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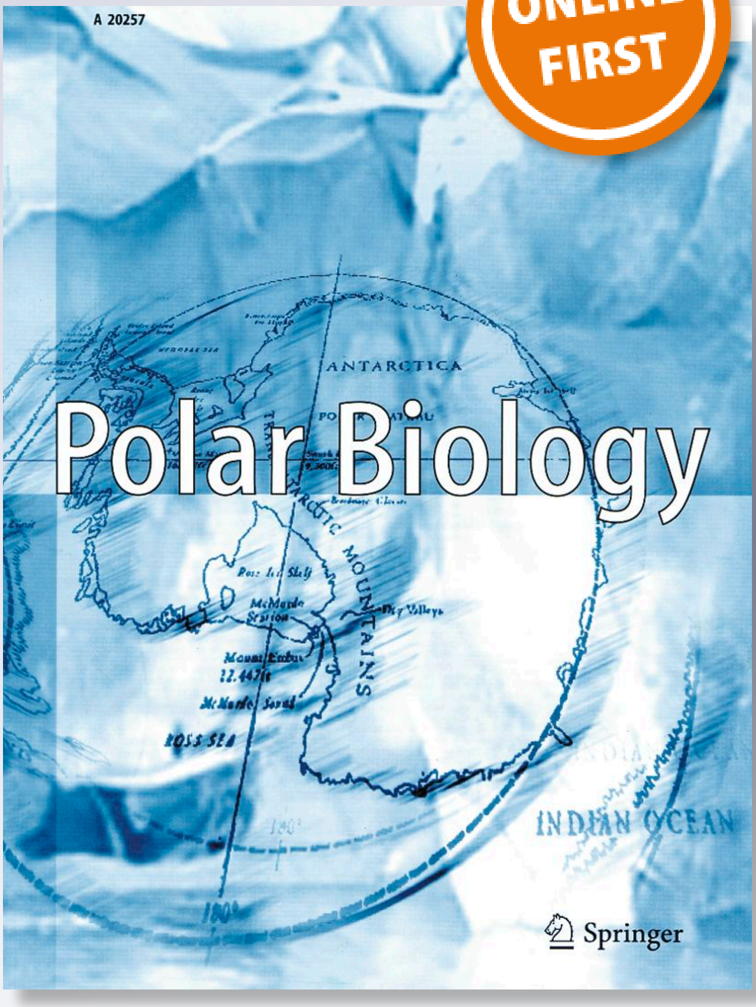

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ORIGINAL PAPER

# Benthic meiofaunal density and community composition in the deep White Sea and their temporal variations

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**Abstract** In spite of the fact that shallow-water meiobenthos of the White Sea is a relatively well studied, the information on meiobenthic fauna from the deepest part of this sea is still very scanty. This study represents the first major study of the meiobenthos from the deep White Sea. The composition of the meiobenthic community, density and vertical distribution was studied during four sampling occasions in the deepest part of the Kandalaksha Depression (White Sea) in July 1998, October 1998, May 1999 and November 1999. Samples were collected from a depth of 270 m with the aid of a multicorer. The total density of meiobenthos in 1998 was twice than in 1999 (on average, 2,356 and 1,464 ind./10 cm$^2$, respectively). The most abundant meiobenthic group was Foraminifera (59 %), followed by Nematoda (26 %) and Harpacticoida (7 %). These relative and absolute abundance values are comparable with the same depth interval in Arctic and temperate regions. The density of foraminiferans and nematodes was higher in the autumn and lower in the summer. This may be explained by the mass propagation of these animals in the autumn season: the density of juvenile nematodes and small-sized foraminiferans increased significantly in the 1- to 4-cm-deep sediment layers in autumn. The size range of the meiobenthos in the deepest part of the White Sea was also comparable to deep-sea meiobenthos (the 63–125 and 125–250 µm size classes were most dominant).

**Keywords** Foraminifera · Harpacticoida · Meiobenthic · Community · Density · Nematoda · Pseudo-bathyal · Seasonality

## Introduction

The White Sea is a small marginal shelf sea semi-enclosed by land areas and connected to the Barents Sea by the long (160 km), narrow (48–56 km wide) and shallow (maximum depth 60–70 m) Gorlo Strait (Berger et al. 2001; Filatov et al. 2005). In spite of its shelf origin, the White Sea has several depressions with a maximum depth of 343 m (Berger and Naumov 2000). The shallow and narrow connecting strait means that environmental conditions in the deep hollows of the White Sea differ strongly from those at the same depth in the Barents Sea: the deep water temperature is very cold, colder than in the Barents Sea (about −1.5 vs. 1–3 °C, respectively), and the salinity is also lower (29.5–30.0 vs. 34–35 ‰, respectively) (Loeng 1991; Berger and Naumov 2000). Deep waters in the White Sea depressions originate from winter inflow from the Barents Sea: cold sea water penetrates the White Sea through the Gorlo Strait, sinking under the lower-salinity and lower-density surface waters of the White Sea.

The term "pseudo-bathyal" was introduced by Andriashev (1977) to designate this type of marginal shelf depression detached from the main oceanic water body by

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a shallow sill. Due to the isolation of such pseudo-bathyal hollows from oceanic deep water, their fauna differs from the oceanic deep-sea fauna and is of mainly shallow-water origin. The deep White Sea is occupied by cold-water Arctic assemblages at depths >150 m, whereas such assemblages have been not found in the strait connecting the White Sea and the Barents Sea (Galkina et al. 2000). It has been proposed that the Arctic fauna has survived in the deep White Sea since the last glacial period (Knipowitsch 1906).

The average annual primary productivity in the White Sea is about 25 gC/m$^2$ per year (Sakshaug 2004). An intensive phytoplankton bloom lasts from April to the beginning of June. A primary production peak (up to 302 mg C/m$^2$ per day) has been observed in May and minimum primary production (49–98 mg C/m$^2$ per day) in October (Fedorov and Bobrov 1977, cit. from Rat'kova 2000). Yearly primary production can vary from 13 to 52 gC/m$^2$ per year (Fedorov et al. 1974, cit. from Rat'kova 2000).

In addition, a cyclonic gyre contributes to the accumulation of sediments in the central pseudo-bathyal part of the White Sea, due to more rapidly sinking sediments in its low-energy centre. This gyre also introduces an unknown quantity of phytodetritus from the tidal and upper subtidal zones in the form of macroalgal thallomes detached during storms (Lukanin et al. 1995).

The White Sea is a relatively well-studied boreal sea. Due to regular scientific activity at two Russian biological stations open since the 1940s, a large quantity of biological data has been collected from this region (see for example Berger et al. 2001). However, although the macrobenthos has been well studied, information on the diversity, distribution and seasonality of the meiobenthos is rather scarce, and meiobenthic studies have mostly been conducted in the intertidal zone (see Platonova and Galtsova 1985; Galtsova 1991).

The meiobenthos plays an important role in marine ecosystems (see Giere 2009 for review), and a short summary of current knowledge on deep-sea meiobenthos in the White Sea has been published by Mokievsky (2000). Galtsova and Sheremetevsky (1985) described the quantitative distribution of meiobenthos along a transect running from shallow water in Onega Bay down to 300 m depth in the White Sea Basin. They reported a prominent decrease in total meiofaunal abundance along the depth gradient, from 1,000 ind./10 cm$^2$ in the tidal zone to 20–130 ind./10 cm$^2$ at a depth range 100-280 m. The taxonomic composition of the Foraminifera was described at the same stations by Lukina (1985).

In the south-eastern part of Kandalaksha Bay, a second transect from the intertidal zone to 300 m depth has also been quantitatively studied for meiobenthos (Golikov et al. 1988; Galtsova and Vladimirov 1988; Galtsova and Platonova 1988). According to these authors, eumeiobenthos of the deep part of the White Sea was represented by Foraminifera, Nematoda, Harpacticoida, Ostracoda and Halacaroidea. Also, the pseudomeiobenthos included Polychaeta, Oligochaeta, Bivalvia, Gastropoda, Nemertina, Isopoda, Cumacea and Insecta. Galtsova and Vladimirov (1988) reported that the total density of eumeiobenthos at depths of 200–300 m was 100–500 ind./10 cm$^2$. Nematodes were most abundant in this depth range, their relative abundance approximately double that recorded in the upper subtidal zone.

Several publications have focused on Foraminifera diversity and distribution in the deep White Sea. Kirienko (1973) reported that agglutinated foraminiferans prevailed there, and Mayer (1977, 1980) recorded 161 Foraminiferan species in the White Sea, but noted that only 95 species were found in the Basin below 150 m. Similarly, Mayer (1977, 1980) found that total foraminiferan density in the 0–1 cm sediment layer was four- to sixfold less below 150 m (51 ind./10 cm$^2$) than at 15–110 m depth.

Several species of Enoplida (Nematoda) from the central Basin of the White Sea have been described by Filipjev (1927). Galtsova and Platonova (1988) recorded a low nematode diversity below 100 m in southeast Kandalaksha Bay, but noted that most species were euribathic with a distribution range of 20–300 m.

