THE MEIOBENTHOS OF THE MOLLOY DEEP (5 600 M), FRAM STRAIT, ARCTIC OCEAN

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MEIOBENTHOS
NEMATODES
DEEP-SEA
MOLLOY DEEP
ABYSSAL PLAINS
TRENCHES

ABSTRACT. – The meiobenthos (including foraminiferans) of the Molloy Deep (Fram Strait, Arctic Ocean) was studied along a 15 km transect crossing the deep in NW-SE direction. Four stations between 5 416 and 5 569 m water depth were sampled during summer months between 1997 and 2001. In comparison with other abyssal and hadal regions of the World Ocean, meiofauna abundances were extremely high, ranging from 2 153 to 2 968 ind./10 cm^2 (values for the uppermost 5 cm of the sediments). The analysis of biogenic sediment compounds (e.g. chloroplastic pigments, particulate proteins) confirmed comparably high amounts of organic matter in the sediments, presumably favouring increased faunal densities and biomasses. Subsurface peaks in meiobenthic abundances at 1-2 cm sediment depth may be due to substantial disturbance and/or predation by dense herds of small holothurians (*Elpidia glacialis*), obviously inhabiting the entire Molloy Deep in very high numbers. Faunal composition of the meiobenthic community of the Molloy Deep was similar to other deep-sea regions. Foraminiferans were the dominant taxa of the total meiobenthos (48.5-59.9%), whereas nematodes dominated the metazoan meiofauna (91.7-95.8%). The total meiofauna of the Molloy Deep consisted of relatively small organisms compared to other/shallower oceanic regions, which could not be explained by reduced food availability to the benthos.

MÉIOBENTHOS
NÉMATODES
MER PROFONDE
DÉPRESSION DE MOLLEY
PLAINES ABYSSALES
FOSSES

RÉSUMÉ. – Le méiobenthos (incluant les Foraminifères) de la dépression de Molloy (Détroit de Fram, Océan Arctique) a été étudié le long d'un transect de 15 km qui recoupe cette dépression selon la direction NO-SE. Quatre stations situées entre 5 416 et 5 569 m de profondeur ont été échantillonnées pendant les mois d'été entre 1997 et 2001. En comparaison avec d'autres zones abyssales et hadales de l'Océan mondial, les abondances de la méiofaune, qui s'échelonnent de 2 153 à 2 968 ind./10 cm^2 (dans les 5 cm supérieurs des sédiments), sont extrêmement élevées. L'analyse des composants biogènes des sédiments (pigments des chloroplastes, protéines particulaires) confirment les taux relativement élevés de matière organique des sédiments, qui pourraient favoriser une augmentation des densités et des biomasses élevées. Les pics d'abondance de la méiofaune proche de la surface, à 1-2 cm de profondeur dans le sédiment, pourraient être dus à une perturbation notable et/ou à la prédation de denses concentrations de petites Holothuries (*Elpidia glacialis*), qui habitent toute la dépression de Molley en très grand nombre. La composition de la communauté méiofaunique de la dépression de Molley est similaire de celle des autres régions de mer profonde. Les Foraminifères constituent le taxon dominant du méiobenthos total (48.5-59.9 %), tandis que les Nématodes dominent la fraction des Métazoaires (91.7-95.8 %). La méiofaune totale de Molley Deep comprend des organismes de taille relativement petite par rapport aux autres zones océaniques moins profondes, ce qui ne peut s'expliquer par des ressources nutritives réduites disponibles pour le benthos.

INTRODUCTION

The presence and persistence of life at the ocean floor can be seen as a response to organic matter input from the upper water levels. Abundance of benthic organisms generally tends to decrease with ocean depth from continental margins to the hadal zone (Rowe 1983, Thiel 1983). Decreasing food supply with increasing water depth and distance from land masses appear to be one of the primary causes for reduced faunal abundance in the deep oceanic basins and on the abyssal plains. Some deep-sea areas, however, support unusually high densities of benthic organisms. These high densities have been related to high surface productivity (e.g. upwelling areas) with subsequently enhanced input of organic matter to the seafloor (Thiel 1982, Soltwedel 1997, 2000), or to the accumulation of organic material in low-energy bottoms (Thiel 1971, 1983).

Hadal regions like trenches are generally located in the vicinity of the continental margins. Such settings adjacent to land masses enhance a natural dumping of terrestrial and coastal, inorganic and organic material. Trenches as well as fracture zones are also characterised by steep walls, which may promote a rapid down slope transport of any kind of material. In this way, enhanced availability of organic matter might promote rich communities of benthic organisms, even at hadal depths.

In the past decades, knowledge of the standing stocks of deep-sea meiobenthos has increased considerably. Due to logistical reasons and limitations in ship time, information on the meiobenthos from abyssal depths deeper than 5 000 m, and especially from hadal regions of the World Ocean is still rather limited. To date about 30 ultra-deep sites have been visited to investigate meiobenthic communities. Most of them are situated in subtropical and tropical regions; except for the study by Vinogradova *et al.* (1993) there is, to our knowledge, no information on ultra-deep meiobenthic communities from higher latitudes.

This paper describes the meiobenthic communities (with special attention on the free-living Nematoda) in the Molloy Deep, the deepest region of the Arctic Ocean (max. depth 5 607 m). On the basis of the Molloy Deep data set, and in comparison with published meiofauna data from other ultra-deep parts of the World Ocean, we address the following questions: Does meiofauna abundance generally correlate with indicators of organic-matter input? Does variation in organic matter availability correlate with changes in the taxonomic composition of the meiofauna? Does the size structure correlate with organic matter input?

MATERIALS AND METHODS

Area of investigation: The seafloor of Fram Strait is part of a complex transform zone between the Knipovich Ridge of the Greenland Sea and the Gakkel Ridge of the Arctic Ocean. The Molloy Deep is a nodal basin formed at the intersection of the Molloy Fracture Zone and the Molloy Ridge (Fig. 1). Especially to the east and to the south, the deep has steep flanks with up to 30º inclination between 3 000 and 5 000 m water depth. The floor of the Molloy Deep as defined by the 5 200 m isobath, measures 12 km (SW-NE) by 22 km (NW-SE). According to Thiede *et al.* (1990), the deep has a maximum water depth of 5 607 m at 79º08.5'N and 2º47.0'E.

