

Deep-sea meiofauna communities in Antarctica: structural analysis and relation with the environment

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ABSTRACT: The metazoan meiofauna in the region off Kapp Norvegia, Antarctica (Weddell Sea; 71° S, 12° W), was collected from depths between 211 and 2080 m. Total meiofaunal abundance ranged from 815 to 5122 ind. per 10 cm² and total biomass from 126 to 966 µg dwt per 10 cm². Nematodes dominated the samples (range 83 to 97%), followed by harpacticoid copepods, polychaetes and kinorhynchans. A typical skewed length frequency distribution was obtained with most nematodes in the 0.4 to 0.6 mm size-class. The meiofauna communities were primarily influenced by bathymetric depth and food availability (e.g. organic matter and microbiota), which in turn are suggested to be directly related to phytoplankton blooms and associated sedimentation pulses. Standing stock and distribution patterns indicate that the meiofauna from the Weddell Sea show similar features to major deep-sea assemblages elsewhere in the world.

KEY WORDS: Meiofauna · Continental margin · Antarctica

INTRODUCTION

The ecology of deep-sea meiofauna has been extensively studied since the first quantitative investigation by Wigley & McIntyre (1964). Most of these studies, however, have focused on the Atlantic, Pacific and Indian Oceans (Vincx et al. 1994). So far only 2 meiofauna studies have investigated sediments from deep polar seas: one in northern boreal waters (Pfannkuche & Thiel 1987) and one in the Weddell Sea, Antarctica (Herman & Dahms 1992).

Compared to other oceanic regions, the pelagic of the Southern Ocean (e.g. south of 50° S) has a very short, but extremely intense, summer phytoplankton bloom, often associated with the melting of the pack-ice. As benthic communities depend heavily on the

supply of resources from the water column, the seasonality, intensity and spatial heterogeneity of depositing matter will certainly affect the size and structure of its components. The intense pulse in primary production results in strong sedimentation of organic matter to the sea bed (Knox 1994).

From macrobenthic studies it appears that Antarctic shelf and slope sediments support high biomasses and large numbers of individuals, characterized by a relative scarceness of infaunal worms. Towards the deep sea (below 1000 m) Antarctic and non-Antarctic biomass levels do not seem to differ greatly (Arntz et al. 1994).

Studies on cycling of organic matter in deep-sea sediments of the northeast Atlantic suggest degradation rates of 0.3 to 2.9% d⁻¹ (Lochte 1992). Remineralization processes in the sediment mainly involve bacteria (Poremba 1994), but meiofauna also play an important role (Findlay & Tenore 1982, Ingham et al. 1985, Alkemade et al. 1992, Giere 1993).

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The objectives of this study are (1) to assess the composition and population densities of the meiofauna off Kapp Norvegia, in the Weddell Sea (71 to 72° S, 12 to 13° W) and describe their distribution across the continental margin; (2) to compare the results with a previous study on meiofauna composition in a similar transect in the Weddell Sea to the south and west of the present study (Herman & Dahms 1992, Halley Bay); and (3) to relate the benthic structures to events occurring in the overlying water column by comparison with other deep-sea areas in the world.

This study serves as background for a more detailed investigation on the meiofauna in the Antarctic environment. In the future, research emphasis will be on the ecological role of the most abundant and ecologically important taxon, the nematodes.

MATERIAL AND METHODS

Study area and treatment of meiofauna samples (Fig. 1, Table 1). Samples were collected off Kapp

Norvegia (Weddell Sea, 71 to 72° S, 12 to 13° W) during the third leg of the European Polarstern Study (EPOS) carried out by the RV 'Polarstern' between 13 January and 10 March 1989). General descriptions of the biological, chemical and physical characteristics of the Weddell Sea during the present investigation are given by Hempel (1993). Characteristic features of sedimentation, hydrography and topography off Kapp Norvegia are described in Grobe (1986). The investigated bathymetric range was between 211 and 2080 m. Ice had started to retreat during the sampling period. The sediments are of glacial marine and biogenic origin (Hough 1956), and mainly consist of fine sands.

Samples were taken with a multicorer with a hydraulic system (MUC; each core 25 cm²; Barnett et al. 1984). A multiboxcorer (MG; each core 240 cm²; Gerdes 1990) was used where sampling with the more fragile multicorer was impossible, because of bad weather conditions and high sediment gravel content. The sampling device and original station numbers are included in Table 1. In both cases meiofauna was sub-sampled using 10 cm² plastic cores and material was

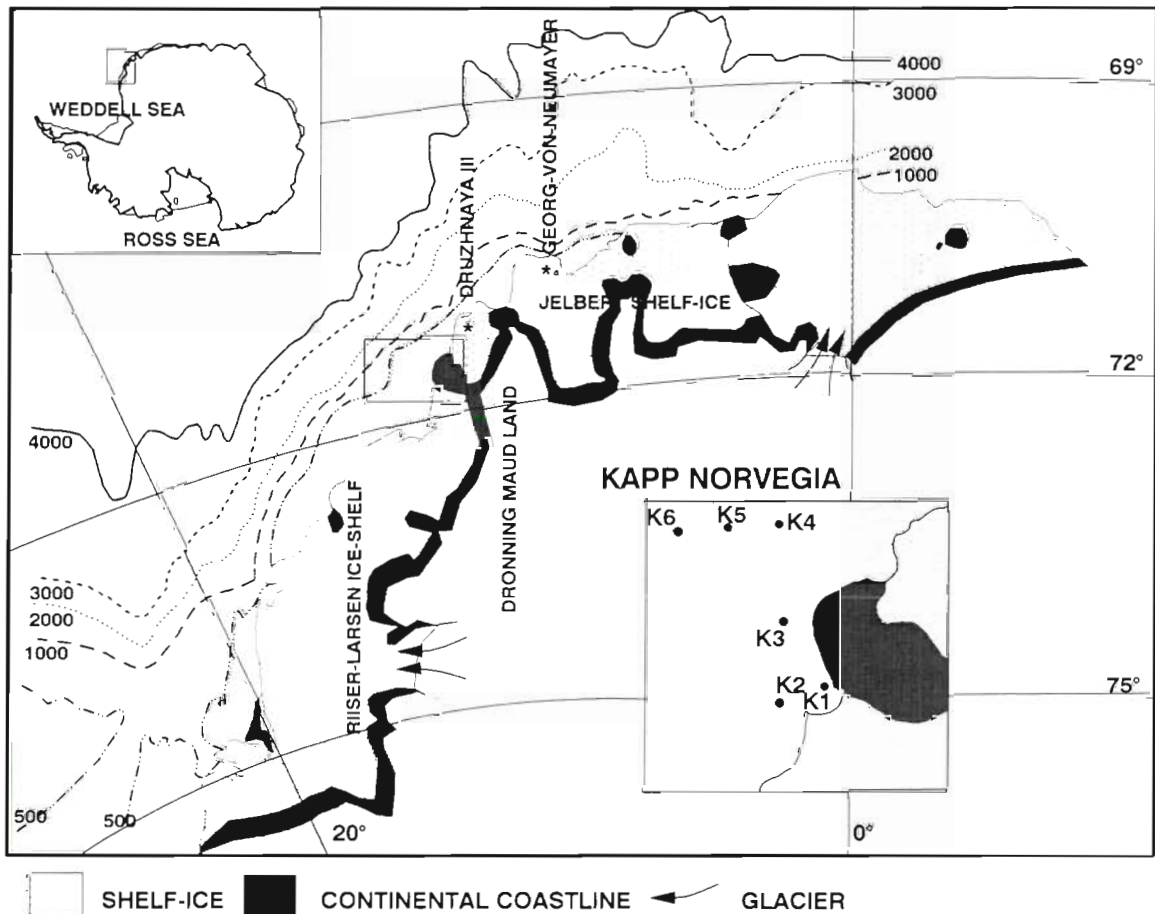


Fig. 1. Map showing the study area in the Weddell Sea, with station locations

Table 1 Environmental characteristics at the study sites in the Weddell Sea. Values are integrated over the top 5 cm, except where stated. Original station numbers and sampling gear employed (MG: multiboxcorer; MUC: multicorer) are added