Most recently, a cooperative German-Russian scientific programme "The investigation of the deep sea ecosystem of the White Sea" supported by INTAS was initiated in 1998 (Rachor 2000). Through this project, a number of research cruises were conducted in the Kandalaksha Depression, at a depth of about 270 m. These cruises enabled qualitative and quantitative meiofaunal sampling and initial results from the first cruise (July 1998) recorded 16 major meiobenthic taxa, with total abundance of about 1,900 ind./10 cm$^2$ in the upper 0–5 cm sediment layer (Mokievsky et al. 2009). Nematoda and Foraminifera were numerically dominant, and fifty-five nematode species belonging to 18 families were identified.

The study reported here forms part of this latter programme, it examines seasonal abundance data of the major meiobenthic taxa collected during 4 cruises conducted during summer and autumn seasons over 2 years. The main aim was to describe in more detail the abundance and composition of the meiobenthic community and to study the possible influence of different temporal scales (years and seasons) on these characteristics.

## Materials and methods

### Sampling area

In the sampling area, the uppermost 0–4 cm sediment layer was a liquid, clayey mud with a minor admixture of silt and a large number of Mn micronodules (0.06–1 mm in diameter). The 4–7 cm sediment layer was a semi-liquid, sand–silt–clayey mud (Strekopytov et al. 2005). Sediment organic carbon content was measured in the summer of 1999 and varied with sediment depth: 1.58 ± 0.08, 1.64 ± 0.06 and 1.74 ± 0.05 % in the sediment layers 0–2, 2–4 and 4–7 cm, respectively (Strekopytov et al. 2005). Agatova et al. (2002) reported 2-times higher values of lipids and carbohydrates in the organic matter of the uppermost, liquid sediment layer compared to deeper layers, but concurrent 2-times lower values for nucleic acids.

## Data sampling and material processing

Meiobenthos was collected in July and October 1998, and in May and November 1999 (Table 1; Fig. 1) during four cruises of the RV "Kartesh" and the RV "Professor Kuznetsov" (Zoological Institute, Russian Academy of Sciences). The sampling area was about 10 square miles, and every effort was made to take samples in the same location on each cruise. However, because of weather conditions and an absence of dynamic positioning systems on the ships, the coordinates of each sampling occasion differed slightly and sampling depth ranged from 251 to 288 m (Table 1; Fig. 1).

Meiobenthos samples were taken using a minicorer, specifically a small model of the Burnett's multiple corer (MUC), bearing four 70-cm long plastic corers with an internal diameter of 5.4 cm. In total, 9 samples were collected in July 1998 (3 replicates from each of 3 deployments); 6 samples in October 1998 (3 replicates/2 deployments); 5 samples in May 1999 (3 deployments, only single samples from the deployments #2 and #3 were taken because of technical problems); and 3 samples in November 1999 (3 replicates/1 deployment).

Meiobenthos was collected from the corers using cut-off syringes with an internal diameter 2 cm (one syringe per core). Each syringe was divided into 5 subsamples of five 1-cm-thick sediment layers from the surface down to 5 cm depth (0–1, 1–2, 2–3, 3–4 and 4–5 cm sediment depth). From each core, overlying water was filtered through a 50-μm mesh sieve and any collected material added to the 0–1 cm layer. An upper phytodetritus layer (up to several centimetres thick) was also combined with the upper 0–1 cm layer. In total, 115 subsamples each with a volume of about 3.14 $cm^3$ were collected. In addition, one complete 17-cm deep sediment core was collected in May 1999. This was sliced into 1-cm-thick layers down to 7 cm sediment depth and then into 2-cm-thick layers down to 17 cm depth. All subsamples were fixed in 10 % buffered formalin.

In the laboratory, each subsample was stained with 1 % Rose Bengal and washed through a set of sieves (32, 63, 125, 250 and 500 μm mesh size). For every size fraction, organisms were identified to major taxa and counted under a stereo microscope using a Bogorov counting chamber. Nematodes were picked out, processed in glycerin using the Seinhorst's method of slow evaporation (Seinhorst 1959) and permanently mounted on glycerin–paraffin slides. The nematodes were then examined under a light microscope and the number of adults and juveniles counted.

## Statistical analysis

The software packages PAST (Hammer et al. 2001), PRIMERv6 (Clarke and Gorley 2006) and SYSTAT were used for statistical analysis.

To analyse the contribution of different spatio-temporal factors (season, deployment date and sample) to the total variance of meiobenthic density, multifactor analysis of variance was carried out. This was undertaken in SYSTAT using a nested general linear model (GML) analysis. Nested factors were sample, deployment and season, in that order, and the contribution to total variance was calculated for each grouping level.

To further understand the influence of temporal (intra- and inter-annual) variations on the composition and density of the meiobenthos, two additional time factors were analysed: "year" (1998 or 1999) and "season" ("summer", May and July or "autumn", October and November).

**Table 1** Location of sampling sites, date of sampling and number of replicates (cores) taken for meiobenthic study from each multicorer deployment

| Station | Date | Deployment (no.) | Latitude (N) | Longitude (E) | Depth (m) | Number of replicates |
|---|---|---|---|---|---|---|
| CBB-20 | 27.07.1998 | 1 | 66°25.99′ | 34°22.47′ | 270 | 3 |
| | | 2 | 66°25.95′ | 34°22.23′ | 270 | 3 |
| | | 3 | 66°26.02′ | 34°21.88′ | 270 | 3 |
| CBB-22 | 15.10.1998 | 1 | 66°26.03′ | 34°19.50′ | 288 | 3 |
| | | 2 | 66°24.93′ | 34°19.86′ | 277 | 3 |
| CBB-23 | 31.05.1999 | 1 | 66°25.59′ | 34°20.75′ | 251 | 3 |
| | | 2 | 66°25.16′ | 34°24.09′ | 274 | 1 |
| | | 3 | 66°24.49′ | 34°24.09′ | 270 | 1 |
| CBB-34 | 24.11.1999 | 1 | 66°25.20′ | 34°22.08′ | 270 | 3 |

It was not possible to collect triplicate samples from every deployment at station CBB-23 because of technical problems

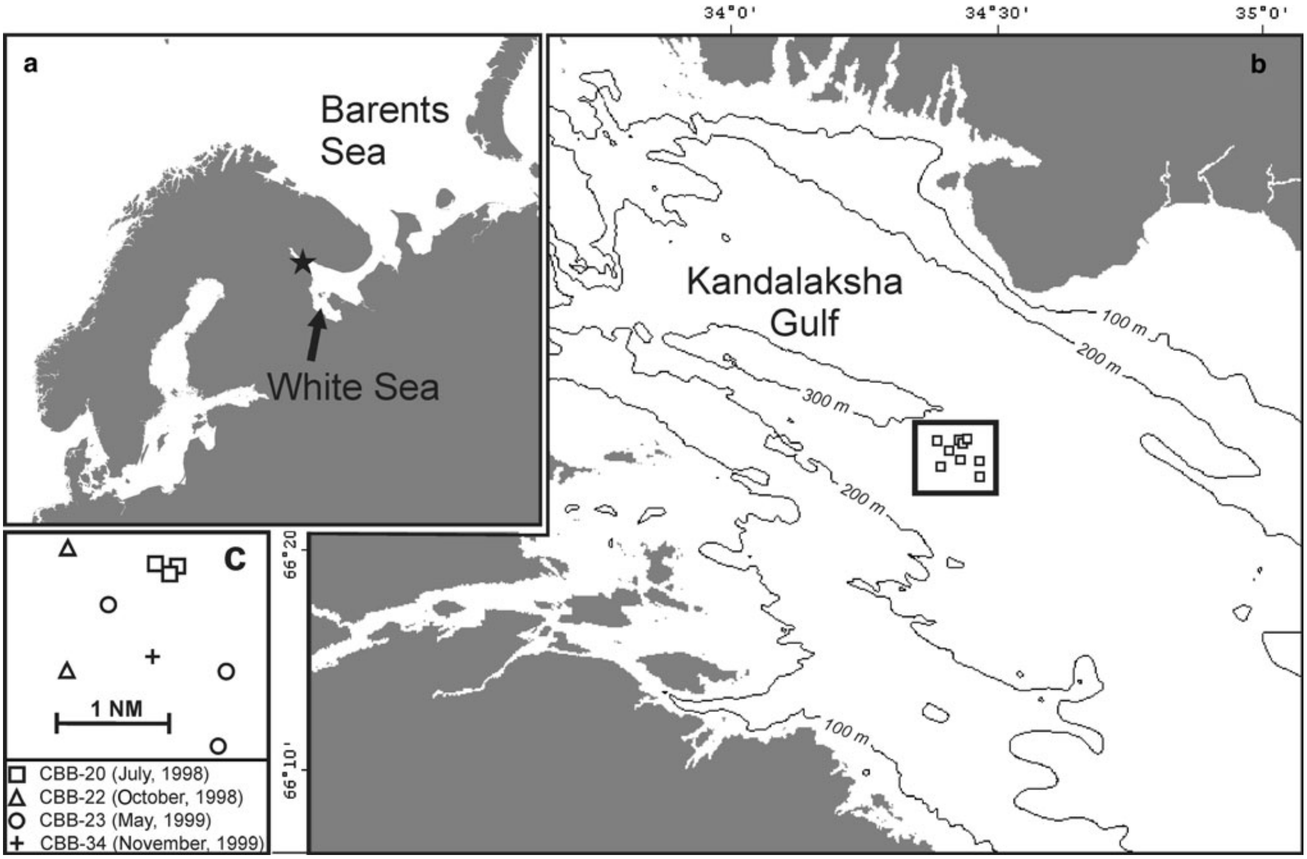

**Fig. 1** Sampling area and location of stations. **a** Large-scale map of the White Sea region (the *star* indicates the sampling area), **b** detailed map of the sampling area (sampling sites are indicated by *squares*), **c** position of deployments within the sampling area

To test for differences between univariate values (density of meiobenthic groups), two-way ANOVA (for log-normalized values), Mann–Whitney *U* and Kruskal–Wallis tests were employed.

