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# The metazoan meiobenthos along a depth gradient in the Arctic Laptev Sea with special attention to nematode communities

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**Abstract** The meiobenthos along a depth transect of oligotrophic sediments in the Arctic Laptev Sea was studied. The meiobenthos followed the general trends reported from other studies: densities decreased with depth in relation to the more limited supply of degradable organic matter at greater depths. Although the sediments along the transect were poor in organic matter in comparison with the NE Atlantic, the densities fitted well with the meiobenthic densities reported from the latter area. It is suggested that the meiobenthos in the cold polar waters is adapted to this extreme environment by a rapid response to short food pulses to the sediments. Nematodes were identified up to genus level and assigned to trophic groups. A total of 32 families comprising 95 genera were found along the transect. The communities were dominated by deposit feeders whose importance increased with depth. Both TWINSPAN and CCA analyses revealed a community shift along the depth transect: a shelf community dominated by *Microlaimus* and *Chromadora* could be distinguished from a slope community dominated by *Monhystera* and *Leptolaimus*. Generic diversity decreased with depth.

## Introduction

The study of the ecology of deep-sea meiofauna started some 25 years ago (Thiel 1972) and focused mainly on the Atlantic (review in Vincx et al. 1994) and the Mediterranean Sea (Soetaert et al. 1991a,b). Studies carried out in polar waters are scarce. Pfannkuche and Thiel (1987) investigated the meiobenthos from the high Arctic NE Svalbard Shelf and the Nansen Basin. Herman and Dahms (1992) and Vanhove et al. (1995) studied the meiobenthic communities from the high Antarctic Weddell Sea.

To date, no information is available on nematode communities from Arctic deep-sea sediments. Data on the biology of the Laptev Sea are scarce (Sirenko et al. 1995). Sheremetevsky (1977) studied the meiobenthos from shallow waters and to our knowledge no taxonomic data on nematode communities from the Laptev Sea are available.

The Arctic Ocean is described as very oligotrophic (Smith and Sakshaug 1990; Luchetta et al. 1994). Its very high latitude and permanent ice cover are limiting factors for primary production, resulting in a greatly reduced amount of low quality organic matter supply to the sea floor (Kröncke 1994; Kröncke et al. 1994).

This paper aims to describe the meiobenthic communities along a depth gradient (65–3237 m) in the Laptev Sea with special attention on the nematode communities, in order: (1) to identify meiobenthic densities and nematode community composition changes along the slope in relation to diminishing food availability, and (2) to compare the nematode communities of extreme environments with those from more temperate deep-sea areas.

## Materials and methods

### Study area

The Arctic Ocean is considered one of the world's most oligotrophic seas because of its very high latitude and permanent ice cover (Smith and Sakshaug 1990). According to Luchetta et al. (1994), nutrient concentrations in the Laptev Sea are low. From May to the end of September, nutrients (mainly nitrate and phosphate) are depleted in the upper water column when large open waters occur. The major source of carbon in the area is allochthonous terrestrial peat, which provides very little nutritional value for most marine organisms. However, some regional differ-

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ences occur. In marginal seas, such as the Laptev Sea, an increased fluvial supply occurs resulting in elevated primary production. In addition to the marine organic carbon produced in the water column, the Lena River may supply large amounts of terrigenous organic matter to the Laptev Sea (Martin et al. 1993). However, the study area of the present paper, located in the western part of the Laptev Sea, is not directly influenced by the Lena River as the organic matter in the area can be considered to be mainly marine (Stein and Nürnberg 1995).

The extended persistence of the ice cover and the ice thickness in the Arctic seas increase with distance from the Arctic coast. The limited primary production in the study area and the reduced quantity and quality of organic matter in deeper water (due to longer sinking times) (Suess 1980; Wakeham and Lee 1993; Wakeham et al.1993) cause a large reduction in the supply of degradable organic matter to the benthos of the central Arctic basin (Kröncke 1994; Kröncke et al. 1994; Wollenburg 1995; Boetius and Damm in press).

## Sampling and treatment of meiofauna samples

Samples were collected in the ice-covered area of the outer shelf and continental slope of the Laptev Sea (Fig. 1) during the ARK IX-4 cruise of RV "Polarstern" (6 August 1993–29 September 1993). Five stations were sampled (depth range: 65–3237 m) (Table 1) using a multicorer (Barnett et al. 1984). Four cores per station were subsampled using a minicore (1.5 cm$^2$) down to 10-cm depth (cf Herman and Dahms 1992). At the same stations, sediment related variables [chlorophyll *a*, chloroplastic pigment equivalents (CPE), grain size] were measured by other research groups (Boetius and Damm in press). Samples were fixed in a hot (70°C) 4% formaldehyde tapwater solution. The meiofauna was extracted by means of centrifugation with Ludox (see Heip et al. 1985). Macrofauna was excluded using a 1-mm sieve. All animals retained on a 40-µm sieve were counted and sorted into major taxa. Per sample, 200 nematodes (or all nematodes when density < 200 ind.) were picked out at random and mounted on glycerine slides for identification to genus level.

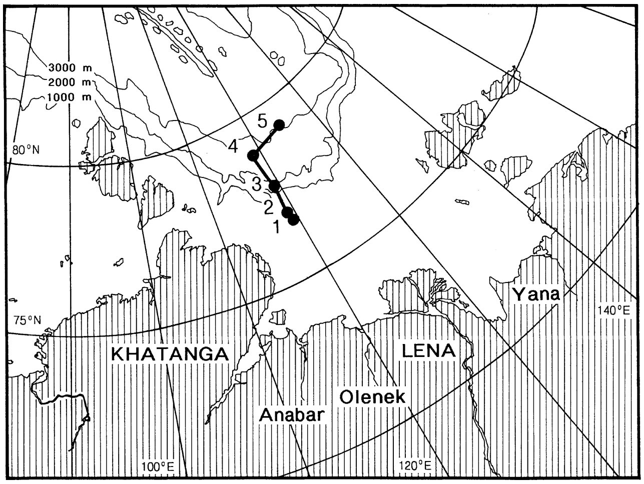

**Fig. 1** Location of the sampling stations in the Laptev Sea

## Diversity and community analysis

In order to test for significant differences in total meiobenthic densities, the non-parametric Kruskal-Wallis analysis by rank was used. Spearman Rank correlation coefficients were calculated to study the relationship between total densities and environmental variables.

All nematodes were identified up to genus level and assigned to trophic groups according to Wieser (1953): selective deposit feeders, 1A-group; non-selective deposit feeders, 1B-group; epistrate feeders, 2A-group and predators/omnivores, 2B-group. According to Jensen (1987), the 1A, 1B and 2A nematodes feed on bacteria, fungi and unicellular algae; the deposit feeders (1A + 1B) by ingestion, and the epistrate feeders (2A) by sucking the prey contents. The 2B nematodes are predators or scavengers.

Hill's diversity numbers were calculated per station (Hill 1973). Hill's diversity number of a certain order "a" is given by:

$$\mathrm{N}_a = \left\{ \sum_{i=1}^{S} p_i^a \right\}^{(1-1/a)}$$

where $S$ = the number of genera, $p$ = the relative abundance of the i$^{\mathrm{th}}$ genus.

$\mathrm{N}_0$ is the number of genera in the sample.

$\mathrm{N}_1$ relates to the Shannon-Weaver index (H′):

$$\mathrm{N}_1 = \exp\,(\mathrm{H}')$$

$$\mathrm{H}' = -\sum_{i=1}^{s} \mathrm{p}_i \ln\,(p_i)$$

with $\mathrm{p_i}$ = the relative abundance of the i$^{\mathrm{th}}$ genus.