Station:	Kapp Norvegia						Halley Bay											
	K1	K2	K3	K4	K5	K6	H1	H2	H3	H4	H5	H6	H7	H8	H9	H10	H11	H12
Station number (according to Arntz et al. 1990)	274	277	278	292	294	295	226	229	230	235	241	245	248	249	250	252	253	258
Depth (m)	211	405	537	561	1199	2080	582	502	247	399	458	492	633	681	806	1183	1958	502
Sampling gear	MG	MG	MG	MG	MUC	MUC	MUC	MUC	MG	MUC	MUC	MUC	MUC	MUC	MUC	MUC	MUC	MG
Sediment granulometry (%)																		
Mean (phi)	4.0	4.1	3.4	5.0	5.7	5.7	4.3	4.0	2.9	4.1	5.4	3.9	2.6	2.5	2.7	4.2	6.7	
Gravel	6.1	34.5	40.1	15.7	1.0	1.0	0.0	0.0	1.5	0.0	7.0	19.1	11.4	17.6	2.1	0.0	0.0	
Very coarse sand	16.0	9.5	16.8	16.2	2.0	2.0	0.1	0.6	11.1	2.9	2.6	8.7	13.6	12.1	6.1	1.2	2.5	
Sand	48.0	33.9	33.8	36.2	26.6	26.6	61.8	67.5	76.0	58.6	25.8	48.1	71.0	66.9	86.7	53.0	6.4	
Silt	24.5	18.5	7.2	20.2	54.3	29.3	29.3	26.7	9.0	32.7	51.0	15.1	2.1	2.5	4.2	42.1	61.3	
Clay	5.3	3.6	2.2	11.8	16.0	8.8	8.8	5.2	2.4	5.8	13.7	9.1	1.9	1.0	0.9	3.8	29.8	
Porosity	60.7	63.4	37.2	51.4	75.4	59.3	57.8	35.5	61.2	72.2	58.3	37.2	38.5	39.4	62.2	81.5		
Sediment organic matter																		
Org C (%)	0.5	0.7	0.4	0.2	0.5	0.2	0.2	0.2	0.1	0.3	0.4	0.5	0.2	0.2	0.2	0.3	0.6	
Tot N (%)	0.1	0.1	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.0	0.0	0.0	0.0	0.1	
C/N	8.8	9.3	8.1	9.0	7.5	6.8	6.7	7.0	6.6	6.8	6.6	6.6	7.9	7.4	9.4	8.1	6.7	
Pore water nutrient content (µM)																		
SiO ₂	334.1			340.1	353.4	375.2	334.1			357.5	358.6	270.9	336.2	376.4	416.0	380.9	212.0	
PO ₄	16.9			14.5	7.8	8.0	27.7			28.0	11.7	22.6	55.8	43.2	27.9	20.2	5.2	
NO ₂	0.6			0.8	0.3	1.2	0.6			0.8	0.7	1.0	0.9	2.8	1.0	0.5	0.7	
NO ₃	40.8			27.0	64.2	27.7	52.1			29.7	17.5	56.2	21.1	28.9	17.4	40.2	54.4	
Sediment pigment content (µg cm ⁻²)																		
Chl <i>a</i>	0.4	0.1	0.0	0.0		0.4	0.2			0.4	0.6	1.1	0.3	0.1	0.0	0.2	0.3	
Pheo	4.3	2.1	3.5	0.5		3.2	3.1			6.4	5.3	7.1	2.0	2.2	1.2	2.4	2.4	
Sediment ATP ^b (mg m ⁻²)	3.2	2.7	5.9	2.1	2.6	1.3	3.3	3.0			3.0	4.2	2.7	1.7	0.8	2.9	2.5	
Benthic microbiota (values integrated over 63 mm) (ng C cm ⁻²)																		
Heterotrophic nanoflagellates	88.2	130.8	118.3	53.6	49.5	341.3	149.4	57.0	51.3	120.3	56.3	101.6	52.0	31.6	16.4	13.0		
Bacteria	103.7	94.6	75.9	68.5		91.1	106.0	55.3	76.1	90.5	102.9	78.7	47.1	78.2	114.6	64.5		
Eh (mV)																		
At -1 cm	506			479	403	608	418			526	526	436	484	433	467	498	556	
At 5 cm	313			359	391	542	406			428	428	419	396	548	-21	440	531	

^aChloroplastic pigment equivalents (chlorophyll *a* and degradation products)

^bUsed as a biomass estimate of bacteria in the sediment

held on a 38 μm mesh sieve. For 6 stations at least 2 cores were analysed for both bathymetric distribution (SD is spatial distribution, bulk sediment) and vertical distribution (VD) within the sediment. The detailed descriptions of the VD replicates will be presented later. Density data presented are concerned with metazoan meiofauna. A description of the species composition of the foraminifers is given by Mateu (1992).

Approximately 200 nematodes were collected from each SD core, while 100 nematodes were used from each sediment interval for the VD analysis. After mounting the nematodes in glycerin slides (Seinhorst 1959), the length and maximum width of each individual were measured. Assuming a specific gravity of 1.13 and a dry/wet weight ratio of 0.25, the biomass of nematodes was calculated using the adjusted method of Andrassy (Soetaert 1989). Parametric (ANOVA, covariance analysis) analysis was performed on respectively square and fourth root transformed data of total biomass and density. Nonparametric analysis (Kruskal-Wallis; Siegel 1956) was used on the data for individual nematode length and nematode biomass, where the assumptions for parametric analysis were not met.

Comparison with Halley Bay. Herman & Dahms (1992) described the structure of the meiofauna along a similar depth transect in the Weddell Sea at Halley Bay. Their results were compared with the current data to assess classification techniques (Two-Way Indicator SPecies ANalysis, TWINSpan, Hill 1979; Group-Average Sorting cluster analysis, GAS, with the Bray Curtis similarities, Bray & Curtis 1957) using taxon composition. The stations off Kapp Norvegia are denoted with K1 to K6, the stations off Halley Bay with H1 to H12. The density data were reduced using a 4% rule (e.g. taxa consisting of less than 4% of the total density after elimination of the nematodes were excluded), and were fourth root transformed prior to this analysis (Jongman et al. 1987). The relation with environmental factors was tested using the nonparametric Spearman rank correlation analysis. Environmental data (sediment properties and microbiota) were obtained simultaneously with similar sampling devices (Table 1) For details on methods consult Arntz et al. (1990). Sediment grain size was calculated using the Wentworth classification (Krumbein & Pettijohn 1938).