In Fram Strait, Atlantic waters flow northward in the West Spitzbergen Current. To the west, surface waters of polar origin flow southwards along the western Greenland margin. The bathymetry of Fram Strait plays a guiding role in water mass modifications (Quadfasel *et al.* 1987). The "Molloy Deep Eddy", a cyclonic gyre of 80-100 km in diameter, is located persistently just north of the Molloy Deep at 79º30'N and 3º00'E. It is induced either by the deep itself (Wadhams & Squire 1983, Smith *et al.* 1984) or by the Molloy Ridge just north of the deep (Quadfasel *et al.* 1987). Based on a modelling study, Schlichtholz & Houssais (1999) confirmed a cyclonic circulation of Eurasian Basin Deep Water in the Molloy Deep region. These specific hydrographic circumstances may favour the sedimentation of particulate matter in the centre of the gyre (see Discussion).

The overall circulation pattern in Fram Strait results in variable sea-ice cover with permanent ice-covered areas in the west, permanently ice-free areas in the southeast, and seasonally varying ice conditions in the central and eastern parts of the area (Vinje 1977, 1985). For most of the year, the Molloy Deep is located in the marginal ice zone, an area characterised by enhanced primary productivity (Sakshaug & Skjoldal 1989).

Photo and video observations (in 1997 with a towed camera system, "Ocean Floor Observation System", in 1999 with the help of the French deep-diving Remotely Operated Vehicle VICTOR 6000, and in 2001 with a video-guided Multiple Corer) gave an impression of the epibenthos, inhabiting the deepest parts of the Molloy Deep (Ritter & Soltwedel, unpubl data). The epibenthic community is characterised by three species: a holothurian (*Elpidia glacialis),* a scavenging amphipod (most probably *Uristes* sp.), and the sea anemone *Bathyphellia margaritacea* (Riemann-Zürneck, pers comm). The holothurian *E. glacialis* is by far the dominating epibenthic organism. Abundances of the 1-2 cm tall holothurian reached 20-30 ind/m^2. Similar numbers at Sites 1997, 1999 and 2001 let us infer that comparable densities occur all over the deepest part of the Molloy Deep. The abundance of the scavenging amphipod was 2-3 ind/m^2. *B. margaritacea* was found, only where hard substrate (clay aggregations?, wooden pieces, drop stones, human debris) occurred on the visually homogenous silty sediments.

Sampling and sample processing: Bottom samples were taken between 1997 and 2001 at 4 sites along a 15 km transect that crossed the Molloy Deep in NW-SE direction (Fig. 1). Water depths ranged from 5 416 to 5 569 m (Table I). Figure 2 shows the depth profile of the Molloy Deep floor along the transect, positions of
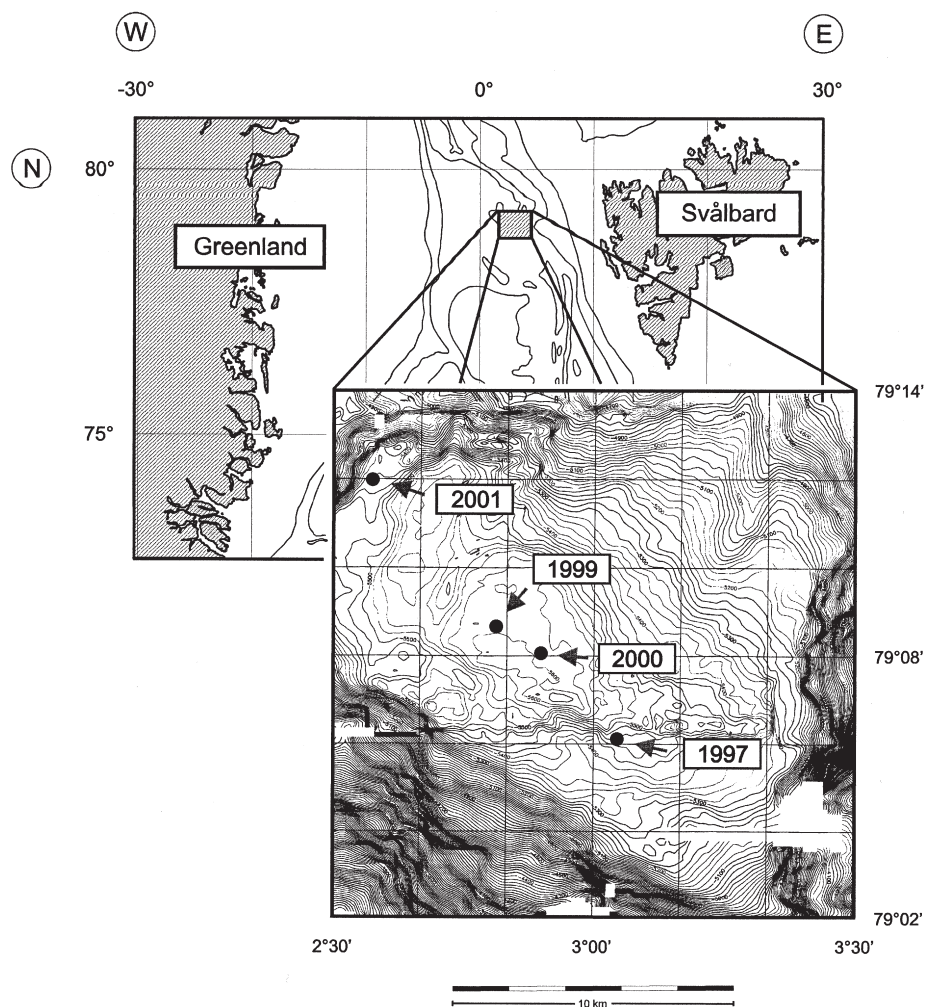
Fig. 1. – Sampling sites between 1997 and 2001 along a NW-SE transect crossing the Molloy Deep, Fram Strait.

the sampling sites, and distances between these sites. Inclinations between outer sampling sites and the bottom of the deep are about 3 degree.

Sediments were sampled with a Multiple Corer (MUC) (Barnett *et al.* 1984) in 1997, 2000 and 2001, and with the French Remotely Operated Vehicle (ROV) VICTOR 6000 in 1999 (Table I). Due to limitations in ship time only one MUC haul could be performed per sampling site. Subsamples for meiobenthic investigations were taken from the core samples by inserting small plastic disposal syringes of 2-cm inner diameter and 5-cm length with cut-off anterior ends. To minimise effects of small-scale variability in meiofauna dispersion at the different sampling sites, we analysed three "pseudo" replicates (Hurlbert 1984) from different MUC cores, and 4 "real" replicates from different push-cores sampled with the ROV, respectively.

