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DEEP-SEA MEIOBENTHOS OF THE CENTRAL ARCTIC OCEAN : DISTRIBUTION PATTERNS AND SIZE-STRUCTURE UNDER EXTREME OLIGOTROPHIC CONDITIONS

I. SCHEWE, T. SOLTWEDEL

Alfred-Wegener-Institut for Polar and Marine Research, Columbusstrasse, 27568 Bremerhaven, Germany
e-mail : ISchewe@AWI-Bremerhaven.de

ARCTIC OCEAN
ICE-COVERAGE
DEEP-SEA MEIOBENTHOS
FORAMINIFERA
COMPOSITION
SIZE-STRUCTURE
FOOD AVAILABILITY

ABSTRACT. – During the expedition “Arctic Ocean ’96” with the Swedish icebreaker ODEN (18.07.-21.09.96), sediments were collected from 20 basin and ridge stations in the deep-sea regions of the central Arctic Ocean north of 85°N at water-depths between 864 m and 4187 m to investigate the influence of extreme food scarceness in the perennially ice covered deep Arctic-Mediterranean on the meiobenthic community. Meiofauna densities (including foraminiferans) ranged between 68-247 ind·10 cm⁻² in the uppermost sediment layers and were very low compared to values from temperate, central oceanic regions. Nevertheless, a decrease in abundance with increasing water depth as well as regional differences in abundance and community structure were detectable. Foraminiferans were by far the predominant taxon (58-86 %), followed by nematodes (10-27 %). Except for harpacticoid copepods all other meiofauna taxa occurred in extremely low densities and very patchy. Very low meiofaunal abundances and a visible trend towards miniaturisation of organisms may be an outcome of the extremely limited food supply to the benthos under perennial ice-coverage of the central Arctic Ocean.

OCÉAN ARCTIQUE
GLACES PERSISTANTES
MÉIOBENTHOS PROFOND
FORAMINIFÈRES
COMPOSITION
STRUCTURE DE TAILLE
RESSOURCES NUTRITIVES

RÉSUMÉ. – Lors de l’expédition « Arctic Ocean ’96 » sur le brise-glace suédois ODEN (18.07-21.09.96), des sédiments ont été prélevés à 20 stations du bassin et de la ride dans les zones benthiques de l’Océan Arctique central, au nord de 85°N et à une profondeur comprise entre 864 et 4187 m, afin de rechercher l’influence de l’extrême pauvreté de la nourriture sous les glaces persistantes de la Méditerranée arctique sur les communautés méiobenthiques. Les densités de la méiofaune (y compris les Foraminifères) varient entre 68 et 247 ind· 10 cm⁻² dans la couche la plus superficielle du sédiment et sont très basses par rapport aux valeurs des régions tempérées et centrales de l’océan. Une diminution de l’abondance alors que la profondeur augmente, ainsi que des différences régionales de l’abondance et de la structure des communautés ont été détectées. Les Foraminifères représentent le taxon dominant (58-86 %), suivis des Nématodes (10-27 %). A l’exception des Copépodes Harpacticoides, les autres taxons méiofauniques ont de très faibles densités et sont répartis par taches. L’abondance très faible de la méiofaune et une tendance visible à la miniaturisation des organismes peuvent être la conséquence de ressources nutritives extrêmement limitées pour le benthos au-dessous des glaces permanentes de l’Océan Arctique central.

INTRODUCTION

Benthic investigations in deep-sea regions of the central Arctic Ocean are scarce. Extreme weather conditions and strong ice-coverage require remarkable financial and logistic effort for the exploration of these areas. First quantitative studies on the meiobenthos of the Arctic Ocean were given by Pfannkuche & Thiel (1987) for the north-

ern Barents Sea and the adjacent Nansen Basin, and by Vanaverbeke *et al.* (1997) for the Laptev Sea continental slope. The Swedish expedition “Arctic Ocean ’96” with the icebreaker ODEN in summer 1996 offered the possibility to carry out quantitative investigations on the meiobenthos of the central Arctic Ocean north of 85°N. Sediment-samples from the deep basins (Amundsen-, Nansen- and Makarov Basin) and submarine ridges (Gakkel- and Lomonosov Ridge) served as a basis

Table I. – Positions of sampling sites during expedition "Arctic Ocean '96".

Date	Station	Transekt	Latitude	Longitude	Depth	Region
27.08.96	25	I	85°24,5'N	143°11,5'E	2523m	Lomonosov Ridge slope
29.08.96	26	I	85°22,0'N	149°16,5'E	1055m	Lomonosov Ridge crest
31.08.96	27	I	85°32,7'N	156°29,9'E	2382m	Lomonosov Ridge slope
01.09.96	31	I	85°40,6'N	160°20,5'E	3346m	Makarov Basin
24.08.96	24	II	86°28,6'N	130°13,1'E	4187m	Amundsen Basin
06.08.96	10	II	86°24,5'N	143°01,4'E	970m	Lomonosov Ridge crest
05.08.96	9	II	86°23,5'N	144°15,4'E	864m	Lomonosov Ridge crest
12.08.96	11	---	86°47,5'N	142°25,7'E	1300m	Lomonosov Ridge crest
18.08.96	16	---	87°01,0'N	144°02,0'E	1782m	Lomonosov Ridge canyon
03.08.96	8	III	87°04,6'N	129°29,6'E	3724m	Amundsen Basin
03.09.96	32	III	87°36,3'N	146°54,3'E	1223m	Lomonosov Ridge crest
06.09.96	33	III	87°09,7'N	169°20,2'E	3883m	Makarov Basin
10.09.96	37	IV	89°55,0'N	152°13,0'E	4142m	Amundsen Basin
08.09.96	36	IV	88°60,0'N	179°58,0'E	2249m	Lomonosov Ridge slope
07.09.96	35	IV	88°40,0'N	178°30,0'E	1111m	Lomonosov Ridge crest
31.07.96	7	V	86°20,0'N	74°27,7'E	3600m	Gakkel Ridge
29.07.96	6	V	85°33,9'N	72°14,9'E	3792m	Nansen Basin
12.09.96	39	VI	87°16,8'N	22°27,2'E	4180m	Amundsen Basin
14.09.96	40	VI	85°31,0'N	12°09,0'E	2265m	Gakkel Ridge
17.09.96	41	VI	84°01,0'N	11°43,0'E	3275m	Nansen Basin

for different investigations on these organisms (community composition and densities, regional distribution patterns, as well as size distribution of the arctic deep-sea meiobenthos).

The input of particulate organic matter (POM) to the seafloor is the main food – and energy-source for heterotrophic benthic organisms in oceanic regions (Jumars *et al.* 1989). Polar regions are dominated by short cycles of production and long periods of low nutrient availability (Thiel *et al.* 1996). The content of organic material, reaching the benthic environment and being a food and energy source, reflects variations in hydrography, perennial ice-coverage, light and water temperature as well as structures in the pelagic food web. Main objective of this study was to clarify how the extreme scarceness of food in the ice-covered Arctic Ocean affects the benthic meiofauna.