Length and biomass of the nematodes of Halley Bay were not presented by Herman & Dahms (1992). A summary of these data is presented in Table 3.

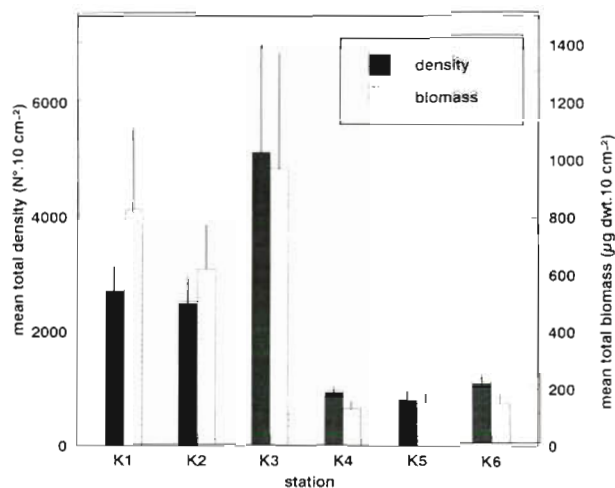


Fig. 2. Mean meiobenthos densities (no. 10 $\text{cm}^{-2} \pm \text{SE}$) and mean total biomass ($\mu\text{g dwt } 10 \text{ cm}^{-2} \pm \text{SE}$) at the 6 stations

RESULTS

Sample replication

The contrast analysis (ANOVA) showed that there was no significant difference between a VD and an SD treatment (SD is bulk sediment; VD is the sum of subsequent sediment slices) of the sediment core. The exception was due to the occurrence of a small-scale spatial heterogeneity within a treatment, probably reflecting patchiness. Consequently VD and SD sam-

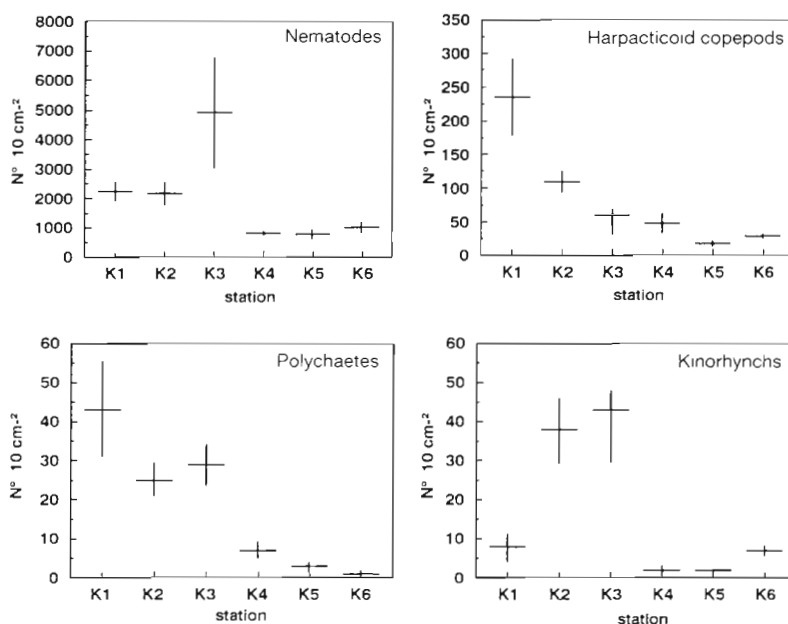


Fig. 3. Bathymetric distribution of nematodes, harpacticoid copepods, polychaetes and kinorhynchans. Values shown are means \pm SE ($n \geq 4$)

ples could be assigned as replicates (the data of the VD treatments are not presented here).

Distribution and composition of the meiofauna off Kapp Norvegia

Total meiofauna densities ranged from 815 ± 321.7 ind. 10 cm^{-2} at 1199 m depth (K5) to 5122 ± 3254.0 ind. 10 cm^{-2} at 537 m depth (K3). Total biomass varied from 126 ± 47.2 $\mu\text{g dwt } 10 \text{ cm}^{-2}$ (K4, 561 m) to 966 ± 698.6 (K3, 537 m) $\mu\text{g dwt } 10 \text{ cm}^{-2}$. The 2 variables were significantly related to each other (dwt: abundance, $p < 0.05$). Covariance analysis showed 2 distinct groups of stations (Tukey, $p < 0.001$). Stns K1, K2 & K3 (Group I) had the highest densities and total biomass, while a noticeably lower stock was found in stations K4, K5 and K6 (Group II) (Fig. 2). There was no clear relationship with bathymetric depth, but 2 separate geographical groups were present: Group I was close to the ice-shelf, while Group II was more off-shore. Mean total biomass was 20% higher in Group I than in Group II. Nematodes were most abundant, and accounted for 83 to 97% of the total. They were followed by nauplii and Harpacticoida, Polychaeta and Kinorhyncha (Fig. 3). The other taxa (19 in total) comprised together less than 4% of the total (Table 2). From this table it is clear that the diversity (number of taxa) did not differ between Groups I and II along the transect. Harpacticoid copepod and polychaete density exhibited a significant negative correlation with depth ($p < 0.01$), whereas the nematodes and the kinorhynchs did not (Fig. 3). The distinction between the ice-shelf and open-water stations can partly be inferred from the taxon composition (Fig. 3, Table 2).

Size structure of nematodes

In order to test the hypothesis of Thiel (1975) (i.e. meiofauna become smaller in size with increasing water depth), nematode sizes were studied along the transect. The length-frequency distributions of the nematodes in the 6 stations showed similar shapes. The end stations of the transect can be considered as representatives for the whole depth transect (Fig. 4). Skewed patterns were obtained with the smaller organisms (0.4 to 0.6 mm) being more highly represented. Only 27% of the nematodes were longer than 1 mm, and only 4 and 0.9% reached

Table 2. Relative abundance of nematodes, and mean metazoan meiofaunal abundance of the less abundant taxa (no. 10 cm^{-2})

	K1	K2	K3	K4	K5	K6
Abundance nematodes	82.5	86.8	96.0	86.9	96.4	95.9
Other taxa (%)	2.7	2.0	0.5	3.4	0.8	0.6
Amphipoda					0.1	0.1
Bivalvia	1.0	8.2	7.5	3.5	2.0	0.4
Bryozoa		9.8		5.0		
Coelenterata	1.0	0.8	0.8	1.8		
Cumacea						1.7
Echinodermata			0.3			
Gastrotricha	0.7	0.3		1.8	0.2	
Halacaroidea	6.7	2.0		0.3	0.5	0.2
Isopoda		0.3		1.0		
Loricifera		0.6	0.5		0.8	0.8
Oligochaeta	0.3	7.2	5.0	1.3	1.4	0.6
Ostracoda	14.7	13.8	8.25	7.8	0.8	1.7
Porifera		0.2				
Priapulida		0.5	0.8	0.5		0.1
Rotifera		3.2	1.0	6.0		
Tanaidacea	0.3	0.2	0.3	0.3	0.3	
Tardigrada	6.0	0.2		1.5	0.5	1.2
Tunicata			0.3			
Turbellaria		3.3	1.0	1.5	0.1	
No. of taxa	8	15	12	13	10	9

lengths over 2 and 3 mm respectively. Mean nematode lengths varied from 743 μm at K4 to 986 μm at K1 (overall mean: $892 \mu\text{m} \pm 579$; geometric mean: 754 μm ; harmonic mean: 646 μm). The high standard deviation indicates a high variation between the replicates. Mean individual nematode lengths were significantly different