$\mathrm{N}_2$ is the reciprocal of the Simpson dominance index:

$$\mathrm{N}_2 = \left( \sum_{i=1}^{s} p_i^2 \right)^{-1}$$

with $p_i$ = the relative abundance of the i$^{\mathrm{th}}$ genus.

$\mathrm{N}_\infty$ is the reciprocal value of the proportional abundance of the dominant genus ($1/p_i$).

Because of the small sampling surface all four replicates were pooled in order to describe the diversity of the complete nematode community sampled.

The nematode community structure was analysed using the classification technique TWINSPAN (Two-Way INdicator SPecies ANalysis, Hill 1979a) using both non-transformed generic densities and relative contributions to the total density. All replicates were considered as stations in order to get an idea about differences in the community composition within one station. A Canonical

**Table 1** List of sampling stations, depth, location, sampling date and variables characterising the surface sediments (0–1 cm) (*Chl a* chlorophyll *a*, *CPE* Chloroplastic Pigment Equivalents, *GS* median grain size)

| Station | Sampling date | Depth (m) | Latitude | Longitude | Chl *a* (µg cm$^{-3}$)$^a$ | CPE (µg cm$^{-3}$)$^a$ | GS (µm) |
|---|---|---|---|---|---|---|---|
| 1 | 18.09.93 | 65 | 77°31,34′ | 114°27,35′ | 0.3 | 3.58 | 50 |
| 2 | 17.09.93 | 230 | 77°15,15′ | 118°33,17′ | 0.18 | 2.83 | 10 |
| 3 | 15.09.93 | 1935 | 77°59,51′ | 118°35,14′ | 0.02 | 1.07 | 3 |
| 4 | 14.09.93 | 2621 | 78°40,00′ | 118°44,48′ | 0.01 | 1.07 | 3 |
| 5 | 12.09.93 | 3237 | 79°13,64′ | 122°51,29′ | 0.02 | 0.56 | 3 |

[a] Data from Boetius and Damm (in press)

Correspondence Analysis (CCA, Hill 1979b) was used to group similar stations together.

## Results

### Study area

Sediment-related variables are mentioned by Boetius and Damm (in press) (Table 1). The coarsest grain size was measured at station 1 (50 μm), followed by station 2 (10 μm). At the deeper stations, a medium grain size of 3 μm was found. Both chlorophyll *a* and CPE values (measured in the superficial centimeters) declined along the slope. At station 1, a chlorophyll *a* value of 0.3 $\mu g\ cm^{-3}$ was noted whereas at station 5 only 0.02 $\mu g\ cm^{-3}$ chlorophyll *a* was found. Deeper than 250 m, chlorophyll *a* values decreased strongly. CPE values ranged from 3.58 $\mu g\ cm^{-3}$ (station 1) to 0.56 $\mu g\ cm^{-3}$ (station 5).

### Meiobenthos

Meiobenthic total densities (Fig. 2) reached a maximum of 2,683 ± 299 (SE) ind./10 $cm^2$ at station 1 and decreased with bathymetric depth to a minimum of 418 ± 93 ind./10 $cm^2$ at station 4. The densities at the two shallow stations were significantly higher than at the three deeper stations (Kruskal-Wallis analysis by rank, $P < 0.01$). Nematodes were the dominant taxon (92% at station 2, 98% at station 5), followed by harpacticoid copepods (4% at station 1, 1% at station 5). Other meiobenthic taxa (turbellarians, polychaetes, kinorhynchs, ostracods, cumaceans, priapulid larvae, gastrotrichs, tanaids and tardigrades) were observed frequently but in lower numbers (0.7–7.9%).

Spearman Rank correlation coefficients showed the densities to be significantly related to sediment chlorophyll *a* contents ($P < 0.01$). No other significant correlation could be detected.

### Nematode community composition

A total of 95 genera belonging to 32 families were found along the transect (Table 2). Table 3 shows the dominant genera for each station together with their relative abundance. The shallow station (station 1, 65 m) showed a strong dominance of *Microlaimus* followed by *Quadricoma* and *Leptolaimus*. From these genera, only *Leptolaimus* was listed among the 20 most dominant genera of station 2 (230 m) and it was the only genus out of the dominant ones from station 1 to be found in relatively high abundances (>5%) at the 3 deepest stations. Station 2 showed a different dominance pattern in comparison with both the shallow and the deeper stations. *Chromadora* was dominant here followed by *Halalaimus*. Stations 3, 4 and 5 showed a more uniform nematode community composition with *Leptolaimus*, *Metalinhomoeus* and *Monhystera* always present among the six most dominant genera. Genera known to be typical of deep-sea areas (e.g. *Acantholaimus* and *Halalaimus*) increased their significance in deeper stations although this trend is not very clear.

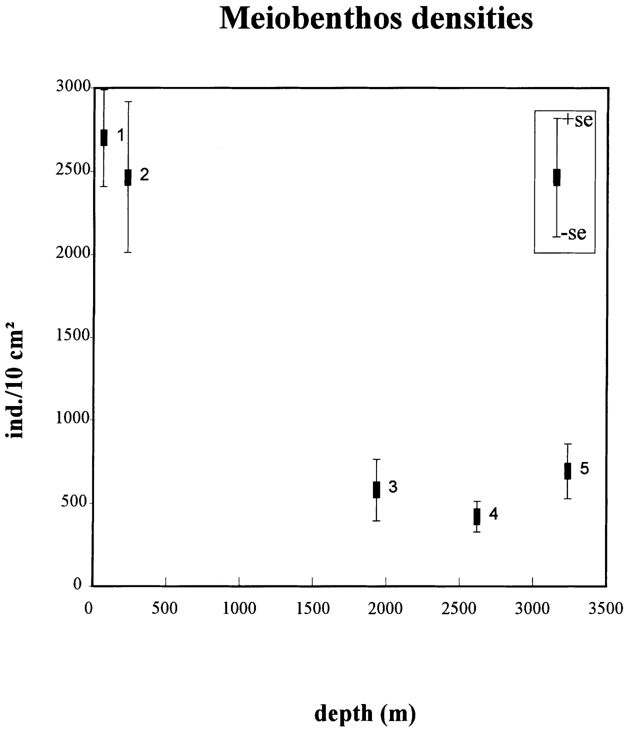

**Fig. 2** Mean meiobenthic densities per station ± standard error

### Trophic structure of the nematode community

At all depths along the transect the deposit feeders (1A + 1B) were dominant (Fig. 3) and their importance increased with depth (Kruskal-Wallis analysis by rank, $P < 0.01$) due to the increasing dominance of the 1B group deeper down the slope (22% at station 1, almost 50% at stations 4 and 5). The 2A group (epistrate feeders) was dominant at station 1 and became less important at deeper stations. The 2B group (predators/omnivores) was much less abundant at all stations.

Hill's diversity numbers $N_0$ and $N_1$ indicated a decrease in nematode generic diversity with depth (Table 4). Station 1 displayed the highest diversity values ($N_0 = 70, N_1 = 42.14$) followed by station 2. At deeper stations, no large differences in diversity numbers were detected. $N_2$ values reflected the same pattern, whereas the distinction between the shallow and deep stations disappeared at $N_\infty$ (less sensitive to rare species).

