The meiofauna:macrofauna ratio across the continental slope of the Goban Spur (north-east Atlantic)

Els Flach*, Jan Vanaverbeke[†] and Carlo Heip*

*Centre for Estuarine and Coastal Ecology, Netherlands Institute of Ecology (NIOO-CEMO), PO Box 140, 4400 AC Yerseke, The Netherlands. [†]University of Gent, Department of Biology, K.L. Ledeganckstraat 35, B-9000 Gent, Belgium

Meio- and macrofauna density and biomass were estimated at the OMEX-transect across the continental slope of the Goban Spur at water depths ranging from 208 to 4460 m in the north-east Atlantic. A linear increase in the ratio between meio- and macrofauna densities with increasing water depth was found. At the continental shelf meiofauna densities were ∼50 times higher than macrofauna densities, whereas in the abyss meiofauna densities were more than 1000 times higher. This change in ratio was due to a significant decrease in macrofauna densities with increasing water depth, whereas the meiofauna densities stayed more or less at the same level. The ratio in biomass between meio- and macrofauna showed a dip at ∼1000 m. At this depth macrofauna biomass was ∼55 times higher than meiofauna biomass, whereas at ∼4500 m macrofauna biomass was only about three times higher. Macrofauna biomass was high at ∼1000 m, due to the high mean individual weight of the macrofauna, whereas meiofauna biomass and mean individual weight were low at this depth.

Meiofauna consisted of ∼90% nematodes. Within the macrofaunal fraction (>0.5 mm) a linear increase in the ratio between nematodes and macrofauna *sensu stricto* with depth was found. At the deepest station ∼20% of the macrofaunal fraction were nematodes, at the shallowest station only ∼2%. Thus, large nematodes became relatively more important with increasing water depth. Within the macrofauna a decrease in the abundance of filter- and surface deposit-feeders relative to the subsurface deposit-feeders with increasing water depth was observed, which may be related to a change in food input. As no decrease in mean individual weight with increasing water depth within either group could be observed, the change in meio:macrofauna ratios along the OMEX-transect merely reflects a change in taxonomic (functional) composition, rather than a change in size.

INTRODUCTION

Benthic fauna can be divided in four size groups (nano-biota, meiofauna, macrofauna and megafauna), which are regarded as distinct functional groups (Gage & Tyler, 1991). A quantitative knowledge of the abundance of various size groups of the benthic fauna is essential for a better understanding of the structures and functions of deep sea communities at the sediment–water interface (Sibuet et al., 1989). Among deep sea organisms both gigantism and dwarfism occur, evolutionary trends that can be explained by selection on optimal foraging strategies (Gage & Tyler, 1991). A foraging animal may adapt to low food levels by increasing its foraging area (increase in size) or decreasing its maintenance costs (decrease in size) (Carney et al., 1983). Sibuet et al. (1993) observed in the north-east tropical Atlantic a relatively smaller impact of decreasing food input on the smaller organisms and a sharper decrease in large organism abundance when food diminished. In general, a decrease in average body-size with depth is reported for most faunal components across the full meio–megafauna size range. This appears to be caused by a replacement of larger species by smaller (Carney et al., 1983).

Vanreusel et al. (1995) observed that mean body size of nematodes is correlated with food availability. At a more eutrophic site a relatively greater abundance of larger nematodes was found compared to an oligotrophic site. Gage & Tyler (1991) report a depth-related decrease in metazoan meiofaunal biomass, which was significantly correlated with the rate of detrital input. Thiel (1975) observed that in general the decrease in meiofauna abundance with depth is smaller than that of macrofauna, i.e. the relative importance of meiofauna increases. He hypothesized for deep sea benthos that: 'With increasing depth and decreasing food concentrations small organisms gain importance in total community metabolisms.' and in general that: 'Associations governed by constantly limited food availability are composed of small individuals on the average.'

However, Thiel (1975) came to this hypothesis by comparing data from different studies conducted in far distant ocean regions. Comparisons of meio- and macrofaunal abundance from the same stations and regions are still few (Gage & Tyler, 1991) and not always in agreement with Thiel's hypothesis. Shirayama (1983), for instance, found no significant differences in slope between the decrease of meio- and macrofauna with depth in the western Pacific and Sibuet et al. (1989) found a first order relationship between meio- and macrofauna abundances and thus a similar decrease in macrofauna as in meiofauna with decreasing food supply. The present study compared the densities, biomass and mean individual weight from meiofauna and macrofauna at the same sites along a

Table 1. *Sampling stations, positions and depth and sampling dates for meio- and macrofauna along the OMEX-transect. Sediment characteristics (median grain-size, % org. C, %N and C:N ratio) are given for the upper 1 cm of the sediment.*

Station	Sampling date	Coordinates	Depth (m)	Median grain-size (µm)	%org. C	%N	C:N (mol)	Meiofauna (N) subcores	Ø (cm)	Macrofauna (N) boxcores	Ø (cm)	O (cm²)
A	26/10/93	49°28.98′N 11°07.97′W	208	91.9	0.267	0.017	18.3					
	23/5/94	49°29.7′N 11°08.4′W	208	96.2	0.185	0.028	7.7	2	10	3	30	2060.6
	18/8/95	49°28.52′N 11°12.45′W	231	95.2	0.57	0.065	10.3			3	30	2120.7
I	19/10/93	49°24.72′N 11°31.86′W	670	53.8	0.326	0.038	10.0	2	10	1	50	1963.5
	23/5/94	49°24.9′N 11°31.4′W	670	61.0	0.256	0.036	8.3	2	10	2	30	1413.7
	19/8/95	49°24.70′N 11°31.86′W	693	48.9	0.622	0.067	10.7			2	50	3927.0
B	20/10/93	49°21.99′N 11°48.09′W	1034	25.6	0.578	0.045	15.0	2	10	1	50	1963.5
	24/5/94	49°22.4′N 11°45.1′W	1034	19.3	0.43	0.057	8.8	2	10	2	50	3927.0
	20/8/95	49°22.00′N 11°47.99′W	1021	14.2	0.721	0.078	10.5			3	50	4339.4
II	21/10/93	49°11.20′N 12°49.18′W	1425	16.3	0.619	0.052	13.9	2	10	1	50	1963.5
	26/5/94	49°11.3′N 12°49.7′W	1425	14.8	0.317	0.053	7.0	2	10	2	50	3927.0
	21/8/95	49°11.19′N 12°49.17′W	1457	10.3	0.684	0.079	10.1			3	50	4417.9
F	25/10/93	49°09.06′N 13°05.40′W	2182	8.5	0.543	0.047	13.5	2	10	2	50	3927.0
	28/5/94	49°09.5′N 13°05.3′W	2254	7.9	0.417	0.068	7.2	2	10	2	50	3769.9
	22/8/95	49°09.06′N 13°05.38′W	2256	7.9	0.459	0.05	11.8			3	50	4339.4
III	30/5/94	49°05.2′N 13°25.9′W	3673	7.1	0.384	0.055	8.2	2	10	2+1	50+30	4633.8
	23/8/95	49°03.99′N 13°25.83′W	3648	6.3	0.218	0.02	12.7			3	50	4417.9
E	1/6/94	49°02.3′N 13°42.2′W	4460	6.9	0.369	0.04	10.7	2	10	2+1	50+30	4633.8
	24/8/95	49°02.29′N 13°42.20′W	4470	7.7	0.301	0.033	10.6	2	10	3	50	4339.4