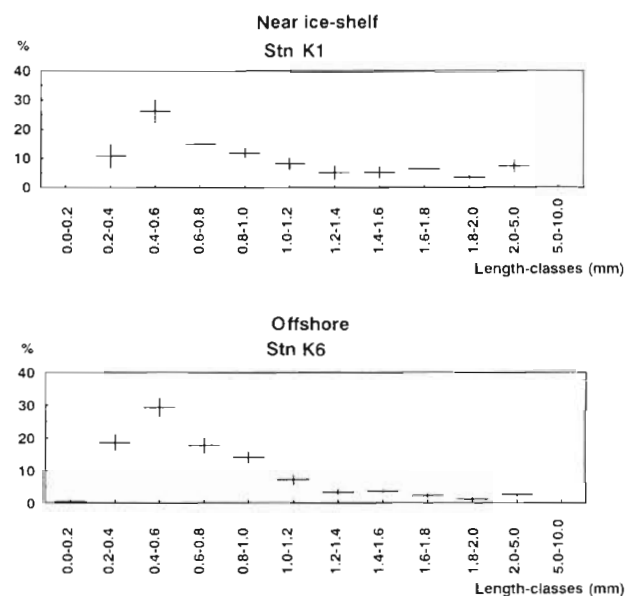


Fig. 4. Length frequency distributions of the nematodes at Stns K1 & K6 off Kapp Norvegia (mean length in mm \pm SE, $n = 3$ and 5). Stns K1 & K6 are representative of the other stations in the study

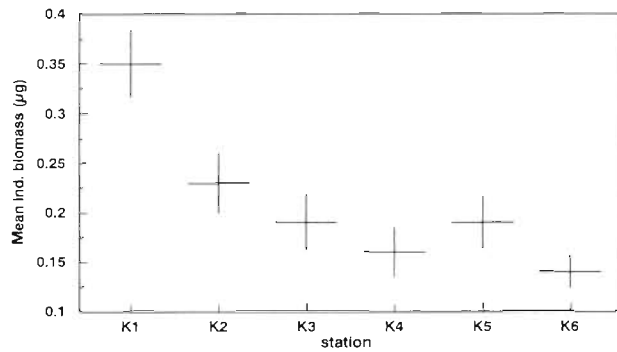


Fig. 5. Mean individual biomass ($\mu\text{g dwt} \pm \text{SE}$) of nematodes at each station off Kapp Norvegia

between the stations (Kruskal-Wallis, $p < 0.001$), but were not related to bathymetric depth. This is consistent with the overall similarity in age structure of the nematodes throughout the transect (53 to 67% of the organisms were juveniles). The smallest mean individual nematode biomass per station of $0.140 \mu\text{g dwt}$ at K6 shifted to $0.352 \mu\text{g dwt}$ at K1 (overall mean: $0.233 \mu\text{g dwt}$; geometric mean: $0.07 \mu\text{g dwt}$; harmonic mean: $0.03 \mu\text{g dwt}$; Fig. 5). Mean individual nematode biomass was significantly different between the stations (Kruskal-Wallis, $p < 0.001$) and negatively correlated with water depth ($p < 0.01$).

DISCUSSION

Halley Bay (74 to 75° S; 25 to 29° W) – Kapp Norvegia (71 to 72° S; 12 to 13° W)

Meiofauna

Table 3 represents a comparison between the 2 regions in the Weddell Sea studied to date. The nematode community in Kapp Norvegia does not markedly differ from Halley Bay (Herman & Dahms 1992). Only slightly higher density and biomass readings were noted in the former area. Similar conclusions can be drawn from the TWINSPLAN analysis (Fig. 6), where no

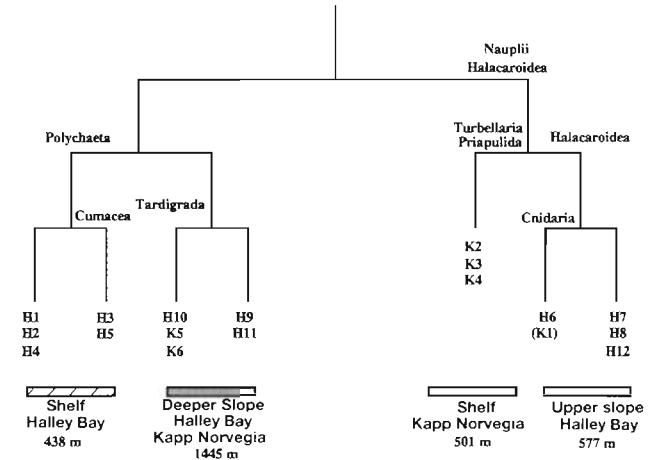


Fig. 6. TWINSPLAN analysis of the samples based on the fourth-root-transformed taxon data with the indicator species (taxa) for each division indicated

clear distinction was found between the 2 transects. Clusters were primarily made on the basis of bathymetric location and/or distance to the ice-shelf, which was also relevant from the correlation analysis, and was also from observations by Herman & Dahms (1992). A strong resemblance was found between the following areas: the shelf stations off Halley Bay (H1, H2, H3, H4, H5; mean depth 438 m; indicator species: polychaetes); the deeper slopes of both transects (K5, K6, H9, H10, H11; mean depth: 1445 m); the shelf stations off Kapp Norvegia (K2, K3, K4; mean depth 501 m; indicator species: turbellarians and priapulids); and the upper slope of Halley Bay (H6, H7, H8, H12 and exception K1, mean depth 577 m, indicator species: halacarids). Comparable sub-divisions were obtained in the GAS analysis (not depicted), with the exception that all the shelf stations were clustered in a single group, and distinctly separated from the deeper localities (upper and deeper slope).

Meso-scale variability in the Weddell Sea

A significant correlation was found between depth and food (e.g. ATP, organic matter, heterotrophic

Table 3. Comparison of the main variables of the nematode communities between Halley Bay and Kapp Norvegia. Data given are the range values at each of the sites; means are in parentheses

	Halley Bay (582–1958 m)	Kapp Norvegia (211–2080 m)
Absolute density (ind. per 10 cm^2)	730.4–2291.0 (1585.7)	823.8–4914.8 (1993.5)
Relative density (%)	88.1–97.1 (93.7)	82.5–96.4 (90.8)
Mean individual length (mm)	0.667–0.972 (0.850)	0.747–0.986 (0.860)
Mean individual biomass ($\mu\text{g dwt}$)	0.124–0.297 (0.188)	0.154–0.351 (0.230)
Total biomass (g dwt m^{-2})	0.087–0.652 (0.285)	0.126–0.966 (0.470)