The TWINSPAN analyses on untransformed density data and on relative abundances showed the same results (Fig. 4). Two groups could be distinguished: one group contained all replicates from station 1 and sta-

**Table 2** Percentage abundance of nematode genera and their feeding type along the transect (–genus not encountered; *0–2%; **2–4%; ***4–8%; ****8–16%)

| Family | Genus | Feeding type | Station 1 | Station 2 | Station 3 | Station 4 | Station 5 |
|---|---|---|---|---|---|---|---|
| Enoplidae | *Enoplus* | 2B | – | * | – | – | – |
| Thoracostomopsidae | *Enoplolaimus* | 2B | – | – | * | – | – |
| | *Mesacanthion* | 2B | – | – | – | * | – |
| | *Oxyonchus* | 2B | * | – | – | – | – |
| | *Paramesacanthion* | 2B | * | – | – | – | – |
| Anoplostomatidae | *Chaetonema* | 1B | * | – | – | – | – |
| Phanodermatidea | *Crenopharynx* | 1A | * | * | – | * | – |
| Anticomidae | *Anticoma* | 1A | – | – | * | – | ** |
| Ironidae | *Syringolaimus* | 2B | – | * | * | – | – |
| Oxystominidae | *Halalaimus* | 1A | ** | *** | * | ** | * |
| | *Oxystomina* | 1A | – | – | * | – | – |
| | *Wieseria* | 1A | * | * | – | – | – |
| Oncholaimidae | *Oncholaimellus* | 2B | * | – | * | – | – |
| | *Viscosia* | 2B | * | * | – | – | – |
| Enchelidiidae | *Bathyeurystomina* | 2B | * | * | – | – | ** |
| | *Eurystomina* | 2B | – | – | * | – | – |
| Tripyloididae | *Bathylaimus* | 1B | – | * | – | – | – |
| Rhabdodemaniidae | *Rhabdodemania* | 1B | * | – | – | – | – |
| Trefusiidae | *Trefusia* | 1A | – | – | – | – | * |
| Lauratonemidae | *Lauratonema* | 1B | * | – | – | – | – |
| Chromadoridae | *Acantholaimus* | 2A | * | ** | ** | *** | *** |
| | *Actinonema* | 2A | – | – | – | – | – |
| | *Chromadora* | 2A | ** | **** | – | * | – |
| | *Chromadorella* | 2A | * | * | * | – | – |
| | *Chromadorita* | 2A | * | * | – | – | – |
| | *Endeolophos* | 2A | * | – | * | – | – |
| | *Neochromadora* | 2A | * | * | * | – | – |
| | *Prochromadorella* | 2A | ** | *** | ** | ** | * |
| | *Spiliphera* | 2A | – | * | – | – | – |
| Ethmolaimidae | *Filitonchus* | 1B | – | * | – | – | – |
| | *Nannolaimus* | 1B | * | – | – | – | – |
| Cyatholaimidae | *Longicyatholaimus* | 2A | – | – | * | – | – |
| | *Marylynnia* | 2A | * | – | – | – | – |
| | *Pomponema* | 2A | – | * | – | – | – |
| Selachinematidae | *Halichoanalaimus* | 2B | * | * | – | * | – |
| Comesomatidae | *Cervonema* | 1B | * | * | – | – | – |
| | *Laimella* | 2A | * | – | – | – | – |
| | *Paracomesoma* | 2A | * | – | * | – | ** |
| | *Paramesonchium* | 2A | * | – | – | * | – |
| | *Pierrickia* | 1A | * | * | – | * | – |
| | *Sabatieria* | 1B | * | ** | – | ** | * |
| Desmodoridae | *Desmodora* | 2A | * | – | – | – | – |
| | *Metachromadora* | 2B | * | – | – | – | – |
| | *Molgolaimus* | 2A | * | ** | – | – | – |
| Microlaimidae | *Bolbolaimus* | 2B | * | – | – | – | – |
| | *Calomicrolaimus* | 2A | ** | – | – | ** | – |
| | *genus 1* | 1A | – | – | * | – | – |
| | *Microlaimus* | 2A | **** | – | *** | – | – |
| Leptolaimidae | *Camacolaimus* | 2A | ** | – | – | ** | – |
| | *Leptolaimoides* | 1B | * | – | – | – | * |
| | *Leptolaimus* | 1A | *** | *** | **** | *** | *** |
| | *Onchium* | 2A | – | – | * | – | – |
| | *Procamacolaimus* | 2A | * | ** | – | – | *** |
| Aegialoalaimidae | *Aegialoalaimus* | 1A | * | * | ** | – | – |
| | *Cyartonema* | 1A | * | ** | ** | – | * |
| | *Diplopeltoides* | 1A | * | – | – | – | – |
| Ceramonematidae | *Ceramonema* | 1A | – | * | – | – | – |
| | *Pselionema* | 1A | * | ** | * | ** | ** |
| Tubolaimidae | *Tubolaimoides* | 1B | * | – | – | – | * |
| Desmoscolecidae | *Desmoscolex* | 1A | *** | ** | ** | – | * |
| | *Gerlachius* | 1A | * | – | * | – | – |
| | *Greefiella* | 1A | * | – | – | – | – |
| | *Quadricoma* | 1A | *** | * | – | – | * |
| | *Tricoma* | 1A | * | – | * | – | – |
| Monhysteridae | *Monhystera* | 1B | * | – | *** | *** | **** |
| Xyalidae | *Ammotheristus* | 1B | * | – | – | – | – |
| | *Amphimonhystera* | 1B | – | *** | * | * | * |

**Table 2** (Continued)

| Family | Genus | Feeding type | Station 1 | Station 2 | Station 3 | Station 4 | Station 5 |
|---|---|---|---|---|---|---|---|
| | *Amphimonhystrella* | 1B | ** | **** | * | ** | ** |
| | *Cobbia* | 2A | * | – | – | * | * |
| | *Daptonema* | 1b | ** | **** | *** | **** | ** |
| | *Gnomoxyala* | 1B | * | * | – | – | – |
| | *Linhystera* | 1A | * | * | * | – | * |
| | *Metadesmolaimus* | 1B | * | * | ** | * | ** |
| | *Paramonhystera* | 1B | * | – | – | – | – |
| | *Promonhystera* | 1B | – | * | – | – | – |
| | *Theristus* | 1B | * | – | ** | * | – |
| Sphaerolaimidae | *Doliolaimus* | 1B | – | * | – | – | – |
| | *Metasphaerolaimus* | 2B | – | * | – | – | – |
| | *Parasphaerolaimus* | 2B | – | * | – | – | * |
| | *Sphaerolaimus* | 2B | * | * | * | ** | *** |
| | *Subsphaerolaimus* | 1B | * | * | – | – | * |
| Linhomoeidae | *Eleutherolaimus* | 1B | * | * | – | *** | – |
| | *Linhomoeus* | 2A | * | * | – | – | – |
| | *Megadesmolaimus* | 1B | – | – | – | – | * |
| | *Metalinhomoeus* | 1B | – | * | **** | *** | *** |
| | *Terschellingia* | 1A | * | * | – | * | – |
| Axonolaimidae | *Ascolaimus* | 1B | * | – | – | – | – |
| | *Axonolaimus* | 1B | * | ** | – | – | – |
| | *Odontophora* | 1B | – | – | – | * | – |
| | *Parodontophora* | 1B | * | * | – | – | – |
| Diplopeltidae | *Campylaimus* | 1B | * | ** | ** | ** | ** |
| | *Diplopeltula* | 1A | * | * | – | – | * |
| | *Southerniella* | 1A | * | – | ** | – | – |
| Coninckidae | *Coninckia* | 1A | * | – | – | – | – |

tion 2 and two replicates from station 4. The deeper stations (except two replicates from station 4) were all listed together in the second group. The nematode communities along the depth gradient in the Laptev Sea could thus be divided into a "shelf" and a "down slope" community although this separation is not strict, and a gentle transition from shallow to deep-sea communities occurred. Table 5 gives the ten most abundant genera of the TWINSPAN groups and their relative abundances. *Microlaimus* was the dominant genus in the shelf community with *Chromadora*, *Leptolaimus*, *Daptonema*, *Halalaimus* and *Quadricoma* being subdominant (> 5%). *Sabatieria*, known as a dominant genus in shelf and upper slope communities, was placed tenth with a relative abundance of 2.7%. The slope community was dominated by *Monhystera* (16.1%); *Leptolaimus* and *Metalinhomoeus* were also present (> 10%) while *Daptonema* was a subdominant genus (> 5%). Dominant genera from the shelf community showed a very low abundance at the deepest stations: *Chromadora* was not among the ten most dominant genera in the second TWIN group but *Leptolaimus* had a high occurrence all over the transect.