Subsamples for meiofauna investigations were split into five 1-cm-thick layers and preserved separately in 4% buffered Formalin. In the laboratory, each sediment sample was washed through a set of sieves with different mesh sizes (500, 250, 125, 63 and 32 µm), stained with Rose Bengal, and sorted under a low-power stereo microscope. Organisms were identified to major taxa, i.e. Foraminifera, Nematoda, Polychaeta, Harpacticoida/

Nauplii. Taxa that occurred in minor quantities (e.g. Kinorhyncha, Isopoda, Gastrotricha, Bivalvia, Gastropoda) were pooled in *one* category, classified as the 'Others'.

Special attention was paid to the nematodes because they generally dominate the benthic metazoan meiofauna. To estimate nematode biomasses, 676 to 988 specimens covering all sieve size fractions and sediment layers were chosen from each of the four sampling sites and transferred to slides for further investigations. Nematode lengths (excluding the filiform tail) and widths were measured by a semi-automated image-analysis system (analySIS® 2.1). Nematode volumes and biomasses (wet weights) were calculated with equations given by Andrassy (1956). Nematoda wet weights were converted to carbon biomass by assuming that 100% wet weight corresponds to 12.4% carbon weight (Jensen 1984).

Subsamples (three "pseudo" replicates from each MUC; Hurlbert 1984) for abiotic and biotic sediment parameters (water content, sediment-bound pigments, as well as two biomass parameters, i.e. phospholipids and particulate proteins) were also taken with modified plastic syringes (1.2 or 2 cm in diameter, and 5 cm in length), and split in five 1-cm-thick layers to investigate vertical gradients in the sediment. Due to limitations in

ship time it was not possible to investigate environmental parameters for the 1999 samples.

Sediment water contents were estimated by weight loss of wet sediment samples dried at 60°C. Concentrations of chloroplastic pigments (chlorophyll *a* and its degradation products) were studied to estimate the amount of plant organic matter reaching the seafloor. Chloroplastic pigments were extracted in 90% acetone and measured with a TURNER fluorometer according to Yentsch & Menzel (1963) and Holm-Hansen *et al.* (1965). This method does not discriminate among individual breakdown products, but distinguishes intact chlorophyll *a* from the bulk of pheopigments. Because the pigment composition in sediments is not completely understood, the term chloroplastic pigment equivalents (CPE) for the bulk of pigments registered with this method is used. Differences in the "total microbial biomass" (TMB), comprising all organisms from bacteria to meiofauna (i.e. fungi, yeasts, flagellates, ciliates, protozoans and small metazoans) within the sediment samples, were assessed with biochemical procedures. Phospholipids (PL), a measure of the amount of cell-wall material, were determined by the method of Findlay *et al.* (1989) with slight modifications as described in Boetius & Lochte (1994). PL concentrations were used

to calculate the total microbial biomass (TMB) in terms of organic carbon by applying a conversion factor of 100 µmol P (g C)$^{-1}$ (Findlay & Dobbs 1993). Particulate proteins (PP) were determined to estimate the bulk of "living" plus "dead biomass", i.e. organisms and the proportion of detrital organic matter in the sediments. PP, operationally defined as γ-globulin-equivalents, were measured following instructions given by Greiser & Faubel (1988).

Statistical analyses: To test variances between stations we performed the Mann-Whitney U-test. SPEARMAN rank-correlation analyses were used to identify relationships between single parameters. All statistical analyses were performed using the computer program STATISTICA®.

RESULTS

Environmental parameters

Data on abiotic and biotic parameters for the uppermost centimetre of the sediment, and cumulative values for the upper 5 cm are summarised in Table I. Water contents, indicating the porosity of sediments, ranged between 54.6 and 63.1% (mean values for 0-5 cm). The highest values were found in the central part of the Molloy Deep (Site 2000). No significant differences among sampling sites were found for cumulative values of the bulk of sediment-bound pigments (CPE) for the upper 5 cm of the sediments (18.4-21.4 µg/5 cm³), but, in the south-easterly part of the deep (Site 1997), CPE concentrations in the uppermost centimetre of the sediments were significantly higher (p = 0.024) than those at the other sampling sites. The relative proportion of comparably "fresh" phytodetrital matter at Site 1997 was an order of magnitude greater (15.2% Chl. *a*) than at all other sampling sites, indicating a significant input of organic mat-
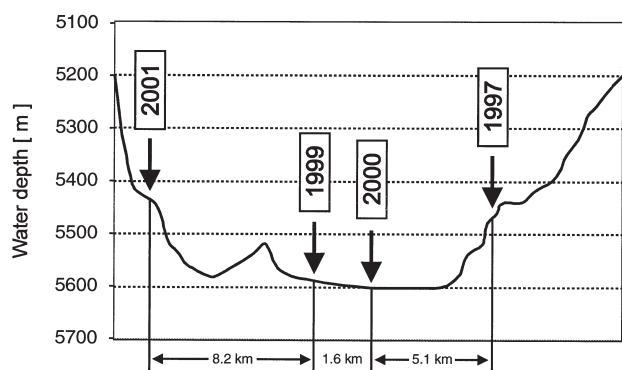

Fig. 2. – Bathymetry of the Molloy Deep along the NW-SE transect.

Table I. – Station data and environmental information. Values for abiotic and biotic parameters are for the uppermost centimetre with cumulative values for 0-5 cm in parentheses. % H$_2$O = water content of the sediments (*means for 0-5 cm. Chl.a = chlorophyll *a*. Pheo. = pheopigments. CPE = chloroplastic pigment equivalents (Chl.*a* + Pheo.). % Chl.*a* = relative proportion of chlorophyll *a*. FDA = bacterial exoenzymatic activity. PL = phospholipids. PP = particulate proteins.