nanoflagellates and bacteria) on one hand, and meiofauna on the other hand (Table 4). Except for kinorhynch, nematode and oligochaete densities, meiofauna distribution was not correlated with sediment texture. Surface oxygen levels (Eh), pore water nutrients (SiO₂, PO₄, NO₂, NO₃), and pigment concentrations (chlorophyll *a*, phaeopigments) also had little impact. High variability between sites was found in the sediment texture, nutrient pore water chemistry, microbiota (bacteria and heterotrophic nanoflagellates), and concentrations of pigments and organic matter (Table 1). Despite this, the sediments within the 4 major TWIN-groups exhibited several abiotic and biotic similarities (Fig. 7). The shelf of Halley Bay was typically characterized by high total density, high numbers of nematodes, kinorhynchs, heterotrophic nanoflagellates, intermediate nematode biomass values and very low nauplii numbers; the sediments were a mixture of silt and sand, and contained high ATP and CPE levels. The shelf of Kapp Norvegia had a dense meiofauna population, coarser sediments and high food concentrations. The deeper slopes of both transects were poor in terms of meiofauna density and biomass compared to the shelves. Low ATP, CPE and flagellate concentrations characterized the fine sediments. Total density and biomass, nematode density, and ATP in the upper slope sediments had a strong affinity with the deep localities, where generally intermediate concentrations were found. The sands were the major component of the sediment, and there was a significant occurrence of gravels. The sedimentation patterns can be related to high energy conditions due

to the effect of the Antarctic Coastal Current in this zone (Rohardt et al. 1990). Such conditions prevent the deposition of finer fractions. At about 400 m deep off Halley Bay (Stns H4, H5, H6) active sedimentation processes were recognizable from the high values of total suspended matter observed during the cruise (Rabitti & Boldrin 1990).

A cluster analysis on macrobenthic densities and biomass in the Weddell Sea region (Galéron et al. 1992) indicated the existence of 2 assemblages according to geographic location (e.g. southern and eastern shelf communities), though high variability within and between these 2 groups was found. For the same reason Gerdes et al. (1992) could not easily distinguish macrobenthic biomass from Halley Bay and Kapp Norvegia. Most stations, therefore, were grouped with the eastern shelf community described by Voß (1988), which is mainly composed of a rich and diverse community of suspension feeders, strongly dependent on depositing food particles.

Small-scale variability in the sediment

A high variation between replicates (as seen for the density and biomass of the meiofauna), was observed. This small-scale (at the cm² level) heterogeneity, inherent to meiofauna in general (Sun & Fleeger 1991), is likely to be strongly influenced by the microtopography and physical structure of the habitat, and hence the patchy distribution of the earlier mentioned environmental factors.

Table 4. Summary of significant Spearman rank order correlations for meiofauna variables with environmental characteristics measured: total meiofauna density; total nematode biomass; individual nematode biomass; number of taxa; nematodes (Nem.); kinorhynches (Kin.); harpacticoids (Har.); cnidarians (Cni.); priapulids (Pri.); naupliids (Nau.); oligochaetes (Oli.); tardigrades (Tar.); ostracods (Ost.); tanaidaceans (Tan.); bivalves (Biv.); polychaetes (Pol)

	Tot. dens.	Tot. biom.	Ind. biom.	No. taxa	Nem.	Kin.	Har.	Cni.	Pri.	Nau.	Oli.	Tar.	Ost.	Tan.	Biv.	Pol.
Depth	***	***	-	***	**	-	*	*	-	*	-	*	**	-	-	***
Porosity	-	-	-	-	*	***	-	-	-	-	-	-	-	-	-	-
Very coarse sand	-	-	-	-	-	*	-	-	-	-	*	-	-	-	-	-
Sand	-	-	-	-	-	**	-	-	-	-	-	-	-	-	-	-
Silt	-	-	-	-	*	***	-	-	-	-	-	-	-	-	-	-
Clay	-	-	-	-	-	*	-	-	-	-	-	-	-	-	-	-
SiO ₂	-	-	-	-	-	-	**	-	-	-	-	-	-	-	-	-
NO ₃	-	-	-	-	-	-	-	-	-	*	-	-	-	*	-	-
Eh at -1 cm	*	-	-	-	*	*	-	-	*	-	-	-	-	-	-	-
ATP	*	*	-	-	*	*	-	-	**	-	-	-	-	-	-	*
Organic carbon	-	-	-	-	-	*	-	-	-	-	-	-	-	**	-	-
Organic nitrogen	-	-	-	-	-	**	-	-	-	-	-	-	-	**	-	-
Biomass bacteria	*	*	*	-	-	-	-	**	*	-	-	-	*	*	*	*
Biomass flagellates	*	*	-	*	-	-	-	**	*	-	-	-	**	-	***	***

*** p ≤ 0.001; ** 0.001 < p ≤ 0.01; * 0.01 < p ≤ 0.05

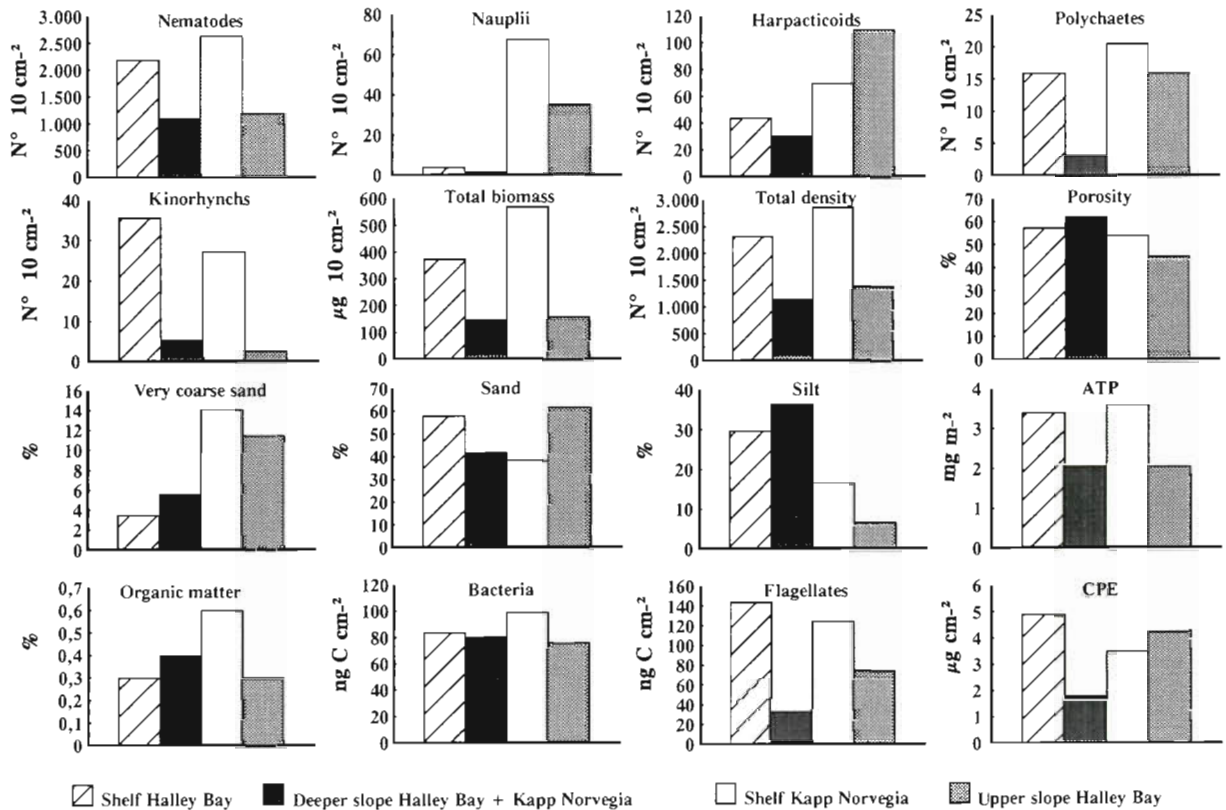


Fig. 7. Sediment characteristics and meiofauna densities in the 4 TWIN groups

Comparison with other deep-sea areas in the world

Meiofauna

Table 5 is restricted to transects crossing continental shelves and upper slopes (e.g. ±200 to 2000 m). The mesh sizes of sieves were similar, except for the study of Shirayama & Kojima (1994). As the use of different gear seriously influences the quantity of meiofauna sampled (Blomqvist 1991, Bett et al. 1994), only boxcore and multicore studies were considered. In this context it is important to note that a mixture of gear types was used in the current study (Table 1). According to Bett et al. (1994), boxcorers are less efficient collectors resulting in lower density records, with possible differences of up to 50%. However, the apparent bias may vary both with time and location. From the present study it is difficult to test the difference in sampling efficiency as both types were not applied at the same sites. If such sample bias occurred, the implication is that density data obtained from multiboxcorer samples would underestimate the true population levels.