N, number of samples; Ø, diameter of core; O, total area sampled; org. C, organic carbon.

transect from 208 to 4460 m across the continental slope of the Goban Spur in the north-east Atlantic. This study is part of the Ocean Margin Exchange (OMEX) project of the EU, the general aim of which is to study the physical, chemical and biological processes that determine the transport of material from the shelf to the deep sea.

MATERIALS AND METHODS

Study site

Samples were taken along the OMEX-transect in October 1993, May/June 1994 and August 1995. The OMEX-transect is situated at the Goban Spur area in the north-east Atlantic. Samples were taken from the continental shelf of the Celtic Sea, along the continental slope, down

to the Porcupine Abyssal Plain at water depths ranging from 208 m (station A) to 4460 m (station E). In Table 1 exact sampling positions, dates and depths are given. Bottom water temperature decreased from ∼11°C at the shallowest stations (∼200 m) to ∼2.5°C at the deepest stations (∼4 km). Salinity also decreased with increasing water depths from ∼35.5 psu at the shallowest stations to ∼34.9 psu at the deepest stations, but showed a small peak around ∼1000 m. Oxygen showed a dip of ∼200 µmol l⁻¹ around ∼1000 m and a maximum of ∼275 µmol l⁻¹ at the shelf (Flach & Heip, 1996b).

Median grain-size decreased from ∼95 µm at 208 m to ∼8 µm below 2000 m (Table 1). The vertical profiles showed very homogeneous sediments to a depth of 15 cm at all stations (Flach & Heip, 1996a) and no changes in grain-size between the three years were observed. The

organic carbon and total nitrogen contents of the upper 1 cm of the sediment are given in Table 1. Both the %N and %org. C (organic carbon) showed a peak at mid-slope depths, with the highest values at station B at ~1000 m. Although the %N and %org. C showed seasonal variation (Flach & Heip, 1996b), the highest values were always found at mid-slope depths. Flow velocities were high at the upper part of the slope (~1000–1500 m), especially during autumn/winter when resuspension could occur (Thomsen & van Weering, 1998). Total particulate matter (TPM) and particulate organic carbon (POC) decreased with increasing water depth within the benthic boundary layer (BBL), whereas chloroplastic pigment equivalents (CPE) showed a small peak at station II at ~1400 m (Thomsen & van Weering, 1998). Carbon input as calculated from concentrations and sedimentation rates in the BBL decreased from $4.6\,\mathrm{g\,C\,m^{-2}\,y^{-1}}$ at station I (670 m) and $4.3\,\mathrm{g\,C\,m^{-2}\,y^{-1}}$ (1425 m) to $1.0\,\mathrm{g\,C\,m^{-2}\,y^{-1}}$ at station III at 3670 m (L. Thomsen, personal communication). The total amount of mineralizable carbon within the sediment as calculated through inverse modelling increased from $4.5\,\mathrm{g\,C\,m^{-2}}$ at station A (208 m), 9.5 at 670 m, 27.5 at 1034 m to $38.5\,\mathrm{g\,C\,m^{-2}}$ at station III at 3670 m (Soetaert et al., 1998).

Macrofauna

Macrofauna samples were taken with the circular boxcorer of the Netherlands Institute of Sea Research (NIOZ). For logistic reasons different numbers of boxes of different sizes were taken at different stations. Boxcores with a diameter of 30 cm (mainly used at the shallow stations) and 50 cm were used. Some subsamples were taken out of some of the boxes for other purposes, resulting in different sample-sizes at the different stations. In Table 1 the sampling dates and the number and size of the boxcore samples are given.

Boxcore samples were taken to a depth of 15 cm and sieved on a 0.5-mm sieve. Samples were stored in 4% formaldehyde, stained and sorted under a stereo microscope. Macrofauna was divided into major taxonomic groups, which were treated separately and combined later to get estimates of total macrofaunal abundance and biomass. Biomass was estimated as wet weight per major taxon after drying the animals a few seconds on absorbent paper. Weighing was done with 0.1 mg accuracy. Because of the small size of most individuals no attempt was made to puncture shells of bivalves to drain them of water. Biomass values were converted into organic C-content per major taxon using the conversion factors given by Rowe (1983). For the macrofaunal sized Nematoda a conversion factor of 12.4% (Jensen, 1984) was used. Nematoda are usually considered to be a meiofaunal taxon and are therefore excluded from the macrofaunal data-set (called macrofauna *sensu stricto*), but data on macrofaunal sized nematodes are given separately.

Meiofauna

In October 1993 and May 1994, two subsamples (one per boxcore) for the meiofauna were taken using 10 cm² plastic cores (Table 1). From the 1995-cruise only data for station E (4460 m) and density of the nearby the OMEX-

transect situated station P4 at 4091 m (situated in the Porcupine Seabight; see Flach & Thomsen, 1998) are available (sorted by Valérie Ryheul, University of Gent). Oxygen microprofiles measured on board and *in situ* were highly comparable (Helder & Epping, 1995), indicating that the boxcore samples were taken carefully. Meiofauna subcores were taken to a sediment depth of 5 cm. Samples were fixed in a hot (70°C), 4% neutral formaldehyde tap water solution. Meiofaunal organisms were extracted from the sediment by centrifugation with Ludox (Heip et al., 1985). Macrofauna was excluded by means of a 1-mm sieve. All animals retained on a 32-μm sieve were counted, and nematodes were picked out at random from each site and mounted in glycerine slides. Nematode length (excluding filiform tails, if present) and maximal width were measured using an image analyser (Quantimet 500+). Nematode wet weight biomass was calculated from volume calculated with Andrassy's formula (Andrassy, 1956) assuming a density of 1.13. Nematode wet weight was converted to organic carbon using the conversion factor (12.4%) given by Jensen (1984). Meiofauna biomass is thus restricted to nematode biomass, but because nematodes were the most abundant meiofaunal taxon (~90%, Vanaverbeke et al., 1997) it gives a good estimate of meiofauna biomass.

