Journal of Experimental Marine Biology and Ecology 502 (2018) 129–141

Contents lists available at ScienceDirect

Journal of Experimental Marine Biology and Ecology

journal homepage: www.elsevier.com/locate/jembe

# Local effects of large food-falls on nematode diversity at an arctic deep-sea site: Results from an *in situ* experiment at the deep-sea observatory HAUSGARTEN

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ARTICLE INFO

*Article history:*
Received 27 September 2016
Received in revised form 24 February 2017
Accepted 8 March 2017
Available online 22 March 2017

*Keywords:*
HAUSGARTEN
Deep sea
*In situ* experiment
Food-fall
Nematodes
Diversity

ABSTRACT

To study the response of the smaller benthic biota to larger food-falls and their possible effects on the biodiversity at the deep seafloor, we deployed the halves of a sagittally bisected porpoise (1.3 m in length; each half approximately 18 kg) at 2500 m and 5400 m water depth at the LTER (Long-Term Ecological Research) observatory HAUSGARTEN in the eastern Fram Strait. Five weeks after the porpoise deployment, sediments beneath the carcasses and at different distances (0, 20, 40 cm) from these artificial food-falls were sampled with push-corers handled by a Remotely Operated Vehicle. The samples provided empirical evidence for a quick response by sediment-inhabiting bacteria and metazoan meiofauna to the carcasses at both water depths. Compared to control sediments, the substantial pulse of organic matter also led to generally increased meiofauna/nematode densities around the artificial food-falls. The comparison of nematode communities in sediments affected by the carcasses with those in control sediments exhibited shifts in the structural composition and the associated trophic and functional diversity of the nematodes. Our results confirmed that the impact of large food-falls on the deep benthic community largely depend on environmental factors (water depth, alternative food sources) as well as the background species composition, i.e., the structure of the prevailing meiofauna/nematode assemblages and the composition of the necrophagous community present in the wider area.

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## 1. Introduction

Food supply for the deep-sea benthos is predominantly derived from particulate organic matter (POM) that originates from the euphotic zone and settles at the seafloor. A yet undetermined fraction of POM consists of carcasses of birds, fish, seals, dolphins and whales (Smith, 1985) as well as parcels of macroalgae and wood (Bernardino et al., 2010). Such large food-falls represent local and highly concentrated organic inputs to the benthos and are of particular importance as food and energy source to benthic necrophagous communities (Goffredi et al., 2008), generally dominated by lysianassoid amphipods and large fishes (Stockton and DeLaca, 1982). Their response to the type, size, and position of the carcass is variable (Armstrong et al., 1991; Witte, 1999; Kemp et al., 2006; Lundsten et al., 2010; Hilario et al., 2015). Generally, scavengers not only arrive quickly but also in high numbers after the settling of large nekton falls (e.g., Hessler et al., 1978; Jones et al., 1998; Premke et al., 2003). Other aspects like which species are attracted, the duration of different stages of local succession, the turn-over rates and the dispersal of the carrion may vary considerably between different deep-sea areas (Witte, 1999; Smith et al., 2003).

In addition to the instantaneous initial effect on scavenging organisms, large food-falls have the potential to affect the species diversity and community structure of the entire benthic community (Kemp et al., 2006; Bernardino et al., 2012; Smith et al., 2014). Via excretion and defecation by the dispersing organisms, the surrounding area of the carcass experiences an organic enrichment from the food-fall, thereby indirectly affecting the sediment-inhabiting biota. Furthermore, sediment perturbations during active feeding at the carcass represent physical disturbances to the seabed, consequently further influencing benthic infauna (Smith, 1985). In general, smaller individuals may be unable to compete for resources at food-falls or even avoid the vicinity of nekton falls due to predation risk (Jones et al., 1998; Barry and Drazen, 2007; Johnson et al., 2010). Biodiversity shifts at food-fall locations were found to be underlain by long-lasting changes in the biogeochemical milieu as accelerated diffusive oxygen respiration concomitant to intensified microbial activities lead to sedimentary oxygen depletion. Instead of aerobic respiration, sulfate reduction and even methanogenesis take over and may create geochemical boundary conditions similar to those found at hydrothermal vents and cold vent locations (Treude et

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http://dx.doi.org/10.1016/j.jembe.2017.03.002
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al., 2009), suggesting the use of large food-fall habitats as stepping stones between chemosynthetic ecosystems (Smith et al., 2015).