From Table 5 it is clear that the meiofauna in the Weddell Sea is characterized by densities within the range of other deep-sea environments (the upper limit

of 5122 ind. 10 cm⁻¹ is a single exceptional high value). Only the warm and oligotrophic deep-sea sediments in the Red and Mediterranean Sea had significantly poorer populations. Hence, the current results fit the regression of total metazoan meiofauna density with water depth, calculated for the northeast Atlantic Ocean (Vincx et al. 1994, Fig. 8). The composition of meiofaunal taxa turned out to be similar to that found in other deep-sea environments, with a predominance of nematodes and a relatively high importance of harpacticoids, polychaetes and kinorhynchs. A body mass of 0.05 to 0.14 µg C is also in accordance with dimensions of deep-sea nematodes recorded from similar depths in the east Atlantic Ocean and Norwegian Sea (Jensen 1988, Soltwedel 1993). Mean individual dwt diminished along the transect, but no correlation was found with median size. This difference is because extremely large individuals are less frequent at greater depths. These results partly support Thiel's hypothesis (1975).

Environmental impact

The factors controlling the standing stock of deep-sea benthos have recently received more attention.

Table 5. Literature data on total metazoan meiofauna density and biomass in deep seas with comparable depths. Box: (multi)box-corer; Mc: multicorer; *unicellular organisms included in total counts, **only nematodes counted. Following Heip et al. (1985), conversion factors of 0.1, 0.4 and 0.5 were used to obtain comparable C equivalents from wet wt, dwt and AFDW respectively

Region	Source	Depth (m)	Gear	Mesh (μm)	Density (ind. 10 cm^{-2})	Biomass (g C m^{-2})
Mediterranean Sea	De Bovée et al. (1990)	672 to 2105	Box	40	36 to 1005	
	Soetaert et al. (1991), Heip et al. (1985)	160 to 1220	Box	38	370 to 724	0.002 to 0.028
Red Sea	Thiel (1979)	507 to 1977	Box	40	39 to 407	
	Thiel et al. (1987)	593 to 1945	Box	42	43 to 195*	
	Pfannkuche (1993)	1223 to 1650	Mc+Box	40	33 to 123*	
Pacific Ocean	Shirayama & Kojima (1994)	245 to 1964	Box	63	438 to 2060*	
Atlantic Ocean -NE Atlantic	Thiel (1971)	290 to 2000	Box	42	30 to 4226	0.020 to 2.850
	Pfannkuche (1985)	500 to 2000	Mc	42	828 to 2604	0.002 to 0.005
	Vanreusel et al. (1992)	190 to 325	Box	38	864 to 915	0.055 to 0.134
-NW Atlantic	Coull et al. (1977)	400 to 800	Box	42	217 to 1408*	
-SE Atlantic	Soltwedel (1993)	551 to 1965	Box	42	277 to 1398	0.030 to 0.890
Norwegian Sea	Dinet (1974)	283 to 2000	Box	40	139 to 971	
	Jensen (1988)	970 to 1255	Box	45	138 to 204**	0.006 to 0.073
	Thiel (1975)	1250 to 2250	Box	40	600 to 1920	
Arctic Ocean -Barents Sea & Nansen Basin	Pfannkuche & Thiel (1987)	226 to 2500	Box	42	1143 to 4339	
Southern Ocean -Weddell Sea	Herman & Dahms (1992), this paper	211 to 2080	Mc+Box	38	815 to 5122	0.040 to 0.480

Gage & Tyler (1991) stated that large areas of the deep-sea floor are subjected to spatial and temporal disturbances on scales ranging from centimeters to tens of kilometers, and from days to decades or longer. The amount of biologically utilizable particulate organic matter settling from the pelagic, in particular, is a function of sedimentation and degradation rates in the water column, and determines the amplitude and

duration of a benthic response (Lutze et al. 1986, Graf 1989, Gooday & Turley 1990, Sayles et al. 1994, Bak et al. in press). Meiobenthic biota have been suggested to be structured by such POC flux and therefore coupled to phenomena in the pelagic (Shirayama & Kojima 1994, Vincx et al. 1994, Soetaert & Heip in press, Vanreusel et al. 1995).

The pelagic regime of the high Antarctic is typically characterized by sudden and pronounced bloom events. Substantial amounts of organic carbon and biogenic opal may sink as a result of high plankton death rates, current activity and melting processes in the vicinity of ice-shelves and polynyas (Fischer et al. 1988, Wefer et al. 1990). Moreover, the sedimentation of faecal pellets originating from the grazing activity of protozoans, copepods and krill is sometimes the main process for the transport of material from the surface to the sea floor in the Weddell Sea (Wefer et al. 1990). The importance of sedimentation pulses, both from the bloom and grazing, decrease with increasing distance from the shelf (Nöthig 1988, Weber 1992). In the coastal/shelf domain off Vestkapp (Weddell Sea) primary production exhibited high figures in the austral summer, ranging from 100 to 1000 $\text{mg C m}^{-2} \text{ d}^{-1}$, with a maximum daily POC flux of 65% at 100 m depth (von Bodungen et al. 1988). For Kapp Norvegia no data on primary production

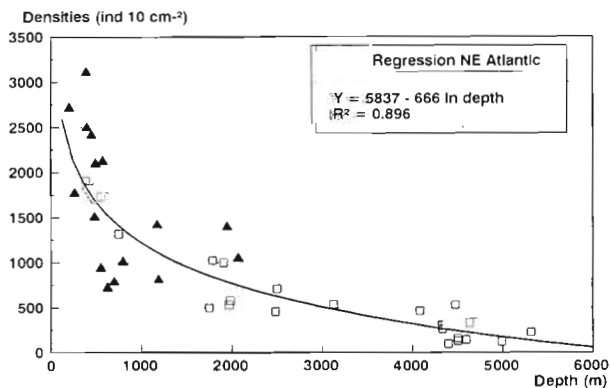


Fig. 8. Regression output of meiofaunal densities in the northeast Atlantic according to Vincx et al. (1994). Data from the Weddell Sea are added (▲) but not included in the regression analysis

were found, but flux rates were 3 to 110 mg m⁻² d⁻¹ at 630 m (Bathmann et al. 1991).

