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Recolonisation of new habitats by meiobenthic organisms in the deep Arctic Ocean: an experimental approach

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Abstract Commercial exploitation and abrupt changes of the natural conditions may have severe impacts on the Arctic deep-sea ecosystem. The present recolonisation experiment mimicked a situation after a catastrophic disturbance (e.g. by turbidites caused by destabilised continental slopes after methane hydrate decomposition) and investigated whether the recolonisation of a deep-sea habitat by meiobenthic organisms is fostered by variations innutrition and/or sediment structure. Two "Sediment Tray Free Vehicles" were deployed for 1 year in summer 2003 at 2,500 m water depth in the Arctic deep-sea in the eastern Fram Strait. The recolonisation trays were filled with different artificial and natural sediment types (glass beads, sand, sediment mixture, pure deep-sea sediment) and were enriched with various types of food (algae, yeast, fish). After 1 year, meiobenthos abundances and various sediment-related environmental parameters were investigated. Foraminifera were generally the most successful group: they dominated all treatments and accounted for about 87 % of the total meiobenthos. Colonising meiobenthos specimens were generally smaller compared to those in the surrounding deep-sea sediment, suggesting an active recolonisation by juveniles. Although experimental treatments with fine-grained, algae-enriched sediment showed abundances closest to natural conditions, the results suggest that food availability was the main determining factor for a successful recolonisation by meiobenthos, and the structure of recolonised sediments was shown to have a subordinate influence.

Keywords Recolonisation · Foraminifera · Sediment tray free vehicle · Arctic deep-sea · Meiobenthos · Long-term in situ experiment

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Introduction

The Arctic deep-sea is characterised by extreme environmental conditions with ambient temperatures around the freezing point and exceptionally low food supply (Bluhm et al. 2011). Benthic organisms are well adapted to the habitat in which they live, and an abrupt change of the environmental conditions may have severe effects on the benthic community. Such a sudden change might act like a disturbance and can be caused by turbidites, benthic storms, food pulses from depositing blooms, sunken vertebrate carcasses and human-induced disturbances like deep-sea mining, gas and oil drilling. Against this background, recolonisation and disturbance experiments can be a valuable approach to assess possible effects of anthropogenic and climate change-related effects on vulnerable deep-sea ecosystems. Colonisation studies with suitable experimental devices, performed over time scales of a few months, over a year up to five years, have already been conducted for several years (Grassle 1977; Thistle 1981; Desbruyères et al. 1985; Grassle and Morse-Porteous 1987; Alve 1999). Compared to the colonisation of azoic shallow-water sediments, the recolonisation of azoic deep-sea sediment is a slow process (Snelgrove et al. 1992). The recolonisation by meio- and macrofauna of the deep-sea floor after physical, biological and human-induced disturbances could be observed in other studies, but the

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colonising population size and diversity was lower compared to the natural community (Kitazato 1995; Ingole et al. 2005). In particular, benthic communities of polar regions are known to need more time to recover from disturbances compared to those of lower latitudes (Gutt and Starmans 2001; Veit-Köhler et al. 2008). However, there are only few studies that investigated recolonisation rates of the deep-sea floor by benthic organisms on a long-term scale of at least 1 year and with regard to the effect of varying food sources as well as sediment types (e.g. Kitazato 1995; Kanzog et al. 2009). Comparable investigations on the recolonisation success of meiobenthic organisms in an Arctic environment are completely lacking. The colonising fauna is characterised by a higher proportion of opportunistic species compared to the surrounding deep-sea sediment (Grassle and Morse-Porteous 1987). Here, it is expected that especially Foraminifera have an advantage over metazoans to react rapidly to changing environmental conditions, since they are characterised by short life-cycles and the ability to respond efficiently to strong food pulses (Schewe and Soltwedel 2003).

The present in situ experiment investigated the recolonisation of azoic sediments by meiobenthic organisms at the Arctic deep-sea observatory HAUSGARTEN. To study the preferences for recolonisation by meiobenthos communities on various habitat characteristics like available types of food or differently structured sediments after a disturbance, different food sources were provided in varying quality and quantity and mixed into various sediments types. While defaunated deep-sea sediment, sediment-sand mixture and pure sand represented natural sediment types, glass beads simulated an artificial environment and acted as a reference in this approach. Two "Sediment Tray Free Vehicles" were deployed in 2,500 m water depth for a period of 1 year on the deep seafloor west of Svalbard. To differentiate between the meiobenthic recolonisation fauna and the meiobenthic community of adjacent undisturbed deep-sea sediments, results were compared with data from the surrounding deep-sea sediment.

In the context of this experiment, we defined a disturbance as a catastrophic event defaunating the environment of almost any organism. This study addresses the questions (1) whether specific taxa have an advantage over others to respond after a disturbance situation in an Arctic deep-sea environment and (2) whether specific food or sediment types will promote the recolonisation of meiobenthic organisms.

Materials and methods

Investigation area

The recolonisation experiment was conducted at the central experimental site of the deep-sea long-term observatory HAUSGARTEN (79°5′N/4°2′E) in the eastern Fram Strait (Fig. 1). Situated on the continental slope west of Svalbard, the investigation area is affected by the inflow of relatively warm nutrient-rich Atlantic Water of the West Spitsbergen Current. The sampling area is situated in the Marginal Ice Zone and thereby affected by strong seasonal pulses of organic matter (Soltwedel et al. 2005).

Experimental design

Two "Sediment Tray Free Vehicles" (STFV; IFREMER design, Desbruyères et al. 1985) were deployed at 2,500 m water depth on the shelf west of Svalbard (79°04′N; 4°13′E) for 1 year in June 2003 during the cruise leg ARK XIX/3c with the RV *Polarstern*. The STFVs were composed of a stable rack carrying four identical round trays (diameter 80 cm, height 13 cm) (Fig. 2). Each tray contained four round chambers (227 cm^2 per chamber), which were covered by a grid (5 mm mesh size) to prevent an interference by macro- and megafauna.

Each STFV carried a current metre fixed at circa 5 m above the bottom. During descent to the deep-sea floor, the trays were closed with lids, which were re-opened mechanically after landing. For a more detailed description of the mechanism, see Kanzog and Ramette (2009).

The chambers were filled with different natural and artificial sediments. In the first STFV (Experiment 1) (Fig. 3a), each tray contained one chamber filled with glass microbeads (diameter 250–500 μm; MHG Strahlanlagen GmbH, Düsseldorf, Germany), one chamber filled with commercially available sand (grain sizes 1–2 mm), one chamber filled with a mixture of the sand and deep-sea sediment at a ratio of 50:50 (sediment mixture), and one chamber filled exclusively with deep-sea sediment. Deep-sea sediments used for the experiments were collected with a multiple corer (MUC) at the same location as the experiments in 2,500 m water depth. To obtain sediments almost depleted of biomass, only sediment horizons deeper than 10 cm were used for the experiments. Coulter counter analyses to analyse sediment structure showed a composition of 43 % silt (4–63 μm), 37 % sand (≥63 μm) and 20 % clay (<4 μm). For additional defaunation, the natural as well as the artificial sediments were frozen at −30 °C for about 48 h.