Station Data						Porosity	Organic Matter Availability				Activity	Biomass	
Site [year]	Date [dd/mm]	Latitude [N]	Longitude [E]	Depth [m]	Gear	H$_2$O [%]	Chl.a [µg/cm³]	Pheo. [µg/cm³]	CPE [µg/cm³]	% Chl.a [%]	FDA [nmol/cm³ h]	PL [nmol/cm³]	PP [mg/cm³]
1997	04.08.	79°06.1'	3°02.6'	5445	MUC	66.7 (58.0)*	1.4 (2.5)	7.6 (17.1)	9.0 (19.6)	15.2 (12.8)	1,4 (1.8)	10.6 (25.7)	0.6 (2.9)
1999	03.07.	79°08.6'	2°49.5'	5552	ROV	--- (---)	--- (---)	--- (---)	--- (---)	--- (---)	--- (---)	--- (---)	--- (---)
2000	16.08.	79°08.2'	2°53.6'	5569	MUC	73.4 (63.1)*	0.1 (0.3)	6.5 (21.1)	6.6 (21.4)	1.6 (1.3)	1,3 (2.1)	18.1 (62.9)	0.2 (1.6)
2001	13.07.	79°12.0'	2°34.5'	5416	MUC	53.3 (54.6)*	0.1 (0.2)	6.0 (18.2)	6.1 (18.4)	1.2 (0.9)	1,2 (3.0)	14.1 (36.8)	0.3 (1.7)

ter from phytoplankton production shortly prior to sampling.

Bacterial exoenzymatic activities (FDA) in the uppermost centimetre of the sediments slightly (non-significantly) decreased in SE-NW, whereas FDA values for 0-5 cm showed an opposite trend. As for the water contents (see above), phospholipid concentrations were greatest in central parts and lower in peripheral areas of the deep. Concentrations of sediment-bound particulate proteins (PP) mirrored the distribution patterns of intact Chl. *a* in the sediments with significantly higher values (p = 0.024) in the SE part of the Molloy Deep, suggesting that enhanced PP concentrations also indicated comparably "fresh" phytodetrital matter at Site 1997.

Meiofaunal abundances and biomasses

Total meiofauna densities (including foraminiferans) at the different sampling sites ranged from $2\ 153 \pm 483$ ind/10 cm^2 to $2\ 968 \pm 613$ ind/10 cm^2 (Table II); the highest numbers were found at Site 1999, and the lowest values appeared at Site 2000. There was no trend in meiofauna densities along the transect: both the highest and lowest values were found at central sampling sites of the Molloy Deep (distance between stations only about 1.5 km). Peripheral sites in the NW and SE had intermediate abundances ($2\ 436 \pm 322$ ind./10 cm^2 and $2\ 636 \pm 420$ ind./10 cm^2, respectively).

Except for Site 1999, metazoan abundances within the sediment columns had distinct sub- surface peaks at 1-2 cm sediment depth inhabiting almost one third of the total metazoan assemblages (number of individuals in 0-5 cm = 100%), whereas foraminiferans generally declined with increasing sediment depth (Fig. 3). That rather high meiofauna densities found in 4-5 cm sediment depth (49-94 ind./10 cm^2) suggest that significant numbers of meiofauna live deeper than 5 cm in the sediment, but, in this study, no attempts were made to quantify these densities.

Free-living nematodes were by far the dominant taxon within the metazoans (91.7-95.8%) and therefore were of special interest. Nematode lengths and widths were measured to calculate nematode biomasses at the different sampling sites and for comparison with estimates of total microbial biomass (TMB) calculated from biochemical analyses (phospholipid measurements, see above). Mean nematode biomass varied from 0.026 to 0.037 μgC (Table III) and showed no significant differences between the four sampling sites. Total nematode biomass per sampling site generally increased from SE to NW sites (Table III). The relative proportion of nematode biomass from the TMB per site ranged between 0.51 and 1.17% (Table III), with lowest values at a central Molloy Deep site.

Faunal composition and size spectra

Meiobenthic assemblages of the Molly Deep were dominated by foraminiferans (48.5-59.9%) and nematodes (36.7-49.4%). The relative proportion of all other taxa ranged between 2.1 and 3.4% (mean values for polychaetes: 0.1%, harpacticoids: 1.0%, nauplii: 0.9%, others: 1.0%). A comparison of the faunal composition at the different sampling sites showed some clear trends. Relative proportions of nematodes along the transect declined from NW to SE, whereas that of foraminiferans increased in NW-SE direction (Fig. 4). An U-test confirmed significant differences (p = 0.049) in the relative abundance of nematodes and foraminiferans between the outer sites of the transect (Sites 1997 and 2001, respectively). The relative proportion of other meiofaunal taxa showed no significant differences between the sampling sites.

Table II. – Meiofauna densities (ind./10 cm^2) for the uppermost centimetre and cumulative values for 0-5 cm (in parentheses).

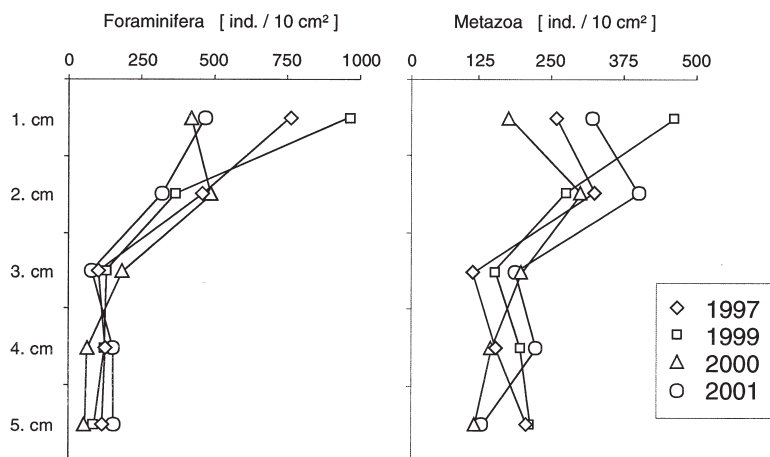| Year/ Site	Foraminifera	Nematoda	Polychaeta	Nauplii	Harpacticoidea	Others	Total Metazoans	Total Meiofauna
1997	763 (1582)	238 (966)	2 (2)	6 (16)	6 (29)	4 (41)	256 (1054)	1019 (2636)
1999	963 (1673)	427 (1187)	1 (1)	13 (28)	10 (31)	11 48	462 (1295)	1421 (2968)
2000	424 (1218)	168 (875)	0 (6)	2 (23)	4 (23)	1 (5)	175 (935)	599 (2153)
2001	466 (1183)	308 (1201)	0 (0)	4 (26)	4 (15)	4 (11)	322 (1253)	788 (2436)

Fig. 3. – Vertical profiles of foraminifera and nematodes in the uppermost 5 cm of the sediments (mean values from 3-4 subsamples).

Table III. – Relative proportion of nematodes of the total meiobenthos (i.e. including foraminiferans), mean biomass per nematode, total nematode biomass per site, and the proportion of the total microbial biomass estimated from biochemical analyses that is nematode biomass.