Little is known about the effects of large nekton falls on the smaller benthic biota (size range: bacteria to meiofauna). Sediment-inhabiting bacterial assemblages were studied at different meter distances (up to 100 m) from whale-falls in the Santa Catalina and the Santa Cruz Basins (Smith et al., 1998; Treude et al., 2009), and in the Monterey Canyon (Goffredi et al., 2008) off North-West America. Debenham et al. (2004) and Rhett (2014) reported on deep-sea meiofauna communities in the surroundings of an experimentally deployed sub-adult gray whale carcass in the Santa Cruz Basin and natural whale falls in the Monterey and Soquel Canyons (Eastern Pacific), respectively. Their studies focused on nematode abundances, however, no special emphasis was put on potential shifts in nematode community composition related to the local organic enrichment from the whale carcass. To our knowledge, Pavlyuk et al. (2009) were the only authors to date who have investigated nematode community compositions both in the immediate surroundings and in the vicinity of the remains of a Minke whale carcass, although at a shallow water site (Peter the Great Bay; 30 m water depth) in the northern Japanese Sea.

To increase our understanding of the response of the smaller benthic biota to larger food-falls and the possible effects of large nekton falls on benthic biodiversity, we followed a similar experimental approach, this time by placing each half of a sagittally bisected porpoise at 2500 m and 5400 m water depth, respectively, at the deep-sea observatory HAUSGARTEN in Fram Strait (Arctic Ocean). Nematode assemblages and the temporal development of their community were a key focus of our investigations. The experimental design further enabled comparisons to be drawn between the community responses to food-falls at different water depths in the same geographical region. Our experiment was conducted to test the following hypotheses: (1) sediment-inhabiting bacteria and metazoan meiofauna quickly respond to large nekton carcasses and organic matter enrichment via excretion generated by the scavenging organisms dispersing the food-falls; (2) nekton carcasses cause an increase in meiofauna/nematode densities in the near surroundings of the carrion; (3) the massive pulse of organic matter leads to shifts in community composition and changes in diversity patterns of nematode assemblages in the vicinity of the carcass.

## 2. Material and methods

### 2.1. Experimental set-up and sampling

The experiment was conducted at the arctic LTER (Long-Term Ecological Research) observatory HAUSGARTEN in the eastern Fram Strait (Soltwedel et al., 2005, 2015). The halves of a lengthwise bisected porpoise (*Phocoena phocoena* Linnaeus, 1758; 1.3 m in length; each half approximately 18 kg), found dead and stranded at the German North Sea coast, were deployed on 19th August 2005 during RV "Polarstern" expedition ARK-XXI/1b. One half was deployed at 79°04.5′N, 04°06.5′E in 2500 m water depth on the Vestnesa Ridge, with the second placed at 79°05.6′N, 03°07.9′E in the Molloy Hole at 5400 m water depth. These artificial food-falls were brought to the seafloor using free-falling systems (bottom-lander) with 2 m long outriggers holding the carcasses during descent and placing them directly on the seafloor after landing. Time-lapse cameras attached to the bottom-lander frames provided still image footage (1.5 h time interval) of the decaying carcasses. The sediments directly beneath the carcass halves and at different distances from the cadavers were sampled with push-corers handled by the French Remotely Operated Vehicle (ROV) "Victor 6000" during an expedition with RV "L'Atalante" 32 days (carcass at 5400 m water depth) and 35 days (carcass at 2500 m water depth) after the deployments. Pushcoring (with tubes of 6 cm inner diameter) was done along short transects (0, 20, and 40 cm) in front of the head, at a right angle to the mid-section of the corpse, and at a projected extension of the tail tip (Fig. 1). Finally, pushcoring beneath the carcasses was done after carefully removing the remains of the porpoise halves. Control sediments were taken with a multiple corer during the RV "Polarstern" expedition ARK-XXI/1b at 1 nm (2500 m) and 4 nm (5400 m) distance to the two experimental sites, temporally coincident with the carcass deployments.