In addition to the varying sediment types, the chambers of the four trays of Experiment 1 were enriched with different food sources. Simulating natural sedimentation events, the food sources were placed at the sediment surface. The different sediments of each chamber in the first tray were enriched with 300 ml of a solution of the microalgae *Nannochloropsis sp.* (2.4 mg C cm^{-3}; Z + L, Langen, Germany). Sediments in chambers of the second tray were enriched with commercially available yeast (26 mg C cm^{-3}). Sediments in chambers of the third tray

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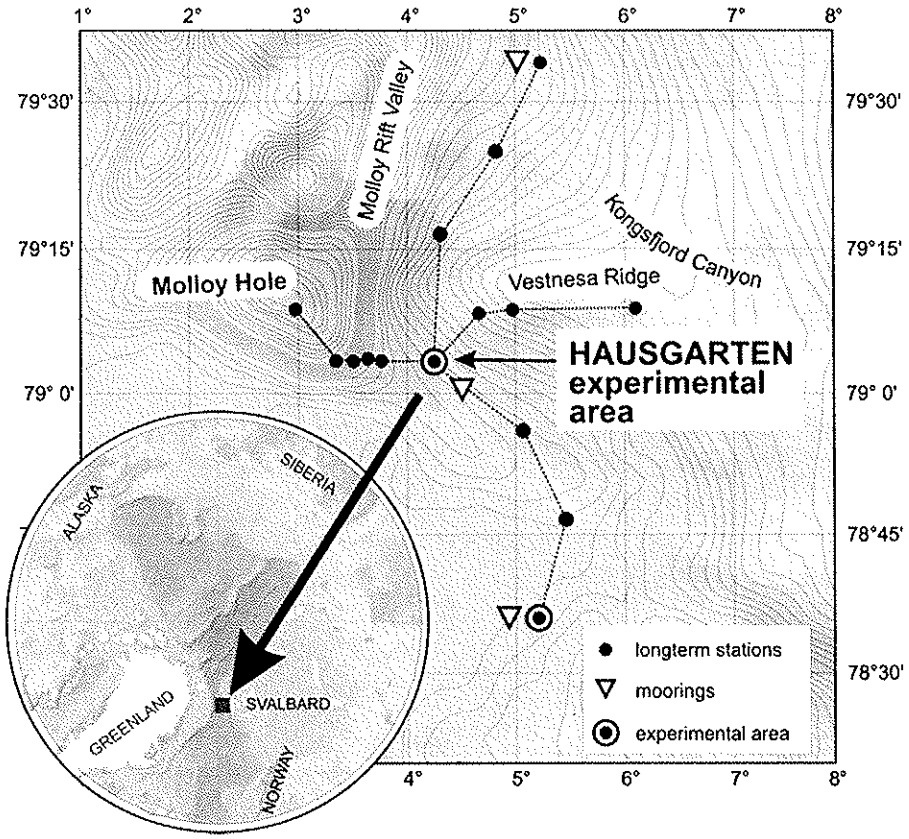

Fig. 1 The investigation area at HAUSGARTEN in the eastern Fram Strait, west of Svalbard

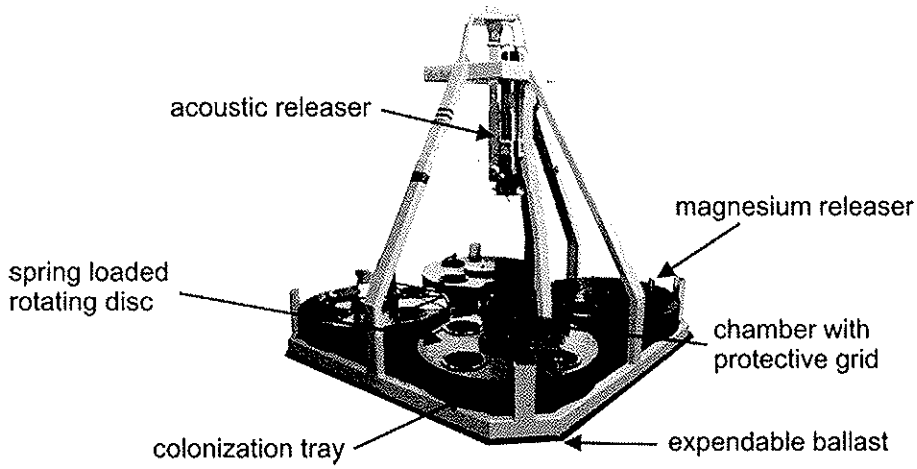

Fig. 2 Sediment tray free vehicle (STFV) consisting of a stable rack with four recolonisation trays, which were composed of four separate round chambers covered by a grid

were enriched with 80 g cod fish (33 mg C cm^{-3}), and those of the fourth tray served as a control and were not enriched with any substrate.

In the second STFV (Experiment 2) (Fig. 3b), two chambers of each tray were filled with deep-sea sediments. Furthermore, one chamber was filled with sand, and one chamber contained a mixture of sand and deep-sea sediment at a ratio of 50:50 (sediment mixture).

To quantitatively simulate a varying phytodetritus input, sediments in Experiment 2 were enriched by algae suspensions with different concentrations of the microalgae *Nannochloropsis sp.*: 150-ml detritus solution (1.2 mg C cm^{-3}) was used for the sediments of the first tray, 75 ml (0.6 mg C cm^{-3}) for the second tray and 15 ml (0.12 mg C cm^{-3}) for the third. The sediments of the fourth tray served as a control and were not enriched with any substrate.

To analyse the natural conditions of the deep-sea environment that surrounded the deployed experiments, two virtually undisturbed sediment samples were taken at the same position as the two STFV with a multiple corer