The CCA plots (Fig. 5) show the depth gradient along the first axis. Again, the gradient is relatively weak and station 4 was plotted in between stations 2 and 3. The shift in community structure is mainly associated with sediment organic matter (CPE and chlorophyll *a*). Stations 1 and 2 are separated along the second axis, probably as a result in different sediment texture. The species plot reveals the same pattern as observed in Tables 3 and 5, with *Microlaimus* and *Quadricoma* being associated with station 1, and *Monhystera* and *Metalinhomoeus* with deeper stations.

## Discussion

### Meiobenthic densities and nematode community composition in the Laptev Sea

The decrease of meiobenthic densities with depth reflects the findings of other studies on depth gradients (Thiel 1983; Tietjen 1992; Vincx et al. 1994). Pfannkuche and Thiel (1987) reported similar results from the high Arctic NE Svalbard shelf and the Nansen Basin. More recently, Vanhove et al. (1995), De Bovée et al. (1996) and Vanaverbeke et al. (in press) showed the same trends in the Weddell Sea, the Skaggerak and the Goban Spur respectively. The inverse relation between meiofaunal stocks and depth is generally explained by the decreased availability of organic matter with depth in terms of both quantity and quality (Thiel 1983; Shirayama 1984; Pfannkuche 1985; Alongi and Pichon 1988; Rowe et al. 1994).

Chlorophyll *a* concentrations were measured to describe recent sedimentary input of organic matter in the form of phytodetritus (Boetius and Damm in press). The decrease in meiobenthic densities is consistent with the lower sediment chlorophyll *a* contents at greater depths.

The central Arctic Basin appeared oligotrophic: the CPE concentrations were considerably lower than those

**Table 3** List of the 20 most abundant nematode genera per station and their relative significance ($n$ = mean ind.10 cm$^{-2}$)

| Station 1 ($n$ = 2462) | % | Station 2 ($n$ = 2133) | % | Station 3 ($n$ = 540) | % | Station 4 ($n$ = 361) | % | Station 5 ($n$ = 678) | % |
|---|---|---|---|---|---|---|---|---|---|
| *Microlaimus* | 14.52 | *Chromadora* | 10.44 | *Leptolaimus* | 15.45 | *Daptonema* | 14.10 | *Monhystera* | 16.83 |
| *Quadricoma* | 7.26 | *Halalaimus* | 7.70 | *Metalinhomoeus* | 10.07 | *Monhystera* | 6.73 | *Metalinhomoeus* | 12.81 |
| *Leptolaimus* | 6.56 | *Daptonema* | 6.96 | *Monhystera* | 7.73 | *Leptolaimus* | 6.65 | *Leptolaimus* | 7.32 |
| *Desmoscolex* | 4.33 | *Amphimonhystrella* | 5.31 | *Daptonema* | 4.48 | *Acantholaimus* | 5.77 | *Acantholaimus* | 5.85 |
| *Chromadora* | 3.35 | *Prochromadorella* | 4.21 | *Microlaimus* | 4.48 | *Eleutherolaimus* | 5.77 | *Procamacolaimus* | 4.39 |
| *Daptonema* | 3.35 | *Leptolaimus* | 4.03 | *Southerniella* | 4.03 | *Metalinhomoeus* | 4.81 | *Sphaerolaimus* | 4.39 |
| *Prochromadorella* | 2.93 | *Amphimonhystera* | 3.18 | *Acantholaimus* | 3.56 | *Calomicrolaimus* | 3.85 | *Anticoma* | 3.9 |
| *Halalaimus* | 2.79 | *Cyartonema* | 2.93 | *Desmoscolex* | 3.56 | *Halalaimus* | 3.85 | *Daptonema* | 3.29 |
| *Amphimonhystrella* | 2.51 | *Procalacolaimus* | 2.93 | *Metadesmolaimus* | 3.56 | *Prochromadorella* | 3.85 | *Bathyeurystomina* | 3.29 |
| *Calomicrolaimus* | 2.42 | *Axonolaimus* | 2.75 | *Campylaimus* | 2.69 | *Pselionema* | 3.85 | *Campylaimus* | 3.29 |
| *Camacolaimus* | 2.23 | *Sabatieria* | 2.75 | *Prochromadorella* | 2.69 | *Sabatieria* | 3.85 | *Paracomesoma* | 3.29 |
| *Gnomoxyala* | 1.82 | *Desmoscolex* | 2.44 | *Theristus* | 2.69 | *Amphimonhystrella* | 3.21 | *Pselionema* | 3.29 |
| *Pierrickia* | 1.68 | *Molgolaimus* | 2.20 | *Halalaimus* | 2.02 | *Sphaerolaimus* | 3.21 | *Amphimonhystrella* | 2.44 |
| *Campylaimus* | 1.54 | *Viscosia* | 2.20 | *Neochromadora* | 2.02 | *Campylaimus* | 2.89 | *Metadesmolaimus* | 2.44 |
| *Aegialoalaimus* | 1.40 | *Pselionema* | 2.02 | *Pselionema* | 2.02 | *Camacolaimus* | 2.56 | *Linhystera* | 2.20 |
| *Ascolaimus* | 1.40 | *Aegialoalaimus* | 1.96 | *Sphaerolaimus* | 2.02 | *Amphimonhystera* | 1.92 | *Halalaimus* | 1.95 |
| *Neochromadora* | 1.40 | *Campylaimus* | 1.96 | *Amphimonhystrella* | 1.34 | *Chromadora* | 1.92 | *Amphimonhystera* | 1.46 |
| *Theristus* | 1.30 | *Sphaerolaimus* | 1.96 | *Anticoma* | 1.34 | *Cobbia* | 1.92 | *Cobbia* | 1.46 |
| *Sabatieria* | 1.26 | *Acantholaimus* | 1.83 | *Chromadorella* | 1.34 | *Crenopharynx* | 1.92 | *Cyartonema* | 1.46 |
| *Sphaerolaimus* | 1.26 | *Chromadorella* | 1.47 | *Cyartonema* | 1.34 | *Halichoanalaimus* | 1.92 | *Desmoscolex* | 1.46 |

reported from the NE Atlantic abyssal plain at similar depths (Pfannkuche 1992). However, the meiobenthic densities are comparable to those reported for the NE Atlantic at similar depths (Vincx et al. 1994). The Laptev Sea was completely ice covered in the study area till the beginning of August when the ice cover decreased to 80–40% above the shelf and the upper slope. By mid-August, the sea was completely ice covered again (Eicken et al. 1997; Boetius and Damm in press). The short opening of the ice cover was reflected in an increased pigment concentration in the surface sediments of the stations at 200- to 1000-m depth (Boetius and Damm in press). The fact that the meiobenthic densities are not significantly lower than at more eutrophic sites in the NE Atlantic might be explained by a rapid and efficient response to the brief food supply occurring during the ice opening, as suggested by Vanhove et al. (1995) for Antarctic meiobenthos. This is supported by Relexans

