



Meiobenthos of the central Arctic Ocean with special emphasis on the nematode community structure

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Abstract

We investigated the abundance of the meiobenthos and the biomass and community structure of the nematodes in the central Arctic Ocean along two separate transects during 1991 and 1994. Meiobenthos abundances ranged from < 100 to 600 individuals per 10 cm^2 , in the same order of magnitude as in other oligotrophic areas of the world's deep ocean. Nematodes were the numerically dominant meiofaunal group at every station. Nematode biomass ranged from < 1 to $48\ \mu\text{g}$ dry weight per 10 cm^2 . A combination of water depth and latitude explained 55% of the variability among stations in nematode biomass and 67% of the variability of total abundance, implying that both vertical and advective fluxes are important sources of food to the meiofaunal communities. The dominant nematode genus was *Monhystera*, a detritivorous/bacterivorous deposit feeder, suggesting that bacteria may play an important role in the food web of the meiobenthos in the Central Arctic. Multivariate analysis of genera abundances revealed differences among stations in the Eurasian and Amerasian Basins. During 1994, however, the deep stations in the Eurasian Basin were more similar to the other Amerasian stations, while the single deep station in the Makarov Basin was most similar to the other Eurasian Basin stations. The structure of meiofaunal communities in the central Arctic may provide insight into spatial variability in the Arctic Ocean. © 2000 Elsevier Science Ltd. All rights reserved.

Keywords: Meiobenthos; Nematodes; Central Arctic Ocean; Community analysis

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1. Introduction

Recent measurements of biological production in the Arctic have shown that the central Arctic Ocean is not as barren as originally thought (Wheeler et al., 1996). Estimates of pelagic production indicate that while the Arctic region is less productive than other oligotrophic ocean regions in terms of pigment concentrations, primary production and DOC, active cycling of carbon is occurring (Rich et al., 1997; Hansell and Carlson, 1998). Similar reevaluations are occurring for other components of the Arctic ecosystem. For example, with reference to benthic bacterial activity, the central Arctic Ocean has alternatively been described as a “benthic desert” (Soltwedel and Schewe, 1998) but also as being similar to temperate continental slopes (Kröncke et al., 1994; Boetius and Damm, 1998). There is a large range in densities and biomass of larger (>250 or $>500 \mu\text{m}$) infauna, but in all cases active mixing and, by extension, active processing of the sediment by benthic organisms is occurring (Kröncke, 1994; Clough et al., 1997; Kröncke, 1998). For Arctic metazoan meiobenthos, the only published data are from the Laptev sea (Van Averbeke et al., 1997). Van Averbeke et al. (1997) assumed that some taxa adapted to this extreme environment by rapidly responding to short-lived food pulses, suggesting that the meiobenthic compartment might be uncoupled from low annual primary productivity of overlying waters.

The purpose of our study was to investigate the meiobenthos (less than 1 mm, greater than $32 \mu\text{m}$) collected along two transpolar transects in the central Arctic Ocean (Fig. 1). Both transects were located in the perennially ice-covered regions of the Arctic and crossed the Lomonosov Ridge, a few degrees from the geographical pole. The Lomonosov Ridge separates the Amerasian and Eurasian Basins, with the Makarov and Canadian Basins on the Amerasian side and the Amundsen and Nansen basins on the Eurasian side. The 1991 transect started in the Makarov basin, crossed the Lomonosov Ridge, and continued to the Morris Jesup Rise beyond the pole. The 1994 transect began in the Chukchi Sea and proceeded to about 6° beyond the pole. We present data on the density and composition of the meiobenthos, and the biomass and composition of the nematode communities. We relate differences in community structure of the Arctic meiobenthos among areas to differences in environmental factors such as concentration of food and physical characteristics of the substrate that were analyzed during the same cruises and published elsewhere (Clough et al., 1997). Finally we compare distribution and abundance of meiobenthos to (1) macrobenthos of the central Arctic Ocean (Clough et al., 1997; Kröncke, 1998) and (2) other meiobenthic communities from oligotrophic regions of the world ocean.

2. Material and methods

2.1. ARK VIII/3 — 1991 transect

Samples were collected in September 1991 during the *Polarstern* cruise ARK VIII/3 to the central Arctic Ocean. Sampling started in the Makarov basin, crossed the

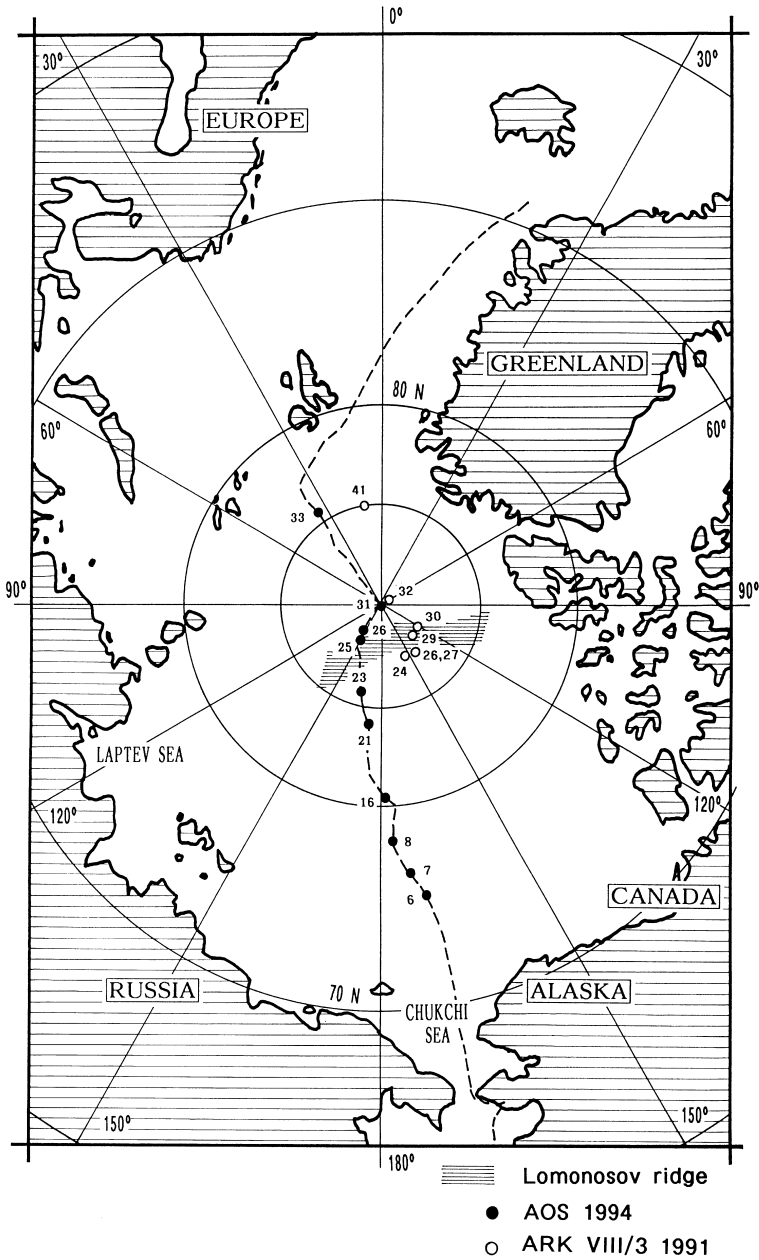


Fig. 1. Map of the central Arctic Ocean showing sampling transects from 1991 and 1994.