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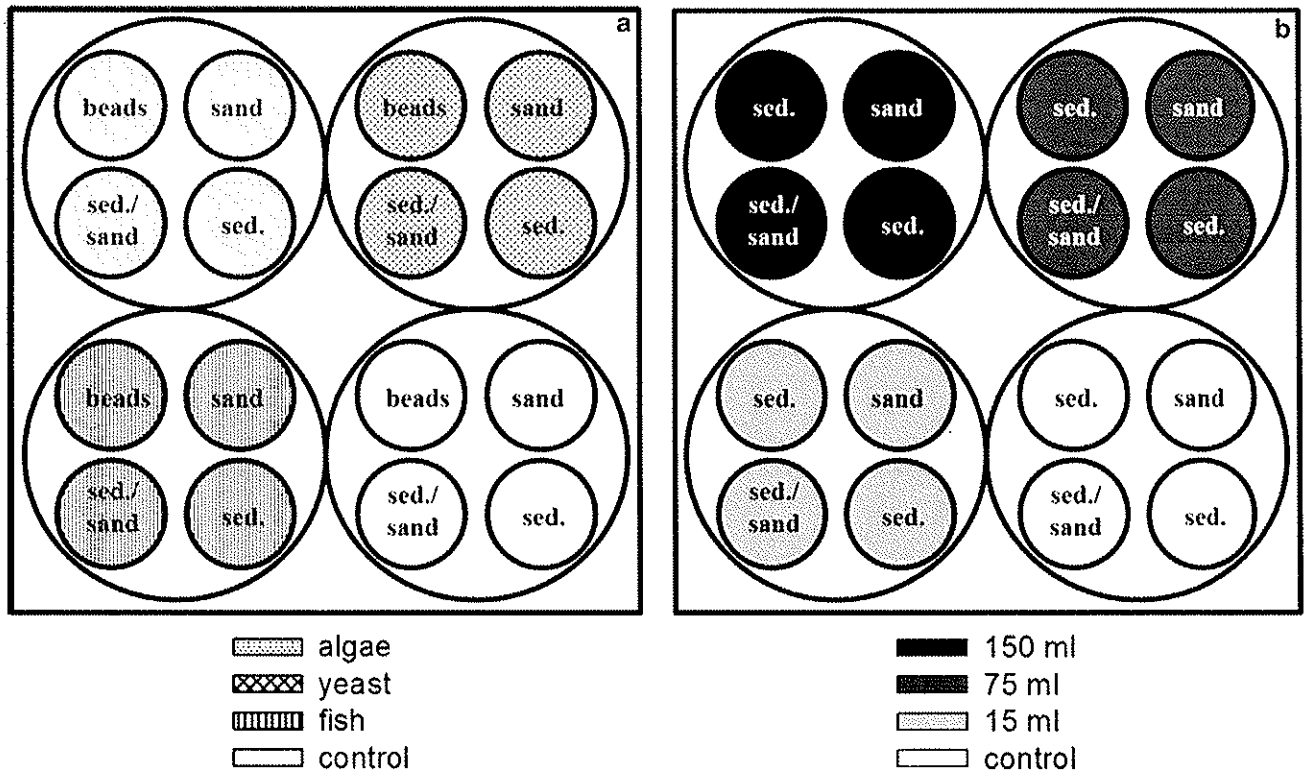

Fig. 3 Schematic overview of Experiment 1 (**a**) and 2 (**b**). For Experiment 1, chambers of the different trays were enriched with different organic food sources and sediments, and for Experiment 2, chambers were enriched with different microalgae concentrations and sediments

(MUC). Serving as a reference to the data gained from the recolonisation experiment, the first sediment centimetre of these samples was used for meiobenthic investigations and biochemical analyses of environmental parameters.

Sampling and sample processing

After the recovery of the STFV, one subsample of the upper sediment centimetres was taken for each investigated parameter from each treatment with plastic syringes (volume/sediment horizon: 3.24 cm^3) with cut-off anterior ends. For meiobenthos, the topmost sediment centimetre from each syringe was cut horizontally and preserved in 4 % formalin until further investigation. For biochemical analyses, sediment samples were stored at −20 °C until further processing.

Meiobenthic investigations

A low-power stereo microscope was used to identify meiobenthic organisms in the sediment samples. Subsamples were stained with Rose Bengal and washed through a series of sieves with different mesh sizes (500, 250, 125, 63 and 32 μm). Only stained, per definition-living organisms were counted. Organisms were identified to major taxa, for example Nematoda, Harpacticoidea/Nauplii, Polychaeta, Gastrotricha, Bivalvia and Turbellaria. Foraminifera were determined at least down to family level, in most cases also down to genus level. Taxonomic analyses of Foraminifera were initially also statistically investigated. Because those approaches gave no significant results, we decided to exclude them from further description and focused the distinction for multivariate statistics on calcareous, chitinous and agglutinated Foraminifera shell-forms as well as metazoan organism types. However, all raw data of taxonomic analyses are uploaded to the open access database PANGAEA and are available via its persistent identifier (doi:10.1594/PANGAEA.785298).

Biochemical analyses of environmental parameters

Food availability at the seafloor can be estimated by determining the concentration of sediment-bound chlorophyll *a* (Chl *a*) and its degradation products, the phaeopigments (Phaeo) (Thiel 1982). Pigments were extracted with 90 % acetone and measured with a Turner Fluorometer (Yentsch and Menzel 1963). The bulk of pigments registered with this method were termed chloroplastic pigment equivalents (CPE; Thiel 1978).

The capability of bacteria to cleave available organic matter in a certain time period is referred to as their potential hydrolytic activity. Bacterial enzymatic activities

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(FDA) were determined by measuring exo-enzymatic esterase turnover rates using the fluorogenic substrate fluorescein-di-acetate (FDA) according to the method by Köster et al. (1991).

Phospholipids were extracted from the sediments, and afterwards, phosphate groups were solubilised and stained. Measurements were conducted with a photometer according to a method of Findlay et al. (1989). Phospholipid concentrations were used to calculate the total microbial biomass (TMB) by applying a conversion factor of 100 μmol P g^{-1} C (Findlay and Dobbs 1993).

For ash-free dry weight (AFDW), the dried sediment subsamples were oxidised (ashed) in a muffle furnace at high temperature and re-weighed. The loss upon oxidation was referred to as AFDW.

Relative water content (% H2O) of sampled sediments was determined by subtraction of AFDW from sediments' wet weight.

Data analysis

The STATISTICA software (StatSoft 1995) was used to perform a Spearman rank-correlation to investigate the relationship between meiofauna abundances and selected environmental parameters. PRIMER V 6.1.6 software (Clarke and Gorley 2006) and procedures were applied to examine the effects of treatments from both STFVs on the meiobenthic composition in relation to recolonised sediments and available food types. Non-metric multidimensional scaling (MDS) plots were based on matrices that were computed using the normalised Euclidean distance of the environmental data. For multivariate community analyses, we used the ANOSIM method to falsify the hypothesis that there is no effect of the various sediment and food treatments on meiobenthic recolonisation. The BioEnv method was used to test the influence of various "environmental" factors on multivariate patterns among samples.

Results

As measured by the current metre attached to the STFVs, mean current velocity during the recolonisation experiment was about 10 cm s^{-1}. In the different sediments of both recolonisation experiments, no visual or olfactory signs of anoxia were found.

Biochemical analyses for Experiment 1

Chlorophyll *a* concentrations ranged between 0.002 μg cm^{-3} in the sediment mixture enriched with fish and 0.91 μg cm^{-3} in the chamber filled with sand of the algae-treatment (Fig. 4a). The lowest phaeopigment concentration of 0.22 μg cm^{-3} was found in the sediment mixture enriched with fish, whereas the highest concentration of 3.94 μg cm^{-3} was observed in the sand chamber of the fish-treatment (Fig. 4b). The chlorophyll *a* concentrations in all algae-treatments and in the fish-treatment of the sand chamber exceeded the concentration found in the natural deep-sea sediments from the control site (reference, 0.31 μg cm^{-3}). In contrast, phaeopigment concentrations were generally lower in all experimental treatments compared to the reference samples (17.29 μg cm^{-3}).