The multivariate data of meiobenthic community composition (square root transformed) were analysed by Bray–Curtis similarity distances. This was then used to produce non-metric multidimensional scaling (nMDS) plots and undertake analyses of sample similarity (ANOSIM). Additionally, similarity percentage (SIMPER) was used to assess which taxa were primarily responsible for any observed differences between groups of samples.

## Results

### Meiofaunal density

#### *Cumulative 0–5 cm sediment layer*

In total, 16 major taxonomic groups were found (Table 2). In addition, nauplii were recorded separately from adult crustaceans, although it appeared that most belonged to the order Harpacticoida. Across the 4 sampling occasions, average density of total meiobenthos was 1,910 ind./10 cm$^2$, and the average density of metazoan meiobenthos was 746 ind./10 cm$^2$ (Table 2).

The most abundant group was Foraminifera (1,164 ind./10 cm$^2$ on average) followed by Nematoda (502 ind./10 cm$^2$) and Harpacticioda + nauplii (122 ind./10 cm$^2$). Other taxonomic groups were much less abundant (Table 2), with the exception of rotifers in one sample taken in July 1998 (station CBB-20, deployment 3, tube B). In this sample, rotifers were unusually abundant in the 3–4 cm sediment layer (1,319 vs. 0–150 ind./10 cm$^2$ in all other subsamples).

The nested GLM analysis showed that total variance in meiobenthic density predominantly reflected microscale fluctuations in density between samples, accounting for 55 % of the variance in total meiobenthic and Foraminifera density, 78 % of the variance in Nematoda density and 42 % of the variance in Harpacticoida density. Also, 32 % of the variance in density of the total meiobenthos (7.5 % of the variance in Nematoda, 31 % in Harpacticoida and 34.5 % in Foraminifera) was explained by season. Only 13 % of the variance in total meiobenthic density related to differences between deployments. Therefore, most variation

**Table 2** Average density (mean ± SE, ind./10 $cm^2$) of each meiobenthic group, and of total meiobenthos, in the 0- to 5-cm deep sediment layer on each sampling occasion

| Group | July 98 | October 98 | May 99 | Nov 99 | Mean |
|---|---|---|---|---|---|
| Foraminifera | 989 ± 202 | 1,725 ± 210 | 973 ± 61 | 969 ± 218 | 1,164 ± 187 |
| Nematoda | 480 ± 90 | 825 ± 167 | 289 ± 52 | 413 ± 134 | 502 ± 115 |
| Harpacticoida | 107 ± 22 | 96.6 ± 31.6 | 22.9 ± 1.9 | 34.0 ± 12.9 | 65.1 ± 21.4 |
| Nauplii | 88.1 ± 29.4 | 71.7 ± 20.9 | 12.7 ± 3.9 | 56.3 ± 27.1 | 57.2 ± 16.2 |
| Aplacophora | 0.35 ± 0.35 | 0 | 0 | 0 | 0.09 ± 0.09 |
| Bivalvia | 2.48 ± 1.74 | 0 | 1.27 ± 0.78 | 1.06 ± 1.06 | 1.08 ± 0.52 |
| *Boreohydra symplex* | 2.83 ± 1.24 | 5.84 ± 3.01 | 7.64 ± 3.57 | 5.31 ± 1.06 | 5.41 ± 1.00 |
| Gastrotricha | 0.71 ± 0.71 | 0 | 0 | 0 | 0.18 ± 0.18 |
| Halacaroidea | 3.54 ± 1.80 | 3.72 ± 2.65 | 7.01 ± 2.74 | 7.43 ± 4.63 | 5.43 ± 1.04 |
| Kinorhyncha | 11.0 ± 5.0 | 26.0 ± 12.7 | 5.10 ± 2.38 | 18.0 ± 3.8 | 15.0 ± 4.5 |
| Oligochaeta | 0.35 ± 0.35 | 0 | 0 | 0 | 0.09 ± 0.09 |
| Ostracoda | 17.7 ± 8.6 | 12.2 ± 8.0 | 1.27 ± 0.78 | 3.18 ± 1.84 | 8.59 ± 3.86 |
| Polychaeta | 33.3 ± 4.1 | 18.6 ± 3.8 | 15.9 ± 6.0 | 28.7 ± 11.0 | 24.1 ± 4.1 |
| Rotifera | 149 ± 146 | 0 | 29.9 ± 29.9 | 0 | 44.7 ± 35.5 |
| Sponges | 3.89 ± 3.13 | 2.65 ± 2.08 | 0 | 0 | 1.64 ± 0.98 |
| Tanaidacea | 0 | 1.06 ± 1.06 | 0 | 0 | 0.27 ± 0.27 |
| Turbellaria | 7.08 ± 2.99 | 2.12 ± 1.06 | 14.0 ± 7.6 | 4.25 ± 1.06 | 6.86 ± 2.59 |
| Unidentified | 22.6 ± 14.5 | 3.18 ± 1.42 | 1.27 ± 0.78 | 6.37 ± 3.68 | 8.36 ± 4.86 |
| Total metazoan meiobenthos | 930 ± 190 | 1,068 ± 206 | 408 ± 73 | 577 ± 146 | 746 ± 153 |
| Total meiofauna | 1,919 ± 336 | 2,793 ± 407 | 1,381 ± 128 | 1,546 ± 363 | 1,910 ± 315 |

in meiobenthic density was at the scale of tens of centimetres (i.e. the distance between corers in one multicorer deployment).

According to the two-way ANOVA analysis, the density of total meiobenthos also varied significantly with sampling "year" (1998 vs. 1999: $p = 0.046$), but not with season (summer vs. autumn: $p = 0.088$). Mean density in 1998 was 2,356 and 1,464 ind./10 $cm^2$ in 1999. Regarding the different meiofauna groups, nematodes and harpacticoids + nauplii were significantly more numerous in 1998 than 1999 (653 vs. 351 ind./10 $cm^2$, $p = 0.026$; and 182 vs. 63 ind./10 $cm^2$, $p = 0.004$, respectively).

The abundance of juvenile nematodes, however, varied significantly with "season" ($p = 0.025$): in 1998, their summer density was 241 ± 62 ind./10 $cm^2$ compared with 309 ± 110 ind./10 $cm^2$ in the autumn, whilst in 1999, these values were 97 ± 39 and 165 ± 52 ind./10 $cm^2$, respectively.

In contrast to the nematodes and harpacticoids, the density of foraminiferans varied signficantly with "season", but not with "year" ($p = 0.031$). However, their density changed with season in 1998 only (989 in summer vs. 1,725 ind./10 $cm^2$ in autumn) and not in 1999 (973 vs. 969 ind./10 $cm^2$).

### *Vertical distribution*

Total meiobenthic density varied with sediment depth and was highest in the 0–1 and 1–2 cm layers (Fig. 2). Across the 4 sampling occasions, total meiobenthos density in the upper 0–1 cm layer averaged 693 and 563 ind./10 $cm^2$ in the 1–2 cm layer. The average density of metazoan meiobenthos in these sediment layers was 276 and 248 ind./10 $cm^2$, respectively.

According to the two-way crossed ANOVA, there was no significant influence of "year" or "season" on the total meiobenthic density in the 0–1 cm layer. However, the factor "season" significantly influenced the total density in the 1–2 and 2–3 cm layers ($p = 0.002$ and 0.002, respectively). Taking these two layers together, the average density was 2–2.5 times higher in the autumn (691 and 502 ind./10 $cm^2$ in 1998 and 1999, respectively) than in the summer (242 and 278 ind./10 $cm^2$ in 1998 and 1999, respectively) (Fig. 2).

The density of foraminiferans in the 1–2, 2–3 and 3–4 cm sediment layers varied significantly with "season" ($p = 0.031$, 0.024, and 0.028, respectively). Averaging across these three layers, foraminifera density was 1.5–3 times higher in the autumn (357 and 233 ind./10 $cm^2$ in 1998 and 1999, respectively) than in the summer (122 and 175 ind./10 $cm^2$ in 1998 and 1999, respectively). Foraminifera density in the uppermost centimetre of the sediments did not vary significantly with any factor (Fig. 2).