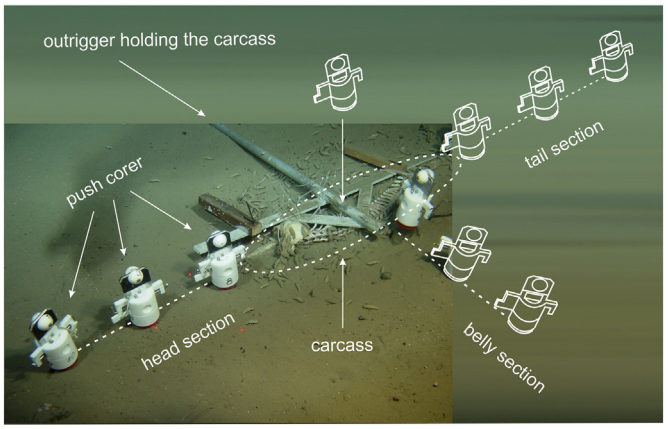


**Fig. 1.** Sediment sampling using ROV-handled push corers beneath the artificial food-falls and along short transects at different distances from the corpses.

### 2.2. Sample processing

Sediment cores taken with push corers and a multiple corer were subsampled using plastic syringes (5 ml and 20 ml) with cut-off anterior ends. Subsamples from the push corers were analyzed for meiofauna, bacterial numbers, biomasses and activities, the total microbial biomass, and phytodetritial matter at the seafloor. Due to the overall limited number of push corers available during the ROV dive, the relatively small area covered by the push corers and the need to sample for various parameters, we had to refrain from taking replicate samples at the different positions beneath and around the carcasses. Control sediments (three sub-samples per parameter) taken with a multiple corer have to be considered as pseudoreplicates, as they come from different tubes from a single multiple corer haul. All investigations were restricted to the uppermost centimeter of the sediments.

The occurrence of phytodetritus as a potential food/energy source for benthic organisms was assessed by analyzing sediment-bound chloroplastic pigments, which were extracted in 90% acetone and measured with a TURNER fluorometer (Shuman and Lorenzen, 1975). The bulk of pigments (chlorophyll *a* and its degradation products) identified with this method was termed chloroplastic pigment equivalents (CPE; Thiel, 1978). Phospholipid (PL) concentrations in the sediments were determined following a method provided by Findlay et al. (1989), with slight modifications as described in Boetius and Lochte (1994). PL concentrations were used to calculate the total microbial biomass (TMB) in terms of organic carbon, applying a conversion factor of 100 μmol P $g^{-1}$C (Findlay and Dobbs, 1993). Bacterial hydrolytic activities were estimated using the fluorogenic substrate fluorescein-di-acetate (FDA). FDA measurements, determining the amount of free available exo-enzymes (thus indicating the potential hydrolytic activity of bacteria) were carried out according to Köster et al. (1991). Sediment samples for bacterial studies were preserved in a 0.2 μm filtered formalin-seawater solution (2%). Bacterial numbers (BN) were counted after staining with acridine orange using epifluorescence microscopy according to Meyer-Reil (1983). Volumetric determinations were conducted with the Porton grid, as described by Grossmann and Reichardt (1991). Bacterial biomass (BB) was estimated using a conversion factor of 3.0 $10^{-13}$ g C $cm^{-3}$, as given by Børsheim et al. (1990). Chloroplastic pigments, exo-enzymatic activities, and bacterial cell numbers and biomasses were analyzed from subsamples taken with 5 ml disposable syringes.

Larger syringes (20 ml), covering 3.14 $cm^2$ of surface sediments, were used to retrieve subsamples for meiofaunal investigations (excluding foraminiferans). Samples were preserved in 4% formaldehyde-seawater solution. At the home lab, sediments were washed through a set of sieves with 1000, 500, 250, 125, 63, and 32 μm mesh sizes. The 1-mm sieve was used to exclude any potential macrofauna organisms. All other sieve fractions were stained with Rose Bengal and sorted under a low power stereo microscope (cf. Pfannkuche and Thiel, 1988). Organisms were identified to major taxa. For data analyses, all taxa occurring in minor quantities (e.g., harpacticoids/nauplii, polychaetes, turbellarians, gastrotrichs, tardigrades, kinorhynchs, ostracods, bivalves, gastropods) were pooled in one category, classified as 'Others'. Meiofaunal densities were standardized to individuals per 10 $cm^2$.