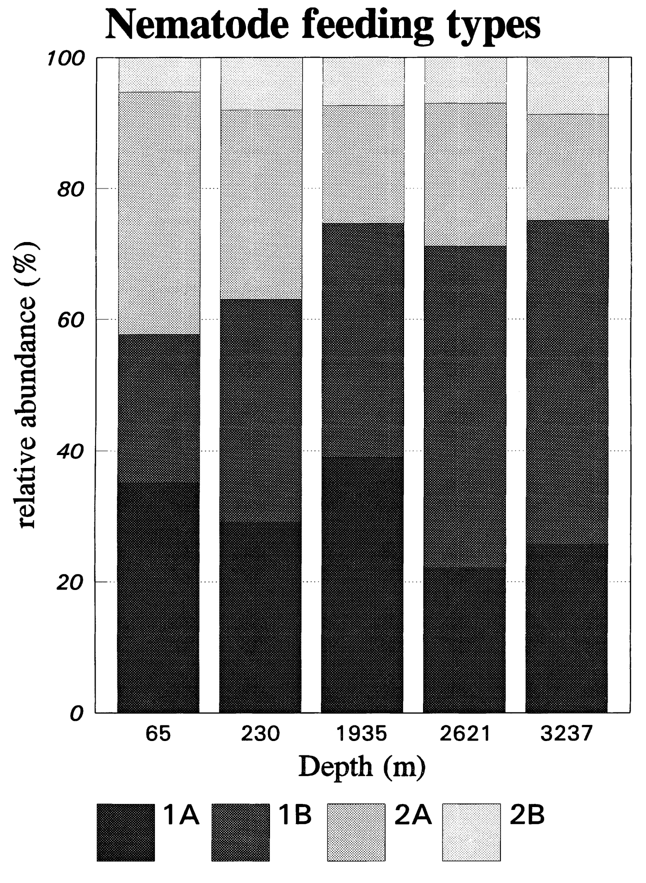

**Fig. 3** Relative abundance of nematode feeding types (according to Wieser 1953) per station

**Table 4** Hill diversity numbers

| | Station 1 | Station 2 | Station 3 | Station 4 | Station 5 |
|---|---|---|---|---|---|
| $N_0$ | 70 | 56 | 36 | 30 | 33 |
| $N_1$ | 42.14 | 35.79 | 25.71 | 21.86 | 21.22 |
| $N_2$ | 23.32 | 25.72 | 17.59 | 17.82 | 14.61 |
| $N_\infty$ | 6.89 | 9.57 | 6.47 | 7.09 | 5.94 |

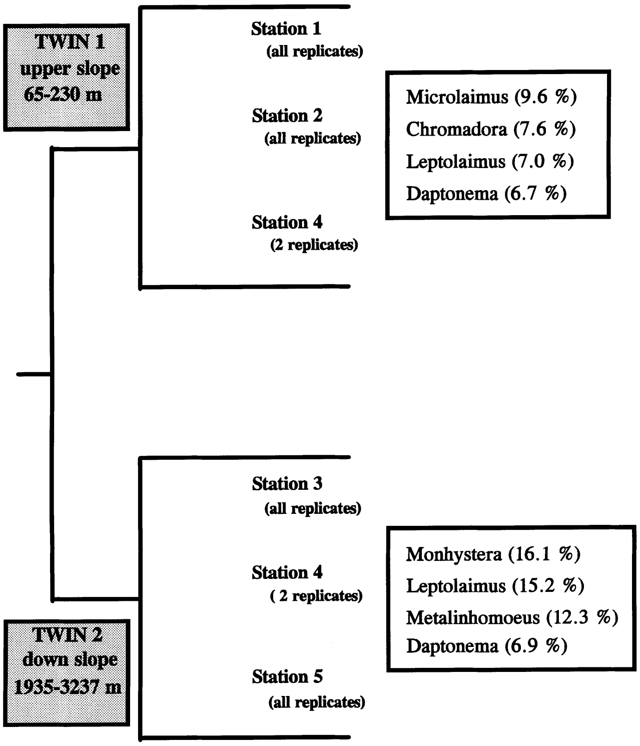

**Fig. 4** TWINSPAN dendrogram based on nematode total generic abundances with the four most abundant genera per group

et al. (1996), who hypothesised that benthic organisms of deep areas (that are relatively oligotrophic) may be more efficient in utilising the organic supply then those living in rich shallow zones.

To date, no data are available on nematode communities in the Arctic region. Therefore, data in this study can be compared only with results of deep-sea studies in other areas. Vincx et al. (1994) compiled a list of the dominant nematode genera in six areas in the Atlantic Ocean; two of them are situated in the east Atlantic (Dinet and Vivier 1979; Vanreusel et al. 1992) and four in the west Atlantic (Tietjen 1971, 1976, 1989; Thistle and Sherman 1985). Two recent studies, Soetaert et al. (1995) and Vanaverbeke et al. (in press) from the Goban Spur (NE Atlantic), have been added to the table of Vincx et al. (1994) to compare Laptev Sea nematode communities with other areas (Table 6). It should be noted that different depth ranges are covered in Table 6. Studies covering a wide depth range (Soetaert et al. 1995; Vanaverbeke et al. in press, this study) show a higher number of genera abundant for > 1%. Therefore, deep areas in the Laptev Sea transect are compared with the deeper areas from the transect studies and the studies from Dinet and Vivier (1979), Tietjen (1971, 1976, 1989) and Thistle and Sherman (1985). Shallow areas from the NE Atlantic (Vanreusel et al. 1992; Vanaverbeke et al. in press) and the Mediterranean Sea (Soetaert et al. 1995) are compared with the shallow stations from the present study.

In deep areas in the Atlantic, three genera were dominant at all study sites (*Theristus*, *Microlaimus* and

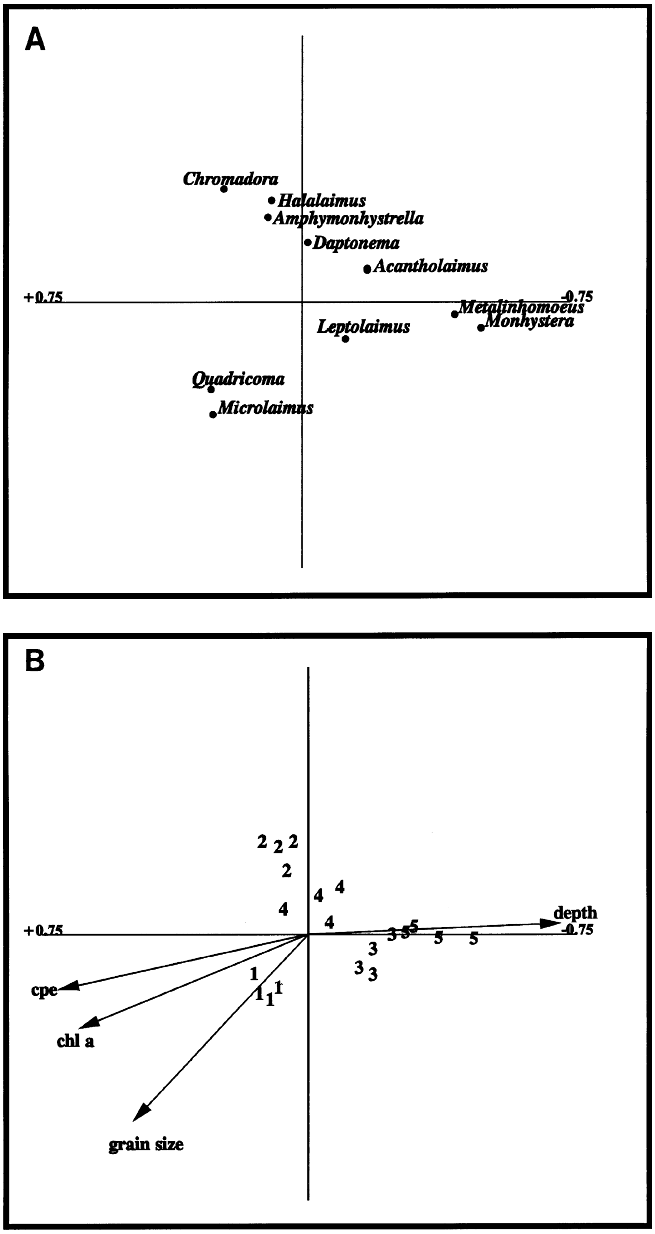

**Fig. 5** **A,B** CCA plot based on nematode total generic abundances. Same *numbers* indicate different replicates from the corresponding station. **A** Species plot; **B** Stations plot