Nematode density also varied significantly with "season" in the 1–2 and 2–3 cm layers ($p = 0.006$ and 0.040, respectively), being higher in the autumn than the summer

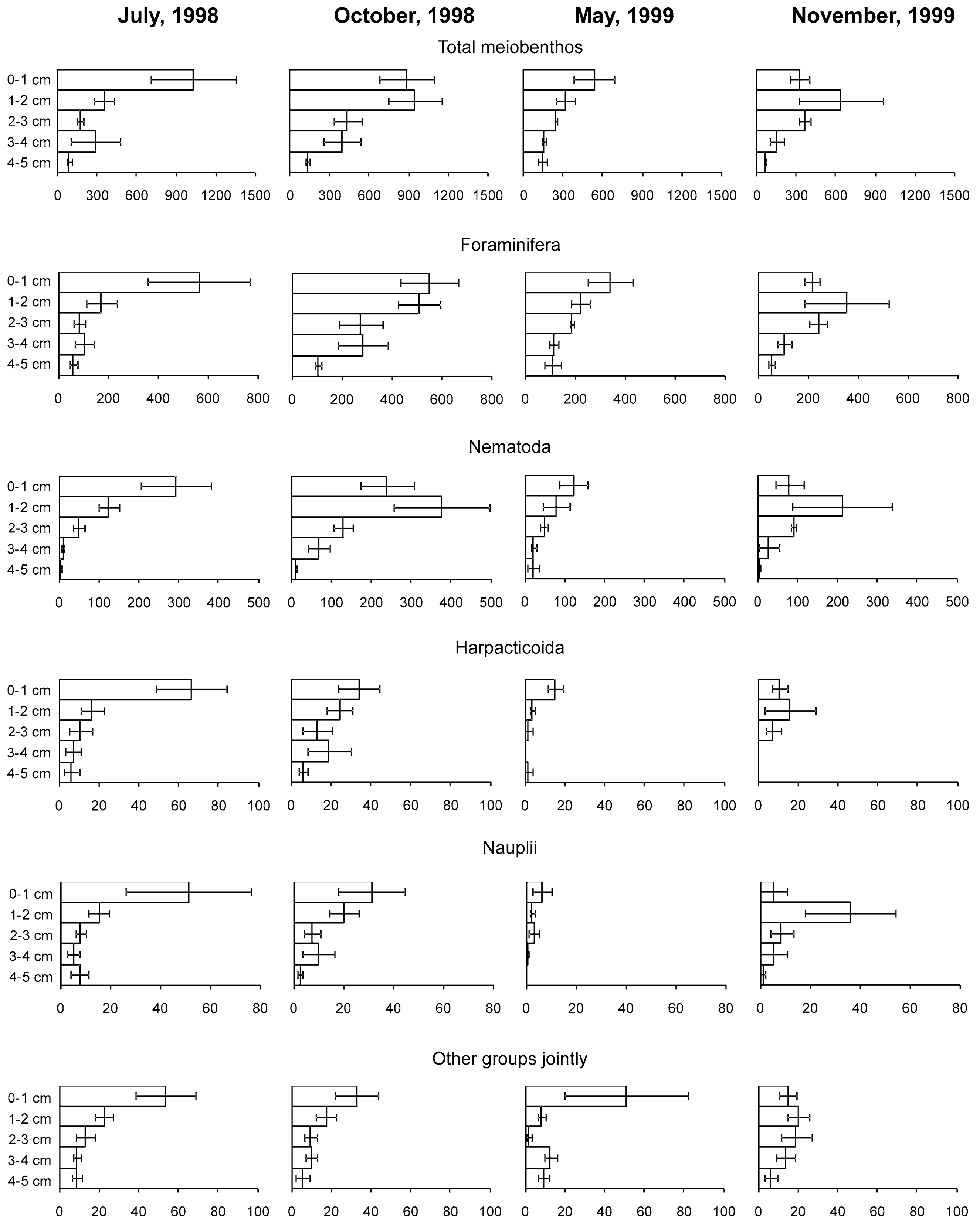

**Fig. 2** Density (mean ± SE, ind./10 cm$^2$) of total meiobenthos and the dominant groups in each 1-cm-thick sediment layer

(202 vs. 75 ind./10 cm$^2$, averaged across years and the two layers). It also varied significantly with "year", but in the 2–3 cm layer only ($p = 0.026$). In this layer, nematodes were significantly more abundant in 1998 than in 1999 (90 and 69 ind./10 cm$^2$, respectively). Nematode density in the uppermost 0–1 cm sediment layer did not vary significantly with any factor ("year", $p = 0.063$; "season", $p = 0.417$). The significant relationships identified reflected changes in the abundance of juvenile nematodes (Fig. 3), and the density of adult nematodes did not vary significantly with any factor ("year", $p = 0.169$; "season", $p = 0.616$).

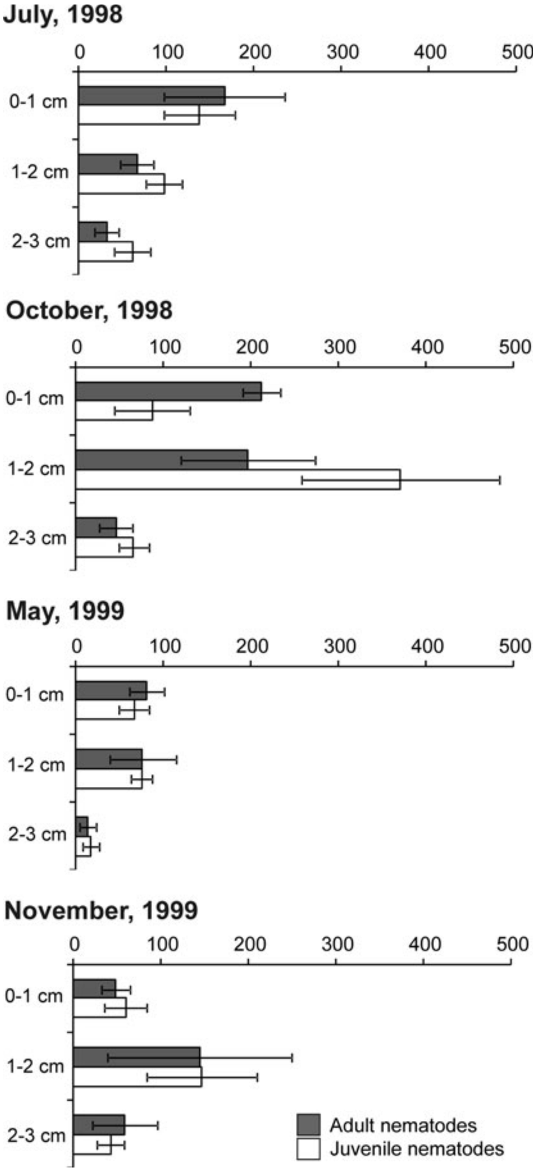

**Fig. 3** Density (mean ± SE, ind./10 cm$^2$) of adult and juvenile nematodes in the three uppermost 1-cm-thick sediment layers

In contrast to total meiobenthic, foraminiferan and nematode density, the density of adult harpacticoids and nauplii varied significantly with "year" only, and only in the uppermost 0–1 cm sediment layer (adult harpacticoida, $p = 0.017$; nauplii, $p = 0.044$). The combined abundance of adult harpacticoids and nauplii was significantly higher in 1998 than in 1999 in this layer (on average, 92 and 19 ind./10 cm$^2$, respectively) (Fig. 2).

## Composition of meiofaunal communities

### *Cumulative 0–5 cm sediment layer*

In the uppermost 5 cm of the sediments, foraminiferans averaged 59.3 % of total meiobenthic abundance, followed by Nematoda (26.2 % of total meiobenthos and 67.4 % of meiobenthic Metazoa) and Harpacticoida + nauplii (7.1 % of the total meiobenthos or 16.6 % of the meiobenthic Metazoa) (Table 3).

The percentage abundance of foraminiferans ranged from 55 % in July 1998 to 70 % in May 1999, being very similar during the two autumnal sampling campaigns (October 1998, 62 %; November 1999, 63 %). The percentage abundance of nematode varied little across the sampling occasions (22–30 %), whilst for harpacticoids + nauplii, it

**Table 3** Average percentage abundance of meiobenthic groups in the 0- to 5-cm deep sediment layer

| Group | % of total meiobenthos | % of metazoan meiobenthos |
|---|---|---|
| Foraminifera | 59.3 ± 2.5 (25.8–80.4) | – |
| Nematoda | 26.2 ± 1.6 (8.9–38.9) | 67.4 ± 3.5 (11.9–91.0) |
| Harpacticoida | 3.9 ± 0.7 (0.9–15.6) | 9.3 ± 1.3 (2.4–22.6) |
| Rotifera | 3.3 ± 2.1 (0–47.6) | 3.9 ± 2.9 (0–64.2) |
| Nauplii | 3.2 ± 0.6 (0.3–10.3) | 7.3 ± 1.3 (0.7–24.4) |
| Polychaeta | 1.3 ± 0.3 (0.1–5.7) | 4.6 ± 0.9 (0.2–16.4) |
| Kinorhyncha | 0.73 ± 0.13 (0–2.25) | 1.7 ± 0.3 (0–4.9) |
| Ostracoda | 0.55 ± 0.12 (0–2.15) | 1.0 ± 0.3 (0–5.7) |
| Turbellaria | 0.35 ± 0.15 (0–3.20) | 1.3 ± 0.5 (0–11.5) |
| *Boreohydra symplex* | 0.25 ± 0.08 (0–1.34) | 0.88 ± 0.32 (0–6.9) |
| Halacaroidea | 0.24 ± 0.09 (0–1.27) | 0.93 ± 0.26 (0–4.4) |
| Porifera | 0.11 ± 0.08 (0–1.76) | 0.28 ± 0.19 (0–4.2) |
| Bivalvia | 0.07 ± 0.03 (0–0.58) | 0.12 ± 0.05 (0–0.78) |
| Tanaidacea | 0.014 ± 0.022 (0–0.46) | 0.05 ± 0.05 (0–1.6) |
| Gastrotricha | 0.014 ± 0.009 (0–0.23) | 0.03 ± 0.02 (0–0.3) |
| Oligochaeta | 0.007 ± 0.013 (0–0.34) | 0.02 ± 0.02 (0–0.88) |
| Aplacophora | 0.007 ± 0.009 (0–0.20) | 0.02 ± 0.02 (0–0.47) |
| Unrecognized forms | 0.55 ± 0.03 (0–4.72) | 1.3 ± 0.5 (0–10.6) |