Bacterial activity (FDA) ranged between 0.02 and 2.52 nmol cm^{-3} h^{-1} in the sediments of Experiment 1 (Fig. 4c). The lowest activity was found in the deep-sea sediment of the algae- and fish-treatments, and the highest bacterial activity was determined in the sediment mix of the yeast-treatment. However, bacterial activities in the sediments of Experiment 1 were between 2.6 and 5.1 nmol cm^{-3} h^{-1}; lower compared to the surrounding deep-sea sediment (reference, 5.12 nmol cm^{-3} h^{-1}).

Phospholipids (PL) indicating the total microbial biomass (TMB) in the sediment samples ranged between 5.32 and 240.87 μg C cm^{-3} in the sediments of Experiment 1 (Fig. 4d), with the lowest microbial biomasses in the chamber filled with deep-sea sediment of the control-treatment and the highest concentration in the chamber with deep-sea sediment of the yeast-treatment. PL concentrations found in the reference samples (95.31 μg C cm^{-3}) were higher compared to all experimental treatments except for the deep-sea sediment, sand and sediment mixture of the yeast-treatment and the chamber with sand of the fish-treatment.

Biochemical analyses for Experiment 2

In Experiment 2, chlorophyll *a* concentrations ranged between 0.003 μg cm^{-3} in the sediment mixture of the control-treatment and 0.84 μg cm^{-3} in the sediment mixture of the 150-ml treatment (Fig. 5a). Therefore, the concentration of the latter treatment was almost three times higher compared to the chlorophyll *a* concentration found in the surrounding deep-sea sediment (reference, 0.31 μg cm^{-3}). Chlorophyll *a* concentrations observed in the 300-ml treatment of Experiment 1 were similar to the concentrations found in Experiment 2, except for the chamber filled with sand. The lowest phaeopigment concentration (0.27 μg cm^{-3}) was found in the sediment mixture of the control-treatment, and the highest in the sediment mixture of the 15-ml treatment (2.86 μg cm^{-3}) (Fig. 5b). Phaeopigment concentrations that were found in Experiment 2 were comparable to those found in Experiment 1 and were also considerably lower compared to the surrounding deep-sea sediment (reference, 17.29 μg cm^{-3}).

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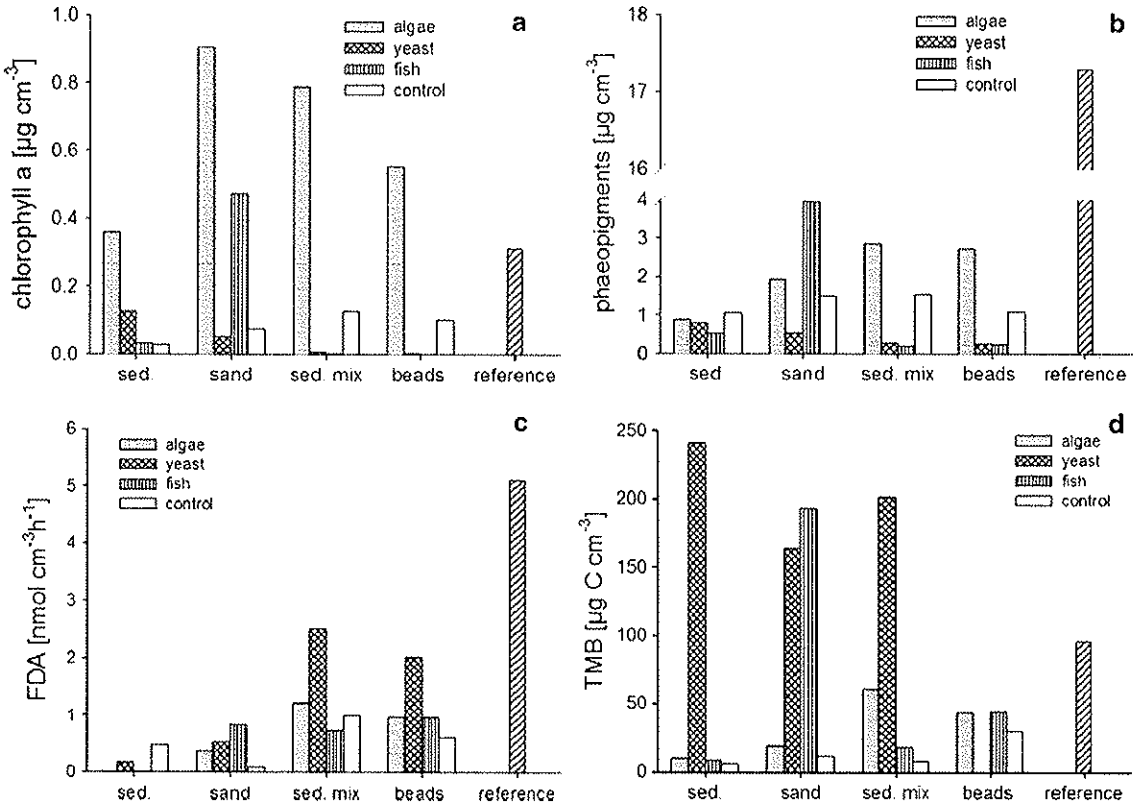

Fig. 4 Environmental parameters in the sediments in the different chambers of Experiment 1 and the surrounding deep-sea sediment (reference). Concentrations of chloroplastic pigment equivalents [µg cm^{-3}], chlorophyll *a* (**a**) and phaeopigments (**b**), bacterial enzymatic activities (FDA) [nmol cm^{-3} h^{-1}] (**c**) and total microbial biomass (TMB) [µg C cm^{-3}] (**d**)

In the sediments of Experiment 2, bacterial activity (FDA) ranged between 0.16 nmol cm^{-3} h^{-1} in the chamber with sand of the control-treatment and 1.27 nmol cm^{-3} h^{-1} in the sediment mixture enriched with 75 ml phytodetritus (Fig. 5c). Bacterial activity was generally lower in all sediments of Experiment 2 compared to the surrounding deep-sea sediment (reference, 5.12 nmol cm^{-3} h^{-1}) but was comparable to the activity found in the 300-ml treatment of Experiment 1.

Total microbial biomass (TMB) ranged between 20.26 µg C cm^{-3} in the chamber filled with sand of the 75-ml treatment and 91.50 µg C cm^{-3} in the sediment chamber of the 150-ml treatment (Fig. 5d). The highest concentrations were similar to those found in the surrounding deep-sea sediments (reference, 95.31 µg C cm^{-3}). PL concentrations found in the sediment of Experiment 2 were comparable to concentrations found in the 300-ml treatment of Experiment 1.