Data analyses

The ratio in density between meiofauna and macrofauna along the OMEX-transect was calculated for the three years separately as significant differences in macrofauna densities between the years were observed, due to high numbers of recruits at the upper part of the slope in May 1994 (Flach & Heip, 1996b). Macrofauna biomass was not significantly different between the years (Flach & Heip, 1996b), and mean values were used. Meiofauna (=nematode) biomass was only available for the stations A, I, B, II and F for 1993 and station E for 1995. Standard errors of the ratios were calculated as:

$$\mathrm{SE}\,\frac{\bar{x}}{\bar{y}} = \left(\frac{\bar{x}}{\bar{y}}\right) \times \sqrt{\left\{\frac{\mathrm{var}\bar{x}}{\bar{x}^2} + \frac{\mathrm{var}\bar{y}}{\bar{y}^2}\right\}} \qquad (1)$$

Regression lines for the ratios along the depth gradient were calculated and differences in ratios between stations were estimated with a *t*-test. Correlation was estimated using the Pearson Product-Moment Correlation Coefficient. Correlation was estimated between all available ratios and the %N and %org. C within the sediment, the total amount of mineralisable carbon within the sediment, the input of organic carbon, and the mean concentrations of TPM, POC and CPE within the BBL. Meiofauna and macrofauna densities along the depth gradient were tested with ANOVA using the replicates.

RESULTS

Density

The ratio in density between meiofauna and macrofauna along the OMEX-transect showed a linear increase with increasing water depth (Figure 1; $y = -118.7 + 0.31 \times x$, $r = 0.94$, N = 14, $P < 0.0001$). At the continental shelf station
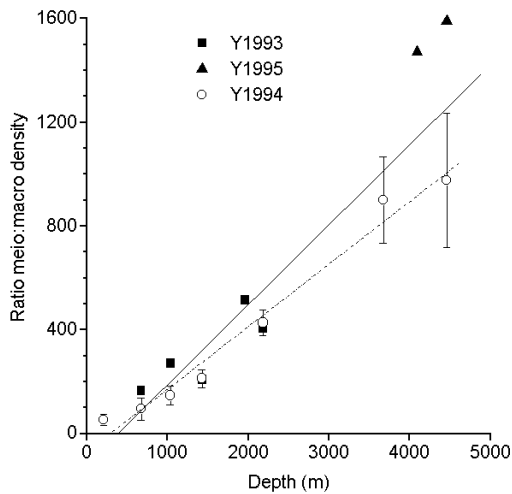
Figure 1. Ratios between meiofauna and macrofauna density (±SE for 1994) and the regression lines for all data (solid line) and for 1994 (dotted line).

Figure 2. Mean density ±SE of macrofauna (ind m^{-2}) and meiofauna (ind m^{-2}) along the OMEX-transect in May 1994.

A meiofauna densities were only ~50 times higher than macrofauna densities, whereas in the abyss meiofauna densities were >1000 times higher than macrofauna densities. Because a complete data set was only available from May 1994, and macrofauna densities showed seasonal variation (Flach & Heip, 1996b), 1994 was also treated separately. The ratio from 1994 showed a linear increase with water depth, but the slope was less steep (y = −68.3+0.24 × x, r=0.99, N=7, P<0.001) than the slope of the regression line of all data (Figure 1). Figure 2 shows that macrofauna densities in 1994 decrease significantly (ANOVA, r=0.97, N=17, P<0.001) with increasing water depth, whereas meiofauna densities were not significantly different (ANOVA, r=0.58, N=14, P=0.73) throughout the depth gradient. Meiofauna densities in May 1994 were not significantly different (t-test, P>0.2) from densities in 1993 at the stations I, B, II and F (given in Vanaverbeke et al., 1997) nor was the density at station E
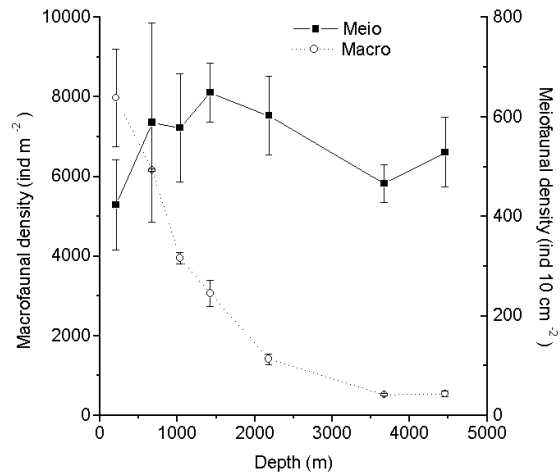
significantly (t-test, P>0.1) different from 1995. Thus, with increasing water depth meiofauna and therefore mainly nematodes become relatively more important.