Values given are average ± SE, with minimum and maximum values in parentheses

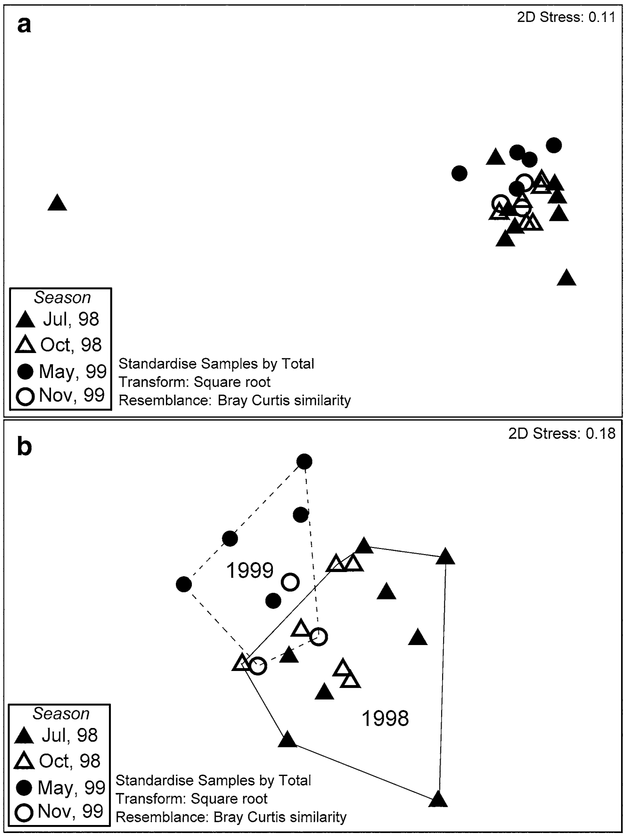

**Fig. 4** nMDS *plots* of Bray–Curtis similarity of the meiobenthic communities in the 0- to 5-cm-deep sediment samples (% data). **a** All samples, **b** one sample taken in July 1998 with an abnormal high abundance of rotifers excluded. The *polygons* indicate the position of samples collected in 1998 and 1999

ranged from 10 % in July 1998 to 3 % in May, 1999 and was again similar for both autumnal sampling periods (6 %). The percentage abundance of all other taxonomic groups combined varied from 3 to 7 %.

Using LINKTREE analysis (a software PRIMER v6), 23 cumulative 0–5 cm samples (where one sample was one core from the multicorer) were tested for distinctness of the meiobenthic assemblage in terms of relative taxon abundances. This showed that one sample (station CBB-20, deployment 3, tube B) was significantly different from the others ($p = 0.002$), and that heterogeneity within all other samples was lower, though still statistically significant ($p = 0.050$). The nMDS plot (Fig. 4a) illustrates this result. As was mentioned above, this single unusual sample was characterized by an extremely high abundance of rotifers. It was therefore excluded for further analyses. However, according to the two-way nested ANOSIM test ("deployment" within "sampling occasion"), there were no significant distinctions between stations and deployments (Global $R = -0.025$ and 0.18, respectively; $p = 0.554$ and 0.162, respectively). Therefore, there were no significant distinctions between different sampling occasions in composition of meiobenthic communities in the upper 5 cm layer if sediments, in spite of the fact that samples taken in 1998 and 1999 were located quite separately on the nMDS plot (Fig. 4b).

### *Vertical distribution*

Mean relative abundance of foraminiferans increased with increasing sediment depth, from 50–60 % in the upper 0–1 cm layer to 70–80 % in the deepest 4–5 cm layer. Nematode average percentage abundance in the 0–1 cm sediment layer was about 25 %, peaked in the 1–2 cm layer (25–40 %) and then decreased with decrease in sediment depth to 5–14 % in the 4–5 cm layer. Harpacticoids + nauplii and other meiobenthic groups were distributed relatively evenly across the different sediment layers.

The two-way crossed ANOSIM test found no significant influence of either "year" or "season" on the composition of the meiobenthic community in the different sediment layers (global tests: $p = 0.072$ and 0.434, respectively). However, the meiobenthic communities varied significantly with "sediment layer" when the analysis was crossed as "year" versus "sediment layer" (global tests: $p = 0.416$ and 0.0001, respectively) and when crossed as "season" versus "sediment layer" (global tests: $p = 0.991$ and 0.0001, respectively). Therefore, the composition of the meiobenthic communities was independent of time factors but was influenced by the sediment depth.

According to the ANOSIM test, the meiobenthic communities recorded in the 0–1 cm and 1–2 cm layers were not significantly different ($p = 0.381$). Insignificant differences were also found between communities from 3–4 and 4–5 cm sediment depth ($p = 0.716$). The meiofauna community in the 2–3 cm layer was significantly different from that in the 0–1 cm layer, but not from the 1–2 cm layer ($p < 0.05$ and $p = 0.055$, respectively). However, the 0–1 and 1–2 cm layers both differed significantly from the 3–4 and 4–5 cm layers ($p < 0.001$ for all pair-wise comparisons). The main dissimilarities in the meiobenthic assemblages between the two upper layers and the two lower layers were greater dominance of Foraminifera in the lower layers (73 vs. 56 %) accompanied by lower percentage abundances of Nematoda (11 vs. 30 %) and Harpacticoida (5 vs. 3.5 %). These differences were significant (*U* test: Table 4).

### Distribution in 17-cm-long sediment column

Meiobenthic organisms were found in all sediment layers of the single 17-cm core (Fig. 5). In the 0–5 cm sediment layers, the density of all groups decreased gradually with

**Table 4** Mean relative abundance of the different meiobenthic groups in the uppermost and deepest sediment layers of 0- to 5-cm deep samples

| Meiobenthic group | Mean percentage (%) | | Contribution to dissimilarity (%) | Result of $U$ test ($p$) |
|---|---|---|---|---|
| | 0–1 + 1–2 cm layers | 3–4 + 4–5 cm layers | | |
| Foraminifera | 56.3 | 73.3 | 34.0 | <0.001* |
| Nematoda | 30.5 | 11.2 | 32.2 | <0.001* |
| Harpacticoida | 5.14 | 3.52 | 9.09 | <0.001* |
| Polychaeta | 1.16 | 5.54 | 8.16 | 0.037* |
| Nauplii | 3.45 | 2.63 | 6.36 | 0.034* |
| Halacaroidea | 0.21 | 1.81 | 2.82 | 0.081 |
| Kinorhyncha | 1 | 0.05 | 1.49 | <0.001* |
| *Boreohydra symplex* | 0.32 | 0.66 | 1.37 | 0.029* |
| Turbellaria | 0.61 | 0.35 | 1.26 | 0.011* |
| Sponges | 0.14 | 0.65 | 1.13 | 0.943 |
| Ostracoda | 0.55 | 0.25 | 1.06 | 0.001* |
| Rotifera | 0.37 | 0 | 0.55 | 0.186 |
| Bivalvia | 0.19 | 0.07 | 0.36 | 0.056 |
| Gastrotricha | 0.06 | 0 | 0.09 | 0.160 |
| Oligochaeta | 0.01 | 0 | 0.02 | 0.328 |
| Aplacophora | 0.01 | 0 | 0.01 | 0.328 |

The contribution of each group to the dissimilarly (%) of the meiobenthic communities recorded in sediment layers is also given (SIMPER analysis), alongside results of the Mann–Whitney $U$ test (significance level $p$) for which $H_0$ was that the meiofaunal populations in each layer had equal median abundances

* Difference is statistically significant at $p < 0.05$

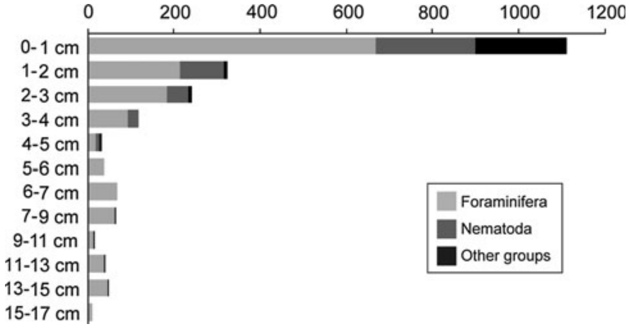

**Fig. 5** The distribution (density, ind./10 cm$^2$) of the total meiobenthos and dominant groups in the different sediment layers of a single 17-cm deep core

increasing depth. In all deeper sediment layers, meiofaunal density was approximately constant.

