonchium	2A	0.01
Gammanema	2B	0.01
Syringolaimus	2B	0.01
Paracanthonchus	2A	0.00
		100

First, *in situ* microphytobenthic production around Signy Island can be substantial and highly variable, amounting to slightly over 100 mg C m⁻² during the ice-free summer, with peaks of 700 mg C m⁻² d⁻¹. This production might have led to an increase in sediment-chlorophyll concentrations in the period prior to the phytoplankton bloom (in November/December) (Gilbert 1991).

Second, sediment-bound organic sources might become part of the microbial loop. In benthic food chains, microbial communities are important because of their fast growth and high metabolic activity. In association with organic material (Meyer-Reil 1983), and along with diatoms, bacteria may belong to the food available to the meiobenthos (Admiraal et al. 1983, Montagna et al. 1983, Ansari et al. 1993, Moens & Vincx 1997, Moens et al. 1999). Meiofaunal density and biomass fluctuations in the current study coincided with the highs and lows of the respiratory activity of microbial communities (Nedwell et al. 1993). This occurred partly during the 'winter stop' in pelagic production. A great portion of deposited organic matter is, however, refractory (Tyson 1995). This older detritus is less
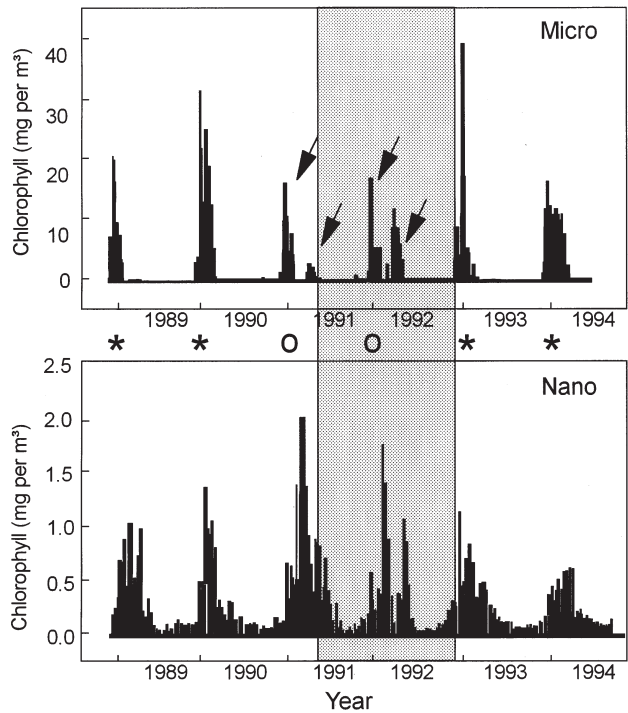

Fig. 9. Standing crop (mg m⁻³) chlorophyll *a* in microplankton (>20 µm) and nanoplankton (2 to 20 µm), Signy Island, December 1988 to April 1994. Note differing vertical scales for the 2 size fractions. ★: Usual year, with 1 bloom; O: unusual year, with 2 blooms (arrows). Shading covers: present study period. (From Clarke & Leaky 1996)

assimilatable than fresh, labile, organic matter (Rudnick 1989). This might be the reason why in our study only few meiofaunal taxa were correlated with bulk organic matter (organic C and N) in the sediments. Therefore, this variable is of little value in predicting meiofaunal standing stock and seasonality at Signy Island.

Third, many taxa have the ability to switch their diet when a specific food item is limited (Moens & Vincx 1997) or when the quality of organic matter available to the deposit- and epistratum-feeders changes with season (Grémare et al. 1997). In Signy Island, *Daptonema* spp. may be opportunistic feeders. The frequent occurrence of intact pennate diatoms in the alimentary duct (i.e. observed trough the transparent wall of the nematodes under the light microscope) led us to believe that this genus can switch to a diet consisting solely of diatoms. In periods of low diatom abundance, this non-selective deposit-feeder consumes bacteria or flagellates. The ability to switch diet may also explain why the dominance structure in the nematode communities did not alter appreciably during the study period, despite frequent fluctuations in the abundance. The results underscore the importance of the experimental approach.