Substantial transport of phytodetritus to the sea bed (after ice-cover-related bloom events) and supplementary lateral transport mechanisms were thought to give rise to high concentrations of CPE in high Arctic waters (Pfannkuche & Thiel 1987). Low temperatures induce low microbial metabolic rates, and hence low organic degradation. Therefore, according to Thiel (1983), food is available to the benthos for longer periods in these cold environments. In combination with low benthic respiration, which is thought to slow down growth rates and increase individual life spans, these high food concentrations gave rise to high meiobenthic standing stocks in the Arctic (Pfannkuche & Thiel 1987).

The same could apply to the cold waters (0.4 to 1.9°C; Rohardt et al. 1990) of the study area. In this region about 60% of phytoplankton derived detritus is mineralized within 16 d by the microbial community in the pelagic (Knox 1994). However, phytodetritus can deposit relatively rapidly and rates of 100 to 150 m d⁻¹ have been reported (Billet et al. 1983). This result implies that a great amount of utilizable organic matter still reaches the sea bed within a few days. Concentrations of pigment and organic matter recorded in sediments in this study were, however, low (Table 3). It is likely that the sampling periods here were not immediately after phytodetrital sedimentation events. Deposited organic matter had probably been utilised by the benthic faunal assemblages. Under the assumption that primary production and POM fluxes to the sea bed showed similar features as in former years (i.e. high and very time-restricted), this would imply that benthos respond rapidly and efficiently to the episodic food supply.

CONCLUSION

Meiobenthic density and biomass data encountered in the Weddell Sea are comparable to major deep-sea environments. Features such as very high, but patchy primary production, with subsequent variable fluxes to the sea bed, induce small- and meso-scale variability between and within substrates (e.g. food resources and sediment texture), and are reflected in meiobenthic distribution patterns. It seems that the meiofauna in these regions has, therefore, developed strategies favourable to the conditions prevalent in deep-sea environments (e.g. high variability within the environment and unpredictability of food sources). Year round surveying of meiofauna and sediment properties, and a detailed investigation of age structure, metabolic activity and diversity of the populations, is now needed before further conclusions about the Antarctic deep-sea meiofauna can be drawn.

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LITERATURE CITED

- Alkemade R, Wielemaker W, de Jong SA, Sandee AJJ (1992) Experimental evidence for the role of bioturbation by the marine nematode *Diplolaimella dievengatensis* in stimulating the mineralization of *Spartina anglica* detritus. Mar Ecol Prog Ser 90:149–155
- Arntz W, Brey T, Gallardo VA (1994) Antarctic zoobenthos. Oceanogr mar Biol A Rev 32:241–304
- Arntz W, Ernst W, Hempel I (1990) The expedition ANTARKTIS VII/4 (EPOS leg 3) and VII/5 of RV 'Polarstern' in 1989. Ber Polarforsch 68:1–214
- Bak RPM, van Duyl FC, Nieuwland G (in press) Organic sedimentation and macrofauna as forcing factors in marine benthic nanoflagellate communities. Microb Ecol
- Barnett PRO, Watson J, Connolly D (1984) A multiple corer for taking virtually undisturbed samples from shelf, bathyal and abyssal sediments. Oceanol Acta 7:399–408
- Bathmann U, Fischer G, Müller PJ, Gerdes G (1991) Short-term variation in particulate matter sedimentation off Kapp Norvegia, Weddell Sea, Antarctica: relation to water mass advection, ice cover, plankton biomass and feeding activity. Polar Biol 11(3):185–195
- Bett BJ, Vanreusel A, Vincx M, Soltwedel T, Pfannkuche O, Lamshead PJD, Gooday AJ, Ferrero T, Dinét A (1994) Sampler bias in the quantitative study of deep-sea meiobenthos. Mar Ecol Prog Ser 104:197–203
- Billet DSM, Lampitt RS, Rice AL, Mantoura RCF (1983) Seasonal sedimentation of phytoplankton to the deep-sea benthos. Nature 302:520–522
- Blomqvist S (1991) Quantitative sampling of soft-bottom sediments: problems and solutions. Mar Ecol Prog Ser 72: 295–304
- Bray JR, Curtis JT (1957) An ordination of the upland forest communities of southern Wisconsin. Ecol Monogr 27: 325–349
- Coull BC, Ellison RL, Fleeger JW, Higgins RP, Hope WD, Hummon WD, Rieger RM, Sterrer WE, Tietjen JH (1977) Quantitative estimates of the meiofauna from the deep sea off North Carolina, USA. Mar Biol 39:233–240
- De Bovée F, Gudi LD, Soyer J (1990) Quantitative distribution of deep-sea meiobenthos in the northwestern Mediterranean (Gulf of Lions). Cont Shelf Res 10: 1123–1145
- Dinét A (1974) Données quantitatives sur le méiobenthos bathyal de la mer de Norvège. In: Géochimie organique des sédiments marins profonds. Orgon 1, Mer de Norvège (extract). CNRS, Paris, p 13–14
- Findlay SEG, Tenore KR (1982) Effect of a free-living marine nematode (*Diplolaimella chitwoodi*) on detrital carbon mineralization. Mar Ecol Prog Ser 8:161–166