About 69 % of all meiobenthic organisms (60 % of foraminiferans and 94 % of metazoans), 97 % of the nematodes and all harpacticoids and nauplii inhabited the upper 5 cm of the sediments. From the 5–6 cm downwards, foraminiferans were dominant (97 % of total meiobenthic abundance), and of the metazoan taxa, only nematodes, polychaetes and Halacaroidea (in descending order of abundance) were recorded. Only foraminiferans, nematodes and halacarids were found in the deepest 16–17 cm layer.

## Size spectra

Meiobenthic organisms were predominantly recorded in the 63–125 μm size class (44 % of all meiobenthic organisms), followed by the 125–250 size class (29 %) (Fig. 6a). The 32–63, 250–500 and >500 μm size classes represented 14, 8 and 5 % of total meiobenthic abundance, respectively. Foraminiferans and harpacticoids were most abundant in the 63–125 μm size class (46 % of foraminiferans and 38 % of harpacticoids) and then in the 125–250 μm size class (31 and 35 %, respectively). In contrast, nematodes were predominantly in the 125–250 μm size class (38 % of all nematodes) and then in the 63–125 μm size class (29 %) (Fig. 6b). Ratio of the 63–125 μm size class differed significantly with season (two-way ANOVA: $p = 0.021$). It was significantly higher in the autumn season compared with the summer season (49 % of all nematodes vs. 39 %, respectively; $U$ test: $p = 0.016$). Ratios of the other size factions did not change significantly over time. In the autumn season, smaller nematodes (size fractions 32–63 and 63–125 μm) prevailed in the 1–2 and 2–3 cm sediment layers (in average, 63 % of all nematodes found in these sediment layers vs. 38 % in summer). This result corresponds with an increased density of juvenile nematodes in the autumn. In the uppermost 0–1 cm layer, the relatively high percentage of these two smaller fractions did not vary depending on the time of the year (73 % of all nematodes found in this layer in the summer and 72 % in the autumn).

A similar picture was seen for foraminiferans. The portion of smaller individuals increased in the autumn, mainly in the 1–2 and 2–3 cm sediment layers: 44 and 71 % of all foraminifers belonged to the 32–63 and 63–125 μm size classes in the summer and in the autumn,

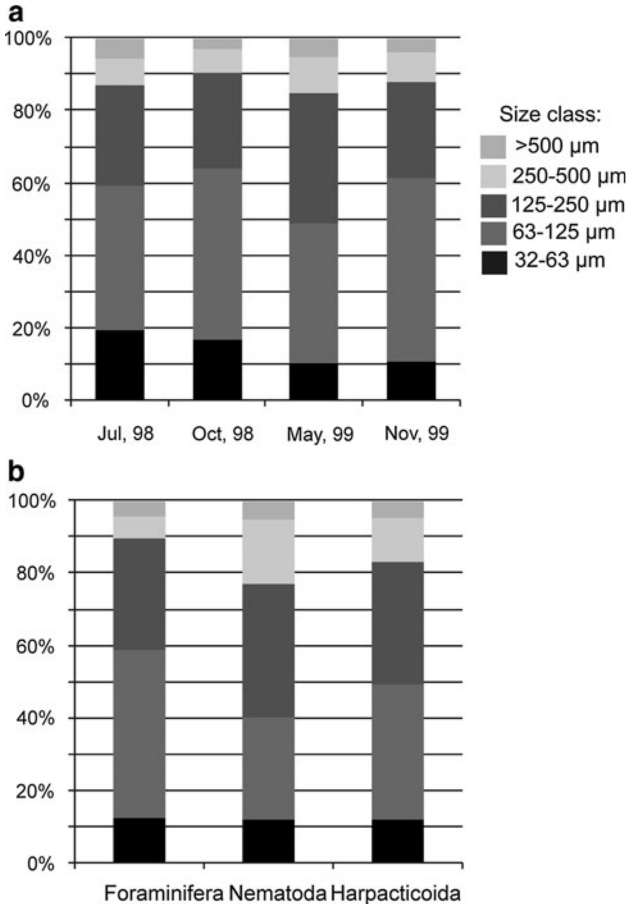

**Fig. 6** Size spectra distribution of total meiobenthos on each sampling occasion (**a**), and of the three most abundant meiobenthic groups averaged across the study period (**b**)

respectively. In the upper 0–1 cm layer, this percentage did not depend on the time of the year significantly (56 % in the summer and 62 % in the autumn).

## Discussion

### Meiofaunal standing stock and size spectra in the upper 5 cm sediment layer

#### *Comparison with other areas*

The dominant meiobenthic organisms in the Kandalaksha Depression, the deepest part of the White Sea, were foraminiferans, nematodes and harpacticoids including nauplii (in descending order). In total, these three taxa represented 93 % of the total meiobenthic community.

Total meiobenthic density (1,910 ind./10 $\text{cm}^2$ on average) and metazoan meiobenthic density (746 ind./10 $\text{cm}^2$) were similar to corresponding densities in the central Arctic Ocean and Arctic shelf seas (Pfannkuche and Thiel 1987; Vanaverbeke et al. 1997a; Soltwedel et al. 2000; Vanreusel et al. 2000). In these regions, similar meiobenthic densities were reported from the same depth range as in the Kandalaksha Depression (around 300 m) down to about 2000 m. Meiobenthic density was also comparable with records from temperate regions over the same depth interval (Tietjen 1971; Shirayama and Kojima 1994; Vanreusel et al. 1995; Vanaverbeke et al. 1997b).

Previous studies in the White Sea reported that total meiobenthic density ranged from 1,000 ind./10 $\text{cm}^2$ in the tidal zone to 51 ind./10 $\text{cm}^2$ at 300 m depth (Galtsova and Sheremetevsky 1985; Galtsova and Vladimirov 1988; Galtsova 1991). These values are much lower than recorded in this present study at 270 m but may be explained by the extraction technique formerly used. The smallest size fraction of meiofauna (<63 µm) is almost entirely absent in shallow water sediments but becomes quite abundant in the deep sea. Whilst in the present study, a minimum sieve mesh size of 32 µm was employed, in the earlier studies, a minimum sieve mesh size of 90 µm was used (Galtsova and Sheremetevsky 1985; Galtsova and Vladimirov 1988; Galtsova 1991). Thus, in these earlier studies, with increasing water depth a decreasing proportion of the meiobenthos was probably retained, resulting in a significant underestimation of abundance at the deepest sites. The discordance between sieve mesh sizes used in earlier studies and this current one therefore probably explains the tenfold difference in abundance values recorded (Mokievskii and Malykh 2002).

The proportion of foraminiferans in meiobenthic communities usually increases with increasing depth, and as a rule, their relative abundance is about 50 % at depths >500 m (Tietjen 1971; Gooday 1986; Shirayama and Horikoshi 1989). In the Arctic Ocean, however, the proportion of foraminiferans tends to be higher, constituting 62–75 % of meiobenthic animals at depths >240 m (Pfannkuche and Thiel 1987; Schewe and Soltwedel 1998; Soltwedel et al. 2000). Therefore, the data presented here show that the proportion of foraminiferans (59 %) in the "pseudo-bathyal" Kandalaksha Depression of the White Sea was most similar to that found at the same depth in Arctic regions.

Nematodes are usually the most dominant meiobenthic metazoans (Mokievsky et al. 2004, 2007), their relative abundance increasing with depth and usually reaching 70–95 % at 200–400 m depth in polar and temperate regions (Wigley and McIntyre 1964; Tietjen 1971; Pfannkuche and Thiel 1987; Vanreusel et al. 1992; Vincx et al. 1994; Vanaverbeke et al. 1997a; Schewe and Soltwedel 1998; Soltwedel 2000). Our results were in agreement with these findings, nematodes representing about 67 % of the meiobenthic Metazoa.

Harpacticoids (including nauplii) were the second most abundant metazoan group of metazoans after nematodes, as is usually the case in oceanic sediments. Studies in the temperate North-East Atlantic Ocean and Arctic Ocean have recorded percentage abundance values between 1 and 17 % over 190–4,850 m depth (Snider et al. 1984; Pfannkuche 1985; Vanreusel et al. 1992, 2000; Vincx et al. 1994; Vanaverbeke et al. 1997a, b; Schewe and Soltwedel 1998; Soltwedel et al. 2003). Thus, harpacticoid relative abundance recorded in the Kandalaksha Depression during this present study (17 % of meiobenthic metazoans) was at the upper limit of reported values, and their relative abundance can be considered as fairly high.