Nematodes become also relatively more important with increasing water depth within the macrofaunal fraction. At the deepest stations ~20% of the macrofauna were nematodes, whereas at the shallowest station A this fraction was only ~2%. The ratio between macro Nematoda and macrofauna *sensu stricto* increased linearly with increasing water depth (Figure 3A; y = −0.00135+0.00007x, r=0.99, N=7, P<0.0001). However, the relationship between meio:macro nematodes showed no consistent trend with depth (Figure 4). Figure 5A shows the Nematoda densities found within the meio- and macrofaunal fractions. Within the macrofaunal fraction a peak in nematode density at around 670–1034 m was found, thus at this depth relatively high numbers of large nematodes occurred. This is also shown in the dip at ~1000 m in the ratio between meio:macro nematodes (Figure 4).
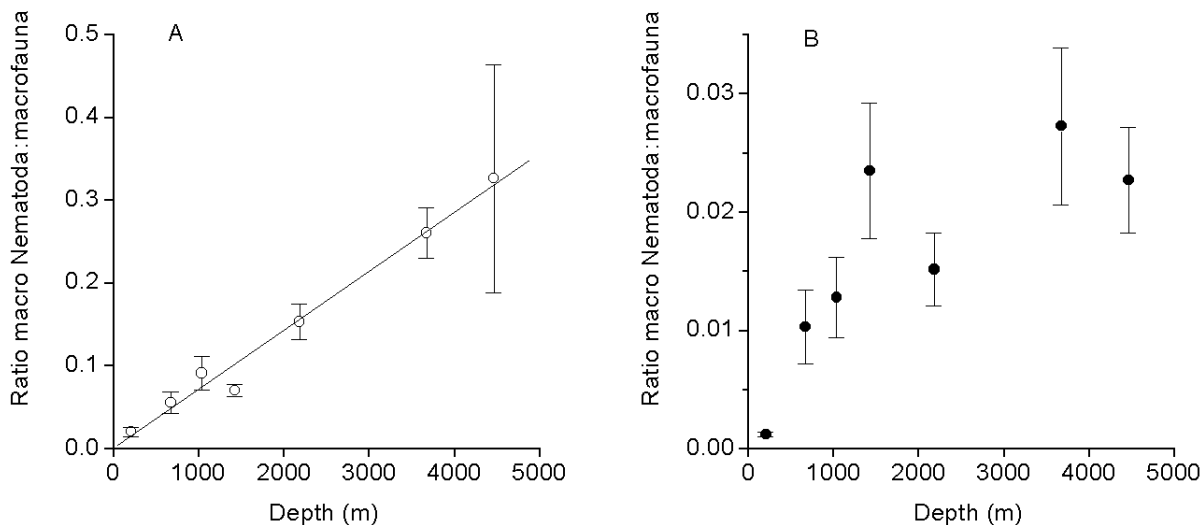

Figure 3. Ratios ±SE between macrofaunal sized Nematoda (>0.5 mm) and macrofauna *sensu stricto* (>0.5 mm) in density (A) and biomass (B).
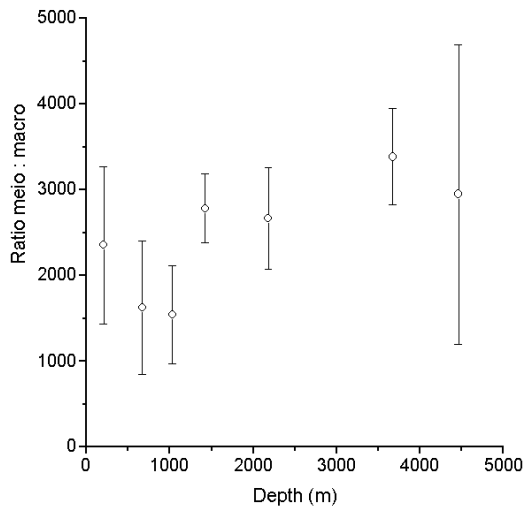
Figure 4. Ratio ±SE in density between meiofaunal and macrofaunal Nematoda.

Biomass

The ratio in biomass between meiofauna (=Nematoda) and macrofauna *sensu stricto* showed a dip at ∼1000 m (Figure 6A). The biomass ratio at station B (1034 m) was significantly lower (*t*-test, $P < 0.05$) than at station I (670 m) and station II (1425 m). The ratio at station A (208 m) was significantly higher (*t*-test, $P < 0.01$) than at station I, but not significantly different from station II, and F (2182 m). The biomass ratio at the deep station E (4460 m) was significantly higher (*t*-test, $P < 0.05$) than at station F. At ∼1000 m macrofauna biomass was ∼55 times higher than meiofauna biomass. Even with the exclusion of a few extremely large individuals from the macrofauna data (see Flach & Heip, 1996a,b), macrofaunal biomass is still ∼35 times higher. At the shelf station A, macrofaunal biomass was about 15 (with exclusion of large individuals only about eight) times higher than meiofaunal biomass, values that are more or less comparable with the values found at ∼2000 m depth (about eight and nine times higher macrofaunal biomass). At ∼4500 m water depth macrofauna biomass was only around three times higher than meiofauna biomass.

Figure 7A shows that the biomass of the meiofauna decreased from ∼71 mg C m^{-2} at the shelf station to ∼15 mg C m^{-2} at ∼1000 m and remained more or less constant at the deeper stations. The macofauna biomass, on the other hand, was high at the shelf and upper slope (∼500 mg C m^{-2} with the exclusion of some extremely large individuals, see Flach & Heip, 1996 a,b) and then dropped to ∼100 mg C m^{-2} at stations deeper than ∼1400 m. This pattern is mainly due to the changes in individual weight of the organisms. Whereas the densities
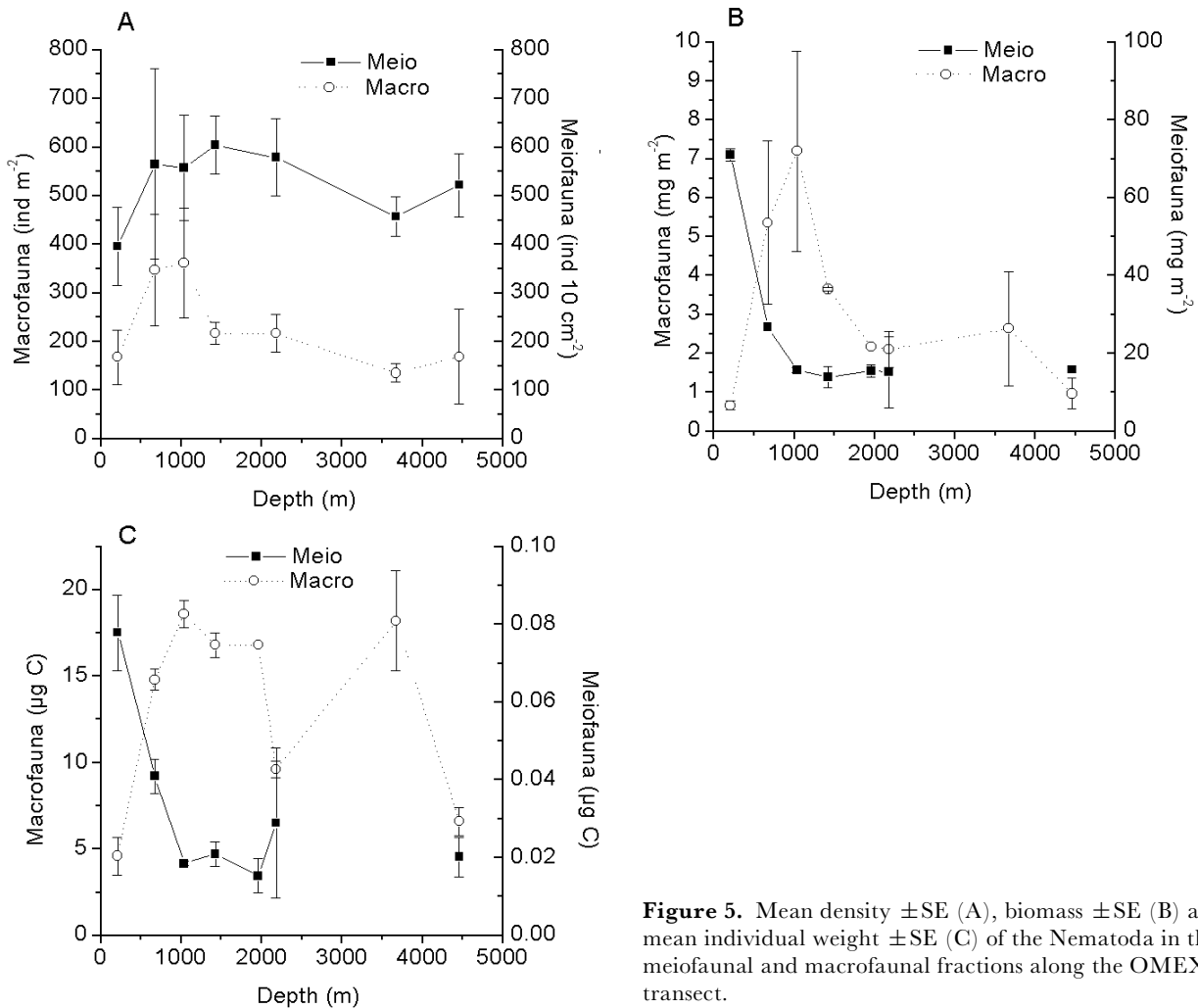