Meiobenthos recolonisation patterns

After 1 year of deployment, the meiobenthos abundances in both experiments were similar to those observed in the surrounding deep-sea sediments.

The highest meiobenthos abundances were found in chambers, which contained deep-sea sediments enriched with algae, that is, the 300-ml treatment in Experiment 1 (566.1 ind. 10 cm^{-2}) and the 150-ml treatment in Experiment 2 (581.1 ind. 10 cm^{-2}). The surrounding deep-sea sediment revealed 654 individuals per 10 cm^2. Foraminifera were dominant in all treatments of both experiments. They occurred with a relative abundance of 87.2 ± 13.5 % of the total meiobenthos and constituted a higher proportion of the meiobenthos than in the reference samples. Calcareous Foraminifera were most abundant followed by Foraminifera with chitinous and agglutinated shells. In all samples, 78–94 % of the Foraminifera were found in the 63 µm size class. In the surrounding deep-sea sediment, approximately 73 % of the Foraminifera occurred in the 63 and 32 µm fraction. Metazoans were dominated by nematodes with a relative abundance of 6.6 ± 21.8 % of the total meiobenthos. In the following, Foraminifera and metazoan abundances will be presented separately.

Experiment 1

After 1 year of incubation, only a few bones of the cod fish carcasses were left in the fish-treatment. The lowest

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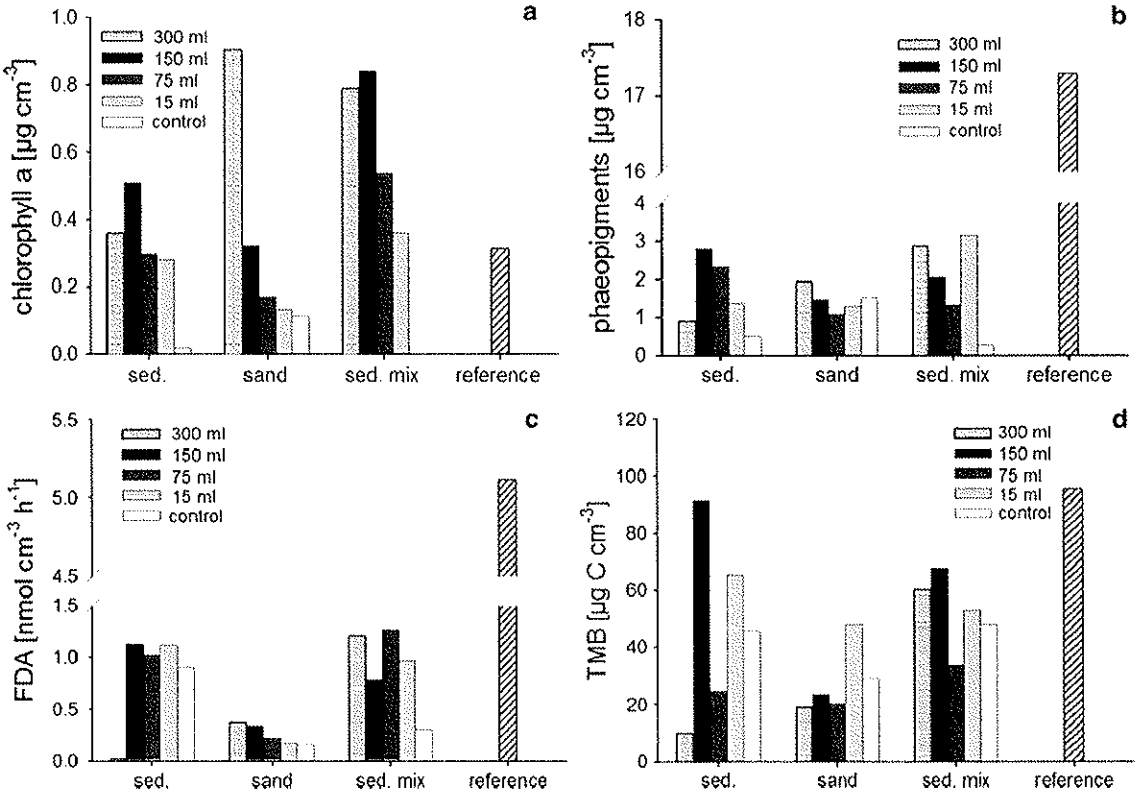

Fig. 5 Environmental parameters in the sediments of the different chambers of Experiment 2 and the surrounding deep-sea sediment (reference). For the purpose of comparison, the results of the 300-ml algae solution of Experiment 1 were included in this graph. Concentrations of chloroplastic pigment equivalents [µg cm^{-3}] chlorophyll *a* (**a**) and phaeopigments (**b**), bacterial enzymatic activities (FDA) [nmol cm^{-3} h^{-1}] (**c**) and total microbial biomass (TMB) [µg C cm^{-3}] (**d**)

Foraminifera abundances were observed in the chamber with deep-sea sediment of the fish-treatment (13 ind. 10 cm^{-2}) (Fig. 6a). The highest Foraminifera abundance were found in the chamber filled with deep-sea sediment of the algae-treatment (556 ind. 10 cm^{-2}), which was even higher than in the surrounding deep-sea sediment (reference, 441 ind. 10 cm^{-2}).

Generally, the numbers of metazoans were low compared to the recolonisation by Foraminifera. Metazoan abundances ranged between zero individuals in the glass beads of the control-treatment and 217 ind. 10 cm^{-2} in the chamber with sand of the fish-treatment, which was as high as in the surrounding deep-sea sediment (reference, 213 ind. 10 cm^{-2}) (Fig. 6b). This sample was dominated by Harpacticoidea and their nauplii.

Experiment 2

Foraminifera abundances in Experiment 2 were the highest in the chamber with deep-sea sediment of the 150-ml treatment (559 ind. 10 cm^{-2}) and comparable to the individual numbers found in Experiment 1 in the 300-ml treatment (556 ind. 10 cm^{-2}) (Fig. 7a). Foraminifera numbers exceeded the abundances observed in the surrounding deep-sea sediment (441 ind. 10 cm^{-2}). Metazoan abundances in Experiment 2 were highest in the 15-ml treatment of the chambers filled with deep-sea sediment (28 ind. 10 cm^{-2}) and considerably lower compared to the surrounding deep-sea sediment (213 ind. 10 cm^{-2}) (Fig. 7b). The lowest metazoan abundances were found in the control-treatment of the sediment chamber (2 ind. 10 cm^{-2}). Overall, the sum of all metazoans in Experiment 2 (215 ind. 10 cm^{-2}) was lower than in Experiment 1 (520 ind. 10 cm^{-2}).

Similarity analysis

Similarities between the different treatments of both experiments are presented with multi-dimensional scaling (MDS) plots (Fig. 8). Environmental parameters determined for the sediments of each tray were set in relation to meiobenthos abundances in the different chambers, which were indicated by their relative bubble sizes.