Of the other metazoan groups, rotifers were most numerous (about 8 %), but only due to a single subsample with an abnormally high concentration of these animals (10–1,000 × more abundant than in any other subsample). Other groups were not numerous. This was again in agreement with the majority of studies on meiobenthos from the subtidal zone, the continental slope and the abyss (e.g. Snider et al. 1984; Renaud-Mornant and Gourbault 1990; Vincx et al. 1994; Soltwedel 1997, 2000). These groups (polychaetes, ostracods, kinorhynchs, turbellarians and bivalves) tend to be most abundant in shallower waters (Soltwedel 2000).

The number of meiobenthic organisms was highest in the mesh size classes 63–125 and 125–250 µm. It is well known that the size of meiobenthic animals tends to decrease with increasing depth (Pfannkuche and Thiel 1987; Soetaert and Heip 1989; Renaud-Mornant and Gourbault 1990; Udalov et al. 2005). The majority of deep-sea Arctic (Schewe and Soltwedel 1998; Schewe 2001; Soltwedel et al. 2003) and NE Atlantic (Pfannkuche 1985; Vanreusel et al. 1995) meiobenthic organisms fall within the 63–125 and 125–250 µm size classes. Thus, the size range of the meiobenthos in the Kandalaksha Depression is equivalent to that of deep-sea meiobenthos. The size range is notably shifted towards smaller size classes in comparison with the meiobenthos of intertidal fine sands in the White Sea (Mokievsky et al. 2009).

### *Spatial and temporal variations*

Unfortunately, the pattern of sampling lacked for a spatial overlap in stations among sampling periods (stations differed each from other not only in time of sampling, but also in their coordinates and depth), This creates difficulties in interpretation of results, as seeming differences between sampling occasions could be effected not only by a time period but also by spatial distinctions between stations. However, the nested GLM analysis showed that only small part (13 %) of the variance in meiobenthos density was related with differences between multicorer deployments and 32 % of the variance was explained by seasonality. The other part was explained by microscale fluctuations in density between samples (cores of the same multicorer). This indicates that the density varied slightly between deployments in the same sampling occasion, and differences in the coordinates and depth of deployments were of no great importance. Therefore, it is correct to suppose that differences between seasons were caused not by differences in coordinates and depth of stations, but by an effect of seasonality.

Seasonal changes in meiobenthic density were most likely connected to seasonal phytoplankton blooms, which result in increased phytodetrital flux to the sea bed. However, during the present study, maximum densities of foraminiferans and nematodes were recorded in autumn, whereas the maximum primary production in the White Sea occurs in spring and early summer. Therefore, after its production in the photic zone, a substantial time lag may regulate the availability of organic matter to the meiobenthos. Nevertheless, peak periods of availability and consumption may still exist. Significant seasonality of meiofaunal abundance, influenced by inter-annual fluctuations in the input of phytodetritus and organic particles to the deep-sea bed, has been reported previously (Pfannkuche 1993; Danovaro et al. 2000, 2001; Galeròn et al. 2001; Lampitt et al. 2001; Vanreusel et al. 2001; Gambi and Danovaro 2006).

The peaks in meiobenthic density recorded here appeared to result from *en masse* reproduction of nematodes and foraminiferans in the autumn, as indicated by an increased abundance of juvenile nematodes and small foraminiferans but no consistent change in adult nematode or large foraminifer numbers. The other evidence of seasonal bulk reproduction of the most abundant taxa, such as the Nematoda and Foraminifera, is an autumnal increase in smaller meiobenthic size groups of these taxa.

Similarly, in the deep Western Mediterranean Sea, increased abundance of small-sized nematodes (presumably juveniles) was found to correlate with increased food availability (Gambi and Danovaro 2006). Also, Vanreusel et al. (2001) reported an increased abundance of juvenile opheliid polychaetes in response to the supply of organic material to the deep sea.

## Vertical distribution

In the deepest part of the White Sea (and the deep sea proper), the big depth of oxygen penetration (the reduced layer occurs at 26 cm sediment depth) and the very high concentration of organic matter (Dr. V. Strekopytov, pers. obs.) allow meiobenthic organisms to penetrate deep into the sediment. Meiobenthic organisms were found throughout a 17-cm long sampling column, and although their total density decreased sharply down to the 4–5 cm layer, it then remained low but relatively constant into deeper sediments. Usually, only the uppermost 0–5 cm sediment layer is examined in meiobenthic studies, because it is presumed that 90–95 % of meiobenthic organisms inhabit this layer. Our results confirm that this method is appropriate for the Metazoa, but suggest that it is not suitable for Foraminifera, since at least 40 % of foraminiferans inhabited sediments deeper than 5 cm.

Within the upper 5-cm layer of sediments, the portion of foraminiferans in the 3–4 and 4–5 cm layers was higher, than in 0–1 and 1–2 cm layers. The reversed situation was in nematodes.

For nematodes, increased density in the 1–3 cm layers in the autumn was caused by an increased density of juveniles, whereas adult densities did not vary significantly. The density of all nematodes and, particularly juveniles, did not decrease in the 0–1 cm layer during the same period, indicating that an in situ mass breeding event occurred in the 1–3 cm sediment layer. The other, indirect, evidence of this intense reproductive phase is an increased proportion of nematodes in the smaller size classes in these lower layers during the autumn. In addition, the annual fluctuations in nematode density were predominantly seen in these sediment layers, their abundance greater in 1998 than 1999 and mainly due to changes in juvenile density. This also suggests inter-annual variation in breeding intensity, with greater reproductive success in 1998 compared to 1999.

Possibly, foraminiferans also exhibited intensive propagation in 1–4 cm sediment layers during the autumn season, whilst again their density in the uppermost 0–1 cm layer showed no dependence on time factors. An increased number of small foraminiferans in the autumn was restricted to the lower layers.

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## References

Agatova AI, Lapina NM, Kirpichov KB (2002) On the organic matter of sediments of the Kandalaksha Bay (White Sea). Geochimiya 7:734–741 (in Russian)

Andriashev AP (1977) Some additions to schemes of the vertical zonation of marine bottom fauna. In: Llano GA (ed) Adaptations within Antarctic ecosystems. Gulf, Houston, pp 351–360

Berger VY, Naumov AD (2000) General features of the White Sea. Morphology, sediments, hydrology, oxygen conditions, nutrients and organic matter. In: Rachor E (ed) Scientific cooperation in the Russian Arctic: ecology of the White Sea with emphasis on its Deep Basin, vol 359. Elsevier, Amsterdam, pp 3–9

Berger V, Dahle S, Galaktionov K, Kosobokova X, Naumov A, Rat'kova T, Savinov V, Savinova T (2001) White Sea. Ecology and environment. Derzavets, St. Petersburg

Clarke KR, Gorley RN (2006) PRIMER v6: user manual/tutorial. PRIMER-E, Plymouth

Danovaro R, Tselepides A, Otegue A, Della Croce N (2000) Dynamic of meiofaunal assemblages on the continental shelf and deep-sea sediments of the Cretan Sea (NE Mediterranean): relationships with seasonal changes in food supply. Progr Oceanogr 46: 367–400

Danovaro R, Dell'Anno A, Fabiano M (2001) Bioavailability of organic matter in the sediments of the Porcupine Abyssal Plain, Northeastern Atlantic. Mar Ecol Progr Ser 220:25–32

Fedorov VD, Bobrov YA (1977) Seasonal variations of selected parameters of the phytoplankton production in the White Sea. Vestnik MGU (Biologiya) 1:104–112 (in Russian)

Fedorov VD, Korsak MN, Bobrov YA (1974) Selected results of the investigations of phytoplankton primary production in the White Sea. Hydrobiol Zhurnal 10:9–14 (in Russian)

Filatov NN, Pozdnyakov DV, Johannessen OM, Pettersson LH, Bobylev LP (2005) White Sea: its marine environment and ecosystem dynamics influenced by global change. Springer-Praxis, Chichester

Filipjev IN (1927) Les Nematodes libres des mers septentrionales appartenant a la famille das Enoplidae. Arch Naturgesch 91A:1–216

Galeròn J, Sibuet M, Vanreusel A, Mackenzie K, Gooday AJ, Dinet A, Wolff GA (2001) Temporal patterns among meiofauna and macrofauna taxa related to changes in sediment geochemistry at an abyssal NE Atlantic site. Progr Oceanogr 50:303–324

Galkina VN, Fedyakov VV, Naumov AD (2000) Life in the depth of the White Sea—what is known about it. In: Rachor E (ed) Scientific cooperation in the Russian Arctic: ecology of the White Sea with emphasis on its Deep Basin. Ber Polarforsch Meeresforsch vol 359, pp 14–20

Galtsova VV (1991) Meiobenthos in marine ecosystems (with special reference to free-living nematodes), vol 224. Trudy Zoologicheskogo Inst, Leningrad (in Russian)

Galtsova VV, Platonova TA (1988) Organization and species structure of nematodes taxocoenosis in south-eastern part of Kandalaksha Bay of the White Sea. In: Benthic ecosystems of south-east part of Kandalaksha Bay and adjacent area. Exploirations of the fauna of the seas, vol 38. Nauka, Leningrad, pp 75–85 (in Russian)

Galtsova VV, Sheremetevsky AM (1985) Meiobenthos of Onega Bay of the White Sea. In: Ecosystems of Onega Bay of the White Sea. Zoologicheskij Institut, Leningrad, pp 88–112 (in Russian)