After Thiel's (1975, 1983) hypothesis, the importance of small organisms, for the total benthic metabolism, is enhanced with decreasing input of organic matter. Especially low "metabolic size" may be advantageous for benthic organisms in ecosystems where the sedimentation rate is very low, and the limited food supply reaching the abyssal bottom restricts faunal abundance. Thus, we expected a big share of especially small organisms and very low abundances in the meiofaunal community.

MATERIAL AND METHODS

Area of investigation: During the expedition "Arctic Ocean '96" with the Swedish ice-breaker ODEN from 18.07. to 21.09.1996 sediment samples were taken in the central Arctic deep-sea basins (Nansen-, Amundsen- and Makarov Basin) as well as along submarine ridges (Lomonosov- and Gakkel Ridge) crossing the Arctic Ocean. A total of 20 stations with water depths ranging between 864 m (station 9) on the top of the Lomonosov Ridge and 4,187 m (station 24) in the deep Amundsen Basin (Fig. 1, Table I) were sampled.

The Arctic Ocean is characterised by its more or less permanent ice-coverage in the central regions and a highly seasonal ice-coverage in the marginal seas. A strong density layer results in a decoupling of deep currents from wind driven water-circulations at the surface. Along the continental slopes and the deep-sea ridges strong border-currents form cyclic gyre systems (Rudels *et al.* 1997): the Beaufort Gyre in the Canadian Basin, a gyre circulating in the Makarov Basin and one in the Eurasian Basin, the latter divided into two parts by the Gakkel Ridge (Fig. 2). Aagaard (1981) found evidence for an easterly overflow of Eurasian Waters into the Makarov Basin. The Transpolar Drift transports high amounts of terrigenous and organic material via sea-ice from the large marginal shelf regions into the central Arctic Ocean (Schubert & Stein 1996). High quantities of this material may be loaded-off especially over the Lomonosov Ridge, released from crushed and melting ice-floes, caused by the interaction of opposite currents along the ridge.

Sampling and sample processing: Bottom samples were taken with a multicorer (MC) bringing to the surface

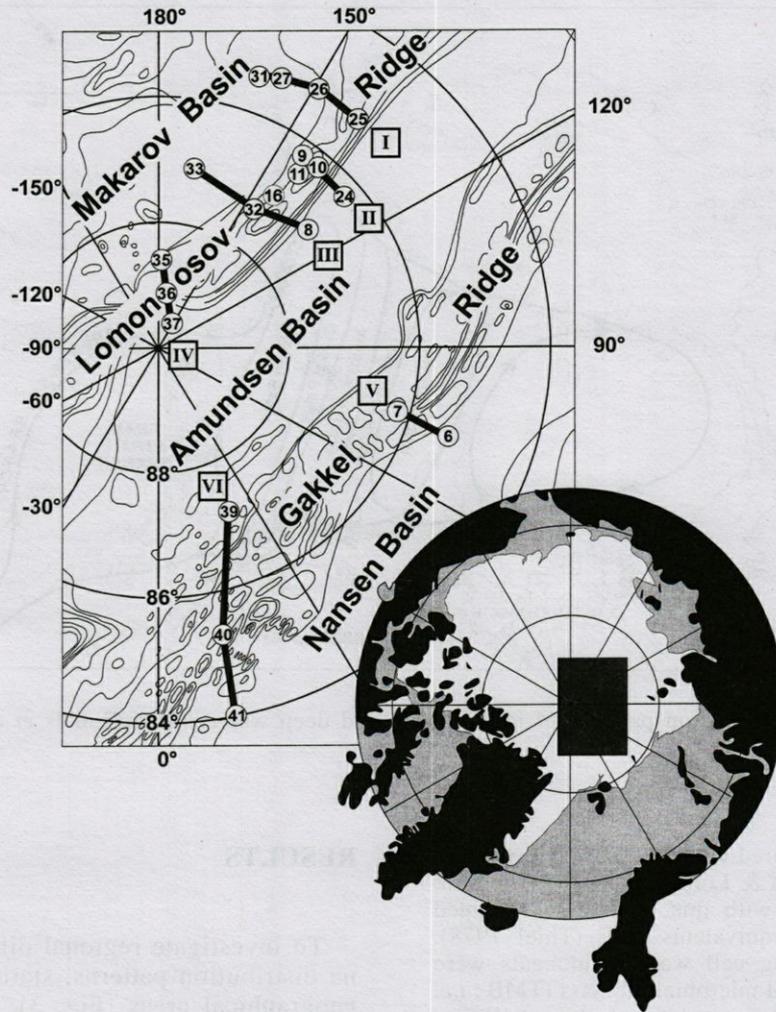


Fig. 1. – Location of sampling stations (arabic numbers) and transects (roman numbers) in the central Arctic Ocean during the expedition “Arctic Ocean ’96” with the Swedish icebreaker ODEN.

virtually undisturbed sediment samples (Barnett *et al.* 1984). Three parallels for meiofaunal investigation were taken from different cores of the MC by inserting small piston corers (20 ml disposable syringes with cut off anterior ends). For ship time reasons and the extreme environmental conditions (ice drift), commonly it is hardly possible to retrieve valid replicates from several MC hauls per station. Sampling was done down to 5 cm sediment depth; cores were sectioned horizontally in 1 cm-layers. All samples were preserved in 4% buffered formalin and later analysed in the lab. After staining (min. 12 h) with 1% Rose-Bengal, sediment samples were fractionated by wet sieving into five size-classes (> 500 μm , > 250 μm , > 125 μm , > 63 μm , > 32 μm). Sorting of each fraction was done in Bogorov-dishes under a low power stereo microscope. Exemplary evaluations down to 5 cm sediment depth showed a very strong decrease in meiofauna abundances within the uppermost centimetres; sediment layers below three centimetres were almost not colonised. Therefore, in order to reduce sorting time, sediment samples were further on generally sorted just down to maximally 3 cm sediment depth.

Organisms were identified to major taxa, *i.e.* Foraminifera, Nematoda, Harpacticoida/Nauplii. For statistical analyses all taxa appearing in minor quantities (*e.g.* Bivalvia, Loricifera, Ostracoda, Oligochaeta and Polychaeta) were pooled in one category named “others”. Foraminiferans appeared to be the most abundant group of meiobenthic organisms. Therefore, it was decided to investigate this group in more detail. All foraminiferans were grouped into three morphological classes: individuals with calcareous shells (*e.g.* *Miliolina*, *Rotaliina*), chitinous forms (*Allogromiina*) and agglutinating forms (*Textulariina*). Frequently appearing foraminiferans, were determined down to genus level. Only individuals with completely stained protoplasm were counted; those with “Inner Organic Lining” stained only, were not taken into account (Douglas 1979).