The Pearson & Rosenberg model of eutrophication may explain the temporal patterns in meiofaunal structure at Signy Island (Pearson & Rosenberg 1978). The increased amounts of organic material in the sediments may result in increased heterotrophic metabolism of bacteria and hence grazing of detritus-feeding animals. Eventually this led to increases in benthic biomass, density and diversity. However, excess labile organic matter may also accumulate, producing a high demand for oxygen and leading locally (in space and time) to hyperoxic, sulphidic bottom-water. In this case, structural characteristics such as high abundance and biomass with low diversity typify the faunal communities (as found during the summer of 1994: Vanhove et al. 1998). In a more advanced state of eutrophication, if enrichment continues, fauna may depauperate despite high food availability. This could explain the sudden troughs in the meiobenthic population sizes.

Table 4. Results of Spearman rank correlation between meiofaunal and environmental variables. Water column, n = 20 (20 mo): microchlorophyll *a*, microphaeopigments, nanochlorophyll *a*, nanophaeopigments, picochlorophyll *a*, picophaeopigments, temperature (from A. Clarke, BAS, Cambridge). Sediment: pigments (n = 10, chlorophyll *a*, chlorophyll *c*, fucoxanthin, β-carotene); dissolved organic carbon (n = 11), particulate organic carbon (n = 36), particulate organic nitrogen (n = 36). ns: not significant; –: significantly negative (p ≤ 0.05); ––: highly significantly negative (0.05 < p ≤ 0.01); –––: very highly significantly negative (0.01 < p ≤ 0.001); +: significantly positive (p ≤ 0.05); ++: highly significantly positive (0.05 < p ≤ 0.01); +++: very highly significantly positive (0.01 < p ≤ 0.001)

| | Water column | | | | | | | Sediment | | | | | | |
	Micro-chl *a*	Micro-phaeo	Nano-chl *a*	Nano-phaeo	Pico-chl *a*	Pico-phaeo	*T*	Chl *a*	Chl *c*	Fuco	β-car	DOC	Org C	Org N
Meiofauna														
Total density	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Number of taxa	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Taxon densities														
Amphipods	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Bivalves	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Harpacticoids	ns	ns	+	ns	ns	ns	+	+ +	+ + +	+ + +	+ + +	ns	ns	+
Ostracods	ns	ns	+	ns	ns	ns	+	ns	ns	ns	ns	ns	ns	ns
Turbellarians	+ + +	ns	+ + +	ns	ns	ns	+ +	ns	ns	ns	ns	ns	ns	ns
Nematodes	ns	+	+ +	ns	ns	ns	+ +	ns	ns	ns	ns	ns	ns	ns
Nematodes														
Total biomass	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Genus densities														
Daptonema	ns	ns	+	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Aponema	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Neochromadora	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Sabatieria	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Microlaimus	ns	+	ns	+	ns	ns	ns	ns	+	+	+	ns	ns	ns
Chromadorita	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Trophic category														
1A	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
2A	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
1B	ns	ns	+	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
2B	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	–	ns	ns

Finally, apart from trophic characteristics of the Antarctic environment, another important factor may explain the variability in the meiofaunal communities at Signy Island. A critical factor for benthos living in the Southern Ocean may be low temperature. Energetic consequences that have often been proposed include slow growth, delayed maturation, longevity, large size, low fecundity, and low metabolic rate (Knox 1994). Likewise, low temperature imposes specific reproductive strategies in the subantarctic nematodes of the Kerguelen Islands, as nematode development time has been found to vary between 30 and 75 d, at 10 and 2°C, respectively (Bouvy & Soyer 1989).