Year	rel. proportion of nematodes from the total meiobenthos [%]	mean biomass of nematodes [µg C]	total nematode biomass per site [µg C / 10 cm²]	total microbial biomass from biochemical analyses [mg C / 10 cm²]	rel. proportion of nematodes from TMB [%]
1997	36.65	0.029	29.95	2.57	1.17
1999	39.99	0.026	30.86	---	---
2000	40.64	0.037	32.38	6.29	0.51
2001	49.30	0.032	39.02	3.67	1.06

Size spectra for the different taxa from the various sampling site were rather similar. For foraminiferans, 95.3% of individuals appeared in size fractions 32-63 µm and 63-125 µm (42.8% and 52.5%, respectively). Nematodes showed a peak (55.7%) in size fraction 63-125 µm, with rather similar proportions in size fractions 32-63 µm and 125-250 µm (24.5% and 17.5%, respectively); only about 2.5% of nematodes were found in sieve sizes > 250 µm. Approximately 90% of all other meiofaunal taxa appeared in size fractions < 250 µm (i.e. 32-63 µm: 22.7%; 63-125 µm: 31.8%; 125-250 µm: 36.4%).

DISCUSSION

Quality of the data set

Due to limitations in ship time it was impossible to sample the different sites during a single expedition. Results presented in this study derive from samples obtained in four different years (1997-2001) with sampling dates from the beginning of
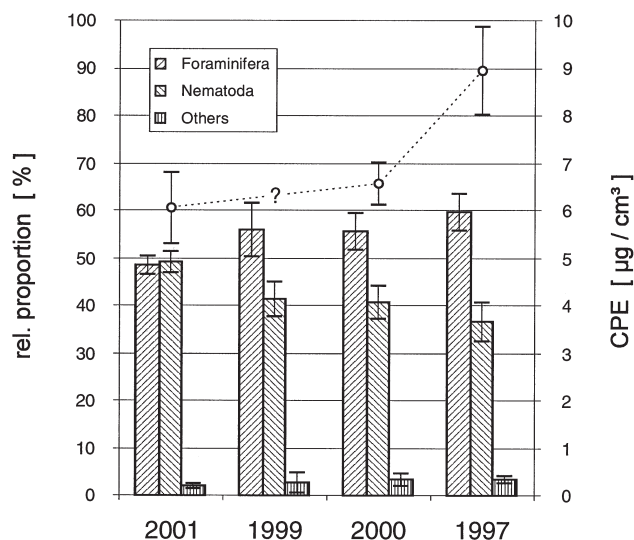

Fig. 4. – Relative proportion of foraminifera, nematoda and other meiofauna taxa along the NW-SE transect in relation to concentrations of sediment-bound chloroplastic pigments (? = no pigment data for Site 1999).

July to the middle of August. Therefore, a comparison of data from the different sampling sites could be affected by seasonal and interannual variability,

for example in phytoplankton production or organic-matter sedimentation. The time lag between the most recent input of organic matter to the seafloor and the sampling date might be of crucial importance. Gooday (1988), Pfannkuche (1993) and Gooday *et al.* (1996) described a rapid and pronounced response of deep-sea foraminiferans to the pulsed input of phytodetrital matter in some areas of the NE Atlantic. Lambshead *et al.* (1995) and Galéron *et al.* (2001) reported that meiobenthic organisms move vertically in the sediment in response to the impoverishment of surface layers and the downward mixing of organic matter by the bioturbation of larger benthic organisms. De Bovée *et al.* (1990) even detected changes in the taxonomic composition of the metazoan meiofauna at deep sampling sites (> 2000 m) following the productive phase in the north-western Mediterranean Sea. Soltwedel *et al.* (1996) found indications that deep-sea nematode assemblages might show growth responses to an episodic food supply. A measurable response in metazoan abundances following the input of particulate organic matter, however, has yet to be observed in oceanic regions (Pfannkuche 1993, Gooday *et al.* 1996, Galéron *et al.* 2001).

Sediment sampling during 1997, 2000, and 2001 was done with a multiple corer (MUC). In 1999, however, we were able to use a Remotely Operated Vehicle (ROV) and push-corers to sample. As deduced from the comparison of box corers and multiple corers, different sampling equipment can influence quantitative estimates of the deep-sea meiobenthos (Bett *et al.* 1994). Compared to the use of any kind of coring gear lowered to the seafloor at a certain speed (thereby producing a bow wave), push-coring with the help of an ROV is probably the best way of getting undisturbed sediment samples from the deep sea. In 1999, the ROV allowed targeted sampling of areas of the seabed that appeared visually to be perfectly undisturbed, i.e. also without any kind of (larger) biogenic structuring. In contrast, MUC hauls delivered a set of ("pseudo") replicates generally including cores with plain sediments and sediment surfaces modified by larger organisms. Therefore, push-coring with a ROV, and the use of a MUC for sediment sampling might lead to different results.

Looking at vertical gradients of meiobenthic organisms we, in fact, found striking differences between ROV and MUC samples. Whereas at Site 1999, metazoan densities gradually decreased with increasing sediment depth, all other (MUC) sampling sites had subsurface peaks for metazoans abundance at 1-2 cm depth. A bow-wave effect of the MUC might have blown away the uppermost millimetres of the sediments (including associated organisms) and therefore could be responsible for reduced densities in the uppermost sediment layer at Sites 1997, 2000, and 2001. Subsurface peaks

were, however, only found for metazoans, whereas foraminiferans generally decreased with increasing sediment depth. Because all abiotic and biotic parameters investigated in this study also did not show consistent subsurface peaks at any of the sampling sites, we suggest that the observed differences in meiofauna gradients are not caused by different sampling methods but come out for other reasons, as discussed in one of the following sections.

Meiobenthic assemblages in the Molloy Deep

Our investigations discovered extremely high meiofaunal densities for all sites visited along the transect across the Molloy Deep (mean: ~ 2 500 ind./10 cm^2). Meiobenthic abundances showed no correlation with station depth, and no general trend along the transect. Looking at relative proportions of foraminiferans and metazoans at the different sites, however, we found significantly increasing values for foraminiferans in south-easterly direction, and an opposite trend for nematodes (Fig. 4). Differences among sites in organic-matter supply (food source) to the benthos might explain these trends. Although the pigment inventory of the sediments (CPE values for the upper 0-5 cm of the sediments) showed no significant differences between sampling sites, pigment concentrations in the uppermost centimetre of the sediments (and especially the relative proportion of Chl. *a*) increased in south-easterly direction. These differences in food-supply markers could be explained by differences among sites in ice-cover because of generally enhanced primary production in ice-free areas. According to long-term observations, the marginal ice zone is, for most of the year, located in the Molloy Deep area. The probability of ice-free surface water increases towards the southeast.