Lomonosov Ridge and ended in the Amundsen Basin (Fig. 1, Table 1). An additional station was sampled at the Morris Jesup Rise. All seven stations were situated beneath the permanent icepack in water depths from 1072 to 4273 m. Benthic samples were

Table 1
Station parameters including cruise identification, sampling date, station numbers, area, coordinates, and waterdepth (m)

Cruise	Date	Station #	Region	Coordinates	Depth
ARK VIII/3	01.09.1991	24 (2181)	Makarov Basin	87°35.75'N 153°03.56'E	3112
ARK VIII/3	01.09.1991	26 (2183)	Lomonosov Ridge	87°36.13'N 148°55.31'E	2031
ARK VIII/3	01.09.1991	27 (2184)	Lomonosov Ridge	87°36.67'N 148°12.12'E	1654
ARK VIII/3	04.09.1991	29 (2186)	Lomonosov Ridge	88°36.37'N 139°54.41'E	1867
ARK VIII/3	05.09.1991	30 (2187)	Amundsen Basin	88°44.15'N 126°53.56'E	3844
ARK VIII/3	07.09.1991	32 (2190)	North pole	90°00.73'N 57°55.59'E	4273
ARK VIII/3	16.09.1991	41 (2200)	Morris Jesup Rise	85°19.48'N 14°00.33'W	1072
AOS	30.07.1994	6	Chukchi Slope	75°21.99'N 170°32.77'W	540
AOS	01.08.1994	7	Chukchi Abyssal Plain	76°41.30'N 173°28.00'W	2220
AOS	03.08.1994	8	Arlis Plateau	78°08.17'N 176°53.00'W	1000
AOS	08.08.1994	16	Mendeleev Ridge	80°20.35'N 178°42.87'W	1520
AOS	13.08.1994	21	Wrangel Abyssal Plain	84°05.58'N 174°57.84'W	3180
AOS	15.08.1994	23	Siberia Abyssal Plain	85°54.44'N 166°40.88'W	3475
AOS	18.08.1994	25	Lomonosov Ridge	88°03.66'N 147°47.50'W	2150
AOS	19.08.1994	26	Lomonosov Ridge	88°47.50'N 143°07.46'W	1020
AOS	22.08.1994	31	North pole	89°58.85'N 40°56.80'W	4190
AOS	26.08.1994	33	Barents Abyssal Plain	84°16.14'N 34°44.39'W	3440

collected with a multi-corer (Barnett et al., 1984), and two replicate meiobenthos samples were obtained at each station. The samples were fixed on board with 4% neutralized formalin solution.

2.2. AOS 1994 transect

Samples were collected from 30 July to 26 August 1994 during the Arctic Ocean AOS - expedition in the Central Arctic Ocean on board the *USCGC Polar Sea*. The transect, which included 10 benthic stations, started in the Chukchi Sea (75°22'N, 170°33'W) and ended at the Barents Abyssal Plain at 84°16'N, 34°45'W. All stations were located beneath permanent ice. Water depths ranged between 540 and 4190 m. (Table 1 and Fig. 1). A US Naval Engineering laboratories Mark III box corer collected sediment that was subsampled for meiofauna with cut-off syringes (Internal diameter of 3.5 cm). Subsamples were collected only from those boxes that had clear overlying water present; drained or disturbed boxes were not sampled. Three replicate meiofauna samples were collected at each station. All samples were fixed on board with a 10% buffered formalin solution.

All samples underwent further processing upon return to the laboratory. Metazoan meiofauna was extracted from the sediment by the Ludox centrifugation technique (Heip et al., 1985) using a 32 μm sieve for the lower size limit and a 1 mm sieve for the upper size limit. Following staining with rose bengal, the meiofauna were sorted under a stereoscopic microscope to higher taxon levels. For most samples, 100 nematodes were picked out at random and mounted on slides for identification to genus level. A formalin–ethanol–glycerol technique was used to prevent dehydration of the nematodes (Seinhorst, 1959). If less than 100 nematodes were present, all were identified. Mean individual nematode biomass of each sample was estimated according to Andrassy's formula (1956).

$$\text{Wet weight } (\mu\text{g}) = \text{Length } (\mu\text{m}) \times \text{Width}^2(\mu\text{m})/1\ 600\ 000.$$

This formula was used to calculate the individual biomass of all selected nematodes.

Total biomass was estimated by multiplying the mean individual biomass by the total density in each sample.

In order to assess relationships among variables (density, biomass versus concentrations of food, latitude and water depth), Spearman Rank Correlation analysis (r coefficients) and regression analysis were performed using the STATSOFT Statistica program. In the case of multiple regression R^2 was adjusted for the number of independent variables (R^2 adj.), and regression coefficients were standardized (β). After fitting a regression equation, assumptions for residuals were tested. Differences in the total meiobenthos abundances among stations were tested with ANOVA and Tukey HSD post-hoc comparison after log transformation of the data.

A multivariate analysis was used to examine relationships among stations. Samples were classified into clusters based on nematode genera composition using the classification program TWINSPAN (Two-Way INDicator SPecies ANALYSIS) from Hill (1979). This multivariate technique was applied on arcsine transformed relative abundances. TWINSPAN also yields indicator taxa characterizing the delineated

communities. In order to take the quantitative differences in relative abundances of the taxa into account, the programme defines the so-called pseudo-species, a qualitative equivalent for the abundances. By the cutlevels one can define the abundance levels by which the user wants to distinguish between pseudo-species. The cut levels, which provide an optimal distribution over the pseudospecies, used here were 0, 5, 7, 11 and 17.

3. Results

3.1. Total meiobenthos densities

3.1.1. ARK VIII/3 — 1991 transect

Meiobenthos densities (Table 2 and Fig. 2) along the Lomonosov Ridge transect ranged from 56 to 87 individuals/10 cm². The station at the Morris Jesup Ridge was characterized by higher densities, with an average of 120 individuals/10 cm². However, no significant differences were found among the seven stations ($F = 2.383$; $df = 6$, $n = 14$, $p > 0.05$).

A total of 11 different major taxa were found along the transect. Nematodes were the numerically dominant taxon at every station, constituting a minimum of 88% of total meiobenthic abundance. Other taxa were, in order of importance, harpacticoids (up to 4 individuals/10 cm²), nauplii (maximum of 3 individuals/10 cm²), polychaetes (2 individuals/10 cm²), bivalves, isopods, ostracods, turbellarians, gastropods, tardigrades and loriciferans (the last 7 taxa all had on average less than 1 individual/10 cm²). The number of taxa per station varied between 4 and 7.