All nematodes found in the samples were transferred to anhydrous glycerol and mounted on permanent slides for further studies (De Grisse, 1969). Nematodes were identified to genus level (Schmidt-Rhaesa, 2014). The classification into different feeding types was done according to Wieser (1953, 1960). Groups 1A and 1B describe selective and non-selective deposit feeders without teeth, respectively. Group 2A defines epigrowth feeders, and group 2B contains predators as well as omnivores with teeth. The first three groups of deposit and epigrowth feeders mainly graze on bacteria and microalgae (Jensen, 1987). Predators and omnivores also use their teeth to tap plant objects, but their most important feeding mode is predation and scavenging (Soeteart and Heip, 1995).

To further characterize the sedimentary milieu around the artificial food-falls, we conducted *in situ* microprofiler measurements beneath the carcasses (after removing them from the deployment position) and in the vicinity of the carcasses using a ROV handled autonomous microprofiler unit (De Beer et al., 2006) carrying Clarke type microsensors (Unisense A/S, Denmark) with ~15 μm tip diameter. Oxygen profiles were recorded with a preset vertical resolution of at least 0.5 mm.

### 2.3. Data analysis and statistics

All data were analyzed using the statistical software Primer v6 (Clarke and Gorley, 2006).

The structural diversity of the nematode communities at the different sampling positions around the carcasses and in the control sediments was calculated using the estimated number of genera for a given number of organisms selected randomly from the existing samples ($ES_n$) (Sanders, 1968; Hurlbert, 1971), the evenness index J′ (Pielou, 1966), and the Shannon-Wiener index $H'_{(log2)}$ (Shannon and Weaver, 1963).

Moreover, we measured the beta diversity of the nematode assemblages across depth and at the different sampling positions around the carcasses using the similarity percentage routine (SIMPER) based on Bray-Curtis matrixes and expressed as percentage of dissimilarity.

Non-metric multi-dimensional scaling (NMDS) based on genera-abundance data was applied to compare community structure across depth and positions around the carcasses. Square-root transformations were used prior to multivariate analyses to balance the importance of common and rare species (Clarke and Warwick, 2001). Analyses of similarities (ANOSIM) were performed on groups, identified *a priori*, to determine the significance differences observed in multivariate plots (Clarke and Warwick, 2001). The similarity percentage routine (SIMPER) was also used to identify the nematode genera contributing to the separation of groups (Clarke and Warwick, 2001).

The nematode community data at genus level were analyzed by means of the PERMANOVA (permutational analysis of variance) routine (Anderson, 2001; Anderson et al., 2008) to assess differences between water depths and at different positions around the carcasses. The PERMANOVA was designed with two factors, water depth (fixed) and position (random) for the whole data set, and with distance (fixed) and position (random) separately for each water depth. All PERMANOVA tests were conducted on fourth-root transformed Bray-Curtis similarity matrices and the residuals were permutated under a reduced model. Partitioning of variation is done by Type III SS (partial) of sums of squares, as these type tend to be the most conservative (Anderson et al., 2008).

DistLM (Distance-based linear model) routines (McArdle and Anderson, 2001; Anderson et al., 2008) were performed (selection procedure = forward, selection criterion = adjusted $R^2$) to analyze the relationship between nematode diversity ($H'_{log2}$) and biotic background parameters (CPE, PL, FDA, BB) as predictor variables. Euclidean distance was used as resemblance measure; data of background parameters were $log_{(0.1 + v)}$ transformed.

The BIO-ENV procedure was carried out to link multivariate patterns of the nematode assemblage to the best explanatory background variables by calculating Spearman's rank correlation coefficient (ρ) between the biotic and abiotic resemblance matrices. As the parameters bacterial numbers and bacterial biomass were correlated, the DistLM routine and BIO-ENV procedure were not applied on the full set of environmental variables, with the parameter bacterial number omitted prior to the analyses.

The Index of Trophic Diversity was calculated as ITD = $\sum \Phi$, where Φ is the contribution of density of each trophic group to total nematode density (Heip et al., 1985). ITD values range between 0.25 (equivalent to highest trophic diversity; the four trophic guilds each accounting for 25% of total nematode density) and 1.0 (equivalent to lowest diversity; one trophic guild representing 100% of the total nematode density).