Figure 5. Mean density ±SE (A), biomass ±SE (B) and mean individual weight ±SE (C) of the Nematoda in the meiofaunal and macrofaunal fractions along the OMEX-transect.
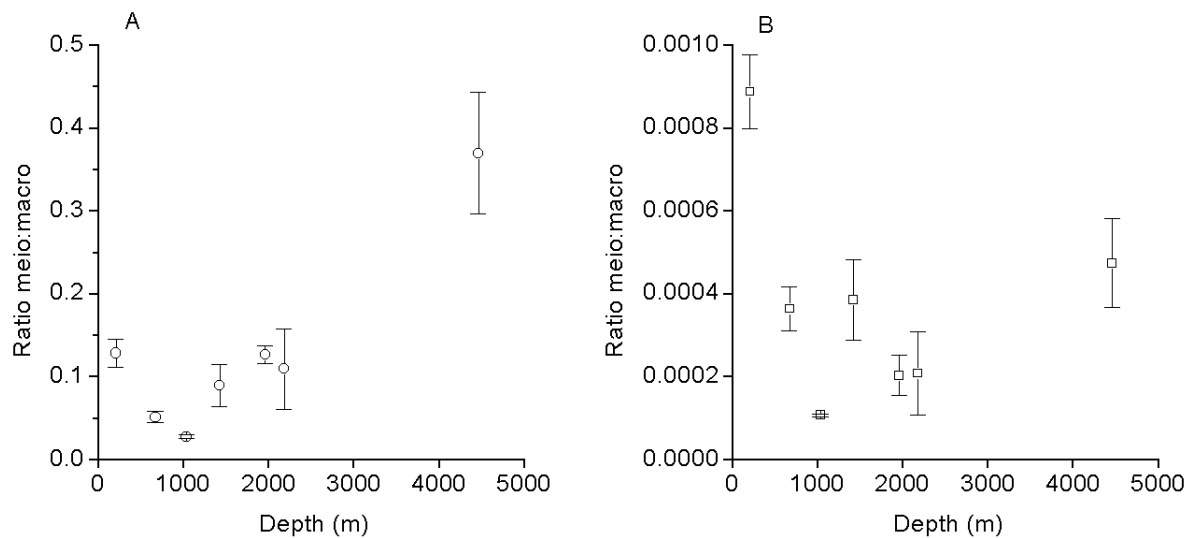
Figure 6. Ratios between meiofauna and macrofauna *sensu stricto* biomass ±SE (A) and mean individual weight ±SE (B). Meiofauna biomass and mean individual weight were only available from 1993 (station A–F) and 1995 (station E). Macrofauna biomass was calculated out of all years with and without a few extremely large specimens, these large ones were omitted in the mean individual weights of the macrofauna.
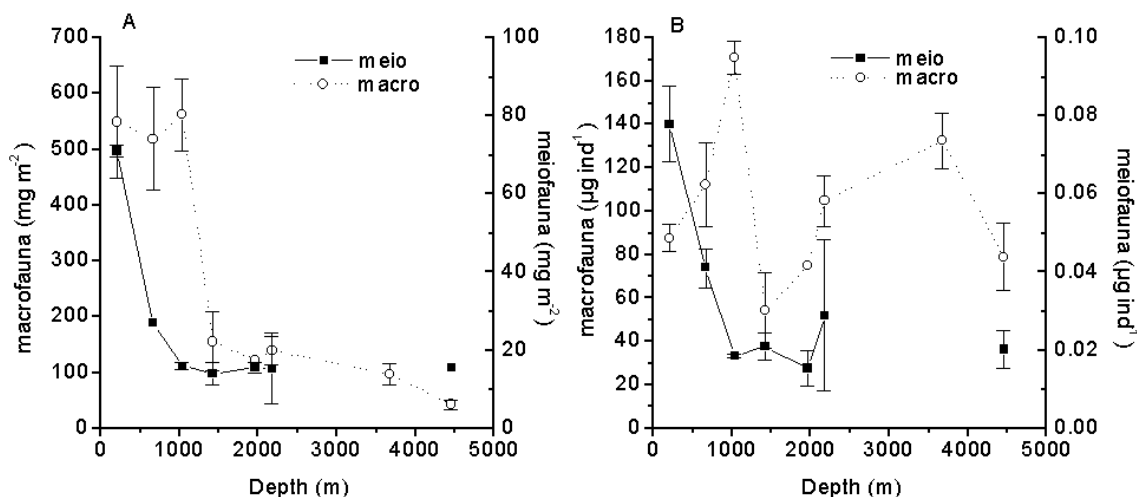

Figure 7. Biomass ±SE (mg org. C m^{-2}) of macrofauna *sensu stricto* with exclusion of some extremely large individuals and meiofauna (A). Mean individual weight ±SE (μg org. C) of macrofauna with exclusion of some extremely large individuals and meiofauna (B).

of meiofauna remained more or less constant along the depth gradient, the mean individual weight decreased with increasing water depth to ~1000 m, after which it remained more or less constant (Figure 7B). Macrofauna densities decreased with increasing water depth, but the mean individual weight showed a peak at station B at ~1000 m and a dip at station II at ~1465 m (Figure 7B). The ratio between mean individual weights of meiofauna and macrofauna therefore shows a dip at ~1000 m (Figure 6B), indicating that at this depth, there was a large difference in size between meio- and macrofauna. At the shelf station A the ratio of the mean individual weights was high, thus the size difference between meio- and macrofauna was relatively small. Meiofauna was relatively large and macrofauna relatively small at this shallow station. At station II both meio- and macrofauna were relatively small (Figure 7B).