3.1.2. AOS — 1994 transect

Meiofaunal densities (Table 2 and Fig. 2) ranged from 28 to 639 individuals/10 cm², with the highest density at the shallowest station (540 m). This station was situated along the ice-edge, at 75°N on the Chukchi Slope. Meiobenthos abundance was lowest in the Barents Abyssal Plain (84°N, 3440 m). Densities were also low at the pole at 4190 m depth (34 individuals/10 cm²), at the Siberian Abyssal Plain at 3475 m (63 individuals/10 cm²) and at the southern side of the Lomonosov Ridge at 2150 m depth (48 individuals/10 cm²). However, station 26 at the top of the Lomonosov Ridge (1020 m) was characterised by much higher densities (254 individuals/10 cm²) compared to the surrounding stations at the base and the slope of the ridge. An ANOVA comparison of total density among stations and a post hoc comparison revealed significant differences among stations resulting in three groups: station 6 with significantly higher densities than all other stations; stations 7, 8, 16, 21 and 26 with intermediate densities; and finally stations 23, 25, 31 and 33 with the lowest densities ($F = 44.3$, $df = 9$, $n = 30$, $p = 0.0000$).

A total of 15 different meiofaunal taxa were found. Nematodes were the numerical dominant at each station, representing a minimum of 91% of the total meiofauna abundance. Harpacticoid copepods were the second most abundant taxon, representing at most 6.3% of total abundance. Other taxa were, in order of importance, nauplii,

Table 2
Mean density and standard deviation per 10 cm² of all metazoan meiofauna taxa from: (A) 1991 and (B) 1994 Central Arctic Ocean transects

A.													
Station #	24	26	27	29	30	32	41						
Depth (m)	3112	2031	1654	1867	3844	4273	1072						
Cruise	ARKVIII/3	ARKVIII/3	ARKVIII/3	ARKVIII/3	ARKVIII/3	RKVIII/3	ARKVIII/3						
Amphipoda													
Bivalvia			0.2 ± 0.2										
Bryozoa													
Copepoda	1.2 ± 0.7	3.9 ± 1.0	3.2 ± 0.0	3.2 ± 0.0	4.4 ± 0.7	1.4 ± 0.5	4.0 ± 0.0						
Cumacea													
Gastropoda			0.2 ± 0.2										
Gastrotricha													
Halacarida													
Hydrozoa													
Isopoda					0.2 ± 0.2								
Kinorhyncha													
Loricifera					0.2 ± 0.2								
Nauplii	2.3 ± 1.2	2.1 ± 1.5	1.2 ± 0.2	0.7 ± 0.0	1.1 ± 1.5	2.8 ± 0.0	3.3 ± 2.2						
Nematoda	51 ± 6.7	53.0 ± 12.1	69.0 ± 39.8	62.0 ± 12.4	80.0 ± 16.1	51.8 ± 8.9	110.0 ± 2.9						
Oligochaeta													
Ostracoda	0.5 ± 0.2	0.9 ± 0.2	0.2 ± 0.2	0.2 ± 0.2	0.2 ± 0.2	0.2 ± 0.2	0.4 ± 0.5						
Polychaeta	1.1 ± 0.0				0.7 ± 0.5	1.4 ± 0.5	2.1 ± 0.0						
Tanaeida													
Tardigrada	0.2 ± 0.2												
Turbellaria			0.2 ± 0.2			0.2 ± 0.2							
Sum	56.3 ± 9	59.9 ± 14.8	74.2 ± 40.8	66.1 ± 12.6	86.8 ± 19.4	57.8 ± 10.3	119.8 ± 5.7						
nr of taxa	6	4	7	4	7	6	5						

(continued on next page)

Table 2 (continued)

B.																				
Station #																				
Depth (m)	540	1000	1520	3180	3475	2150	1020	4190	33	3440										
Cruise	AOS'94	AOS'94	AOS'94	AOS'94	AOS'94	AOS'94	AOS'94	AOS'94	AOS'94	AOS'94	AOS'94	AOS'94	AOS'94	AOS'94	AOS'94	AOS'94	AOS'94	AOS'94	AOS'94	AOS'94
Amphipoda	0.3 ± 0.4	1 ± 0.4																		
Bivalvia																				
Bryozoa				5.7 ± 5.9																
Copepoda	37.50 ± 6.9	5.3 ± 2.3	0.3 ± 0.4	2.6 ± 1.2	3.3 ± 0.9	1.0 ± 0.8	3.7 ± 2.3	0.7 ± 0.5												
Cumacea	0.3 ± 0.4																			
Gastropoda																				
Gastrottricha																				
Halacarida			0.3 ± 0.4	0.3 ± 0.5																0.3 ± 0.4
Hydrozoa	0.3 ± 0.4																			
Isopoda	0.7 ± 0.4																			
Kinorhyncha	1.3 ± 1.3			0.3 ± 0.5																
Loricifera																				
Nauplii	6.0 ± 2.5		5.0 ± 4.3	0.7 ± 0.9	1.0 ± 0.8	1.3 ± 0.4	2.3 ± 0.9	0.7 ± 0.9	0.3 ± 0.4	0.3 ± 0.4										
Nematoda	586.3 ± 86.5	231.3 ± 47.7	236.7 ± 84.6	00.3 ± 38.2	57.3 ± 12.4	43.6 ± 3.8	246.3 ± 66.6	31.7 ± 4.1	27.3 ± 7.3											
Oligochaeta					0.3 ± 0.5															
Ostracoda	3.7 ± 0.3		0.7 ± 0.4	0.3 ± 0.5																
Polychaeta	3.0 ± 0.8	4.6 ± 4.6	0.3 ± 0.4	3.3 ± 2.5	0.7 ± 0.5	1.7 ± 1.3	1.3 ± 1.9	0.7 ± 0.5												
Tanaodiacea				0.3 ± 0.5																
Tardigrada																				
Turbellaria																				
Sum	639.3 ± 78.7	241.7 ± 44.9	247.6 ± 85.8	136.3 ± 25.0	214.0 ± 40.3	62.7 ± 11.6	254.3 ± 68.5	34.0 ± 4.9	28.0 ± 8.8											
nr of taxa	10	4	8	6	9	5	6	4	4	6	4	4	4	3						

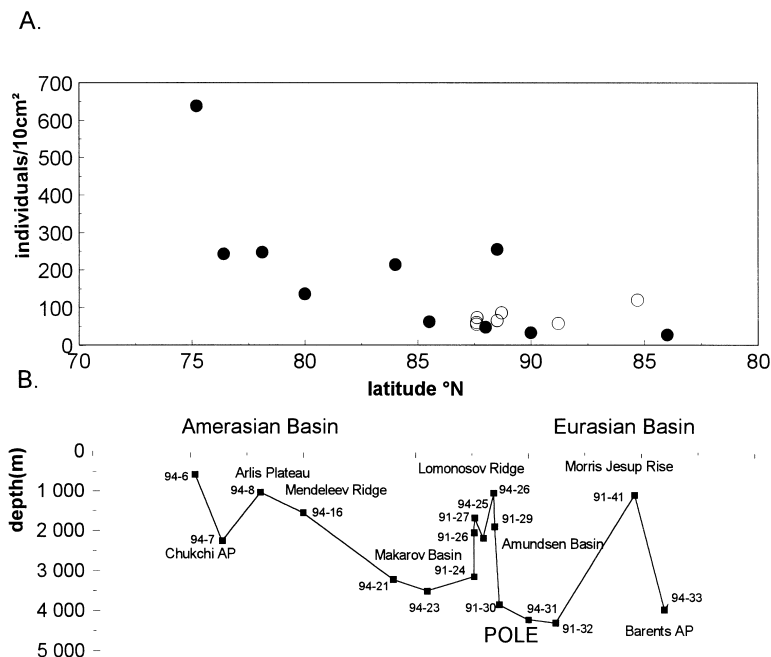


Fig. 2. (A) Relationship between meiobenthos densities and latitude. Open circles indicate stations sampled in 1991 by means of a multi-corer, and closed circles indicate stations sampled in 1994 by means of a box-corer; (B) Location of the actual stations taken relative to the bathymetry and nomenclature of the Arctic Ocean (station numbers are preceded by the year of sampling).