To segregate nematodes on the basis of their known and assumed life history traits and relative sensitivity to stress, nematode genera were assigned to the 'colonizer – persister' (c–p) scale according to their r and K characteristics following Bongers (1990) and Bongers et al. (1991, 1995). Maturity Indices (MI) were calculated as the weighted mean c–p values for the respective taxa, to provide indices that indicate ecosystem conditions based on the composition of the nematode community (Bongers, 1990; Bongers and Bongers, 1998).

## 3. Results

### 3.1. Degradation of the carcasses

Still camera footage taken during the first days after the deployment showed that the artificial food-falls were quickly discovered by high numbers of scavengers and demersal fish. However, the images revealed major differences in the degradation of the two identical carcass halves deployed at the 2500 m and 5400 m water depths (Fig. 2).

At the intermediate depth deployment on the continental margin off Svalbard, zoarcid fish (*Lycodes frigidus*) and large lysianassoid amphipods (*Eurythenes gryllus*) were the first scavengers, arriving at the carcass within minutes (Fig. 2A). *L. frigidus* apparently did not feed directly on the carcass, but on the amphipods attracted by the food-fall. Large isopods (*Saduria megalura*) entered the scene 7–8 h after the deployment. After 3–4 days, fish density considerably decreased, while the density of *S. megalura* markedly increased. Three weeks after deploying the carcass, larger numbers of smaller amphipods surrounded the food-fall. During sampling, five weeks after the deployment, the carcass flesh was observed to be completely consumed, with only the bones remaining. A large number of isopods was still present (Fig. 2C), potentially feeding on meiofauna and food particles left by the sloppy feeding of the scavenging amphipods and/or their faeces potentially released in the area.

At hadal depth off Svalbard the macroscopic scavenging fauna consists exclusively of small amphipods (*Uristes* sp.) occurring in extremely high numbers (Fig. 2B). Unfortunately, due to technical problems, camera footage stopped on the second day following the carcass deployment. Neither fish nor any other potential scavenger was sighted on the images from the first 24 h of the deployment. During the sediment sampling in the vicinity of the carcass five weeks after the deployment,