For Experiment 1, MDS generally revealed a clustering of the sediments that were enriched with the same nutrition. The controls clustered together with three chambers of the fish-treatment (Fig. 8a). All sediments of these chambers were characterised by relatively low meiobenthos abundance.

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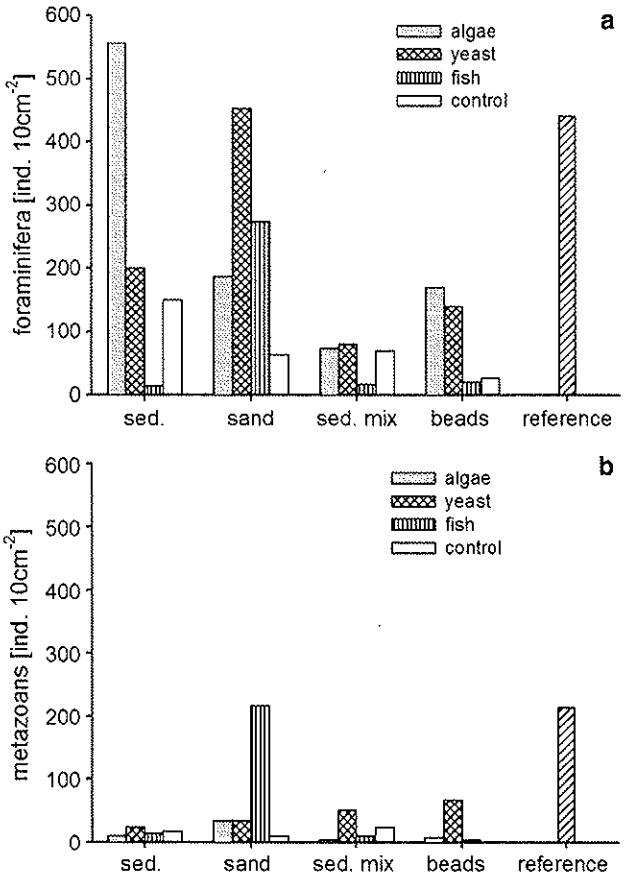

Fig. 6 Absolute numbers of meiobenthos [ind. 10 cm^{-2}] [Foraminifera (**a**) and metazoan (**b**)] for the first sediment centimetre. Meiobenthos data of Experiment 1 and the surrounding deep-sea sediment (reference)

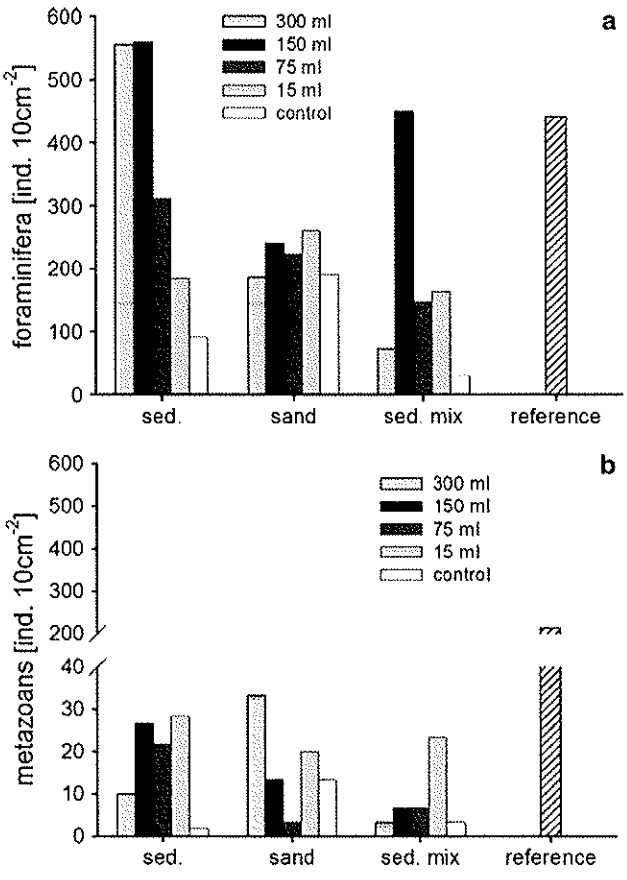

Fig. 7 Absolute numbers of meiobenthos [ind. 10 cm^{-2}] [Foraminifera (**a**) and metazoan (**b**)] for the first sediment centimetre. Meiobenthos data of Experiment 2 and the surrounding deep-sea sediment (reference). For the purpose of comparison, the abundance from the 300-ml treatment was included from STFV 1

The MDS for the data of Experiment 2 showed a relatively heterogeneous distribution of bubbles with similar size, except for a clustering of all chambers filled with sand (Fig. 8b).

Dissimilarities between treatments (ANOSIM)

The statistical significance of multivariate dissimilarities between the various treatments of both trays was tested with the ANOSIM-procedure (analysis of similarity), which is a permutation-test based on Clarkes R statistics (Clarke and Warwick 2001).

We tested the hypothesis that pairwise similarities between the groups of treatments were higher than between the samples from different groups. To do this, the samples were grouped in the food-type treatments (detritus, yeast, fish and blank) and for a second test in sediment-type treatments (deep-sea sediment, sediment mixture, pure sand and artificial glass beads).

In this context, the global test of samples from different food treatments revealed a significant global R of 0.404 ($p = 0.1$ %), which means that the similarity between investigated groups of food types was generally higher than between single samples. A more detailed pairwise test showed that detritus treatments significantly differed from fish-treatments with an R of 0.819 ($p = 0.1$ %), while less distinct but still significant differences were seen for comparisons of the detritus with yeast ($R = 0.390$) and for fish with blank groups ($R = 0.375$). All other groupings (detritus–blank, yeast–blank, yeast–fish) were not significantly distinguishable.

The same tests with groupings of several sediment types showed no significance on the global test level ($R = 0.142$, $p = 3.1$ %), which means that sediment types generally have no influence on the meiobenthic assemblages. Only a pairwise comparison between grouped samples of glass and deep-sea sediment samples revealed reasonable differences between both groups ($R = 0.496$, $p = 1$ %). All other pairings (glass–sand, glass–mixture, sand–mixture, sand–deep-sea sediment, mixture–deep-sea sediment) showed no significant dissimilarities between pairings ($R < 0.25$).