ostracods, polychaetes, kinorhynchs, amphipods, isopods, bivalves, cumaceans, halacarids, tanaediacans, oligochaetes, hydrozoans and bryozoans. Three to 10 different taxa were found at each station, with higher taxonomic diversity occurring in the Amerasian Basin than in the the Eurasian Basin. Specifically in the Eurasian Basin, the number of major taxa never exceeded 6, whereas in the Amerasian Basin three of the five stations had 8 or more different taxa.

3.1.3. Correlations with environmental factors

Meiobenthic densities decreased significantly with depth (Table 3, Fig. 3). However Fig. 3 also shows that the obtained regression is driven mainly by the most shallow and rich (in terms of densities) station. Density was highly variable within the 1000 to 2500 m depth range. A latitudinal pattern is suggested, since stations that were situated far beneath the regression line, and thus characterized by low densities, were on the slopes of the Lomonosov Ridge (latitude between 87° and 88°51'), i.e. the stations furthest from the shelf. Clearly meiofaunal densities changed according to both latitude and depth. A highly significant multiple regression was found which describes the densities as a log function of both latitude and depth. (R^2 adj. = 0.67, $F = 17.6$, $df = 2, 14$, $p < 0.001$, β (lat.) = -0.48 ; β (depth) = -0.49).

Table 3

Significant ($p < 0.05^{**}$, $p < 0.001^{***}$) Spearman rank correlation coefficients between total meiobenthos densities and total nematode biomass, and environmental and macrofaunal variables. (Probability levels were not corrected for multiple testing)

	n	Densities		Biomass	
		r	p	r	p
Latitude	17	-0.59	**		
Depth	17	-0.71	**	-0.69	**
Polychaeta densities	10	0.66	**	0.84	**
Metazoa densities	10	0.78	**	0.78	**
Foraminifera densities	10	0.77	**	0.83	**
Infauna densities	10	0.76	**	0.80	**
Metazoa biomass	10	0.63	**		
Foraminifera biomass	10	0.77	**	0.83	**
Infauna biomass	10	0.72	**	0.73	**
Mixing depth phaeopigments	9	0.78	**	0.93	***

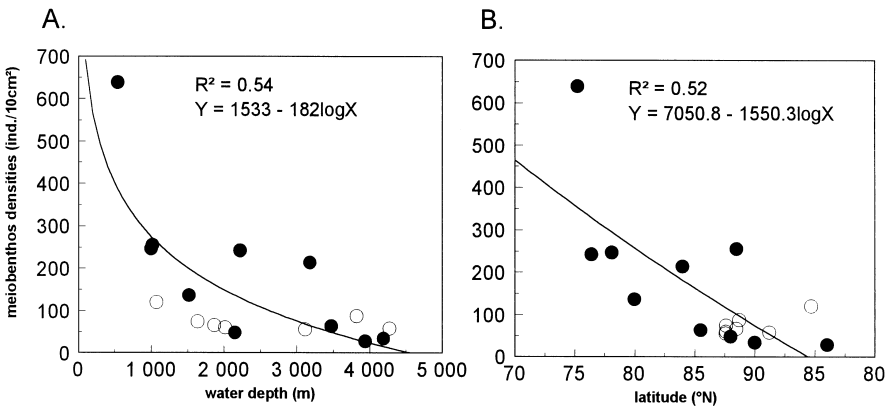


Fig. 3. Relationship between (A) meiobenthos density and water depth; (B) meiobenthos density and latitude. Open circles indicate stations sampled in 1991 and closed circles indicate stations sampled in 1994.

Macrofauna (>250 μm mesh) densities and biomass (including Foraminifera) were estimated by Clough et al. (1997) from the same stations and sampling cruise as the 1994 transect. Their study also provides data on different measures for food supply (mainly as pigment concentrations and total organic carbon), sediment mixing depth and rates, and porewater irrigation. Meiobenthos and nematode densities were significantly correlated ($p < 0.05$) with macrobenthic infauna densities and biomass values (Table 3). In terms of food supply, meiobenthos densities, were significantly related only to mixing depth (in cm) of the excess in phaeopigments. Briefly, excess phaeopigments are defined as the inventory of phaeopigments in excess of a

presumably refractory baseline seen at depth within the sediments (see Clough et al., 1997 for further details). The mixing depth of excess pigments is defined as the maximum penetration of the excess pigments below the sediment–water interface. The total organic carbon (TOC) content was measured simultaneously for 1994 and 1991 stations and did not show a significant correlation with either meiobenthos or nematode densities ($r = 0.29$, $n = 17$, $p > 0.05$).

Kröncke (1994) investigated the macrobenthos ($> 500 \mu\text{m}$) from 6 stations of the 1991 transect. Along this transect, there was no significant correlation between mei- and macrobenthos densities, but macrobenthos densities were lower than in 1994. The use of a larger mesh size is likely to be responsible for the lower macrobenthic abundance in 1991 compared to 1994.

3.2. Nematode biomass

3.2.1. ARK VIII/3 — 1991 transect

The mean individual nematode biomass for 1991 stations was characterized by a high variation among stations with a minimum of $0.03 \mu\text{g}$ dry weight at station 30 in the Amundsen Basin to a maximum of $0.15 \mu\text{g}$ dry weight per individual at station 27 near the top of the Lomonosov Ridge (Fig. 4). The mean values on the ridge also