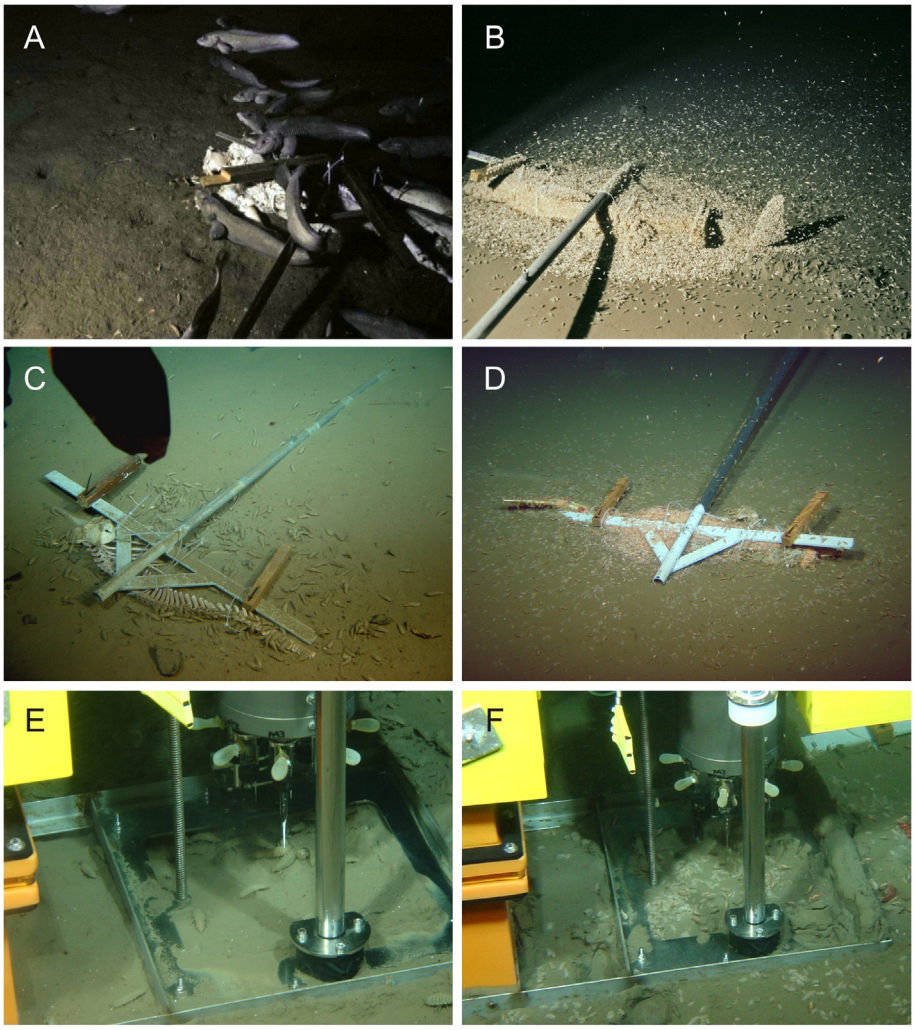


**Fig. 2.** Demersal fish (*Lycodes frigidus*) and small amphipods (*Uristes* sp.) as early visitors at the food-falls a few hours after the deployment at 2500 m (A) and 5400 m (B); large isopods (*Saduria megalura*) and holothurians (*Elpidia heckeri*) feeding on the food-fall remains ~5 weeks after the deployment at 2500 m (C) and 5400 m (D); oxygen microprofiling beneath the carcasses (after removing them from the original spot) at 2500 m (E) and 5400 m (F).

the carcass was observed to be only partly skeletonized and amphipods still fed on remaining corpse tissue. Large numbers of small holothurians (*Elpidia heckeri*) besieged the food-fall, obviously intensively reworking the surrounding sediments (Fig. 2D).

### 3.2. Meiofauna

Metazoan meiofauna densities around the carcasses and in control sediments ranged between 223 and 1733 ind. 10 $cm^{-2}$ at 2500 m water depth, while densities at 5400 m were only slightly lower, ranging between 132 and 1429 ind. 10 $cm^{-2}$ (Table 1). At bathyal and hadal depths, mean abundances at the food-falls were generally (non-significantly) higher compared to the respective control sites (Fig. 3). Interestingly, highest meiofauna numbers were usually found at 20 cm distance to the carcasses both at 2500 m and 5400 m water depth. Nematodes clearly dominated the metazoan meiofauna assemblages (76–95% at 2500 m; 87–96% at 5400 m). Compared to the deeper site, the composition of the other metazoan meiofauna was clearly more divers at 2500 m water depth (9 taxa at 2500 m; 4 taxa at 5400 m). The proportion of all "Other" meiofauna taxa (mainly harpacticoid copepods and their nauplii) was slightly higher in the sediments around the food-falls, compared to the control samples (Fig. 3). However, while densities of the "Other" taxa around the carcass at hadal depth showed no clear trend with increasing distance to the food-fall, "Other" metazoan meiofauna around the carcass at bathyal depth was about 3-times lower underneath and right next to the food-fall, compared to sampling sites at 20 and 40 cm distance to the carcass (data not shown).

### 3.3. Nematodes

The total of 545 nematodes found in the samples taken at 2500 m could be assigned to 20 families and 54 genera, whereas the 519 individuals found in an equal number of samples taken at 5400 m water depth were identified as belonging to only 29 genera from a total of 14 families. Table 2 provides an overview on the families and genera found in the uppermost centimeter of the sediments at the two experimental sites.

At 2500 m water depth, *Tricoma* (Desmoscolecidae) dominated the nematode community, comprising 18% of the total nematode community around the carcass and even 37% in the control sediments, followed by *Molgolaimus* (Desmodoridae) with 10% around the carcass and 9% in the controls, and by *Thalassomonhystera* (Monhysteridae) with 9% around the carcass and 7% within the controls (Fig. 4). At 5400 m water depth, the nematode communities were clearly dominated by *Acantholaimus* (Chromadoridae), with 42% of the nematodes at the carcass and 44% of the individuals within the control samples. *Thalassomonhystera* (Monhysteridae) was the second most common genus, comprising 19% of the total nematodes at the carcass. The

**Table 1**
Environmental, bacterial, and meiofaunal data in surface sediments (0–1 cm) at various positions around the carcasses and adjacent control sediments: Chl *a*: chlorophyll *a* concentrations; Pheo: pheopigment concentrations; CPE: chloroplastic pigment equivalents, i.e., Chl *a* + Pheo; FDA: bacterial exo-enzymatic activities; PL: phospholipid concentrations; BN: bacterial numbers; MBC: mean biomasses per bacterial cell; BB: bacterial biomasses; Nema: nematode densities; Others: all other metazoan meiofauna; Total Meio: total metazoan meiofauna.