**Table 5** List of the ten most abundant nematode genera per TWINSPAN group (based on the abundance of nematode genera) and their relative significance per TWINSPAN group

| TWIN 1 | % | TWIN 2 | % |
|---|---|---|---|
| *Microlaimus* | 9.61 | *Monhystera* | 16.11 |
| *Chromadora* | 7.58 | *Leptolaimus* | 15.21 |
| *Leptolaimus* | 7.02 | *Metalinhomoeus* | 12.30 |
| *Daptonema* | 6.65 | *Daptonema* | 6.94 |
| *Halalaimus* | 6.10 | *Acantholaimus* | 3.36 |
| *Quadricoma* | 5.27 | *Halalaimus* | 2.68 |
| *Amphimonhystrella* | 4.44 | *Metadesmolaimus* | 2.46 |
| *Prochromadorella* | 4.07 | *Prochromadorella* | 2.46 |
| *Desmoscolex* | 3.79 | *Amphimonhystrella* | 2.24 |
| *Sabatieria* | 2.68 | *Microlaimus* | 2.24 |

*Desmoscolex*). Except for *Theristus*, these genera were also found to be dominant in the Laptev Sea transect. *Acantholaimus*, which is considered to be a typical deep-sea genus (Soetaert et al. 1995), although not reported by Tietjen (1971, 1976), was found along the transect in the Laptev Sea with a relative abundance ranging between 1 and 3%. The highest abundance of this genus was found at station 4 (2611 m, 5.3%), which is low compared to the Goban Spur area at comparable depths where *Acantholaimus* had a relative abundance of 19.1% at 2,760-m depth (Vanaverbeke et al. in press).

Studies including shelf break areas (Vanreusel et al. 1992; Soetaert et al. 1995; Vanaverbeke et al. in press) list *Sabatieria*, *Daptonema* and *Halalaimus* among the dominant genera. *Sabatieria* occurs at 1.3% abundance at station 1 whereas this is 2.8% at station 2. *Daptonema* was found among the most dominant genera along the slope (except at station 5). It was also found to be dominant at comparable depths in the Goban Spur area (Vanaverbeke et al. in press) with a relative abundance of more than 5% down to a depth of 2,182 m; at 2,760 m it only accounted for 3.2%.

The very high abundance of *Leptolaimus* (14.5%) among the dominant genera at station 3 is striking. *Leptolaimus* was found to be a dominant genus at the continental slope, continental rise, abyssal plain and hadal depths in the NE Atlantic and the Mediterranean Sea (Soetaert and Heip 1995; Soetaert et al. 1995) and at the continental slope of the Goban Spur (Vanaverbeke et al. in press). However, a dominance of 14.5% has not yet been reported.

When compared to the other transect studies, the Laptev Sea sediments seem to have a greater affinity with the NE Atlantic continental slope of the Goban Spur than with the Mediterranean transect. The Laptev Sea transect displayed 15 genera (> 1%) in common with the Goban Spur area; 9 were found only in the Laptev Sea, 5 only at the Goban Spur. When compared with the Mediterranean Sea, only 9 genera (> 1%) were found at both areas; 15 were found in the Laptev Sea and not in the Mediterranean and 11 genera were restricted to the Mediterranean Sea.

Four genera (*Cyartonema*, *Metalinhomoeus*, *Neochromadora* and *Axonolaimus*) were reported, with a relative abundance of more than 1%, only in the Laptev Sea transect.

Although nematode communities along the Laptev Sea transect showed some clear differences with those of the Mediterranean transect (Soetaert and Heip 1995), there is no indication of a typical Arctic community since there are only minor differences with the nematode communities of the entire North Atlantic.

## Trophic structure of the nematode community

The trophic structure of the nematode communities in the Laptev Sea confirms previous results from other areas. At the DORA site (3,958–4,700 m), Rutgers van der Loeff and Lavaleye (1986) found the deposit feeders to be dominant, followed by epistrate feeders and predators/omnivores. About half of the nematodes belonged to Wieser's 1B group as at stations 4 and 5 in the Laptev Sea. In the west Atlantic (Tietjen 1976, 1984; Thistle and Sherman 1985), deposit feeders were also dominant (50–80%) as in the Norwegian Sea (Jensen 1988). Soetaert and Heip (1995) reported the dominance of deposit feeders both in Mediterranean canyons and shelf-slope areas.

The majority (> 90%) of the nematodes along the Laptev Sea transect belonged to a group without teeth (deposit feeders: 1A + 1B group) or with only small teeth (epistrate feeders: 2A group). Jensen (1987, 1988) suggested that these nematodes feed preferentially on bacteria, fungi or unicellular algae. Many of these bacterial-feeding nematodes secrete mucus to trap organic matter, thus providing a suitable substrate for microbial growth, and the bacteria are grazed upon (Riemann and Schrage 1978; Jensen 1987). Nematodes covered by a bacterial "slime" were found in deep-sea areas in the Mediterranean Sea (Soetaert and Heip 1995) and in the deep eastern central Pacific (Renaud-Mornant and Gourbault 1990). Nematodes in deep-sea areas, where sediments are organic matter depleted, seem to be able to produce "microbial gardens" in order to improve the food availability of these poor sediments (Soetaert and Heip 1995). This could explain the high dominance of the same groups in the Laptev Sea deep-sea sediments where the input of organic material is restricted to very short periods. Such low organic matter input might also explain the low abundances of 2B nematodes. Soetaert and Heip (1995) showed that this group can only be found to be more abundant in the deep sea when relatively large amounts of labile organic matter are available.

The observed decrease of diversity (at the genus level) with depth was also observed for copepods at the species level (Martinez Arbizu unpublished work). These findings are in contrast with the current opinions that benthic diversity increases with depth (Sanders 1968; Coull 1972; Gage and May 1993) or that diversity follows a hyperbolic curve that reaches a maximum between 2000- and 3000-m depth and declines at both shallower and deeper depths (Rex 1976, 1983; Lambshead 1993; Patterson 1993). However, since only five stations along the Laptev Sea slope were available, care should be taken when drawing conclusions. Other studies that investigated nematode diversity at the genus level could not find a clear increase of diversity with depth (Soetaert et al. 1991b; Vanaverbeke et al. in press). A possible explanation for the decrease of diversity in the Laptev Sea transect could be the difference in grain size along the transect. Heip and Decraemer (1974) detected a positive correlation between nematode species diversity and median grain size, which was explained by the wider range of microhabitats available in sandy sediments when compared with muddy sediments. Soltwedel et al. (1996) hypothesised that benthic diversity in the deep sea