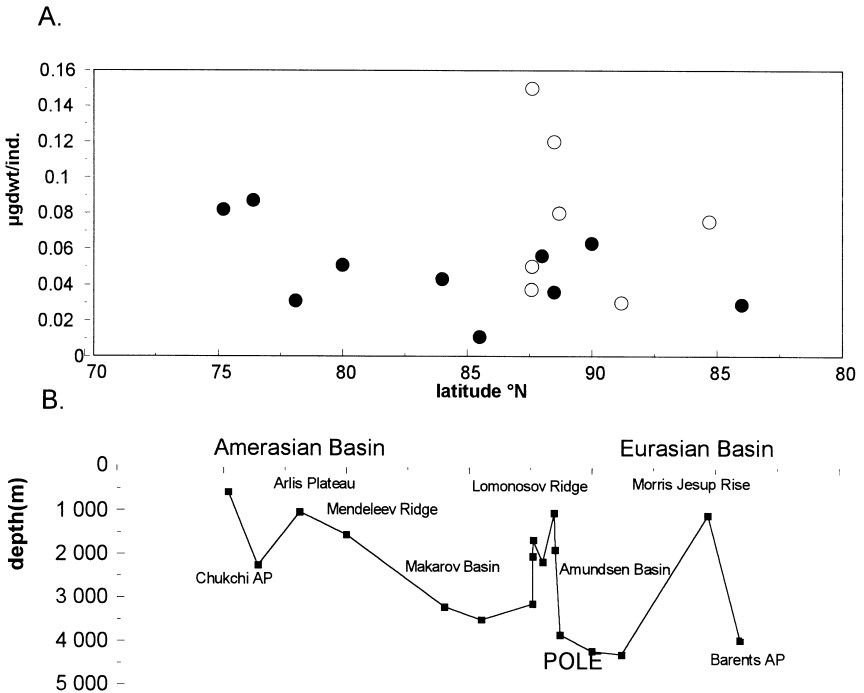


Fig. 4. (A) Relationship between individual nematode biomass and latitude. Open circles indicate stations sampled in 1991 and closed circles indicate stations sampled in 1994; (B) Location of the actual stations taken relative to the bathymetry and nomenclature of the Arctic Ocean.

varied dramatically (0.037–0.15 μg dry weight). While abundances were highest at the Morris Jesup Rise, individual biomass was low with a mean value of 0.075 μg dry weight. Total biomass varied even more, from a maximum of 10.35 μg dwt/10 cm^2 at the ridge (station 27) to a value nearly 10 times smaller (1.56 μg dry weight/10 cm^2) near the pole (station 32).

3.2.2. AOS — 1994 transect

The AOS transect covers a much larger area than the 1991 transect, yet these stations showed lesser variation in individual nematode biomass than the 1991 data. Highest values were found in the Chukchi Sea, with means of ~ 0.08 μg dry weight per individual. The smallest nematodes were found at station 23 in the Makarov Basin, which had an average individual biomass of 0.01 μg dry weight per individual (Fig. 4).

Total biomass followed the same pattern as individual nematode biomass. Highest values were in the Chukchi Sea, with 48 and 20 μg dry weight/10 cm^2 at stations 6 and 7, respectively, and the lowest total biomass was recorded at station 23 on the Siberia AP (0.6 μg dry weight/10 cm^2), with station 33 on the Barents AP being slightly higher (0.8 μg dry weight/10 cm^2).

3.2.3. Correlations with environmental factors

Mean individual nematode biomass was not correlated with any of the environmental factors, nor was there any latitudinal trend. The Lomonosov Ridge was characterized by larger nematodes at stations sampled in 1991 than at other stations (Fig. 4). Nematode size did not show any correlation with total densities or biomass of any of the meiobenthic or macrobenthic groups.

Total nematode biomass was significantly correlated only with water depth, not with latitude (Table 3). However, when the high biomass value from the single shallow station (station 6 at 540 m, sampled in 1994) was excluded from the regression (Fig. 5),

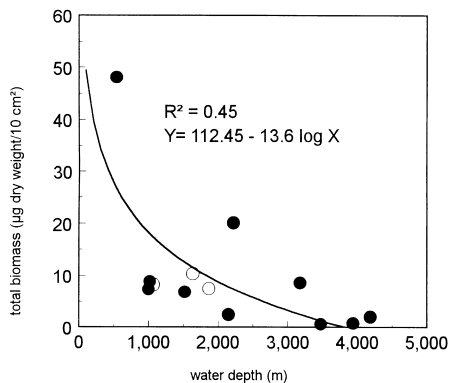


Fig. 5. Relationship between total nematode biomass and water depth. Open circles indicate stations sampled in 1991 and closed circles indicate stations sampled in 1994.

the relationship with depth was less robust ($R^2 = 0.16$). As was seen with meiofaunal density, 55% of the variation in biomass was explained by a combination of latitude and depth (after log transformation of the data: R^2 adj. = 0.55; $F = 10.8$, $df = 14$, $2 p < 0.001$ β (lat) = -0.44 ; β (depth) = -0.45).

Total nematode biomass was significantly correlated with densities of all macrobenthic components including polychaetes, metazoans, foraminiferans and the total infauna for the 1994 transect (Table 3). Nematode biomass was also correlated with foraminifera and the total infauna biomass (Table 3). As with total meiofaunal abundance, only the maximum mixing depth of excess phaeopigments was significantly ($r = 0.93$, $n = 9$) correlated with the nematode biomass (Fig. 6 and Table 3). All other tested correlations were not significant.

3.3. Community structure of the nematodes to genus level

3.3.1. ARK VIII/3 — 1991 transect

In total 50 different nematode genera were identified along the 1991 transect, with a range of 23–39 genera per station. The relative abundances of the 30 most abundant genera are shown in Table 4. All seven stations were dominated by *Monhystera* (Monhysteridae), which accounted for 16–55% of the total abundance. Station 27 showed shared dominance between *Monhystera* (19%) and *Acantholaimus* (24%) (Chromadoridae). In general, *Metalinhomoeus* was the third most abundant genus, making up 4–20% of the nematode community. *Leptolaimus* (Leptolaimidae) and *Halalaimus* (Oxystominidae) were also important genera along this transect.

3.3.2. AOS — 1994 transect

In total, 111 different genera were found along this transect, 41 of which were also found during the 1991 transect. The number of genera per station varied between 16

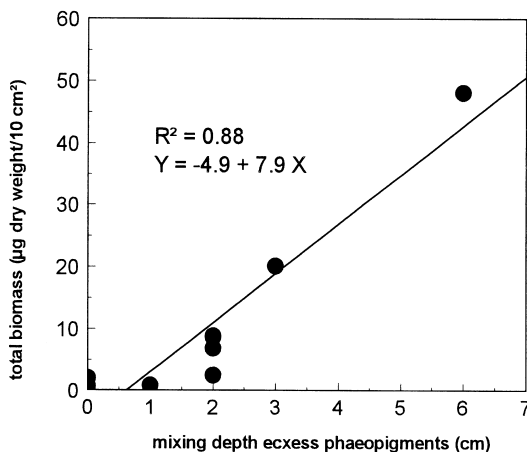


Fig. 6. Relationship between total nematode biomass and mixing depth of excess in phaeopigments in 1994, showing the benefit of meiofauna from increased sediment mixing.

and 52. The maximum number of genera was recorded at station 8 on the Arlis Plateau, followed by the nearby stations on the Chukchi Slope (station 6) and the Mendeleev Ridge (station 16) with 45 and 41 genera, respectively. The lowest number of genera (16) was seen at the Siberia Abyssal Plain (station 23) and the Barents Abyssal Plain (station 33), both of which were also characterized by low numbers of individuals. For seven of the 10 stations, *Monhystera* (Monhysteridae) was the dominant genus, making up 24–62% of the total community. At the three remaining stations *Monhystera* was still very abundant (9–20%). *Acantholaimus* (Chromadoridae) was the most abundant genus at two of the remaining stations (11 and 22%). The Chukchi Slope station was dominated by *Daptonema* (Xyalidae), but *Monhystera* and *Acantholaimus* were the two next most abundant genera at this station, making up 11 and 7% of the total community, respectively. Other common and relatively abundant genera along the transect were *Campylaimus* (Diplopeltidae), *Amphimonhystrella* (Xyalidae), *Halalaimus* (Oxystominidae), *Aegialolaimus* (Aegialolaimidae) and *Sphaerolaimus* (Sphaerolaimidae).