| Position | Distance | Chl *a* | Pheo | CPE | FDA | PL | BN | MBC | BB | Nema | Others | Total Meta |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | (cm) | (μg $cm^{-3}$) | (μg $cm^{-3}$) | (μg $cm^{-3}$) | (nmol $cm^{-3}$ $h^{-1}$) | (μg $cm^{-3}$) | ($10^8$ cells $m^{-3}$) | (fg $cell^{-1}$) | (μg C $cm^{-3}$) | (ind. 10 $cm^{-2}$) | (ind. 10 $cm^{-2}$) | (ind. 10 $cm^{-2}$) |
| 2500 m | | | | | | | | | | | | |
| below whale | – | 0.94 | 10.17 | 11.12 | 4.19 | 9.81 | 2.43 | 0.21 | 9.05 | 537 | 30 | 568 |
| head | 0 | 0.70 | 8.03 | 8.73 | 3.60 | 4.02 | 9.48 | 0.18 | 32.40 | 405 | 41 | 446 |
| head | 20 | 1.03 | 14.03 | 15.07 | 5.90 | 6.76 | 12.25 | 0.19 | 42.09 | 1257 | 132 | 1389 |
| head | 40 | 1.10 | 18.98 | 20.08 | 4.45 | 7.42 | 11.86 | 0.16 | 37.28 | 517 | 132 | 649 |
| belly | 0 | 0.59 | 8.48 | 9.07 | 2.83 | 11.76 | 6.77 | 0.41 | 37.23 | 182 | 41 | 223 |
| belly | 20 | 1.33 | 10.50 | 11.83 | 10.30 | 14.31 | 8.05 | 0.27 | 34.90 | 1581 | 152 | 1733 |
| belly | 40 | 1.12 | 15.71 | 16.84 | 6.46 | 6.63 | 6.88 | 0.14 | 19.81 | 588 | 233 | 821 |
| tail | 0 | 0.92 | 12.39 | 13.31 | 1.40 | 10.68 | 6.68 | 0.45 | 38.92 | 466 | 61 | 527 |
| tail | 20 | 0.65 | 7.74 | 8.40 | 3.80 | 6.03 | 3.07 | 0.21 | 11.29 | 274 | 41 | 314 |
| tail | 40 | 0.92 | 12.39 | 13.31 | 4.06 | 14.39 | 3.09 | 0.21 | 11.40 | 395 | 101 | 497 |
| control | – | 3.14 | 13.12 | 16.26 | 5.75 | 6.45 | 5.87 | 0.30 | 17.46 | 354 | 16 | 370 |
| 5400 m | | | | | | | | | | | | |
| below whale | – | 2.74 | 28.20 | 30.94 | 0.41 | 26.67 | 2.27 | 0.79 | 18.33 | 385 | 61 | 446 |
| head | 0 | 3.75 | 31.82 | 35.57 | 1.11 | 5.53 | 5.19 | 0.15 | 15.52 | 243 | 51 | 294 |
| head | 20 | 3.75 | 31.81 | 35.57 | 1.27 | 15.10 | 4.16 | 0.20 | 15.03 | 1399 | 30 | 1429 |
| head | 40 | 3.30 | 29.98 | 33.28 | 2.03 | 6.05 | 2.84 | 0.16 | 8.92 | 1004 | 122 | 1125 |
| belly | 0 | 2.74 | 28.20 | 30.94 | 0.28 | 11.85 | 5.81 | 0.45 | 33.64 | 781 | 20 | 801 |
| belly | 20 | 2.86 | 25.54 | 28.40 | 1.34 | 13.81 | 8.89 | 0.12 | 23.99 | 466 | 20 | 487 |
| belly | 40 | 3.38 | 31.57 | 34.95 | 1.55 | 24.58 | 6.20 | 0.21 | 23.07 | 132 | 0 | 132 |
| tail | 0 | 3.04 | 28.46 | 31.49 | 0.61 | 13.10 | 1.85 | 0.18 | 6.23 | 558 | 101 | 659 |
| tail | 20 | 3.38 | 31.57 | 34.95 | 1.92 | 16.69 | 2.79 | 0.11 | 7.00 | 598 | 41 | 639 |
| tail | 40 | 3.41 | 31.07 | 34.48 | 0.77 | 13.18 | 3.17 | 0.10 | 7.47 | 781 | 30 | 811 |
| control | – | 3.40 | 22.72 | 26.12 | 2.94 | 5.92 | 9.31 | 0.31 | 29.01 | 238 | 0 | 238 |

nematode community of the control sediments was co-dominated by *Daptonema* (Xyalidae), comprising 18% of the total nematodes (Fig. 4).