The biomass ratio between macro Nematoda and macrofauna *sensu stricto* (without Nematoda) showed a

slight increase with increasing water depth (Figure 3B). The ratio at the shallow station A was significantly lower (*t*-test, $P < 0.005$) than the upper slope station I. The ratios at all other stations were not significantly different, but station II had a relatively high ratio, due to a relatively low biomass of the macrofauna *sensu stricto* (Figure 7A). The biomass of the macrofaunal Nematoda showed a clear peak at ~1000 m, due to high numbers of relatively large individuals (Figure 5). Again there was a divergence in mean individual weights between meio- and macrofaunal Nematoda at station B and a convergence at station A. However, relatively large macrofaunal nematodes were also found at station II and III (Figure 5C). At station OMEX-III mean individual weight of the macrofauna *sensu stricto* was also relatively high, but at station II it was low (Figure 7B). Thus, at station II nematodes seem to respond differently to the physical/chemical conditions than the macrofauna *sensu stricto*.

Relations with the physical environment

No significant correlations between any of the calculated ratios with the %N or %org. C within the sediment were found, nor with the concentration of POC and CPE within the BBL. The ratio between meio:macrofauna densities was significantly and negatively correlated with the calculated carbon input ($r = -0.998$, $P = 0.04$). The ratio between meio:macrofauna biomass ($r = -0.999$, $P = 0.02$) and the ratio between macrofaunal sized nematodes and macrofauna *sensu stricto* ($r = -0.9999$, $P = 0.007$) were also significantly and negatively correlated with the calculated carbon input. Significant negative correlations were also found between on the one hand the density ratios of meio:macrofauna ($r = -0.84$, $P = 0.04$) and large nematodes:macrofauna ($r = -0.9$, $P = 0.01$) with the concentration of TPM within the BBL on the other. The ratios between meio:macrofauna densities ($r = 0.83$, $P = 0.16$), and between macrofaunal sized nematodes and macrofauna *sensu stricto* density ($r = 0.91$, $P = 0.08$) and biomass ($r = 0.92$, $P = 0.07$) were positively correlated (although not significantly) with the estimated mineralizable carbon within the sediment.

DISCUSSION

Although there is an overlap in size between the meiofauna (< 1 mm) and the macrofauna (> 0.5 mm), due to differences in the sieve sizes used, this overlap is constant over the whole depth range and will thus have only a minor impact on the change in meio:macrofauna ratios along the OMEX-transect. It will, however, give some difficulties in comparing the OMEX results with other studies.

Comparison with other studies

The linear increase in the ratio of meiofauna and macrofauna density with increasing water depth, found along the OMEX-transect, is in agreement with the observation by Thiel (1975) that, in general, the decrease in meiofauna abundance with depth is smaller than that of macrofauna. Along the OMEX-transect macrofauna densities decreased exponentially with increasing water depth, whereas meiofauna densities remained more or less similar along the depth range from ~ 200 to ~ 4500 m. Density and biomass of the macrofauna of the Goban Spur, are somewhat higher than most values from the literature (Flach & Heip, 1996a). Comparison of the meiofauna data with the 'best regression' for the entire north-east Atlantic (Vincx et al., 1994) showed that at the shallow OMEX sites (< 1500 m) meiofauna densities were somewhat lower, whereas at the deep OMEX-stations densities were higher. Especially at the deepest station E (4460 m) meiofauna densities were high (528 ind 10 cm^{-2} in 1994 and 867 ind 10 cm^{-2} in 1995), compared to the BIOTRANS site (320 ind 10 cm^{-2} at 4560 m; Pfannkuche, 1993) and the oligotrophic EUMELI site at ~ 4700 m (139 ind 10 cm^{-2}), but they were more or less similar to those from the nearby Porcupine Abyssal Plain (PAP) site at ~ 4700 m (638 ind 10 cm^{-2}) Vanreusel et al. (1995).

In only a few studies, both meiofauna and macrofauna data are given. Comparison between literature values is often difficult because of methodological problems, mainly differences in mesh size of the sieve used (Rowe, 1983). In the Gulf of Biscay Dinet et al. (1985) used a sieve of 250-μm to separate meio- and macrofauna and Sibuet et al. (1989) also used 250-μm at the EUMELI sites. In both studies macrofauna data were corrected by leaving out the meiofaunal taxa (nematodes, ostracods, copepods), which could constitute up to 50% of total number (Sibuet et al., 1989). The meio:macrofauna density ratio of the shallower OMEX sites (at ~ 2000 m) are more or less similar to the values found at the three EUMELI sites (Sibuet et al., 1993) and the three sites in the Bay of Biscay (Dinet et al., 1985) (427 compared to 406 and 519). However, the OMEX-values at the deeper sites are higher than in the Bay of Biscay and the mesotrophic EUMELI site. The value form the deepest OMEX station, was again in agreement with the oligotrophic EUMELI site (~ 1500). Pfannkuche (1993) used a 1-mm sieve for macrofauna at the BIOTRANS site and called the fraction between 0.5 and 1mm large meiofauna. This fraction between 0.5 and 1mm contained around ten times more animals than the > 1mm fraction. For calculating the meio:macrofauna ratio, the total fraction > 0.5 mm was considered as macrofauna, although this also included the meiofaunal taxa, and arrived at a much lower value (160) than at similar depth at the OMEX transect.

The meiofauna (nematodes) within the macrofaunal fraction were treated separately and made up ~ 2–20% of total macrofaunal numbers. Schwinghamer (1985) asserts that distinct bacterial, meiofaunal and macrofaunal peaks occur in benthic size in the deep sea, but that the trough between meio- and macrofauna is found at 512 μm in the fine-grained abyssal samples rather than at the 1024 μm as in coarser shelf and coastal sites. The 500-μm sieve used for the OMEX-samples can thus be expected to give a reasonable separation between meio- and macrofauna.