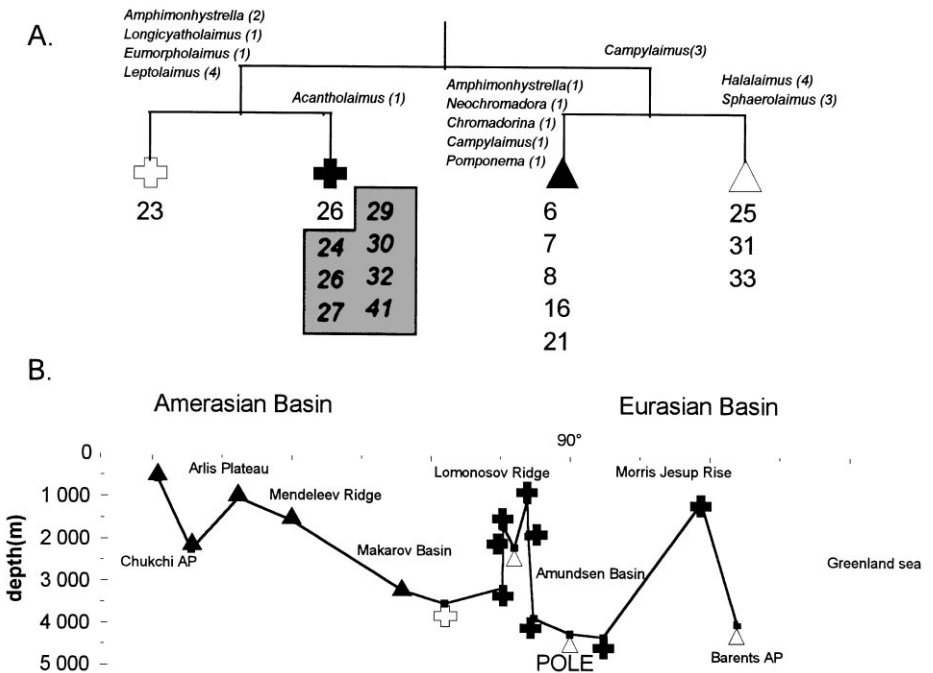


Fig. 7. (A) Dendrogram resulting from a TWINSPLAN on arcsine transformed relative abundances of nematode genera in both transects, with indication of the indicator genera for each division and their respective cut levels. The position of the twingroups is indicated on the depth and latitudinal profile below. The stations sampled in 1991 are grouped in a gray box; (B) Location of the actual stations taken relative to the bathymetry and nomenclature of the Arctic Ocean.

3.3.3. Comparison of both transects

Two Way INDicator SPecies ANalysis (TWINSPAN) revealed a combined effect of latitude and bathymetry on nematode community structure at the genus level. All stations (except station 25) from the base, the slope and the top of the Lomonosov Ridge and the adjacent Morris Jesup Rise group together after the first dichotomy (Fig. 7). The other TWIN-group comprises all stations in the Amerasian basin (except the one adjacent to the Lomonosov Ridge) together with three other stations: one at the Lomonosov Ridge (the depression near the top), one at the Amundsen basin (the pole station) and one at the Barents Abyssal plain. The Lomonosov Ridge and Morris Jesup Rise stations were distinguished from the remaining stations (Amerasian Basin, Amundsen Basin and Barents Abyssal Plain) by the overall high abundance of *Leptolaimus*, a genus that was only subdominant to occasionally present in the second group. Also, the subdominance of *Amphimonhystrella* and the presence of *Eumorpholaimus* and *Longicyatholaimus* separated the ridge and rise from other portions of the transects. *Campylaimus* is an indicator genus for the second group where it reaches higher abundances relative to the first group.

Within the first TWIN group, station 23 from the Makarov basin (adjacent to the Lomonosov Ridge) separated from the remaining stations based on the absence of *Acantholaimus*. Within the second TWIN group, all stations from the Amerasian basin (West from the Lomonosov Ridge) were distinct from the three remaining stations due to the presence of *Amphimonhystrella*, *Neochromadora*, *Chromadorina*, *Campylaimus* and *Pomponema*. High abundances of *Halalaimus* and *Sphaerolaimus* were characteristic for the remaining three stations in the second group (Fig. 7).

4. Discussion

4.1. Meiobenthos standing stock in the central Arctic Ocean

Meiobenthos densities from the central Arctic Ocean were similar for adjacent stations sampled in 1991 and 1994. In 1991, however, samples were collected with a multi-corer, whereas in 1994 a box-corer was used. Bett et al. (1994) showed that the meiobenthos from soft surface sediments can be underestimated when the box-corer is used. In our study the box-corer density data lie completely in the range of the multi-corer data collected at similar depths. This suggests a minor effect of different sampling techniques on the results.

Meiobenthos densities and nematode biomass along the 1994 transpolar transect revealed the same pattern observed by Clough et al. (1997) for the macrofauna, with high densities in the first part of the transect and low densities approaching the pole, with the exception of some locally enriched sites at the top of the Lomonosov Ridge (station 26) and in the Wrangel Abyssal Plain (station 21; Makarov Basin). A significant relationship between macrofaunal density and water depth was found although only 39% of the variability in density was explained by this linear relationship, indicating other unidentified factors must also play a significant role. In our study,

67% of the variation in meiobenthos density and 55% of the variation in nematode biomass was explained by a combination of latitude and depth.

We suggest that the latitudinal effect is driven by either distance from the continental shelf or distance from the ice-edge, two factors that are not mutually exclusive. Both proximity to the continental shelf and proximity to the ice-edge would be expected to impact food supply to the benthos (e.g. Walsh, 1995). Several studies have concluded that food availability is the main determining factor for meio- and macro-benthic standing stock, not only in the deep-sea (Vincx et al., 1995) but also in subarctic environments such as the Barents Sea Slope (Pfnannkuche and Thiel, 1987). While food availability appeared to be the main determining factor, as indicated by the combined effect of latitude and water depth, 33 and 45% of the variability in the meiobenthos density and nematode biomass remain unexplained. For example, at a given water depth benthic standing stock appears to be higher in the Amerasian than in the Eurasian Basin. One factor that may be invoked to explain the remaining variability is lateral advection of biogenic material. There is evidence for the importance of lateral input of biogenic detritus in different areas of the world, including the Arctic (Anderson et al., 1994; Kemp, 1994; Rowe et al., 1994; Wallace et al., 1987). Yet according to Boetius and Damm (1998), independent estimates of vertical organic matter import to the Laptev Slope implied that the advective transport of organic matter was not important for the benthos of the Arctic Sea, because the advected material was old, refractory organic carbon. This was especially true for the eastern Arctic (i.e., the Laptev Sea), where sediments were composed largely of terrigenous organic matter (Stein et al., 1994). The western Arctic, including the Chukchi Sea, however, is characterized by low riverine input. A more thorough investigation of the role of lateral advection in providing food to the benthos of the central Arctic is needed.