Samples for the analysis of biogenic sediment compounds were taken in parallel with the same subsampling device used for the meiofaunal studies. To estimate the input of phytodetritus to the seafloor sediment-bound chlorophyll *a* and phaeopigments were determined. Chloroplatic Pigments were extracted in

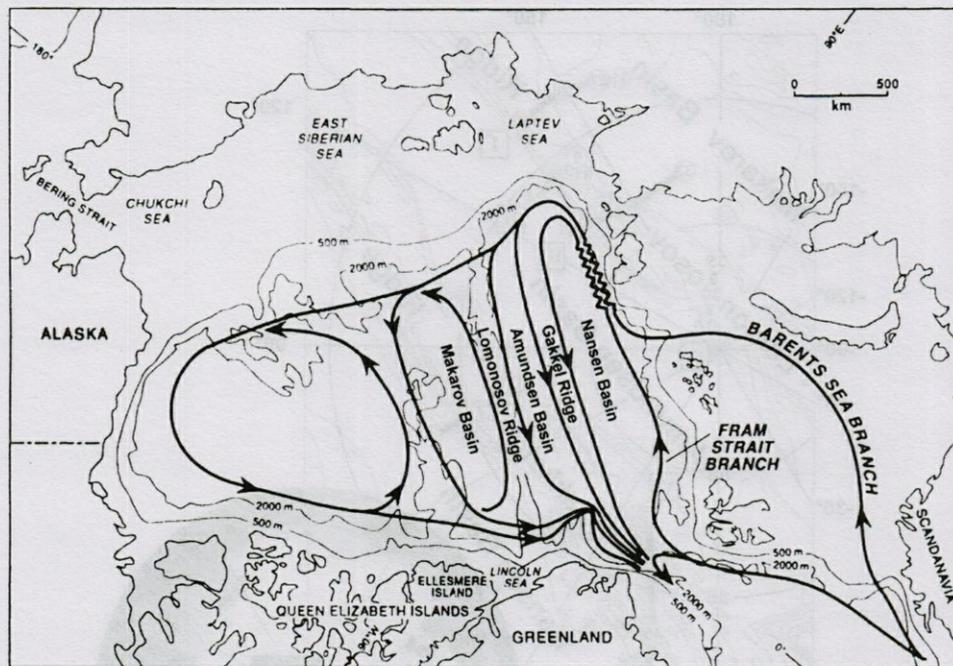


Fig. 2. – Circulation patterns of intermediate and deep waters (after Rudels *et al.* 1994).

90 % acetone and measured with a TURNER fluorometer according to Shuman & Lorenzen (1975). The bulk of pigments registered with this method was termed chloroplastic pigment equivalents CPE (Thiel 1978). Phospholipids, indicating cell wall components were analysed to quantify total microbial biomass (TMB; *i.e.* bacteria, protozoans, fungi, yeasts and also small metazoans) (Findlay *et al.* 1989). A conversion factor of $100 \mu\text{mol P-g}^{-1}\text{C}$ given by Findlay and Dobbs (1993) was used to estimate TMB in terms of organic carbon. Results of biochemical analyses are already presented and discussed in more details in Soltwedel & Schewe (1998).

Phytodetritus as well as sediment inhabiting microorganisms may serve as a potential food-source for meiofauna. In this study data for individual biogenic sediment compounds are included, to proof direct influences of food availability on meiofauna densities, composition and distribution patterns.

Statistical investigations: In general it has to be considered that all parallel samples, taken on one station, are only pseudoreplicates (Hurlbert 1984). Nevertheless, we decided to treat these data alike real replicates. For this reason, statistical investigations were mainly used to support observations made in the raw data set.

To test variances between stations a Mann-Whitney U-test (Mann and Whitney 1947) was performed. We investigated valid differences between areas grouped by multiple stations by the t-test. In order to take especially different meiofaunal community structures of stations into account, we used multidimensional scaling (MDS), a method of multivariate statistical analysis. In addition, we analysed the dependencies of meiofaunal data and different abiotic and biotic parameters by a PEARSON correlation.

RESULTS

To investigate regional differences in meiofauna distribution patterns, stations were grouped in geographical areas (Fig. 3). This arrangement is mainly disposed by water depth and prevailing intermediate- and deep-water currents (Fig. 2). Area A (water-depth > 2,000 m) covers two deep

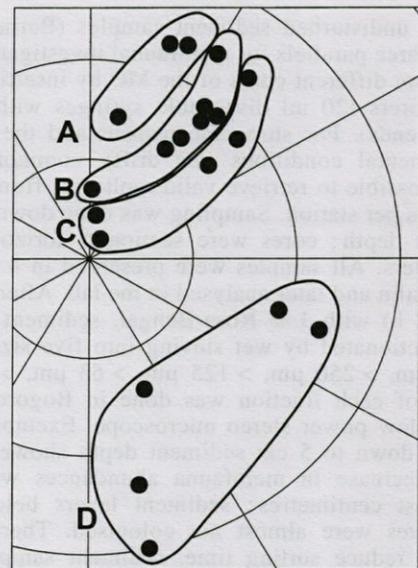


Fig. 3. – Grouping of benthic stations in Areas A-D.

Table II. - Mean meiofaunal abundances (Ind.10 cm⁻²) and standard deviations in the upper three centimetres of sediments (stations arranged by areas).

	A			B							C					D				
	Makarov Basin			Lomonosov Ridge							Amundsen Basin					Gakkel Ridge				
	27	31	33	9	10	11	16	26	32	35	8	24	25	36	37	6	7	39	40	41
Station	2382	3346	3883	864	970	1300	1782	1055	1223	1111	3724	4187	2523	2249	4142	3792	3600	4180	2265	3275
Depth [m]	27	17	14	21	29	18	5	26	29	16	81	30	28	56	38	25	28	14	47	-
<i>Epistominella spec.</i>	±3	±6	±3	±7	±5	±11	±9	±15	±15	±6	±37	±13	±7	±11	±7	±10	±11	±6	±37	-
<i>Ioanella spec.</i>	15	10	2	10	8	11	5	27	36	14	4	-	2	34	-	-	-	-	51	36
	±5	±9	±3	±7	±7	±13	±9	±14	±18	±6	±3	-	±3	±3	-	-	-	-	±15	±7
<i>Buliminella spec.</i>	7	2	-	10	13	4	6	16	22	10	-	-	10	14	-	-	-	-	-	-
	±7	±3	-	±12	±8	±4	±10	±8	±6	±1	-	-	±9	±9	-	-	-	-	-	-
<i>Bolivina spec.</i>	6	4	2	4	7	14	-	8	11	7	-	2	2	-	-	-	-	2	4	6
	±0	±3	±3	±4	±8	±3	-	±2	±3	±8	-	±3	±3	-	-	-	-	±3	±4	±7
<i>Miliolinidae</i>	9	16	4	7	3	9	6	15	32	18	4	-	11	6	9	6	-	-	41	14
	±15	±13	±3	±7	±5	±6	±11	±8	±21	±18	±6	-	±5	±6	±5	±5	-	-	±22	±8
<i>Discorbinella spec.</i>	19	23	7	16	10	14	8	24	29	16	-	2	10	7	0	2	10	-	7	19
	±9	±11	±6	±2	±2	±14	±14	±19	±12	±3	-	±3	±11	±7	0	3	±13	-	±13	±10
<i>Nodosariacea</i>	10	11	2	11	11	18	6	21	12	6	14	25	10	11	12	4	4	2	-	0
	±4	±6	±3	±11	±5	±3	±7	±11	±6	±6	±15	±18	±7	±5	±7	±3	±3	±3	-	-
<i>Reopax spec.</i>	2	-	-	3	12	15	9	14	-	2	2	16	7	2	18	10	4	2	-	0
	±3	-	-	±5	±1	±5	±8	±5	-	±3	±3	±9	±3	±3	±7	±5	±6	±3	-	-
<i>Saccaminidae</i>	10	10	7	28	24	19	8	15	9	22	2	3	15	29	-	29	23	2	6	0
	±10	±5	±2	±3	±1	±7	±10	±3	±8	±9	±3	±6	±2	±11	-	±16	±17	±3	±6	-
<i>Allogromiidae</i>	2	4	-	10	15	16	4	19	7	4	4	4	6	4	17	4	9	2	-	-
	±3	±6	-	±4	±1	±4	±8	±5	±3	±4	±3	±8	±7	±3	±10	±7	±3	±3	-	-
total	183	146	60	184	190	203	87	275	284	162	219	156	146	267	127	145	132	50	205	101
Foraminifera	±80	±58	±25	±66	±19	±29	±111	±73	±62	±75	±53	±36	±13	±49	±15	±60	±62	±1	±65	±22
Nematoda	39	20	20	44	45	57	19	57	44	29	46	39	45	45	41	45	43	23	42	12
	±13	±9	±7	±10	±7	±7	±20	±7	±13	±6	±5	±13	±12	±9	±4	±9	±11	±2	±14	±7
Harpacticoida incl. Nauplii	11	3	2	11	14	12	6	21	15	16	12	4	9	12	6	4	2	9	6	4
	±6	±6	±3	±10	±12	±8	±7	±7	±10	±5	±7	±3	±6	±12	±6	±3	±3	±3	±7	±4
'others'	-	-	±3	±3	±5	±7	-	±6	±3	±8	±5	±8	±5	±0	±3	±16	±3	±6	±10	-
Σ	232	169	84	243	251	284	113	375	347	211	279	203	203	330	177	211	178	86	258	117