Relations with feeding conditions

Thiel (1975) related the change in meio:macrofauna ratio with increasing water depth to changes in food availability and stated that 'associations governed by constantly limited food availability are composed of small individuals on the average.' In our study a decrease of size occurs due to the change in ratio between meiofauna and macrofauna density, but within either group no significant decrease in mean individual weight with increasing water depth was observed. Rather a minimum mean individual weight was found at ~ 1500 m (Figure 7B). Gage & Tyler (1991) report the absence of a significant decrease in mean macrofaunal organism size from 0.4 to 4 km depth, but a decrease in meiofauna median size with depth, which was ascribed to limited food availability with depth. Along the Goban Spur, Soltwedel et al. (1996) also found that nematode size did not gradually decrease with increasing water depths, but that relatively small nematodes were found at 410 m. They related this pattern to relatively low particulate organic matter (POM) deposition at that depth. They also compared the deepest Goban Spur station at 4470 m with three stations at similar depth on the Porcupine Abyssal

Plain (PAP and EC sites) and the BIOTRANS site in the north-east Atlantic and found no significant differences in nematode size between the Goban Spur and any of the other stations. Vanreusel et al. (1995) compared the nematodes of two contrasting abyssal (4700 m) sites in the north-east Atlantic and found significantly smaller mean individual body weight at the oligotrophic EUMELI site compared to the Porcupine Abyssal Plain (PAP). These differences in mean individual weights are caused by the relatively greater abundance of larger nematodes at the more eutrophic PAP site. Large nematodes were found in the macrofaunal fraction of the OMEX stations and showed a peak in density and biomass around 1000 m water depth. Macrofauna *sensu stricto* also had a peak in mean individual weight and a relative high biomass was found at that depth. However, meiofauna biomass and mean individual weight at station B were relatively low, resulting in the dip in meio:macrofauna ratio in biomass and mean individual weight. Thus, at this depth a selection for either very large or very small specimens occurs. This would be expected if competition for food occurs and the food arrives in pulses. Large specimens can gather as much food as possible in a short time, bury it out of the reach of the small fauna and live on it until the next pulse arrives (Jumars et al., 1990). The small fauna, on the other hand, are better suited to feeding continuously on the small (rapidly degrading) fraction that is left.

Sibuet et al. (1989) found a positive linear relationship in abundance of meio- and macrofauna with the 'burial' organic carbon flux (estimated from the mean organic carbon concentration in the surface sediment and the rate of sediment accumulation during the Holocene). They suggest that the flux of particulate organic carbon (POC) to the deep sea-floor controls biomass distribution in the deep Atlantic Ocean. At the OMEX-transect significant negative correlations were found between the ratios between meio:macrofauna density and biomass and the ratio between macrofauna nematodes:macrofauna *sensu stricto* and the calculated carbon input. No significant correlations were found with the mean individual weight of either the macrofauna or the meiofauna, nor between the macrofaunal sized nematodes with carbon input. Thus, with decreasing carbon input meiofaunal taxa (mainly nematodes) become relatively more important, but this does not directly influence size of the fauna.

Feeding types

Meio- and macrofauna are regarded to be distinct functional groups (Gage & Tyler, 1991). Nematodes (constituting up to ∼90% of meiofauna) mainly feed on bacteria, fungi and unicellular algae within the sediment Jensen (1987). Macrofauna can either feed directly from the water column (filter-feeders), ingest bulk sediment either from the sediment surface or from deeper sediment layers (deposit-feeders) or act as predator/scavenger (predating, e.g. on meiofauna). The change in meio:macrofauna ratio with increasing water depth therefore also means a change in functional composition. Also within the macrofaunal fraction, nematodes became more important with increasing water depth and a change in taxonomic composition in favour of the nematodes with increasing water depth could be observed.

Thus, at the deep stations a selective advantage for the nematodes or a selective disadvantage for the macrofaunal taxa occurs.

The change in the meio:macrofauna ratio's with depth was mainly due to changes in the macrofaunal community. At the upper part of the slope (<1500 m) the macrofaunal community is dominated by filter-feeding, interface-feeding (able to switch from filter- to surface deposit-feeding) and surface deposit-feeding taxa (Flach et al., 1998). This coincided with high concentrations of POC and high flow velocities within the BBL (Thomsen & van Weering, 1998). Feeding from the BBL thus seems to be favourable at the upper part of slope. At the lower part of the slope flow velocities and POC concentrations in the BBL are low and the numbers of filter- and surface deposit-feeders decline (Flach et al., 1998). This resulted at the deep OMEX stations in a benthic community mainly feeding within the sediment consisting of subsurface deposit-feeding polychaetes (the most abundant macrofaunal taxon; Flach & Heip, 1996b) and nematodes.

The observed changes in meio:macrofauna ratio's along the OMEX-transect thus reflect changes in taxonomic (functional) composition, caused by a selective disadvantage for filter- and surface deposit-feeders and not a selection for smaller individuals. The mean individual weights of the major macrofaunal taxa did not show a decrease with increasing water depth, in fact the smallest individuals were found at the shallowest station at 185 m (Flach & Heip, 1996a). Also the nematodes did not show an overall decrease in size with increasing water depth (Figure 5C), nor was there a marked decrease in number (Figure 5A). This does not suggest that the feeding conditions for the nematodes deteriorate much with increasing water depth.

Carbon requirements

Thiel (1975) hypothesized for deep sea benthos that with increasing depth and decreasing food concentrations small organisms gain importance in total community metabolism. The carbon requirements for respiration for macrofauna and macrofaunal sized nematodes (Flach & Heip, 1996b) with the meiofauna (Soetaert et al., 1997) were compared. Both meio- and macrofauna respiration were highest at the shelf and decreased with increasing water depth to a depth of ∼1500 m, after which the macrofaunal respiration decreased slightly and the meiofauna even increased again at the deepest station to ∼0.17 g C m^{-2} y^{-1} (calculated from the 1995 data). The respiration, as calculated from biomass, by macrofaunal sized nematodes was very low (∼1%), but highest at ∼1000 m. Total carbon requirements for respiration by the metazoa infauna decreased with increasing water depth from ∼7.6 g C m^{-2} y^{-1} on the shelf to ∼0.6 g C m^{-2} y^{-1} in the abyss. Most of the carbon was used by the macrofauna with a maximum at station B, where 95% of the carbon respired was due to the macrofauna, resulting in a dip in the respiration ratio between meiofauna and macrofauna at ∼1000 m. At ∼2000 m meiofauna accounted for ∼18% of total metazoal infaunal respiration and at ∼4500 m for ∼30%. Thus, meiofauna gains indeed importance in total community

metabolism with increasing water depth as hypothesized by Thiel (1975). But as argued above this reflects a change in taxonomic composition rather than a change in size.