None of the indicators for food we used, such as concentration of chlorophyll and phaeopigments, as determined by Clough et al. (1997), were significantly correlated with the densities or biomass of any of the meiobenthic groups. Clough et al. (1997) found the same lack of relationship between faunal abundances and pigments. Locally enriched sites such as station 26 at the top of the Lomonosov Ridge did show enriched concentrations of phaeopigments and increased meiobenthic abundances, but this pattern did not hold for all stations. The mixing depth of excess phaeopigments was the only factor significantly correlated with meiofauna densities and biomass. This could imply that the meiofauna benefit from increased sediment mixing or that mixing of excess phaeopigment is a better indicator of food input than the standard concentration measurements.

In our study and that of Clough et al. (1997), the overall relationship between TOC and the benthic standing stock was not significant. A marginally significant linear relationship ($R^2 = 0.67$; $F = 8.15$, $df = 1,4$; $p = 0.046$) between meiobenthos density and TOC was found for the deeper stations of the Amerasian Basin (station 7 → 23). Standard organic carbon estimates may prove to be important at regional, but not panregional, scales in the Arctic Ocean. Soltwedel and Schewe (1998) did not find any significant relationship between sediment pigment concentration and either water depth or latitude in the Arctic Ocean, but they did see a significant correlation

between bacterial abundance (and biomass) in the sediment and water depth in the same area. Perhaps the highly refractory organic matter within the sediments of the central Arctic Ocean is used primarily by specialized microorganisms including bacteria, which act as the main food source for higher trophic levels in this extremely oligotrophic environment. Bacteria may represent an important food source for nematodes as was shown for several shallow water species (Moens and Vincx, 1997). Not much is known concerning the feeding strategies of deep-sea or Arctic nematodes, but the dominance of morphotypes with small buccal cavities, such as *Monhystera* and *Metalinhomoeus*, *Leptolaimus*, *Halalaimus* and *Campylaimus*, together with the absence of any buccal armature in these species, is consistent with a bacterivory–detritivory feeding basis for these communities. Microscopic observations on the feeding ecology of several estuarine nematodes demonstrated the exclusively bacterivorous feeding strategy of a *Halalaimus* and a *Leptolaimus* species from the Western scheldt (the Netherlands) (Moens and Vincx, 1997). Hence the absence of a correlation between chl *a* or phaeopigment concentrations in the sediment with meiobenthos standing stock is possibly due to the fact that a portion of the carbon flux to the meiobenthos is channelled through the bacteria. In order to fully understand the processes responsible for the present benthic standing stock, complex interactions between primary production and the different size and taxonomical groups of the secondary producers, and the flux to the sea floor, should be taken into account.

We do not have flux data. During the same transpolar transect (AOS 1994) however, Rich et al. (1997) and Wheeler et al. (1996) found that pigment concentration and algal production in the water column were maximal in the Chukchi Sea (162–437 mg Chl_a/m²), decreased to low values in the Makarov and Amundsen Basins (1–22 mg/Chl_a m²), and then increased slightly towards the Nansen Basin (60 mg Chl_a/m²). Thus, primary production in the overlying water column showed a decreasing latitudinal trend towards the pole. The fact that fluxes of organic material from the surface to the deep-sea floor are largely related to primary productivity in the overlying water column and water depth is generally accepted (Asper et al., 1992; Turley et al., 1995; Relexans et al., 1996). The observations that both meiobenthic abundance and surface primary production decreased with latitude, coupled with the observation that not all the variation in meiobenthos densities and biomass is explained by water depth and latitude, provide support for the existence of a more diverse array of food sources for the meiobenthos of the Arctic Ocean.

In summary, the results from this study provide supplementary evidence that the abundance and distribution of meio- and macrobenthos in the central Arctic Ocean cannot be explained by simple correlations with pigment concentrations or TOC. However, the significant correlation with both water depth and latitude suggests the importance of food availability, and it implies that vertical flux and distance from the continental slope or the ice-edge all play a role in providing food.

4.2. Nematode community structure in the central Arctic

The results of multivariate analysis (TWINSPAN) showed that there is a high similarity among all stations investigated from both transects. Dichotomies are not

based on the dominant genera (see indicator groups) but instead on the rarer genera. Stations from the Lomonosov Ridge and the Morris Jesup Rise are characterized by higher abundances of *Leptolaimus*, *Amphimonhystrella*, *Longicyatholaimus* and *Eumorpholaimus* compared to the remaining stations.

While samples from the central — 1991 transect and the north–south — 1994 transect were similar with regards to the dominance of *Monhystera*, other nematode genera differences did occur. The most striking difference in nematode community structure between 1991 and 1994 was the higher abundance of *Leptolaimus* and *Metalinhomoeus* in 1991. Based on the dominance of these two genera, the 1991 transect shows more similarity with the deepest stations (1935–3237 m) sampled along a Laptev Sea transect (78°N, 120°E), which took place during September of 1993 (Van Averbek et al., 1997), than with the stations from the Lomonosov Ridge sampled during the 1994 transect. We offer three possible explanations for this observation: (1) seasonal differences, (2) circulation patterns, and (3) flow differences.

First, the 1994 samples were collected from the end of July up to the end of August, while the 1991 transpolar transect took place between 1 and 16 September. The algal growing season is assumed to occur from June through September, which means that the 1991 and 1993 transects were sampled at the end of the growing season, while the 1994 sampling took place in midseason. We do not know the average generation time of deep-sea nematodes, nor do we know if in nematode species composition changes in response to episodic enrichment in the deep-sea. Explaining the increase in *Leptolaimus* and *Metalinhomoeus* relative abundances between 1991 and 1994 as a seasonal response would require more work.

The TWINSPAN analysis indicates that the deep station in the Amerasian Basin (lowest in the Makarov Basin) is more similar to the Lomonosov Ridge stations, while the deep stations in the Eurasian Basin during the 1994 transect appear to be more similar to the stations located in the Amerasian Basin. Swift et al. (1997) present evidence showing the deep waters of the Makarov basin to be of Eurasian origin (Russian shelves), so the grouping of station 23 is consistent with the apparent hydrographic patterns. The differences seen in the Eurasian Basin are less easily explained, but may be reflective of changing hydrographic conditions within the central Arctic Ocean (Carmack et al., 1997).

Finally, the separation among stations from both transects may be due to variable flow rather than geographical or temporal changes. The discrepancy of the nematode communities on the Lomonosov Ridge and Morris Jesup Rise from the remaining stations is in accordance with the results of Kröncke (1994) for the macrofauna. Within the macrofauna, the ridge communities consisted of suspension feeders, as opposed to deposit feeders or possibly predators found in the basins. The 1750 km long Lomonosov Ridge has a peak at 1000 m depth running parallel to the 140°E longitude line and passing west of the pole at a few degrees distance and is the highest of all ridges in the central Arctic Ocean. Possibly the divergent nematode genera composition at the Lomonosov Ridge and Morris Jesup Rise is explained by the variable flow rates that act on both the meio- and the macrobenthos.