Galtsova VV, Vladimirov MV (1988) Meiobenthos of the south-east part of Kandalaksha Bay, White Sea. In: Benthic ecosystems of south-east part of Kandalaksha Bay and adjacent area. Exploirations of the fauna of the seas, vol 38. Nauka, Leningrad, pp 47–74 (in Russian)

Gambi C, Danovaro R (2006) A multiple-scale analysis of metazoan meiofaunal distribution in the deep Mediterranean Sea. Deep Sea Res I 53:1117–1134

Giere O (2009) Meiobenthology. Springer, Berlin

Golikov AN, Sirenko BI, Galtsova VV, Golikov AA, Novikov OK, Petryashev VV, Potin VV, Vedyakov VV, Vladimirov VV (1988) Ecosystems of south-east part of Kandalaksha Bay of the White Sea in vicinity of Son-ostrov. In: The distribution and function of the ecosystems of Kandalaksha Bay of the White Sea. Exploirations of the fauna of the seas, vol 40. Zoologicheskij Institut, Leningrad, pp 4–135 (in Russian)

Gooday AJ (1986) Meiofaunal foraminiferans from the bathyal Porcupine Seabight (north-east Atlantic): size structure, standing stock, taxonomic composition, species diversity and vertical distribution in the sediment. Deep Sea Res 33:1345–1373

Hammer Ø, Harper DAT, Ryan PD (2001) PAST: paleontological statistics software package for education and data analysis. Palaeontol Electron 4. http://www.uv.es/pe/2001_1/past/past.pdf. Accessed 22 Mar 2012

Kirienko EI (1973) Distribution of Foraminifera in the upper layer of the White Sea sediments. In: Proceedings of the sixth all-union conference on micropaleontology, Novosibirsk, pp 84–85 (in Russian)

Knipowitsch NM (1906) The fundamentals of European polar ocean hydrology. Zapiski po obschey geografii, vol 13. M.Stasyulevich Press, Saint Petersburg (in Russian)

Lampitt RS, Bett BJ, Kiriakoulakis K, Popova EE, Ragueneau O, Vangriesheim A, Wolff GA (2001) Material supply to the abyssal seafloor in the northeast Atlantic. Progr Oceanogr 50: 27–63

Loeng H (1991) Features of the physical oceanographic conditions of the Barents Sea. In: Sakshaug E, Hopkins CCE, Øritsland NA (eds) Proceedings of the pro mare symposium on polar marine ecology, vol 10, pp 5–18. Trondheim, 12–16 May 1990

Lukanin VV, Naumov AD, Fedyakov VV (1995) General characteristics of the pseudobathyal. In: Berger VYa (ed) The White Sea: biological resources and problems of their rational exploitations. St Petersburg. Zool Inst Russ Acad Sci Publ: pp 215-216 (In Russian)

Lukina TG (1985) Foraminifera of Onega Bay and adjacent part of the White Sea. In: Ecosystems of Onega Bay of the White Sea. Zoologicheskij Institut, Leningrad, pp 113–126 (in Russian)

Mayer EM (1977) Veitical distribution of Foraminifera in the White Sea according to environmental factors. In: Proceedings of the first meeting of Soviet oceanologists, vol 2. Moscow, pp 64–65 (in Russian)

Mayer EM (1980) Quantitative distribution of recent living Foraminifera in the White Sea. Proc White Sea Biol Stn Mosc Univ 5:29–43 (in Russian)

Mokievskii VO, Malykh EA (2002) Methods for quantitative estimation of meiobenthos. Oceanology 42:234–238

Mokievskii VO, Udalov AA, Azovskii AI (2007) Quantitative distribution of meiobenthos in deep-water zones of the World Ocean. Oceanology 47:797–813

Mokievsky VO (2000) Deep-water meiobenthos research in the White Sea. In: Rachor E (ed) Scientific cooperation in the Russian Arctic: ecology of the White Sea with emphasis on its Deep Basin. Ber Polarforsch Meeresforsch vol 359, pp 21–22

Mokievsky VO, Udalov AA, Azovsky AI (2004) On the quantitative distribution of meiobenthos on the shelf of the World Ocean. Oceanology 44:99–109

Mokievsky VO, Miljutina MA, Tchesunov AV, Rybnikov PV (2009) Meiobenthos of the deep part of the White Sea. Meiofauna Marina 17:61–70

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

Pfannkuche O (1993) Bentic response to the sedimentation of particulate organic matter at the BIOTRANS station, 47°N, 20°W. Deep Sea Res 40:135–149

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

Platonova TA, Galtsova VV (1985) Nematodes and their role in the meiobenthos. Washington, DC. Amerind Publishing Co, New Delhi

Rachor E (ed) (2000) Scientific cooperation in the Russian Arctic: ecology of the White Sea with emphasis on its Deep Basin. Ber Polarforsch Meeresforsch vol 359, pp 1–109

Rat'kova TN (2000) The White Sea Basin phytoplankton—a review. In: Rachor E (ed) Scientific cooperation in the Russian Arctic: ecology of the White Sea with emphasis on its Deep Basin. Ber Polarforsch Meeresforsch vol 359, pp 23–29

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

Sakshaug E (2004) Primary and secondary production in the arctic seas. In: Stein R, MacDonald RW (eds) The organic carbon cycle in the Arctic Ocean. Springer, Berlin, pp 57–81

Schewe I (2001) Small-sized benthic organisms of the Alpha Ridge, central Arctic Ocean. Int Revue ges Hydrobiol 86(3): 317–335

Schewe I, Soltwedel T (1998) Deep-sea meiobenthos of the Central Arctic Ocean: distribution patterns and size-structure under extreme oligotrophic conditions. Vie et Milieu 49:79–92

Seinhorst JW (1959) A rapid method for the transfer of nematodes from fixative to anhydrous glycerin. Nematologica 4:67–69

Shirayama Y, Horikoshi M (1989) Comparison of the benthic size structure between sublittoral, upper-slope and deep-sea areas of the Western Pacific. Int Revue ges Hydrobiol 74:1–13

Shirayama Y, Kojima S (1994) Abundance of deep-sea meiobenthos off Sanriku, Northeastern Japan. Jpn J Oceanogr 50:109–117

Snider LG, Burnett BR, Hessler RR (1984) The composition and distribution of meiofauna and nanobiota in central North Pacific deep-sea area. Deep Sea Res 31:1225–1249

Soetaert K, Heip C (1989) The size structure of nematode assemblages along a Mediterranean deep-sea transect. Deep Sea Res I 36:93–102

Soltwedel T (1997) Meiobenthos distribution pattern in the tropical East Atlantic: indication for fractionated sedimentation of organic matter to the sea floor? Mar Biol 129:747–756

Soltwedel T (2000) Metazoan meiobenthos along continental margins: a review. Progr Oceanogr 46:59–84

Soltwedel T, Mokievsky V, Schewe I (2000) Benthic activity and biomass on the Yermak Plateau and in adjacent deep-sea regions northwest of Svalbard. Deep Sea Res I 47:1761–1785

Soltwedel T, Miljutina M, Mokievsky V, Thistle D, Vopel K (2003) The meiobenthos of the Molloy Deep (5,600 m), Fram Strait, Arctic Ocean. Vie et Milieu 53:1–13

Strekopytov SV, Uspenskaya TY, Vinogradova EL, Dubinin AV (2005) Geochemistry of early diagenesis of sediments od Kandalaksha Bay of the White Sea. Geochem Int 43:117–130

Tietjen JH (1971) Ecology and distribution of deep-sea meiobenthos off North Carolina. Deep Sea Res 18:941–951

Udalov AA, Azovsky AI, Mokievsky VO (2005) Depth-related pattern in nematode size: what does the depth itself really mean? Progr Oceanogr 67:1–23

Vanaverbeke J, Arbizu PM, Dahms H-U, Schminke HK (1997a) The metazoan meiobenthos along a depth gradient in the Arctic Laptev Sea with special attention to nematode communities. Polar Biol 18:391–401

Vanaverbeke J, Soetaert K, Heip C, Vanreusel A (1997b) The metazoan meiobenthos along the continental slope of the Goban Spur (NE Atlantic). J Sea Res 38:93–107

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 (NE Atlantic). Belg J Zool 122:185–202

Vanreusel A, Vincx M, Schram D, Van Gansbeke D (1995) On the vertical distribution of the metazoan meiofauna in shelf break and upper slope habitats of the NE Atlantic. Int Revue ges Hydrobiol 80:313–326

Vanreusel A, Clough L, Jacobsen K, William Ambrose W, Jivaluk J, Ryheul V, Herman R, Vincx M (2000) Meiobenthos of the central Arctic Ocean with special emphasis on the nematode community structure. Deep Sea Res I 47:1855–1879

Vanreusel A, Cosson-Sarradin N, Gooday AJ, Paterson GLJ, Galeròn J, Sibuet M, Vincx M (2001) Evidence for episodic recruitment in a small opheliid polychate species from the abyssal NE Atlantic. Progr Oceanogr 50:285–301

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

Wigley RL, McIntyre AD (1964) Some quantitative comparisons of offshore meiobenthos and macrobenthos south of Marta's Vineyard. Limnol Oceanogr 9:485–493