- Fischer G, Fütterer D, Gersonde R, Honjo S, Ostermann D, Wefer G (1988) Seasonal variability of particle flux in the Weddell Sea and its relation to ice-cover. *Nature* 335: 426–428
- Gage JD, Tyler PA (1991) Deep-sea biology, a natural history of organisms at the deep-sea floor. Cambridge University Press, Cambridge
- Galéron J, Herman RL, Arnaud PM, Arntz WE, Hain S, Klages M (1992) Macrofaunal communities on the continental shelf and slope of the southeastern Weddell Sea, Antarctica. *Polar Biol* 12:283–290
- Gerdes D (1990) Antarctic trials of the multi-box corer, a new device for benthos sampling. *Polar Rec* 26(156):35–38
- Gerdes D, Klages M, Arntz WE, Herman RL, Galéron J, Hain S (1992) Quantitative investigations on macrobenthos communities of the southeastern Weddell Sea shelf based on multibox corer samples. *Polar Biol* 12:291–301
- Giere O (1993) Meiobenthology. The microscopic fauna in aquatic sediments. Springer-Verlag, Berlin
- Gooday AJ, Turley CM (1990) Responses by benthic organisms to inputs of organic material to the ocean floor: a review. *Phil Trans R Soc Lond Ser A* 331:119–138
- Graf G (1989) Benthic-pelagic coupling in a deep-sea benthic community. *Nature* 341:437–439
- Grobe H (1986) Spätpleistozäne Sedimentationsprozesse am antarktischen Kontinentalhang vor Kapp Norvegia, östliche Weddell See. *Ber Polarforsch* 27:7–56
- Heip C, Vincx M, Vranken G (1985) The ecology of marine nematodes. *Oceanogr mar Biol A Rev* 23:399–489
- Hempel G (1993) Weddell Sea ecology. Results of EPOS European 'Polarstern' Study. Springer-Verlag, Berlin
- Herman RL, Dahms HU (1992) Meiofauna communities along a depth transect off Halley Bay (Weddell Sea–Antarctica). *Polar Biol* 12:313–320
- Hill MO (1979) TWINSPAN—a FORTRAN program for arranging multivariate data in an ordered two-way table by classification of individuals and attributes. Cornell University, Ithaca, NY
- Hough JL (1956) Sediment distribution in the Southern Ocean around Antarctica. *J sedim Petrol* 26 (4):301–306
- Ingham RE, Trofymov JA, Ingham ER, Coleman DC (1985) Interactions of bacteria, fungi and their nematode grazers: effects on nutrient cycling and plant growth. *Ecol Monogr* 55:119–140
- Jensen P (1988) Nematode assemblages in the deep-sea benthos of the Norwegian Sea. *Deep Sea Res* 35:253–266
- Jongman RHG, ter Braak CJF, van Tongeren OFR (1987). Data analysis in community and landscape ecology. Pudoc Wageningen
- Knox GA (1994) The biology of the Southern Ocean. In: Clarke A, Bliss L, Dewry DJ, Walton DWH, Williams PJ (eds) Studies in polar research. Cambridge University Press, Cambridge
- Krumbein WC, Pettijohn FJ (1938) Manual of sedimentary petrography. Appleton-Century Crofts, Inc, New York
- Lochte K (1992) Bacterial standing stocks and consumption of organic carbon in the benthic boundary layer of the abyssal north Atlantic. In: Rowe GT, Pariente V (eds) Deep-sea food chains and the global carbon cycle, NATO ASI series C: mathematical and physical sciences, Vol 360. Kluwer Academic Publishers, Dordrecht, p 1–10
- Lutze GF, Pflaumann U, Weinholz P (1986) Jungquartäre Fluktuationen der benthischen Foraminiferenfaunen in Tiefsee-Sedimenten vor NW-Afrika. Eine Reaktion auf Produktivitätsänderungen im Oberflächenwasser. 'Meteor' Forsch-Ergebn C40:163–180
- Mateu G (1992) Micropaleontologia sedimentaria del mar de Weddell. In: Lopez-Martinez J (ed) Geologia de la Antártida Occidental. Simposios T 3, III Congreso Geológico de España y VIII Congreso Latinoamericano de Geología. Salamanca, España, 1992, p 213–227
- Nöthig EM (1988) Untersuchungen zur Ökologie des Phytoplanktons im südöstlichen Weddellmeer (Antarktis) im Januar/Februar 1985. *Ber Polarforsch* 53
- Pfannkuche O (1985) The deep-sea meiofauna of the Porcupine Seabight and abyssal plain (NE Atlantic): population structure, distribution, standing stocks. *Oceanol Acta* 8 (3): 343–353
- Pfannkuche O (1993) Benthic response to the sedimentation of particulate organic matter at the BIOTRANS station, 47° N, 20° W. *Deep Sea Res* 40:727–737
- Pfannkuche O, Thiel H (1987) Meiobenthic stocks and benthic activity on the NE-Svalbard Shelf and in the Nansen Basin. *Polar Biol* 7:253–266
- Poremba K (1994) Simulated degradation of phytodetritus in deep-sea sediments of the NE Atlantic (47° N, 19° W). *Mar Ecol Prog Ser* 105:291–299
- Rabitti S, Boldrin A (1990) The Halley Bay-Kapp Norvegia comparison. Suspended matter and oxygen. *Ber Polarforsch* 68:51–66
- Rohardt G, Ruhland G, Schleif U (1990) Physical oceanography. *Ber Polarforsch* 68:39–49
- Sayles FL, Martin WR, Deuser WG (1994) Response of benthic oxygen demand to particulate organic carbon supply in the deep sea near Bermuda. *Nature* 371:686–689
- Seinhorst J (1959) A rapid method for the transfer of nematodes from fixative to anhydrous glycerin. *Nematologica* 4:67–69
- Shirayama Y, Kojima S (1994) Abundance of deep-sea meiobenthos off Sanriku, northeastern Japan. *J Oceanogr* 50:109–117
- Siegel S (1956) Non-parametric statistics for the behavioural sciences. MacGraw-Hill & Kogakusha Ltd, Tokyo
- Soetaert K (1989) An ecological-systematical study of the deep-sea meiofauna and nematode communities in the western Mediterranean Sea. PhD thesis, University of Gent
- Soetaert K, Heip C (in press) Nematode community structure of deep-sea and shelf break sites in the North Atlantic and Mediterranean sea. *Mar Ecol Prog Ser*
- Soetaert K, Heip C, Vincx M (1991) The meiobenthos along a Mediterranean deep-sea transect off Calvi (Corsica) and in an adjacent canyon. *PSZN I: Mar Ecol* 12:227–242
- Soltwedel T (1993) Meiobenthos und biogene Sedimentkomponenten im tropischen Ost-Atlantik. Berichte aus dem Zentrum für Meeres- und Klimaforschung der Universität Hamburg Reihe E: Hydrobiologie und Fischereiwissenschaft, no. 6
- Sun B, Fleeger JW (1991) Spatial and temporal patterns of dispersion in meiobenthic copepods. *Mar Ecol Prog Ser* 71: 1–11
- Thiel H (1971) Häufigkeit und Verteilung der Meiofauna im Bereich des Island-Faröer. *Ber dt wiss Kommn Meeresforsch* 22:99–128
- Thiel H (1975) The size-structure of the deep-sea benthos. *Int Revue ges Hydrobiol (Hydrogr)* 60:575–606
- Thiel H (1979) First quantitative data on the deep Red Sea benthos. *Mar Ecol Prog Ser* 1:347–350
- Thiel H (1983) Meiobenthos and nanobenthos of the deep sea. In: Rowe GT (ed) The sea, Vol 8. Wiley & Sons, New York, p 167–230
- Thiel H, Pfannkuche O, Theeg R, Schriever G (1987) Benthic metabolism and standing stock in the central and northern Red Sea. *PSZN I: Mar Ecol* 8:1–20
- Vanreusel A, Vincx M, Bett BJ, Rice AL (1995) Nematode bio-

- mass spectra at two abyssal sites in the NE Atlantic with a presumed contrasting food supply. *Int Revue ges Hydrobiol* 80(2):287–296
- Vanreusel A, Vincx M, Van Gansbeke D, Gijssels W (1992) Structural analysis of the meiobenthos communities of the shelf break area in two stations of the Gulf of Biscay (N.E. Atlantic). *Belg J Zool* 122 (2):185–202
- Vincx M, Bett BJ, Dinert A, Ferrero T, Gooday AJ, Lamshead PJD, Pfannkuche O, Soltwedel T, Vanreusel A (1994) Meiobenthos of the deep northeast Atlantic. *Adv mar Biol* 30:1–88
- von Bodungen B, Nöthig EM, Sui Q (1988) New production of phytoplankton and sedimentation during summer 1985 in the southeastern Weddell Sea. *Comp Biochem Physiol* 90B:475–487
- Voß J (1988) Zoogeographie und Gemeinschaftsanalyse des Makrozoobenthos des Weddellmeeres (Antarktis). *Ber Polarforsch* 45:6–129
- Weber M (1992) Spätquartäre Sedimentation am Kontinentalrand des südöstlichen Weddellmeeres, Antarktis. *Ber Polarforsch* 109:1–66
- Wefer G, Fischer G, Fütterer DK, Gersonde R, Honjo S, Ostermann D (1990). Particle sedimentation and productivity in Antarctic waters of the Atlantic sector. In: Bleil U, Thiede J (eds) *Geological history of the polar oceans: Arctic versus Antarctic*. Kluwer Academic Publishers, Dordrecht, p 363–379
- Wigley RL, McIntyre AD (1964) Some quantitative comparisons of offshore meiobenthos and macrobenthos south of Martha's Vineyard. *Limnol Oceanogr* 9:485–493

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