Higher relative proportions of protozoans in those areas could be explained by their ability to react comparably fast to any kind of perturbation (including an episodic input of potential food source; Gooday & Lambshead 1989); protozoans (as well as bacteria) can multiply in hours and can also activate dormant cells and resting spores. This ability might be an advantage in areas with pulsed organic matter input (e.g. the SE part of the Molloy Deep), compared to almost permanently ice-covered regions with a more regular (and comparably low) food supply to the benthos, as expected for the north-western part of the Molloy Deep.

Except for Site 1999, vertical gradients of nematodes (and also other metazoans) in the sediment generally revealed distinct subsurface peaks in 1-2 cm depth, whereas densities of foraminiferans, in general, continuously decreased with increasing sediment depth. The occurrence of subsurface peaks

can probably be explained by a high predation pressure by dense herds of holothurians (*Elpidia glacialis*), intensively reworking the upper few millimetres of the sediments. Extremely high abundances of *E. glacialis* (20-30 ind./m^2) were found for Sites 1997 and 1999 (results from photo and video observations; Ritter & Soltwedel, unpubl data), but were also assumed for the two other sites. Highly motile metazoan taxa (e.g. nematodes) are able to escape predation by vertical migration to deeper sediment horizons, whereas most foraminiferans are rather immobile and only passively moved, e.g. by the bioturbation of larger benthic organisms. This fact might result in different vertical distribution patterns within the sediments. No explanation, however, could be given for the lack of a subsurface peak for metazoans at Site 1999.

Looking at size spectra for meiofauna communities of the Molloy Deep, we found no significant differences between the four sites, but, the proportion of individuals in the smallest sieve size fraction (< 63 μm) was relatively high (30-38%). Using the same sizes of sieves (and also including foraminiferans), Schewe & Soltwedel (1999) and Schewe (2001) found similar high proportions (24-40%) in the size class < 63 μm for a number of sampling sites from the central Arctic Ocean (depth range: 864 to 4 187 m). Relative high proportions of small meiofauna individuals in both studies were explained by a tendency towards dwarfism in an area of reduced food availability to the benthos, due to limited primary production in a permanently ice-covered region. As indicated by concentrations of sediment-bound pigments and particulate proteins, food availability in the Molloy Deep should be up to 20-times higher than those at sampling sites in the central Arctic Ocean. Thus, in contrast to suggestions originally given by Thiel (1975), reduced food availability is obviously not the only factor explaining dwarfism in deep-sea meiofauna communities. When comparing meiofauna size spectra with biochemical data indicating food availability (quantity and quality) in Atacama Trench off Chile (7 800 m), Danovaro *et al.* (2002) came to the same conclusion and presented different suggestions to explain the disproportion between meiofauna sizes and food availability. To our mind, pressure-related effects on metabolic processes, and selection of small-sized barophilic or barotolerant organisms are the most probable explanations, but, further investigations are needed to confirm these hypotheses.

Direct biomass measurement were carried out for nematodes exclusively. As expected from sieve size spectra, mean biomasses per nematode were comparably low (Soltwedel *et al.* 2000) and showed no significant differences between sampling sites, however, as the relative proportion of nematodes from the total biomass clearly increased

in north-westerly direction (see above), total nematode biomass per site followed the same trend. The relative proportion of nematode biomass from the total microbial biomass (TMB) estimated from biochemical analyses (concentrations of phospholipids, indicating the total biomass of the bulk of sediment-inhabiting organisms from bacteria to meiofauna) revealed lowest values at a central Molloy Deep site (Table III). Highest TMB values together with intermediate densities of foraminiferans at this site presume a relatively high proportion of nanofauna organisms, i.e. fungi, yeasts, flagellates and ciliates, in the central Molloy Deep.

Meiobenthos in ultra-deep regions of the World Ocean

For logistical reasons (e.g. insufficient cable lengths, lack of availability of deep-diving instruments, limitations in ship time), information on the meiobenthos from abyssal depths deeper than 5 000 m, and especially from hadal regions of the worlds oceans is still rather limited. Some 30 ultra-deep sites have been visited to investigate meiobenthic communities, most of them situated in subtropical and tropical regions (Table IV). Except for investigations by Vinogradova *et al.* (1993) in the Orkney Trench (Antarctica) our study is, to our knowledge, the only work on ultra-deep meiobenthic communities from higher latitudes.

Table IV summarises data on densities and taxonomic composition for ultra-deep meiobenthic assemblages from deep-sea basins and abyssal plains (20 sites) and deep-sea trenches and fracture zones (13 sites). Information on methods (i.e. lower mesh size limits, total sediment depth investigated) were included for better assessment of data comparability. Most investigations focussed on the metazoan meiofauna; only 7 studies included meiobenthic foraminiferans.

Due to lack in standardisation of sampling and sorting techniques, a comparison of meiobenthic standing stocks in the literature is fraught with problems. The use of different sampling devices, subsampling strategies and extraction methods makes a direct comparison of meiofauna data given by different authors quite a challenge. Due to known trends in dwarfism of deep-sea fauna, lower sieve size limits play an especially crucial role for meiobenthos abundance estimates. When comparing results from this study with data from the literature (see below), we tried to take into account these limitations.

A comparison with results from other regions revealed surprisingly high meiofauna densities for the Molloy Deep; mean numbers were about 10-times higher than in other ultra-deep regions of the world ocean. Similarly high numbers were only found by Shirayama & Kojima (1994) for the Japan Trench. These authors investigated the metazoan

Table IV. – Comparison of meiofauna densities from different deep-sea sites > 5 000 m water depth, separated into investigations of abyssal plains and basins, and investigations of trenches and fracture zones. Lower Size Limit refers to the opening of the smallest sieve used. FORAM = foraminifera. NEMA = nematodes. META = metazoan meiofauna. MEIO = total meiofauna.