stations in the Makarov Basin (stat. 31, 33), as well as station 27, localised on the outermost eastern Lomonosov Ridge rise. All stations on the Lomonosov Ridge crest (< 1,500 m) are grouped in Area B (stat. 9, 10, 11, 26, 32, 35 plus canyon station 16, 1,782 m). In Area C (> 2,000 m) all deep stations in the Amundsen Basin and stations at the western Lomonosov Ridge rise are combined (stat. 8, 24, 25, 36, 37). Area D covers stations on the Gakkel Ridge and adjacent deep basins (stat. 6, 7, 39, 40, 41).

Meiofauna densities and composition

Meiofauna densities in the area of investigation were generally low. A complete overview of meiofaunal abundances integrated over all determined sediment layers is given in Table II. Highest abundances (247 ind.10 cm⁻²) in the uppermost sediment layer (0-1 cm, Fig. 5) were found at one of the shallowest stations on the Lomonosov Ridge (stat. 26, 1,055 m), whereas one of the deepest stations (stat. 39, 4,180 m) exhibited the lowest densities (68 ind.10 cm⁻²).

At all stations and in all sediment-layers investigated, foraminiferans clearly dominated all other taxa (X = 76 ± 6 %). Nematodes were the second

most important group. They also appeared at all stations and in all sediment-layers investigated, but the relative proportion of nematodes was generally well below 20 % of the total meiofauna. Harpacticoid copepods (including nauplii) made up more than 4 % of the total meiofauna. All other meiofauna taxa (e.g. Turbellaria, Loricifera, Kinorhyncha, Bivalvia, Oligochaeta, Polychaeta, Acarina and Ostracoda) appeared in extremely low densities and showed very patchy distribution patterns. Highest diversity on taxon-level was found on the shallow stations of the Lomonosov Ridge (Table III); stations in the Makarov Basin exhibited the poorest meiofauna community.

In respect to their dominance, foraminiferans were generally determined down to genus level. Table II summarises the distribution patterns of single families and genera in the investigated regions. The calcareous foraminifera *Epistominella* was clearly most abundant (X̄ = 30 %) and showed low density-fluctuations across all water depths. In contrast the appearance of *Buliminella*, another common genus, was restricted to stations close to the Lomonosov Ridge; no individuals of this genus were found in the Gakkel Ridge region. All other genera and families showed no notable distribution patterns; irregular and/or patchy patterns were typical.

Table III. – Occurrence of 'other' taxa in all investigated samples (stations arranged by areas).

Station	A			B							C					D						
	Makarov Basin			Lomonosov Ridge							Amundsen Basin					Gakkel Ridge						
Depth [m]	27	31	33	9	10	11	16	26	32	35	8	24	25	36	37	6	7	39	40	41		
	2382	3346	3883	864	970	1300	1782	1055	1223	1111	3724	4187	2523	2249	4142	3792	3600	4180	2265	3275		
Turbellaria																					+	
Loricifera						+		+		+		+	+	+								
Kinorhyncha						+																
Bivalvia						+			+			+					+					+
Oligochaeta														+								+
Polychaeta				+		+		+		+	+											
Acarina								+									+	+				
Ostracoda					+	+											+					
'Indets'			+			+		+								+	+	+		+	+	

Distribution within the sediment column

Figure 4 exemplary shows gradients of meiofauna organisms in the uppermost 3 centimetres of the sediment columns at 4 selected stations from each defined region. In all regions, an expected decrease in abundances with increasing sediment depth was clearly noticeable. Foraminiferans showed the steepest gradients in the sediments; less steep gradients were determined for the nematodes. Harpacticoids generally appeared exclusively in the uppermost centimetre. The occurrence of "others" within the sediment columns was very patchy. Individuals of these groups were often just found in single sediment layers, however, these organisms in general also showed a decrease in abundances with increasing sediment depth.

Generally, steepest gradients in total meiofauna abundances were found at deep stations in the Makarov- and Amundsen Basin (stations 33, 39) with more than 80 % of organisms in the uppermost centimetre sharply decreasing to less than 10 % in the following sediment layer (2 cm).

Regional differences in distribution patterns

Total meiofauna abundances (including foraminiferans) in the uppermost centimetre of stations in the Lomonosov- and Gakkel Ridge regions are shown in Fig. 5. Densities were generally higher on the crest of the ridges than at the deeper stations on the slope and in the adjacent basins. Nevertheless only the transects I & III in the Lomonosov Ridge region showed, certified by a Mann-Whitney U-test, significant differences between the respective shallowest ridge station and deepest stations in the adjacent basins (Fig. 6). A significant difference between Amundsen. and

Makarov Basin stations within the same transect, was only apparent for transect III.

A view on meiofauna distribution patterns using MDS analysis showed pronounced regional differences in the community structure between relatively shallow Lomonosov Ridge stations and adjacent deeper stations, especially to those in the Amundsen Basin (Fig. 7). Mean abundances of all identified foraminiferal genera as well as all remaining taxa, appearing in the uppermost 3 centimetres of the sediments, served as the basis for this analysis. Compared to other Lomonosov Ridge stations MDS also exhibited marginally differences in taxonomic composition at station 16, located in a canyon crossing the Lomonosov Ridge and probably influenced by strong currents, flowing between the Makarov- and Amundsen Basins. Furthermore, stations along transect V (Gakkel Ridge East) formed an additional cluster, clearly separated from stations of transect IV (Gakkel Ridge West).

Additionally performed statistical investigations by T-tests showed a significant difference ($p = 0,0051$) in meiofaunal densities between stations grouped in Area B (Lomonosov Ridge) and Area D (Gakkel Ridge). Between all the other areas no further significant differences were detectable.