In our study, many meiobenthic variables were correlated with temperature. As reproductive and development rates of nematodes are positively correlated with temperature, meiobenthic communities were expected to peak in abundance during the warmer months. However, individual taxa often reached their highest abundance at other times of the year. Small temperature oscillations may have accounted for the short-term variations in meiofauna numbers. Similar conclusions were drawn for the meiofauna communities of the subantarctic Kerguelen Islands by de Bovée et al. (1983), Bouvy (1988), and Bouvy & Soyer (1989).

Conclusion

The results support our hypothesis that the metazoan meiofauna at Signy Island (Antarctica) experiences fundamental temporal variations that are more or less coupled to the environmental variations. Although many fluctuations may be due to factors of unknown nature (for example physical disturbance by storm, macrofaunal activity, biological interactions within the meiofauna, etc.) the strong temporal variations in stock sizes emphasise the relatively low impact of the small variations in temperature, compared to the distinct temporal impact of food supply.

Table 5. Results of Spearman rank correlation between meiofaunal and water-column variables: microchlorophyll *a*, microphaeopigments, nanochlorophyll *a*, nanophaeopigments, picochlorophyll *a*, picophaeopigments, temperature (from A. Clarke, BAS, Cambridge). (A) Datamatrix reduced to 1st year (April 1991 to December 1991, n = 9 corresponding to first 9 mo); (B) Datamatrix reduced to 2nd year (January 1992 to November 1992, n = 11 corresponding to last 11 mo). ns: not significant; –: significantly negative (p ≤ 0.05); ––: highly significantly negative (0.05 < p ≤ 0.01); –––: very highly significantly negative (0.01 < p ≤ 0.001); +: significantly positive (p ≤ 0.05); ++: highly significantly positive (0.05 < p ≤ 0.01); +++: very highly significantly positive (0.01 < p ≤ 0.001)

	(A)							(B)						
	Micro-chl *a*	Micro-phaeo	Nano-chl *a*	Nano-phaeo	Pico-chl *a*	Pico-phaeo	*T*	Micro-chl *a*	Micro-phaeo	Nano-chl *a*	Nano-phaeo	Pico-chl *a*	Pico-phaeo	*T*
Meiofauna														
Total density	+	+	+++	+	++	+	+++	ns	ns	ns	ns	ns	ns	ns
Number of taxa	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Taxon densities														
Amphipods	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Bivalves	++	++	ns	ns	+	+	++	ns	ns	ns	ns	ns	ns	ns
Harpacticoid adults	ns	ns	+	+	ns	ns	ns	+	+	+	+	+	+	ns
Harpacticoid nauplii	ns	ns	ns	ns	ns	ns	ns	+	+	ns	ns	ns	ns	ns
Harpacticoid total	ns	ns	ns	ns	ns	ns	ns	+	+	+	+	+	+	ns
Ostracods	ns	ns	+	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Turbellarians	ns	ns	ns	ns	+	ns	ns	ns	ns	ns	ns	ns	ns	ns
Nematodes	++	+	+++	+	++	+	++	ns	ns	ns	ns	ns	ns	ns
Nematodes														
Total biomass	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Genus densities														
Daptonema	++	++	++	+	+++	++	+++	ns	ns	++	ns	++	ns	ns
Aponema	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Neochromadora	ns	ns	++	ns	+	ns	+	ns	ns	ns	ns	ns	ns	ns
Sabatieria	ns	ns	++	ns	ns	+	+	ns	ns	ns	ns	ns	ns	ns
Microlaimus	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Chromadorita	++	++	++	++	++	++	+++	ns	ns	ns	ns	ns	ns	ns
Trophic category														
1A	ns	ns	+	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
2A	+	+	++	ns	+	ns	++	ns	ns	ns	ns	ns	ns	ns
1B	++	ns	++	+	++	++	+	ns	ns	ns	ns	ns	ns	ns
2B	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns

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