4.3. Comparison of deep-sea Arctic and non-arctic meiofauna

The total number of higher taxa (19) over the whole Arctic study area, in addition to the overall dominance of the nematodes, representing 90% and more of the total metazoan meiobenthos communities, is in the same order of magnitude as for other deep-sea areas (Vincx et al., 1995), including the Antarctic Weddel Sea (Vanhove et al., 1995). The study of Vanhove et al. (1995) revealed in general a higher number of taxa per station, varying between 8 and 15, in comparison to the 3–10 taxa counted per Arctic station. The overall presence of the nematodes, harpacticoid copepods, and polychaetes at the Arctic stations is also in accordance with the general trend present in the deep-sea. (Alongi, 1992; Vincx et al., 1995; Vanhove et al., 1995).

When we compare our data on densities and biomass of the meiobenthos with other oligotrophic areas at similar depths, it is obvious that especially the lowest Arctic densities within the 5° latitude zone around the pole are significantly lower than densities in the Antarctic and the Laptev Sea. The densities near the North pole are similar to the extreme low values found in the oligotrophic south-west Pacific and at 4850 m depth on the Cape Verde Abyssal Plain (EUMELI site) (Fig. 8).

Densities of Arctic meiobenthos at the shallow station of the Chukchi Sea are more similar to those in the Weddell Sea. Estimates of water column primary production, however, are more than one order of magnitude lower in the 75°N–80° N area of the Chukchi Sea ($0.032 \pm 0.013 \text{ g C/m}^2/\text{d}$; Wheeler, 1997) compared to the Weddell Sea ($0.114\text{--}0.955 \text{ g C/m}^2/\text{d}$; Brockel, 1981; El-Sayed, 1978). Based on their findings in the Laptev Sea, Van Averbek et al. (1997) assumed that the meiobenthos, especially the nematodes, are adapted to this extreme environment by a rapid response to short food

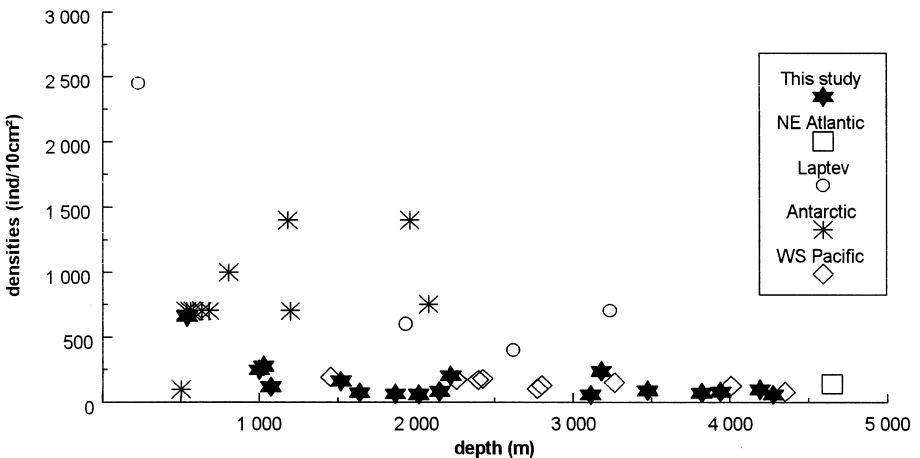


Fig. 8. Meiobenthos densities (ind/10 cm²) in different oligotrophic oceans of the world. Data are from the oligotrophic EUMELI site (Vincx et al., 1995), the Arctic Laptev sea (Van Averbek et al., 1997), the Antarctic Weddell sea (Vanhove et al., 1995) and the Southwest Pacific Solomon and Coral seas (Alongi, 1992).

pulses to the sediments. So far, no evidence exists for the proposed rapid response. The fact that the different estimates of primary production in north and south polar (Chukchi versus Weddell Sea) seas are not translated into differences in meiobenthos densities at shallow depths (<1000 m) may be related to a higher importance of bacterial production in the Arctic compared to Antarctic Seas. As further support for this hypothesis, the Weddell Sea communities are better represented by feeding types that are assumed to have a more epistratum feeding mode, such as *Molgolaimus*, *Microloaimus* and *Dichromadora* (Vanhove et al., 1999), versus the dominance of potentially bacterivorous nematodes found in the Arctic.

Comparing mean individual body sizes (μg dry weight/ind.) in different areas revealed that, with exception of the two outliers at the Lomonosov Ridge (0.12 and 0.15 μg dry weight), nematodes are the same size in the Arctic Ocean (0.011–0.087 μg dry weight) as in the NE Atlantic oligotrophic site (0.0241 μg dry weight \pm 0.006 SD) and even the more eutrophic Porcupine Abyssal Plain site (0.0511 μg dry weight \pm 0.02 SD) (Vanreusel et al., 1995). Both sites are, however, 600 m deeper than the deepest Arctic sites. The individual nematodes are in general larger in the Antarctic Weddell Sea (0.05–0.2 μg dry weight) in the depth range between 600 and 2000 m depth (Vanhove et al., 1995). Differences in individual biomass, in addition to differences in densities, account for the difference in total nematode biomass per unit surface area seen between the Arctic and Antarctic.

The dominance of *Monhystera*, *Daptonema*, *Theristus* and *Acantholaimus* and the subdominance of the genera *Leptolaimus* and *Halalaimus* in the central Arctic Ocean is in accordance with the nematode communities of the deep-sea studied in other parts of the world. *Acantholaimus*, *Halalaimus*, *Theristus*, *Leptolaimus* and Monhysteridae were found to be dominant to subdominant from the rise to the Abyssal Plain in the NE Atlantic (Soetaert and Heip, 1995 and Vincx et al., 1995), the NW Atlantic (Tietjen, 1971, 1976, 1989, Thistle and Sherman, 1985), the Indian Ocean (Muthumbi, 1998) and the Pacific (Vanreusel et al., 1997). A higher abundance of *Sabatieria* at the shallow slope as described for the NE Atlantic and Mediterranean (Soetaert and Heip, 1995) was not found in the transpolar transect. The higher abundance of *Metalinhomoeus* in this study seems to be the dominant distinguishing characteristic for the Arctic Ocean. *Metalinhomoeus* was never abundant in other deep-sea areas except for the Laptev Sea (Van Averbek et al., 1997). The number of genera present at the different stations is rather low for the deep sea.

5. Conclusions

- (1) The meiobenthic standing stock in the permanently covered central Arctic Ocean appears to be influenced by both water depth and latitude. We infer that both vertical and advective fluxes play a role in providing organic matter to the meiobenthos, yet other factors must be considered as well.
- (2) The dominance of bacterivory–detritivory nematodes in the Arctic suggests an important role of bacteria in the meiobenthic food web, at least in comparison to the Antarctic, where epistratum feeders are dominant.

- (3) The nematode communities in the central Arctic Ocean are similar in terms of dominant genera and average sizes to the communities observed at similar depths in the Atlantic Ocean.
- (4) The nematode communities of the central arctic ocean are fairly homogeneous among the areas sampled, showing only minor spatial changes in the dominant genera composition. Further study is required to explain the separation of stations on and near the Lomonosov Ridge and adjacent Morris Jesup Rise on the basis of nematode community.

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