Size structure of meiobenthos

In order to test regional differences in mean organism body sizes, meiofauna size class frequencies were calculated as percentages of the relative abundance retained on the various mesh sizes used (Fig. 8). In all regions investigated in this study the dominant organism body size was 63-125 μm (41-48 %), closely followed by the smallest size group investigated with organisms

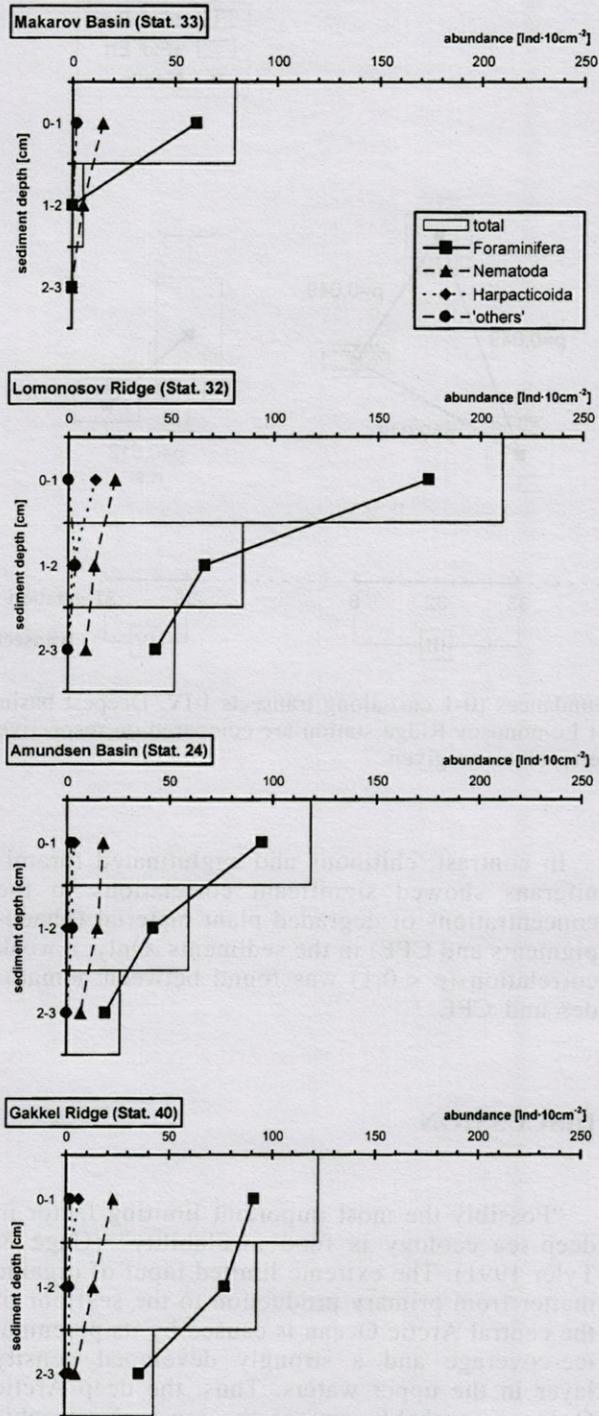


Fig. 4. – Profiles for major meiofauna taxa in the uppermost 3 centimetres of sediments from selected stations in various regions.

body sizes ranging from 32-63 μm (24-40 %) (Fig. 8). The fraction of bigger organisms (125-1,000 μm) was low in all regions (< 22 %).

A slightly, non-significant trend towards an increasing proportion of the smallest size class (32-63 μm) from the Makarov Basin (34 %) via

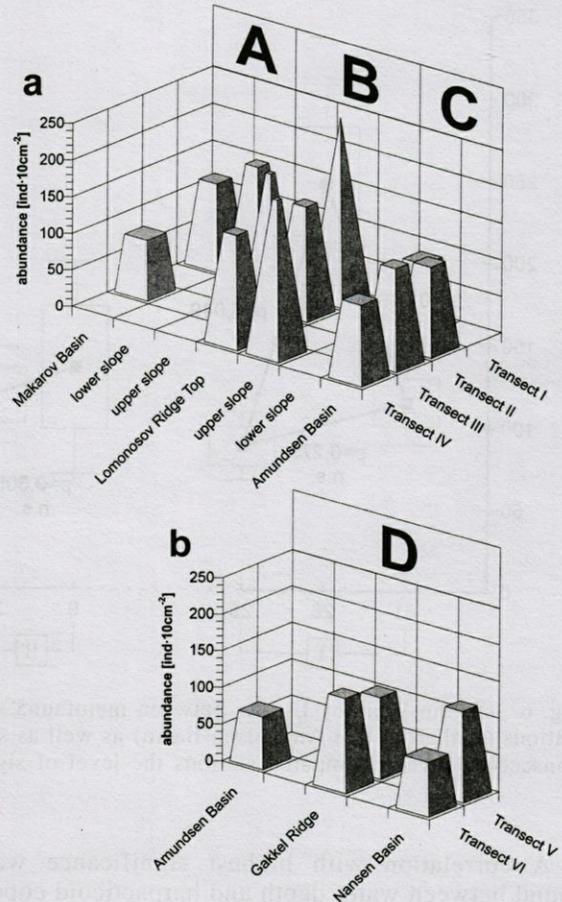


Fig. 5a, b. – Total meiobenthic abundances (including foraminiferans) in the uppermost sediment layer (0-1 cm) along transects I-IV crossing the Lomonosov Ridge (a) and transects V, VI crossing the Gakkel Ridge (b).

the Lomonosov Ridge (38 %) to the Amundsen Basin (41 %) was detectable.

Gakkel Ridge stations showed a comparably high proportion of organisms with a body size of 63-125 μm (~ 53 %).

Correlations between meiobenthic abundances, water depth and various biogenic sediment compounds

A PEARSON correlation analysis (Table IV) was performed with meiofaunal data (total abundances of major taxa), water depth, sediment-bound chloroplastic pigments (indicating deposited particulate organic matter from phytoplankton production) and total microbial biomass (representing a further potential food source for meiofauna organisms). CPE and TMB data were already published by Soltwedel and Schewe (1998).