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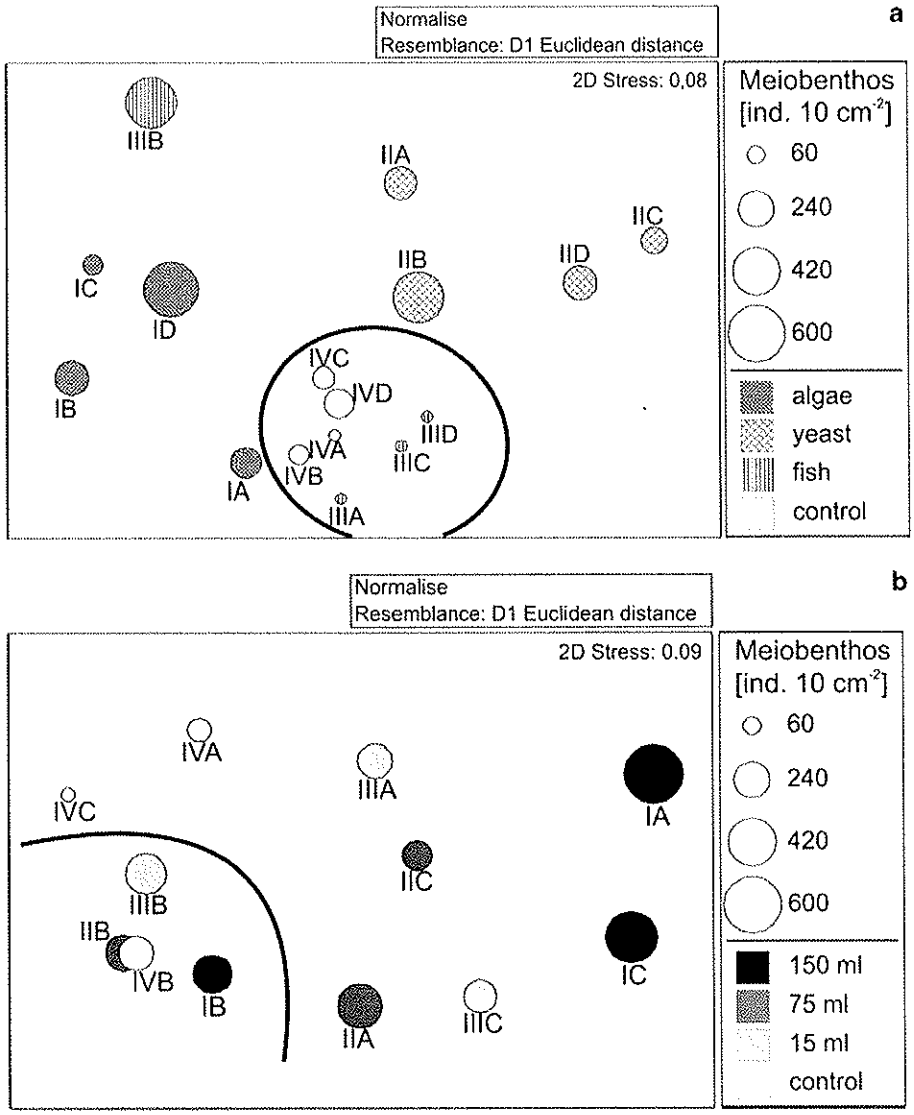

Fig. 8 MDS plots of the environmental data determined for all chambers of both trays. Environmental parameters are superimposed bubble plots of meiobenthos abundances. *T* tray *I–IV*; *A*, *B*, *C*, *D* chambers. **a** Experiment 1 (*TI* algae; *TII* yeast; *TIII* fish; *TIV* control; *A* glass beads; *B* sand; *C* sediment mixture; *D* deep-sea sediment). **b** Experiment 2 (*TI* 150 ml algae; *TII* 75 ml algae; *TIII* 15 ml algae; *TIV* control; *A* deep-sea sediment; *B* sand; *C* sediment mixture)

Relation of meiobenthos recolonisation to environmental parameters

To gain deeper insight into linkages between meiobenthic assemblages and environmental parameters, we used the BioEnv module of the Primer software package. Parameters like sediment-bound chloroplastic pigments were used as indicators for the availability of fresh food, while bacterial esterase activity (FDA) and total microbial biomass (TMB) represented proxies of potential bacterial food for meiobenthic organisms. Sediment water content and ash-free dry weight (AFDW) were used to characterise the different sediment treatments. Unfortunately, the BioEnv analysis revealed no statistically significant linkages; however, it at least provided indications that parameters representing food match most closely with meiobenthic patterns. The combination of chlorophyll *a* and total microbial biomass showed the best match ($p = 0.151$), while water content and AFDW did not even show up in the list of potential parameter combinations.

Because BioEnv tests revealed no satisfying results concerning the influence on meiobenthic recolonisation patterns, we used a more direct attempt to analyse whether environmental parameters show at least a general relationship with the total abundances of recolonising meiobenthos (total Foraminifera and metazoa). In this context, a Spearman rank-correlation (Table 1) revealed the strongest correlations between meiobenthos abundances and chlorophyll *a* ($p = 0.0003$) and phaeopigments ($p = 0.0023$). In contrast, no significant correlation was observed between meiobenthos abundances and bacterial activity (FDA) or phospholipids indicating total microbial biomass.

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Table 1 Spearman rank-correlation coefficient (R) and *p* value of the Spearman rank-correlation between meiobenthos abundances and environmental parameters [bacterial enzymatic activities (FDA), chlorophyll *a*, phaeopigments, chloroplastic pigment equivalents (CPE), total microbial biomass (TMB)] for both experiments

	R	*p* value
Meiobenthos/FDA	0.1680	0.3580
Meiobenthos/chlorophyll *a*	0.6002	0.0003
Meiobenthos/phaeopigments	0.5206	0.0023
Meiobenthos/CPE	0.5404	0.0014
Meiobenthos/TMB	0.2763	0.1258

Discussion

Natural disturbances such as strong currents, turbidites, food pulses and anthropogenic impacts like deep-sea mining or exploitation for oil and gas can be the reason for massive perturbation of the deep-sea floor and cause changes in the surface conditions of the sediments (Hollister et al. 1984; Gage and Tyler 1991). This study mimicked such a disturbance-like situation by deploying sediments of varying structures enriched with different food sources.

One year after deployment, meiobenthos abundances in some treatments enriched with food were almost comparable to abundances found in the natural surrounding habitat. In contrast, other recolonisation studies and disturbance experiments found slow recolonisation rates and low species diversities in a disturbed area compared to the natural community (Foell et al. 1990; Kitazato 1995; Ingole et al. 2005). However, food availability in the present experiments conducted in a strongly seasonal deep-sea environment, which is at least occasionally highly oligotrophic, probably promoted the recolonisation of the sediments by meiobenthos (Ingole et al. 2005). In addition, the mesh covers of individual chambers of the present experiment prevented predation by macrofauna and thus facilitated the recolonisation by meiobenthic organisms (Grassle and Morse-Porteous 1987).