Authors	Area	Region	Water Depth [m]	Sediment Depth [cm]	Lower Size Limit [µm]	FORAM Abundances [ind./10cm²]	NEMA Abundances [ind./10cm²]	META Abundances [ind./10cm²]	MEIO Abundances [ind./10cm²]
Abyssal Plains, Basins:									
Dinet (1973)	SE Atlantic	Angola Basin	5170	5	40	-	294	313	-
Ingole et al. (2000)	Central Indian Ocean	Central Indian Basin	5300 - 5330	10	45	-	20 - 24	35 - 45	-
Kamenskaya (1991)	Southern Atlantic	Namibia Abyssal Plain	5230	5	90	-	4	6	-
Kaneko et al. (1997)	Central Pacific	Central Pacific Basin	5300	3	30	-	95	101	-
Parulekar et al. (1982)	NW Indian Ocean	Arabien Basin	5100	10	44	-	9	12	-
Parulekar et al. (1982)	NW Indian Ocean	Somali Basin	5400	10	44	-	5	7	-
Parulekar et al. (1992)	Central Indian Ocean	Central Indian Basin	5250 - 5750	?	63	-	30 - 34	50 - 55	-
Rachor (1975)	NE Atlantic	Tejo Abyssal Plain	5111	5	50	-	23	28	-
Rachor (1975)	NE Atlantic	Canary Basin	5510	6	50	-	76	103	-
Shirayama (1984)	Western Pacific	Eastern Marianen Basin	5820	10	37	87	78	89	176
Shirayama (1984)	NW Pacific	Northwestern Pacific Basin	5580 - 5730	10	37	39 - 214	31 - 257	38 - 317	77 - 317
Sibuet et al. (1989)	NE Atlantic	Cape Verde Basin	5190	?	40	-	-	87	-
Snider et al. (1984)	Central Pacific	Central Pacific Basin	5800	25 - 55	42	100	92	102	202
Soltwedel & Thiel (1995)	Eastern Atlantic	Guinea Basin	5213	5	42	112	193	219	331
Soltwedel (1993)	SE Atlantic	Angola Basin	5027	5	42	156	93	115	271
Thiel (1975)	NE Atlantic	Iberian Basin	5500	4	40	-	-	210	-
Thiel (1975)	Western Indian Ocean	Somali Basin	5000	4	40	-	-	50	-
Thiel (1975)	Central Pacific	Central Pacific Basin	5000	4	40	-	-	100	-
Tietjen et al. (1989)	NW Atlantic	Hatteras Abyssal Plain	5411	15	44	-	85	114	-
Woods & Tietjen (1985)	Caribian Sea	Venezuela Basin	5050	6	44	-	44	49	-
Trenches, Fracture Zones:									
Danovaro et al. (2002)	SE Pacific	Atacama Trench	7800	6	20	-	5072	6378	-
George & Higgens (1979)	NW Atlantic	Puerto Rico Trench	8570	7	62	-	12	17	-
Olu et al. (1997)	W Atlantic	Barbados Trench	5000	?	?	-	790 - 8336	845 - 8438	-
Renaud-Mornant & Gourbault (1990)	Eastern Pacific	Clarion-Clipperton Fracture Zone	5015	2.5	40	-	78	82	-
Saidova (1970)	NW Pacific	Kurile-Kamtchatka Trench	5000 - 9000	1	?	19 - 94	-	-	-
Shirayama (1984)	NW Pacific	Ogasawara Trench	8260	10	37	132	389	430	562
Shirayama & Kojima (1994)	NW Pacific	Japan Trench	5370 - 7460	3	63	-	357 - 470	373 - 488	-
Sibuet et al. (1989)	Central Atlantic	Vema Fracture Zone	5100	?	40	-	-	130	-
Soltwedel (unpubl. data)	Central Atlantic	Romanche Fracture Zone	7628	5	42	43	152	155	-
Richardson et al. (1995)	NW Atlantic	Puerto Rico Trench	8380	20	44	-	66	69	-
Thiel (1979)	Western Pacific	Philippine Trench	9807	?	40	125	?	30	155
Tietjen et al. (1989)	NW Atlantic	Puerto Rico Trench	7460 - 8189	15	44	-	41 - 93	44 - 96	-
Vinogradova et al. (1993)	Antarctica	Orkney Trench	5150 - 6160	3 - 4	40	-	5 - 6	7 - 11	-
This Study	Arctic Ocean	Molloy Deep	5445 - 5569	5	32	1183 - 1673	875 - 1201	935 - 1295	2153 - 2968

meiofauna with a lower size limit of 63 μm and found 373-488 ind./10 cm². When adapting our results from the Molloy Deep to the same size range (simply by subtracting the number of meiofauna individuals found in mesh size class 32-63 μm), we found comparably high densities (205-311 ind./10 cm²). Such an adaptation of data, of course, assumes identical meiofauna size spectra for the different sampling site. Because we do not have information on the entire size spectra from the Japan Trench, these calculations are somewhat speculative.

To our knowledge only one paper (Danovaro *et al.* 2002) reports higher meiofaunal densities than those given in this study. These authors found metazoan meiofauna densities of 6 378 ±3 061 ind./10 cm² for samples from the Atacama Trench (7 800 m) in the upwelling sector off Chile, SE Pacific (Table IV). The lower sieve-size limit used in their study was 20 μm, but even when adapting their results to the lower size limit we used (assuming that more meiofauna individuals would be found when further reducing the lower size limit), metazoan meiofauna abundances in the Atacama Trench were still 6-times higher than those of the Molloy Deep and thus by far the highest abundances ever measured for deep-sea

sites. Although Olu *et al.* (1997) presented comparably high metazoan meiofauna densities from a cold-seep area seaward of the Barbados accretionary prism at about 5 000 m water depth (Table IV), these data should not be considered for direct comparison with results from "normal" deep-sea regions.