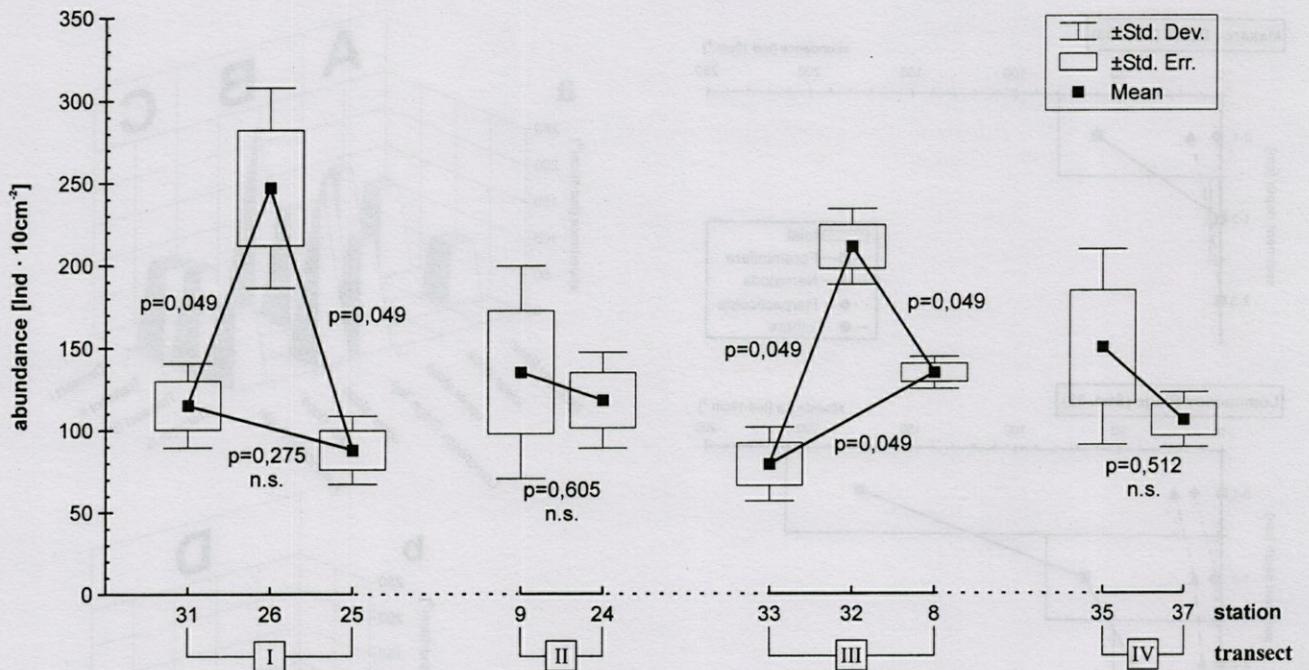


Fig. 6. – Mann-Whitney U-tests between meiofauna station-abundances (0-1 cm) along transects I-IV. Deepest basin stations (Makarov- and Amundsen-Basin) as well as shallowest Lomonosov Ridge station are compared on respective transects. Between compared stations the level of significance (p-level) is given.

A correlation with highest significance was found between water depth and harpacticoid copepods, including nauplii ($p < 0,001$). Calcareous foraminiferans and nematodes showed significant correlations with water depth ($p < 0,01$ and $p < 0,05$, respectively). Harpacticoids and calcareous foraminiferans also exhibited high significant and significant correlations respectively with the content of 'fresh' plant material (indicated by sediment-bound Chl a concentrations).

In contrast, chitinous and agglutinated foraminiferans showed significant correlations to the concentrations of degraded plant material (phaeopigments and CPE) in the sediments. Only, a weak correlation ($p < 0,1$) was found between nematodes and CPE.

DISCUSSION

"Possibly the most important limiting factor in deep-sea ecology is food availability" (Gage & Tyler 1991). The extreme limited input of organic matter from primary production to the seafloor of the central Arctic Ocean is caused by its perennial ice-coverage and a strongly developed density layer in the upper waters. Thus, the deep Arctic Ocean is probably one of the most oligotrophic marine ecosystems on earth. Investigations on benthic meiofauna were carried out to provide information about, densities, distribution patterns and the influence of extreme limited food availability on this size class of benthic organisms.

Meiofauna distribution patterns

The vertical distribution of the benthic meiofauna in the central Arctic Ocean agrees with the observed general characteristic that abundances

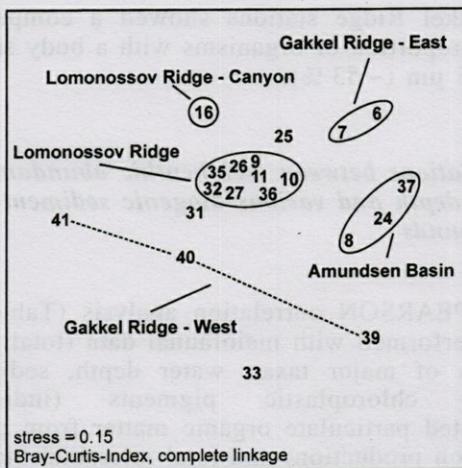


Fig. 7. – Multi Dimensional Scaling (MDS) of results from faunal analyses (including all genera and taxa identified).

Table IV. – Pearson Correlation between meiofauna densities and abiotic and biotic parameters (0-1 cm) : Water **Depth**, **Chlorophylla [Chl a]**, **Phaeopigments**, **Chloroplastic Pigment Equivalents [CPE]**, **Total Microbial Biomass [TMB]**, **calcareous**, **chitinous** and **agglutinating Foraminifera**, **Nematoda**, **Harpacticoida** and **'other'** taxa.

	Depth	Chl a	Phaeo.	CPE	TMB
Foram. calc.	-0,630 p=,005	0,485 p=,041	-0,180 p=,475	-0,040 p=,874	0,214 p=,393
Foram. chit.	-0,390 p=,110	0,298 p=,230	0,489 p=,039	0,537 p=,022	0,277 p=,266
Foram. agglut.	-0,388 p=,111	0,246 p=,325	0,522 p=,026	0,554 p=,017	0,167 p=,507
Nema.	-0,632 p=,005	0,270 p=,279	0,375 p=,126	0,422 p=,081	0,306 p=,217
Harp.	-0,766 p=,000	0,643 p=,004	0,049 p=,848	0,215 p=,391	0,344 p=,162
others	-0,141 p=,577	-0,071 p=,781	0,298 p=,230	0,260 p=,297	-0,281 p=,259

Levels of significance:

p<0,001 ■; p<0,01 ■; p<0,05 □

are normally highest in the surface layers of sediment and rapidly decrease with increasing sediment depth (Vincx *et al.* 1994); ≥ 90 % of individuals may be found within the uppermost 5 cm of sediments (Thiel 1983). Results from the central Arctic Ocean confirmed this general picture. Due to an extremely limited input of POM to the seafloor under perennial ice-coverage, randomly evaluated samples down to 5 cm sediment depth, exhibited that even more than 95 % of the

meiobenthos is concentrated within the upper 3 cm of the sediment. Less steep gradients in nematode distribution may be caused by their mobility and resulting ability to reach further food sources in deeper sediment layers.

Compared to meiofauna-abundances given for the central north-east Atlantic (Scheibe 1990, Table V) the maximum abundances at stations within this study were more than five times lower. The maximum abundances of Pfannkuche & Thiels (1987) investigations at deep stations (2,000 m) on the Barents Sea continental margin were up to four times higher. Abundances given by Vanaverbeke *et al.* (1997) for the Laptev Sea continental rise (2,000 m) were still two times higher, than values determined within this study.

Decreasing numbers of metazoan meiobenthic abundances with increasing water depth are supposed to be a general tendency (Thiel 1983, Tietjen 1992). This trend was also described for continental slopes of polar seas (Pfannkuche & Thiel 1987, Hermann & Dahms 1992, Vanhove *et al.* 1995, Vanaverbeke *et al.* 1997). For the central oceanic transects investigated in this study, mainly those crossing the Lomonosov Ridge, we could demonstrate a similar trend. However, especially in this region such a gradient may slightly be interfered by a north-westerly current-driven transport (Transpolar Drift) of organic material from the Lomonosov Ridge crest into the Amundsen Basin.