REFERENCES

Andrassy, I., 1956. The determination of volume and weight of nematodes. *Acta Zoologica Academiae Scientiarium Hungricae*, **2**, 1–15.

Carney, R.S., Haedrich, R.L. & Rowe, G.T., 1983. Zonation of fauna in the deep sea. In *The sea.* Vol. 8. *Deep-sea biology* (ed. G.T. Rowe), pp. 371–398. New York: John Wiley & Sons.

Dinet, A., DesbruyoDres, D. & Khripounoff, A., 1985. Abondance des peuplements macro- et méiobenthiques dans la zone abyssale BIOGAS: répartition et stratégie d'échantillonnage. In *Peuplements profonds du Golfe de Gascogne, Campagnes BIOGAS* (ed. L. Laubier and C. Monniot), pp. 121–142. Brest: IFREMER.

Flach, E. & Heip, C., 1996a. Vertical distribution of macrozoobenthos within the sediments on the continental slope of the Goban Spur area (NE Atlantic). *Marine Ecology Progress Series*, **141**, 55–66.

Flach, E. & Heip, C., 1996b. Seasonal variations in faunal distribution and activity across the continental slope of the Goban Spur area (NE Atlantic). *Journal of Sea Research*, **36**, 203–215.

Flach, E., Lavaleye, M., Stigter, H. de & Thomsen, L., 1998. Feeding types of the benthic community and particle transport across the continental slope of the Goban Spur. *Progress in Oceanography*, **42**, 209–231.

Flach, E. & Thomsen, L., 1998. Do physical and chemical factors structure the macrobenthic community at a continental slope in the NE Atlantic? *Hydrobiologia* **375/376**, 265–285.

Gage, J.D. & Tyler, P.A., 1991. *Deep-sea biology: a natural history of organisms at the deep-sea floor.* Cambridge: Cambridge University Press.

Heip, C., Vincx, M. & Vranken, G., 1985. The ecology of marine nematodes. *Oceanography and Marine Biology. Annual Review*, **23**, 399–489.

Helder, W. & Epping, E., 1995. Mineralization of organic matter along a transect in the Goban Spur area (Celtic Sea). *Report. Ocean Margin Exchange (Annual)*, part E, 93–104.

Jensen, P., 1984. Measuring carbon content in nematodes. *Helgolânder Meeresuntersuchungen*, **38**, 83–86.

Jensen, P., 1987. Feeding ecology of free-living aquatic nematodes. *Marine Ecology Progress Series*, **35**, 187–196.

Jumars, P.A., Mayer, L.M., Deming, J.W., Baross, J.A. & Wheatcroft, R.A., 1990. Deep-sea deposit-feeding strategies suggested by environmental and feeding constraints. *Philosophical Transactions of the Royal Society* A, **331**, 85–101.

Pfannkuche, O., 1993. Benthic response to the sedimentation of particulate organic matter at the BIOTRANS station, 47ºN, 20ºW. *Deep-Sea Research II*, **40**, 135–149.

Rowe, G.T., 1983. Biomass and production of deep-sea macro-benthos. In *The sea.* Vol. 8. *Deep-sea biology* (ed. G.T. Rowe), pp. 97–121. New York: John Wiley & Sons.

Schwinghamer, P., 1985. Observations on size-structure and pelagic coupling of some shelf and abyssal benthic communities. In *Proceedings of the Nineteenth European Marine Biology Symposium, Plymouth, 1984* (ed. P.E. Gibbs), pp. 347–359. Cambridge: Cambridge University Press.

Shirayama, Y., 1983. Size structure of deep-sea meio- and macrobenthos in the western Pacific. *Internationale Revue der Gesamten Hydrobiologie*, **68**, 799–810.

Sibuet, M., Albert, Ph., Charmasson, S., Deming, J., Dinet, A., Galeron, J., Guidi-Guilvard, L. & Mahaut, M.-L., 1993. The benthic ecosystem in the three EUMELI sites in the northeast tropical Atlantic: general perspectives and initial results on biological abundance and activities. *Annales de l'Institut Océanographique, Paris*, **69**, 21–33.

Sibuet, M., Lambert, C.E., Chesselet, R. & Laubier, L., 1989. Density of the major size groups of benthic fauna and trophic input in deep basins of the Atlantic Ocean. *Journal of Marine Research*, **47**, 851–867.

Soetaert, K., Herman, P.M.J., Middelburg, J.J. & Heip, C., 1998. Assessing organic matter mineralization, degradability and mixing rate in an ocean margin sediment (northeast Atlantic) by diagenetic modelling. *Journal of Marine Research*, **56**, 519–534.

Soetaert, K., Vanaverbeke, J., Heip, C., Herman, P.M.J., Middelburg, J.J., Duineveld, G. & Sandee, A., 1997. Nematode distribution in ocean margin sediments of the Goban Spur (north-east Atlantic) in relation to sediment geochemistry. *Deep-Sea Research*, **44**, 1671–1683.

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. *Journal of the Marine Biological Association of the United Kingdom*, **76**, 327–344.

Thiel, H., 1975. The size structure of the deep-sea benthos. *Internationale Revue der Gesamten Hydrobiologie*, **60**, 575–605.

Thomsen, L. & Weering, T.C.E. van, 1998. Spatial and temporal variability of particulate matter in the benthic boundary layer at the north east Atlantic continental margin (Celtic Sea). *Progress in Oceanography*, **42**, 61–76.

Vanaverbeke, J., Soetaert, K., Heip C. & Vanreusel, A., 1997. The meiobenthos along the continental slope of the Goban Spur (NE Atlantic). *Journal of Sea Research*, **38**, 93–108.

Vanreusel, A., Vincx, M., Bett, B.J. & Rice, A.L., 1995. Nematode biomass spectra at two abyssal sites in the NE Atlantic with contrasting food supply. *Internationale Revue der Gesamten Hydrobiologie*, **80**, 287–296.

Vincx, M. et al., 1994. Meiobenthos of the deep northeast Atlantic. *Advances in Marine Biology* **30**, 2–88.