Benthic Foraminifera have short life-cycles and effectively use food as soon as it is available, which probably gave them an advantage over metazoans when colonising the STFVs. However, they are also supposed to be rather immobile outside of their habitats and attached to substrate, either sediment or phytodetritus (Gooday and Lambshead 1989), which makes their comparably high recolonisation rates in the present experiments surprising: since the experimental trays were slightly elevated from the seafloor, it would be necessary to either actively swim into the chambers or to drift into them. With a relative proportion of about 87 % of the total meiobenthos, Foraminifera, observed in the present study, exceeded the occurrence under natural conditions. A study by Gooday (1986) found Foraminifera comprised 30–70 % of the total meiobenthos population in an undisturbed deep-sea environment in the Northeast Atlantic. For Arctic deep-sea environments, a proportion of 60–70 % is known (Schewe and Soltwedel 2003). Foraminifera dominated in all sediments and treatments and seemed to utilise the sudden food supply in the experimental sediments with an advantage over metazoans (Linke 1992; Nomaki et al. 2005). Individuals with calcareous shells were most abundant in this study, which is in accordance with their predominance in natural plain and unstructured deep-sea sediments (Schewe and Soltwedel 2003). In addition, the present study showed a higher occurrence of small Foraminifera (≤63 μm) in sediments of the experiments compared to the surrounding deep-sea sediment. Small or juvenile Foraminifera were thin and transparent. They probably unfurled their filose pseudopodia, which helped them to drift like meroplanktonic organisms with the measured mean current velocity of 10 cm s^{-1} into the chambers of the experiments (Myers 1963; Alve 1999). Therefore, Foraminifera might have had an advantage over metazoans in overcoming the distance between the chambers and the seafloor. For instance, nematodes are considered to be weak swimmers, and in deep-sea environments, they are known to migrate through the sediments rather than through the water column (Fegley 1985; Ullberg and Ólafsson 2003). Sediment tray experiments are often presumed to suffer from artifacts due to their distance from the seafloor (Levin and Smith 1984, Smith 1985). However, the recolonisation by meiobenthic organisms in the present experiment supports the idea that meiobenthic organisms are also able to colonise areas isolated from the seafloor.

Even though metazoan abundances were comparably low in the experiments, we found a recolonisation by metazoans with nematodes as the dominant group. Nematodes also were the dominant group in other disturbance experiments and in the natural deep seafloor (Schewe and Soltwedel 2003; Ingole et al. 2005). Clearly, the sediments of the yeast- and fish-treatment showed higher numbers of metazoans compared to the sediments enriched with algae and the control-treatment. The yeast and fish used in this experiment had a higher carbon content compared to the algae. The type of organic matter probably determined the occurrence of specific taxa (Snelgrove et al. 1992), and it is presumed that the recolonisation of metazoans is supported by a food supply with a high carbon content (Nomaki et al. 2005). As metazoans were dominated by nematodes and harpacticoid copepods in some treatments, these organisms seemed to be especially capable of utilising the high carbon food sources. Deposit feeders are known to be the dominant feeding type among nematode communities at the deep-sea station HAUSGARTEN (Hasemann 2006).

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Therefore, small particles like yeast, bacteria growing on the fish carcasses and small fish pieces probably were a highly appropriate food source for these nematodes.

Harpacticoid copepods and their nauplii occurred in relatively high abundances in the sand enriched with fish of Experiment 1. Harpacticoid copepods are known to scavenge on fish (Seifried and Dürbaum 2000; Willen 2006). In addition, harpacticoids are considered interstitial fauna, which may explain their relatively high abundance in the sand chamber (Giere 1993). The occurrence of nauplii suggests again an advantage for juvenile stages regarding the recolonisation of the trays. Some benthic harpacticoids are able to swim small distances, which might be another reason for the unexpected high recolonisation of these organisms in the chamber filled with sand (Thistle and Sedlacek 2004).

Food availability seemed to be beneficial for a successful recolonisation of azoic sediment by meiobenthic organisms (Bertram and Cowen 1998). This assumption was supported by the low meiobenthos numbers in the sediments, which were not enriched with food. In addition, Experiment 2 revealed a generally positive correlation of increasing meiobenthic abundances with increasing algae concentrations. A correlation between increasing organic carbon concentration and increasing individual densities could also be shown by similar studies (Menot et al. 2009). The availability of phytodetritus is crucial for a successful recolonisation by Foraminifera (Pascal et al. 2008), and as expected, the highest abundances were observed in the deep-sea sediment enriched with algae solution. The highly significant Spearman rank-correlation between chloroplastic pigment equivalents and meiobenthos confirmed this observation. Even though the deep-sea sediments had been deep-frozen before filling in the chambers, there were still most likely remains of dead organisms (Thistle 1981). These remains could act as additional food or at least carbon source, which would be another explanation for the relative successful recolonisation of deep-sea sediment by meiobenthos in the experiments (Snelgrove et al. 1996). Control sediments were not enriched with any nutrition. Nonetheless, a low recolonisation of these sediments by meiobenthic organisms could be observed, which suggests a vertical food input from the water column into the experiments. This assumption is confirmed by a low but measurable concentration of sediment-bound chloroplastic pigments in the control-treatments of both experiments.

Besides phytodetritus, bacteria are considered to be an important food source for Foraminifera (Pascal et al. 2008). Indeed, Kanzog (2008) found decreased microbial biomass and esterase activity after 1 year in the present experiment, which might be explained by predation by meiobenthos. In addition, total microbial biomass (TMB) found in the present study was low compared to the surrounding deep-sea sediment, which again might point to a strong predation by meiobenthos and Foraminifera in particular.

Clustering in the multivariate analyses of the sediments enriched with the same nutrition supported the determining effect of food on the meiobenthos abundances. In contrast, a study by Urban-Malinga et al. (2005) found sediment structure to be the main factor that determined meiobenthos abundance. Similarity analysis of Experiment 2 of the present study showed a clustering of all chambers filled with sand, which were mainly colonised by harpacticoid copepods. Our investigations revealed that food was the main forcing factor for the recolonisation by meiobenthic organisms. Nevertheless, it was shown that the composition of the recolonised sediments also had at least a certain influence in determining the meiobenthos composition. In particular, the availability of natural sediments such as sand or deep-sea sediment seemed to be crucial, since glass beads as an artificial substrate were only poorly recolonised.

Conclusion

This colonisation experiment demonstrated the effect of quality and quantity of food supply as well as sediment structure on the recolonisation of meiobenthic organisms in an Arctic deep-sea environment. Food availability promoted recolonisation by meiobenthic organisms, and especially fine-structured sediments enriched with phytodetritus seemed to be beneficial and prompted meiobenthos abundances similar to the surrounding deep-sea sediment. Overall, food seemed to be the major driving force for a successful recolonisation by meiobenthic organisms; however, the presence of natural fine-grained sediments was highly beneficial. Due to their ability to respond efficiently to sudden food pulses, our investigation illustrated the high potential of Foraminifera to recolonise azoic sediments compared with metazoan meiobenthos. The present study demonstrates how an Arctic deep-sea meiobenthos community might react to a disturbance-like situation. However, further research has to be done to assess the effect of natural and anthropogenic disturbances on meiobenthos communities of the Arctic deep-sea on a broader temporal and spatial scale.

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