Vertical distribution in the uppermost sediment layers (0-1 cm) was quite different in the various areas investigated. Compared to stations from the Gakkel Ridge region, stations on the Lomonosov

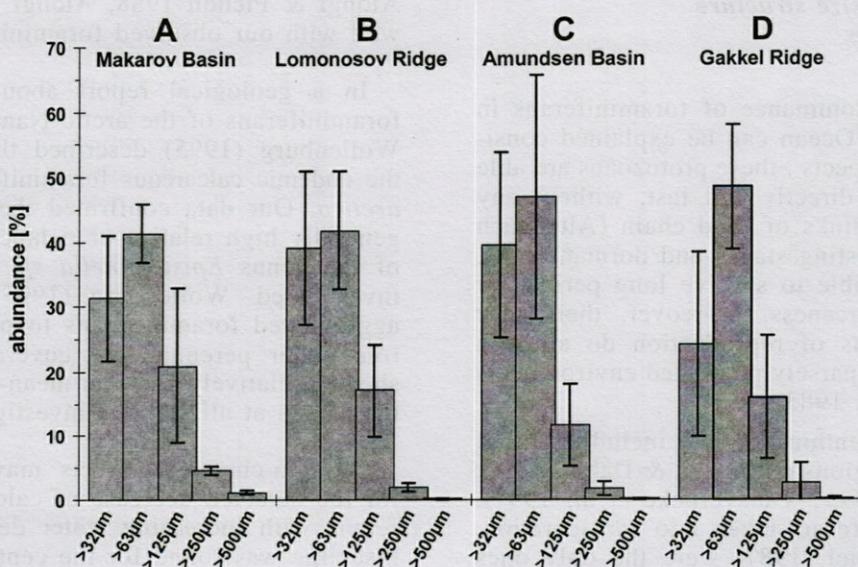


Fig. 8. – Relative abundances of the total meiofauna (incl. foraminiferans) in different size classes (uppermost sediment layer (0-1 cm), mean values for stations in the defined areas).

Table V. – Meiobenthic densities from polar and central oceanic regions.

water depth [m]	min. meshsize [µm]	max. sediment depth [cm]	density [ind. 10cm ⁻²]				region	source
			total meiofauna	foraminiferans	nematodes	'others'		
2090-8260 12 stations	>37	12	76-2421	39-1196	31-1195	11-185	western Pacific Shirayama (1984)	
2500	>42	9	1528	170	1259	99	SW Nansen Basin Pfanckuche & Thiel (1987)	
3270	>42	9	363	130	204	29		
3920	>42	9	418	70	334	14		
1640-3647 10 stations	>30	5	171-2327	98-1324	38-723	12-280	central NE-Atlantik Scheibe (1990)	
1190	>38	10	1427	---1	1385	42	Weddel Sea (Antarctic) Herman & Dahms (1992)	
1960	>38	10	1402	---1	1317	85		
1199	>38	10	815	---1	700	115	Weddel Sea (Antarctic) Vanhove et al. (1995)	
2080	>38	10	1100	---1	1000	100		
1935	>40	10	540	---1	---2	---2	Laptev Sea (Arctic) Vanaverbeke et al. (1997)	
2621	>40	10	361	---1	---2	---2		
3237	>40	10	678	---1	---2	---2		
864-4187 20 stations	>30	3	84-375	50-284	16-57	3-44	central Arctic Ocean this study	

---¹ not included
---² no information

Ridge exhibited significantly higher meiofauna abundances. Crest stations of the Lomonosov Ridge showed higher densities than the flanks or the adjacent basins. Between the Amundsen and the Makarov Basin differences of meiobenthic abundances existed, but only were significant in one case. Especially the results of community analyses were more helpful and pointed out those differences more distinctly.

Composition and size structure of the meiobenthos

The observed dominance of foraminiferans in the central Arctic Ocean can be explained considering different aspects: these protozoans are able to ingest detritus directly and fast, without any need of previous links of food chain (Altenbach 1991). Creating resting stages and dormant cells, they are also capable to survive long periods of extreme food scarceness. Moreover, their very simple mechanisms of reproduction do allow a save offspring in sparsely populated environments (Thiel 1975, Thiel 1983).

In most meiobenthic studies, including those few from polar regions (Hermann & Dahms 1992, Vanhove *et al.* 1995; Vanaverbeke *et al.* 1997), foraminiferans were not taken into consideration. Pfanckuche & Thiel (1987) were the only ones including those protozoans into their investigations of the arctic meiobenthos from the northern Barents Sea and the adjacent deep Amundsen

Basin. For three investigated deep stations ($\geq 2,500$ m) they found an unusual dominance of nematodes, whereas all other stations exhibited a higher relative proportion of foraminiferans. Studies from central oceanic regions generally showed a dominance of foraminiferans with a relative proportion of up to 70 % (Shirayama & Horikoshi 1989, Scheibe 1990, Alongi 1992, Pfanckuche 1993); an increasing dominance of foraminifers with increasing water-depth is especially described for continental slope regions (Thiel 1983, Alongi & Pichon 1988, Alongi 1992) which fits well with our observed foraminiferal dominance.

In a geological report about recent benthic foraminiferans of the arctic Nansen Basin region Wollenburg (1995) described the dominance of the endemic calcareous foraminifera *Epistominella arctica*. Our data confirmed these findings with generally high relative abundances of individuals of the genus *Epistominella sp.* at most stations investigated. Wollenburg (1995) also described agglutinated foraminiferans to play an important role under perennial ice coverage. Our studies showed relatively constant mean-level densities of these taxa at all stations investigated.

Physico-chemical effects may be responsible for the detected decrease of calcareous foraminiferans with increasing water depth. By now no lysocline was found for the central Arctic Ocean (Stein 1996). However, with increasing water depth, it generally gets energetically more and more sumptuous for calcareous foraminiferans to

build up their shell and to preserve it, respectively (Murray 1991).

The metazoan meiofaunal composition observed for the central Arctic Ocean was similar to that found for deep sites in the north-eastern Atlantic and the western Pacific (Vincx *et al.* 1994, Vanaverbeke *et al.* 1997, Shirayama & Horikoshi 1989), with nematodes being by far the dominant taxon, followed by harpacticoids and nauplii. However, the density of metazoan organisms rapidly decreased with increasing water depth, which fits well with results of other authors (Table V) from investigations on polar continental margins and adjacent deep-sea regions (Pfannkuche & Thiel 1987, Hermann & Dahms 1992, Vanhove *et al.* 1995).

A comparison of stations concerning the composition of selected faunal elements (MDS) exhibited a clear separation of crest stations on the Lomonosov Ridge, from those of the adjacent basins (Makarov- and Amundsen Basin). A distinct composition of Gakkel Ridge Stations indicated a further different community structure and was proved by statistical testing.

A closer inspection of meiofauna size spectra from investigated regions exhibited a clear trend for 'dwarfism'. Apart from generally low total abundances, the predominance of especially small meiofauna organisms in the observed regions of the central Arctic Ocean can be taken as an indicator for an extremely limited input of POM to the benthic realm.