**Table 6** Comparison of the nematode generic dominance in different seas (northeast Atlantic, west Atlantic), Mediterranean Sea (*MS*) and the Laptev Sea (*LS*) (* > 1%; ** > 3%)

| Genera | Dinet and Vivier 1979 | Vanreusel et al. 1992 | Vanaverbeke et al. in press | Tietjen 1971 (< 1500 m) | Tietjen 1976 (< 1500 m) | Thistle and Sherman 1985 | Tietjen 1989 | Soetaert et al. 1995 | This study |
|---|---|---|---|---|---|---|---|---|---|
| *Theristus* | ** | | * | ** | ** | ** | ** | | |
| *Spiliphera* | ** | | | | | | | | |
| *Halalaimus* | ** | ** | * | ** | | ** | ** | ** | ** |
| *Microlaimus* | ** | * | * | ** | ** | ** | ** | * | ** |
| *Acantholaimus* | ** | * | ** | | | ** | ** | ** | * |
| *Desmoscolex* | ** | | ** | ** | ** | * | ** | * | * |
| *Syringolaimus* | ** | | | | | * | * | * | |
| *Leptolaimus* | * | * | ** | | ** | | ** | * | ** |
| *Campylaimus* | * | | * | | | | * | | * |
| *Diplopeltula* | * | ** | | | | | * | * | |
| *Thalassoalaimus* | * | | | | | | * | | * |
| *Sphaerolaimus* | * | | ** | ** | ** | | ** | | |
| *Longicyatholaimus* | * | | | | ** | | | | |
| *Tricoma* | * | | | ** | | | ** | ** | |
| *Cervonema* | * | | | | | | * | | |
| *Sabatieria* | * | ** | * | ** | ** | * | * | ** | * |
| *Daptonema* | | ** | * | | | | | * | * |
| *Richtersia* | | ** | | | | | | ** | |
| *Prochromadorella* | | ** | | | | | | | * |
| *Actinonema* | | ** | | | | ** | ** | | |
| *Pselionema* | | ** | | * | | | | | * |
| *Amphimonhystera* | | | | | | | | | * |
| *Amphimonhystrella* | | | | | | | | ** | ** |
| *Bolbolaimus* | | | * | | | | | | |
| *Camacolaimus* | | | * | | | | | | * |
| *Calomicrolaimus* | | | * | | | | | * | * |
| *Chromadora* | | | * | | | | | | * |
| *Chromadorita* | | | * | | | | | | * |
| *Linhystera* | | | * | | | | | | |
| *Metadesmolaimus* | | | * | | | | | | ** |
| *Monhystera* | | | ** | | | | | | |
| *Oxystomina* | | | ** | | | | | * | |
| *Pareudesmoscolex* | | | * | | | | | | |
| *Pselionema* | | | * | | | | | | * |
| *Quadricoma* | | | * | | | | | | * |
| *Viscosia* | | | * | | | | | | |
| *Aegialoalaimus* | | | | | | | | * | |
| *Dichromadora* | | | | | | | | ** | |
| *Diplopeltoides* | | | | | | | | * | |
| *Diplopeltula* | | | | | | | | * | |
| *Molgolaimus* | | | | | | | | * | |
| *Monhystrella* | | | | | | | | * | |
| *Cyarthonema* | | | | | | | | | * |
| *Metalinhomoeus* | | | | | | | | | ** |
| *Neochromadora* | | | | | | | | | * |
| *Axonolaimus* | | | | | | | | | * |
| | EAST ATLANTIC | | | WEST ATLANTIC | | | | MS | LS |

was influenced by pulses of organic matter sedimentation. Both the higher chlorophyll *a* contents and the coarser sediment at the shallow station from the Laptev Sea transect may be responsible for the higher generic diversity in comparison with the stations deeper down the slope.

Along the transect, nematode communities are separated into a group containing the most shallow stations and a slope community, although the separation is not very strong. *Microlaimus* (9.6%), *Chromadora* (7.6%) and *Leptolaimus* (7.0%) are dominant at the shallow stations, while *Monhystera* (16.1%), *Leptolaimus* (15.2%) and *Metalinhomoeus* (12.3%) are dominant at the deeper stations. The same trend was found in the Goban Spur area (Vanaverbeke et al. in press), Mediterranean Sea (Soetaert et al. 1995) and the NE Atlantic (Soetaert and Heip 1995). The division between shallow and deeper stations found in the Laptev Sea depth transect follows the general trend observed in other areas. Nevertheless, there is a difference in dominant nematode genera within the groups distinguished. The absence of *Sabatieria* and *Daptonema* at the shallow stations of the Laptev Sea is remarkable.

*Sabatieria* is a genus associated with anoxic mineralisation pathways (Soetaert and Heip 1995). This pathway might be absent in the transect studied because this part of the Laptev Sea is ice covered during most of the year, thereby strongly limiting direct input of phytodetritus to the seafloor. This determines the presence of an oxic mineralisation pathway, even at shallow depths, thus maintaining a high oxygenation of the sediments. This is reflected in the high oxygenation of the sediment (Boetius and Damm in press). Such environmental conditions are probably responsible for the abundance of typical deep-sea genera (e.g. *Microlaimus* and *Leptolaimus*) at shallow depths in the Laptev Sea.

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## References

Alongi DM, Pichon M (1988) Bathyal meiobenthos of the western Coral Sea: distribution and abundance in relation to microbial standing stocks and environmental factors. Deep Sea Res 35:491–503

Barnett PRO, Watson J, Cornelly D (1984) A multiple corer for taking virtually undisturbed samples from shelf, bathyal and abyssal sediments. Oceanol Acta 7:399–408

Boetius A, Damm E (in press) Benthic oxygen uptake, hydrolytic potentials and microbial biomass at the Laptev Sea continental slope. Deep Sea Res I

Boetius A, Nöthinger EM, Liebezeit G, Kröncke I (in press) Distribution of plant pigments in Eastern Arctic sediments: indication of recent marine organic input. Ber Polarforsch

Coull BC (1972) Species diversity and faunal affinities of meiobenthic Copepoda in the deep sea. Mar Biol 14:48–51

De Bovée F, Hall POJ, Hulth S, Hulthe G, Landén A, Tengberg A (1996) Quantitative distribution of metazoan meiofauna in continental margin sediments of the Skagerrak (northeastern North Sea). J Sea Res 35:189–197

Dinet A, Vivier MH (1979) Le Méiobenthos abyssale du Golfe de Gascogne. II. Les peuplements de nématodes et leur diversité spécifique. Cah Biol Mar 20:109–123

Eicken H, Reimnitz E, Alexandrov V, Martin T, Kassens H, Viehoff T (1997) Sea-ice processes in the Laptev Sea and their importance for sediment export. Cont Shelf Res 17:205–233

Gage JD, May RM (1993) A dip into the deep seas. Nature 365:600–610

Heip C, Decraemer W (1974) The diversity of nematode communities in the southern North Sea. J Mar Biol Assoc UK 54: 251–255

Heip C, Vincx M, Vranken G (1985) The ecology of marine nematodes. Oceanogr Mar Biol Annu Rev 23:399–489

Herman RL, Dahms HU (1992) Meiofauna communities along a depth transect off Halley Bay (Weddell Sea-Antarctica). Polar Biol 12:313–320

Hill H (1979a) TWINSPAN – A FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. Ecology and Systematics, Cornell University, Ithaca, New York

Hill H (1979b) DECORANA – A FORTRAN program for detrended correspondence analysis and reciprocal averaging. Ecology and Systematics, Cornell University, Ithaca, New York

Hill MO (1973) Diversity and eveness: a unifying notation and its consequences. Ecology 54:427–432

Jensen P (1987) Feeding ecology of free-living aquatic nematodes. Mar Ecol Prog Ser 35:187–196

Jensen P (1988) Nematode assemblages in the deep-sea benthos of the Norwegian Sea. Deep Sea Res 35:253–266

Kröncke I (1994) Macrobenthos composition, abundance and biomass in the Arctic Ocean along a transect between Svalbard and the Makarov Basin. Polar Biol 14:819–829

Kröncke I, Tan TL, Stein R (1994) High bacteria standing stock in deep Arctic basins. Polar Biol 14:423–428

Lambshead PJD (1993) Recent developments in marine benthic biodiversity research. Océanis 19:5–24