When plotting meiofauna abundances from the papers listed in Table IV against water depth, we found major differences between stations from basins or abyssal plains, and trenches or fracture zones (Fig. 5). Whereas there is no obvious relationship between metazoan densities and water depth on the plains (Fig. 5A), data from trenches show an exponential decrease of individuals with increasing depth (Fig. 5B). The weak correlation between metazoan meiofauna densities and water depth on abyssal plains could be explained by the varying productivity of the overlying water (and a subsequently varying food supply to the benthos) in the different regions considered in this comparison. The same should hold for trench regions, however, because of the specific topographic settings of trenches (it should make a difference, whether the samples came from the central parts or from the flanks of a trench) variability should probably be even greater. The significant correlation (R^2 =
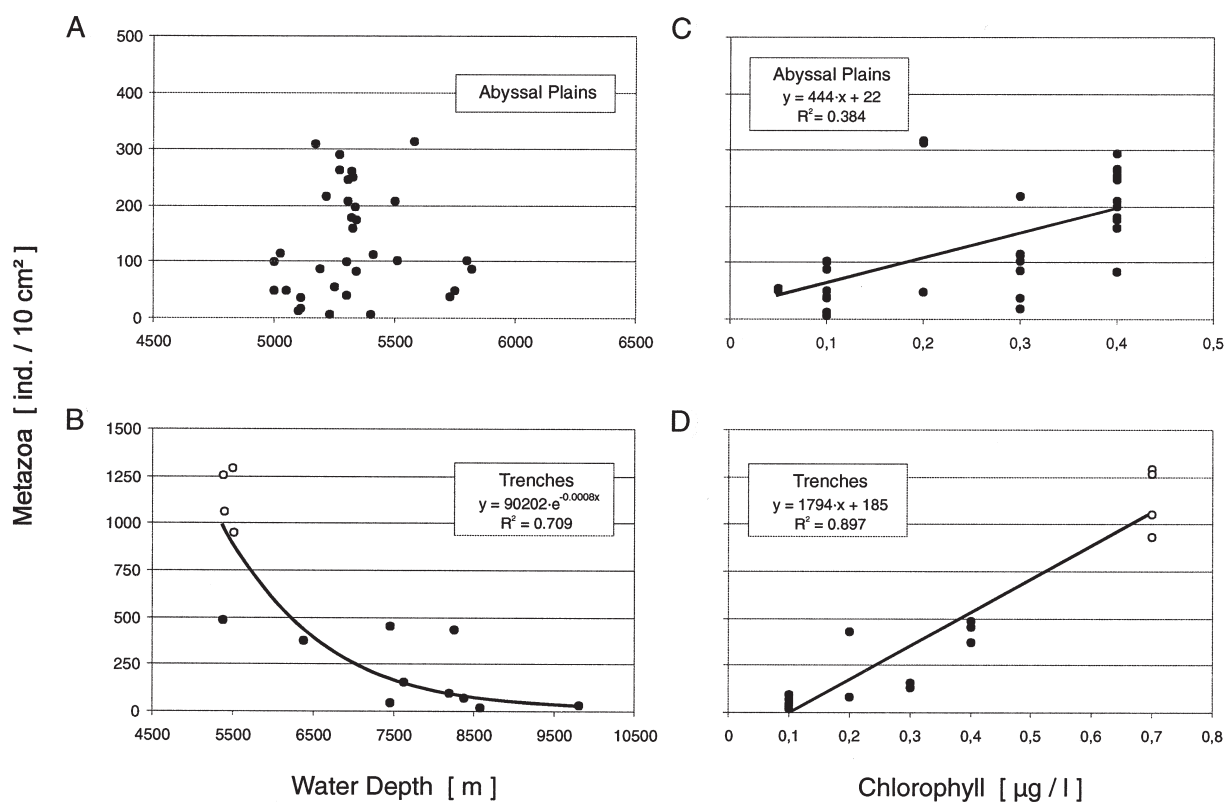

Fig. 5. – Graphs of metazoan meiofaunal densities against water depth and primary productivity data (World Ocean Atlas 1998) for abyssal plains (a, c) and trenches (b, d) on the basis of faunal data listed in Table IV (data of Olu *et al.* 1997 and Danovaro *et al.* 2002, excluded). The open circles indicate the data from this study.

0.709) between meiofauna numbers and water depth in the data set for trenches (Table IV, neglecting the extremely high values for Atacama trench and the Barbados cold seep area; Fig. 5B) was probably caused by the immense range in water depth (~ 5 000-9 800 m) covered by the different studies.

Benthic standing stocks are known to generally decrease with increasing water depth, and a number of studies suggest that food supply is one of the major controlling factors (e.g. Thiel 1983, Sibuet *et al.* 1989, Vincx *et al.* 1994). Bathymetric settings of the Molloy Deep and the special hydrographic conditions in the area of investigation together with enhanced primary productivity associated with processes in the marginal ice zone favour a strong input of particulate organic matter to the seafloor. The whole system might act as a huge sediment trap accumulating organic matter at the bottom of the Molloy Deep, consequently allowing a rich benthic community with surprisingly high meiofauna numbers but also allowing high standing stocks of megafaunal organisms (e.g. dense herds of small holothurians; see above). Comparably high remineralisation rates (3.74 mg C/m² d), obtained during the deployment of a free-falling grab respirometer in summer 2000 in the central Molloy Deep (Soltwedel unpubl data), and steep oxygen gradients in the uppermost sediment layers obtained with a micro-profiling unit in summer 2002 (Sauter pers comm) confirm the picture of an unusually eutrophic region at hadal depths.

Only a very few investigations on meiofauna assemblages from ultra-deep regions included parameters assessing environmental settings, e.g. food availability, grain sizes, oxygen contents of bottom waters. To study relationships between meiofauna densities and food availability at ultra-deep sites, we compared primary-production estimates based on satellite-derived data (World Ocean Atlas 1998) from the different regions with the meiofauna data given in the papers listed in Table IV. Assuming that local primary productivity supports benthic assemblages in the same region (which for current-driven lateral advection might not always be the case; Soltwedel 1997), we found good correlations ($R^2 = 0.384$ and $R^2 = 0.897$, respectively, when neglecting data of Olu *et al.* 1997 and Danovaro *et al.* 2002) between chlorophyll concentrations in the upper water layers and meiofauna numbers at abyssal depths (Fig. 5C), and trenches (Fig. 5D), further demonstrating that food supply plays a major role in determining meiobenthic standing stocks.

CONCLUSIONS

In comparison with other abyssal and hadal regions of the World Ocean, meiofauna abundances in the Molloy Deep were extremely high. Analyses of biogenic sediment compounds confirmed comparably high amounts of organic matter in the sediments, presumably favouring increased faunal densities and biomasses. Variations in organic matter availability correlate with changes in the taxonomic composition of the meiofauna. Subsurface peaks in meiobenthic abundances are most probably due to substantial disturbance and/or predation by dense herds of small holothurians (*Elpidia glacialis*), obviously inhabiting the entire Molloy Deep in very high numbers. The total meiofauna of the Molloy Deep consisted of relatively small organisms compared to other/shallower oceanic regions, which could not be explained by reduced food availability to the benthos. Pressure-related effects on metabolic processes, and the selection of small-sized barophilic or barotolerant organisms might explain the occurrence of comparably small meiofauna individuals in the Molloy Deep.

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