Size spectra at central Arctic Ocean stations showed no water-depth depending gradients, also shown by Scheibe (1990) for the central North-Atlantic. While such a gradient seems not necessarily expectable in central oceanic regions, Pfannkuche & Thiel (1987) described similar for nematode size spectra on the Barents Sea continental slope. They reported a continuous decrease of the size classes $\geq 100 \mu\text{m}$ from 50 % on shelf stations down to 18 % on the deepest basin station (3,920 m). Nevertheless in these investigations the proportion of smallest nematodes ($< 63 \mu\text{m}$) never reached higher levels than 17 %, while in the existing study the lowest mean proportion of smallest meiofauna ($< 63 \mu\text{m}$) was never lower than 20 %.

Abundance, composition and size spectra in relation to food supply

Beside quantity, quality of sedimentary particulate organic matter, sunken to the seafloor, is of great importance for meiofauna distribution patterns (Dinet 1979). Residence time of POM in the water column plays an important role, because bacterial decomposition of organic material takes

place during the passage to the seafloor (Suess 1980).

Different Antarctic studies suppose, that up to 76 % of primary production can already be utilised in the microbial loop of the upper water column (Cota *et al.* 1990, Sullivan *et al.* 1990). Additionally, if primary production is low, densities of phytoplankton cells might be substantially reduced. Thus, dead phytoplankton organisms will not aggregate, may sink as single cells and sedimentation will be very slow. Because of long residence times in the water column, the largest part of phytodetritus, reaching the bottom of the Arctic Ocean, is highly degraded by zooplankton and bacteria (Grebmeier & Barry 1991). In consequence, gradients of meiofaunal colonisation in the sediments may be steep and densities generally lower.

For the Lomonosov Ridge region, Gordienko & Laktionov (1969) reported an increased, current driven crushing of ice-floes opening leads in the ice shield. For Summer 1996 we could confirm this observation. Crushed ice floes in this region often showed slimy brown mats of ice-algae at the bottom of the floes. Such detached algae may sink down to the seafloor as aggregates in very short periods of time. Billett *et al.* (1983), Rice *et al.* (1986) described a similar rapid transfer of POM via 'fluffy' aggregates in oceanic regions with seasonally high primary production. A comparable rapid transport of POM to the seafloor may explain relatively high amounts of sediment-bound Chla found at single stations on the Lomonosov Ridge (*e.g.* stat. 25).

Benthic protozoans are able to react rapidly to episodic sedimentation events of detritus (Turley & Lochte 1990, Boetius & Lochte 1994). Because of the spatially and temporally extremely patchy input of POM to the seafloor, abundances of microorganisms are irregularly distributed as well. A significant correlation between TMB (including bacteria, nanofauna and meiofauna) and CPE indicated a good adaptation of these organisms to utilise phytodetritus of any quality.

Spontaneous growth as a reaction to episodic food-pulses have already been described for foraminiferans from the Norwegian Sea (Altenbach 1991). There is also evidence for growth reactions of metazoan meiofauna to episodic food supply. Soltwedel *et al.* (1996) found indications for growth reactions of nematodes to the seasonal input of POM to the deep-sea floor in the North-Western Atlantic.

The influence of detritus quality on foraminiferal growth and density is described by Lamshead and Gooday (1990). A correlation analysis exhibited that at least for our data, calcareous foraminifers were found especially in the presence of 'fresh' phytodetritus (significant

correlation ($p < 0,05$) with sediment-bound Chl *a*-concentration), whereas proteinaceous and agglutinated foraminifers seemed to be well adapted to utilise more degraded phytodetritus, as confirmed in a significant correlation ($p < 0,05$) between these taxa and concentration of sediment-bound phaeopigments. This may reflect higher demands of calcareous foraminifers on utilisable detritus.

Harpacticoids seemed clearly depended on the availability of 'fresh' phytodetritus. Correlation analysis exhibited a significant relation between their abundances and Chl *a* concentrations within the sediments. Nematode densities generally decreased with increasing water depth. However, no correlation was found between nematode abundances and indicators of phytodetritus, neither in quantity nor in quality. Data of TMB, from the same set of samples (Soltwedel & Schewe 1998), were used to estimate the importance of microorganisms, being a further potential food source for meiofauna organisms. However, correlation analysis showed no clear relations between TMB and single meiofauna-taxa. We suggest that, the variety of organisms, determined by phospholipids, is probably too complex to identify clear trophic interrelations between meiofauna organisms and the bulk of micro-organisms traced by phospholipid determinations. Different feeding strategies (deposit feeders, microbial grazers) might explain such a lack of significant correlations.

Clear regional differences in mean body size, for instance influenced by regionally increased food availability, were not provable. Soltwedel *et al.* (1996) discovered a trend towards miniaturisation on nematodes as a response to an overall declined availability of utilisable food. Confirmed by relatively high proportions in the smallest size class investigated (32-63 μm), we also found indications for a dwarfism of meiofauna organisms in the highly oligotrophic central Arctic Ocean. This fact, together with the low quantity and expected poor quality of organic material reaching the benthic realm, suggests a higher importance of so called nanofauna (size-class: 2-32 μm , mainly small protozoans, flagellates, yeasts and fungi) in this extreme oligotrophic environment. Biomass data of organisms with adequate body size are only available from biochemical bulk-determinations (Soltwedel and Schewe 1998). A direct determination of this size-class was not the aim of this work, but examinations of especially this size-group of benthic micro-organisms is highly recommended for future studies in the central Arctic Ocean.

The availability of food seems to have an important influence on meiofaunal distribution patterns. In this connection the abiotic factor 'water depth' may just exert in secondary influence. Especially the results of community ana-

lyses indicate an outcome of meiofauna community structure by a large-scale, current driven transport of POM. The higher values to the west of the Lomonosov Ridge probably reflect such oceanwide distribution patterns, mainly caused by the Transpolar Drift. There was no clear indication for a lateral input of POM from the ice-free marginal seas. However especially on the shallowest stations of the Lomonosov Ridge we found a slightly, non significant, northerly decrease of values in our data.

CONCLUSIONS

Meiobenthic investigations in a perennially ice-covered central region of the Arctic Ocean exhibited a clear relation between the limited availability of sedimentary organic matter and resulting extremely low organism densities. Nevertheless meiofauna standing stocks clearly differed between the crest of the Lomonosov Ridge and its adjacent basins as well as between Gakkel Ridge stations. These differences were underlined by varying community structures in corresponding areas. Our investigations exhibited a slight, non-significant trend with northward decreasing meiofaunal densities at crest stations of the Lomonosov Ridge, probably indicating a lateral transport of POM from ice-free marginal regions. Additional sampling of benthic meiofauna between stations sampled for this study north of 85°N and benthic investigations in the Laptev Sea has to be done, to clarify the large scale distribution between these areas.

Food scarceness in the extremely oligotrophic environment of the central Arctic Ocean is probably also responsible for a detected tendency towards dwarfism. Nanofauna organisms (2-32 μm) probably play an important role for the total metabolism in the deep-sea ecosystem of the Arctic Ocean. By now, only limited information about biomass of organisms with adequate body size are available via biochemical bulk-measurements. Future benthic investigations in the deep Arctic Ocean should probably put more emphasis on the smallest size-classes ("sub-meiofauna range") of sediment inhabiting organisms, especially done by direct counts and taxonomic investigations of nanofauna organisms.

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