Luchetta A, Poniz P, Ilyin G (1994) Nutrients and oxygen. In: Fütterer DK (ed) The expedition Arctic '93 LEG ARK-IX/4 of RV "Polarstern" 1993. Ber Polarforsch 149:37–39

Martin JM, Juan DM, Elbaz-Pouliochet F, Thomas AJ, Gordeev VV (1993) Preliminary assessment of the distributions of some trace elements (As, Cd, Cu, Fe, Ni, Pb and Zn) in a pristine aquatic environment: the Lena River estuary (Russia). Mar Chem 43:185–199

Patterson GLJ (1993) Patterns of polychaete assemblage structure from bathymetric transect in the Rockall Trough, NE Atlantic Ocean. PhD Thesis, University of Wales

Pfannkuche O (1985) The deep-sea meiofauna of the Porcupine Seabight and abyssal plain (NE Atlantic): population structure, distribution, standing stock. Oceanol Acta 8:343–353

Pfannkuche O (1992) Organic carbon flux through the benthic community in the temperate abyssal Northeast Atlantic. In Rowe: GT, Pariente V (eds) Deep sea food chains and the global carbon cycle. Kluwer, Dordrecht, pp 183–198

Pfannkuche O, Thiel H (1987) Meiobenthic standing stocks and benthic activity on the NE Svalbard Shelf and in the Nansen Basin. Polar Biol 7:253–266

Relexans J-C, Deming J, Dinet A, Gaillards J-F, Sibuet M (1996) Sedimentary organic matter and micro-meiobenthos with relation to trophic conditions in the tropical northeast Atlantic. Deep Sea Res I 43:1434–1468

Renaud-Mornant J, Gourbault N (1990) Evaluation of abyssal meiobenthos in the eastern central Pacific (Clarion-Clipperton fracture zone). Prog Oceanogr 24:317–329

Rex MA (1976) Biological accommodation in the deep-sea: a comparative evidence on the importance of predation and productivity. Deep Sea Res 23:975–987

Rex MA (1983) Geographical patterns of species diversity in the deep-sea benthos. In: Rowe GT (ed) The seas, vol 8. Wiley, New York, 453–472

Riemann F, Schrage M (1978) The mucus-trap hypothesis on feeding of aquatic nematodes and implications for biodegradation and sediment texture. Oecologia 34:75–88

Rowe GT, Boland S, Phoel WC, Anderson RF, Biscaye PE (1994) Deep-sea floor respiration as an indication of lateral input of biogenic detritus from continental margins. Deep Sea Res II 41:657–668

Rutgers van der Loeff MM, Lavaleye MSS (1986) Sediments, fauna and the dispersal of radionuclides at the N.E. Atlantic dumpsite for low level radioactive waste. Report of the Dutch DORA program. Nederlands Institut Ozolerzen der Zee, Texel:1–134

Sanders HL (1968) Marine benthic diversity: a comparative study. Am Zool 102:243–282

Sheremetevsky AM (1977) Meiobenthos in the intertidal zone of the Laptev Sea and the New Siberian Islands. Gidrobiol Zh 13:63–70

Shirayama Y (1984) The abundance of deep-sea meiobenthos in the Western Pacific in relation to environmental factors. Oceanol Acta 7:113–121

Sirenko BI, Petryashov VV, Rachor E, Hinz K (1995) Bottom biocoenoses of the Laptev Sea and adjacent areas. Ber Polarforsch 176:211–221

Smith WO, Sakshaug E (1990) Polar phytoplankton. In: Smith WO (ed) Polar oceanography, Part B. Chemistry, biology and geology. Academic Press, San Diego, pp 477–525

Soetaert K, Heip C (1995) Nematode assemblages of deep-sea and shelf break sites in the North Atlantic and Mediterranean Sea. Mar Ecol Prog Ser 125:71–183

Soetaert K, Heip C, Vincx M (1991a) The meiobenthos along a Mediterranean deep-sea transect off Calvi and an adjacent Canyon. PSZNI Mar Ecol 12:227–242

Soetaert K, Heip C, Vincx M (1991b) Diversity of nematode assemblages along a Mediterranean deep-sea transect. Mar Ecol Prog Ser 75:275–282

Soetaert K, Vincx M, Heip C (1995) Nematode community structure along a Mediterranean shelf slope gradient. PSZN I Mar Ecol 16:1–18

Soltwedel T, Pfannkuche O, Thiel H (1996) The size structure of deep-sea meiobenthos in the north-eastern Atlantic: nematode size spectra in relation to environmental variables. J Mar Biol Assoc UK 76:327–344

Stein R, Nürnberg D (1995) Productivity proxies: organic carbon and biogenic opal in surface sediments from the Laptev Sea shelf and the adjacent continental slope. Ber Polarforsch 176:286–296

Suess E (1980) Particulate organic carbon flux in the oceans – surface productivity and oxygen utilization. Nature 288:260–263

Thiel H (1972) Die Bedeutung der Meiofauna in küsternfernen benthischen Lebensgemeinschaften verschiedener geographischer Regionen. Verh Dtsch Zool Ges 65:42–57

Thiel H (1983) Meiobenthos and nanobenthos of the deep sea. In: Rowe GT (ed) The sea, vol 8. Wiley, New York, pp 167–230

Thistle D, Sherman K (1985) The nematode fauna of a deep-sea site exposed to strong near-bottom currents. Deep Sea Res 32:1077–1088

Tietjen JH (1971) Ecology and distribution of deep-sea meiobenthos off North Carolina. Deep Sea Res 18:941–957

Tietjen JH (1976) Distribution and species diversity of deep-sea nematodes off North Carolina. Deep Sea Res 23:755–768

Tietjen JH (1984) Distribution and species diversity of deep-sea nematodes in the Venezuela Basin. Deep Sea Res 31:119–132

Tietjen JH (1989) Ecology of deep-sea nematodes from the Puerto Rico Trench area and Hatteras Abyssal Plain. Deep Sea Res 36:1567–1575

Tietjen JH (1992) Abundance and biomass of metazoan meiobenthos in the deep sea. In: Rowe GT, Pariente V (eds) Deep sea food chains and the global carbon cycle. Kluwer, Dordrecht, pp 45–62

Vanaverbeke J, Soetaert K, Heip C, Vanreusel A (in press) The metazoan meiobenthos along the continental slope of the Goban Spur (NE Atlantic). J Sea Res:38

Vanhove S, Wittoeck J, Desmet G, Van den Berghe B, Herman RL, Bak RPM, Nieuwland G, Vosjan JH, Boldrin A, Rabitti S, Vincx M (1995) Deep-sea meiofauna communities in Antarctica: structural analysis and relation with the environment. Mar Ecol Prog Ser 127:65–76

Vanreusel A, Vincx M, Van Gansbeke D, Gijselinck 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 122:185–202

Vincx M, Bett BJ, Dinet A, Ferrero T, Gooday AJ, Lambshead PJD, Pfannkuche O, Soltwedel T, Vanreusel A (1994) Meiobenthos of the deep Northeast Atlantic. Adv Mar Biol 30:2–88

Wakeham SG, Lee J (1993) Production, transport and alteration of particulate organic matter in the marine water column. In: Engel MH, Macko S (eds) Organic chemistry: principles and applications. Plenum Press, New York, pp 145–169

Wakeham SG, Lee J, Farrington JW, Gagosian RB (1993) Biogeochemistry of particulate organic matter in the oceans: results from sediment trap experiments. Deep Sea Res 31:509–528

Wieser W (1953) Beziehungen zwischen Mundhöhlengstalt, Ernährungsweise und Vorkommen bei freilebenden marinen Nematoden. Ark Zool 2:439–484

Wollenburg J (1995) Benthic foraminiferal assemblage in the Arctic ocean: indicators for water mass distribution, productivity and sea ice drift. Ber Polarforsch 179:1–277