The different dominance patterns in nematode community composition between the two water depths were also reflected by the proportion of the genera with <5% presence, summarized as 'Rest' (Fig. 4). At the shallower station, the percentage of the 'Rest' constituted up to 33% of the total nematodes, comprising between 20 genera (control samples) and 47 genera (carcass samples), whereas at the deeper station the proportion of 'Rest' individuals accounted for 19% of the total nematodes, comprising 13 nematode genera within the control samples and 16 genera around the carcass.

Diversity metrics for individual nematode assemblages found at the different sampling positions at the carcasses showed no discernable spatial trends and were thus not considered separately. The (combined) samples around the carcass at 2500 m water depth exhibited the greatest diversity in terms of genera number ($G = 49$), evenness ($J' = 0.77$), estimated number of genera ($EG_{(30)} = 12.39$), and heterogeneity ($H' = 4.31$) (Table 3). Within the control sediments at 2500 m water depth these diversity measures were slightly reduced compared to the carcass associated sediments, except for genera number ($G = 26$), which was about half that observed at the carcass, and heterogeneity ($H' = 3.59$), which was about 20% lower than observed around the carcass (Table 3).

Nematode structural diversity at 5400 m water depth was clearly lower than that at the shallower experimental site (Table 3). Diversity patterns around the carcass resembled the patterns of the nematode community within the control sediments, though with some more pronounced differences for the estimated number of genera ($EG_{(30)}$: 9.5 around the carcass, $EG_{(30)}$: 8.0 within controls).

The nematode beta diversity between depths was high (72%), whereas beta diversity among control and carcass samples was lower and ranged between 61% at 2500 m water depth and 56% at 5400 m water depth.

NMDS analysis also provided strong evidence of nematode community separation between depths, over both the carcass and control samples (Fig. 5). Nearly all nematode community samples at 2500 m water depth clustered separately from all samples at 5400 m water depth (ANOSIM, $R = 0.538$, $p = 0.01\%$). *Tricoma* (15%), *Acantholaimus* (13%), *Halalaimus* (11%) and *Leptolaimus* (10%) together contributed nearly 50% of the within group similarity at the shallower experimental site, whereas within group similarity at 5400 m water depth was to >50% caused by high abundances of only two genera, i.e., *Acantholaimus* (39%) and *Daptonema* (12%). *Acantholaimus* (11%), *Tricoma* (8%), *Thalassomonhystera* (7%) and *Daptonema* (7%) also contributed most to the average dissimilarity between the shallow and the deep nematode communities. The 26 remaining genera each contributed <5% to the differences in the nematode communities between the shallow and the deep site.

Testing for differences in community structure and composition between the control and carcass samples, the ANOSIM analyses showed no significant differences at 2500 m water depth, but significant differences at 5400 m water depth (ANOSIM, $R = 0.447$, $p = 2.7\%$). Similarity within the groups of control and carcass samples both were mainly caused by *Acantholaimus* (36% and 28%, respectively). Within the control samples, *Desmoscolex* together with *Acantholaimus* described over 59% within group similarity, whereas similarity within the carcass samples was to 58% caused by *Thalassomonhystera* and *Sphaerolaimus*, together with *Acantholaimus*. Dissimilarity between the two groups was to 50% caused by *Thalassomonhystera*, *Sphaerolaimus* (~10%, each), *Daptonema*, *Theristus*, *Leptolaimus*, *Amphimonhystrella* and *Halalaimus* (5–7%, each).

Results of the PERMANOVA for the multivariate structure of nematode assemblages showed significant differences between water depths ($p = 0.0001$, unique perms = 9939, pseudo-F = 7.862). In addition, at 2500 m water depth the interaction term of sampling position (head, tail, and belly) × distance (0 cm, 20 cm, and 40 cm) is approaching statistical significance ($p = 0.056$, unique perms =

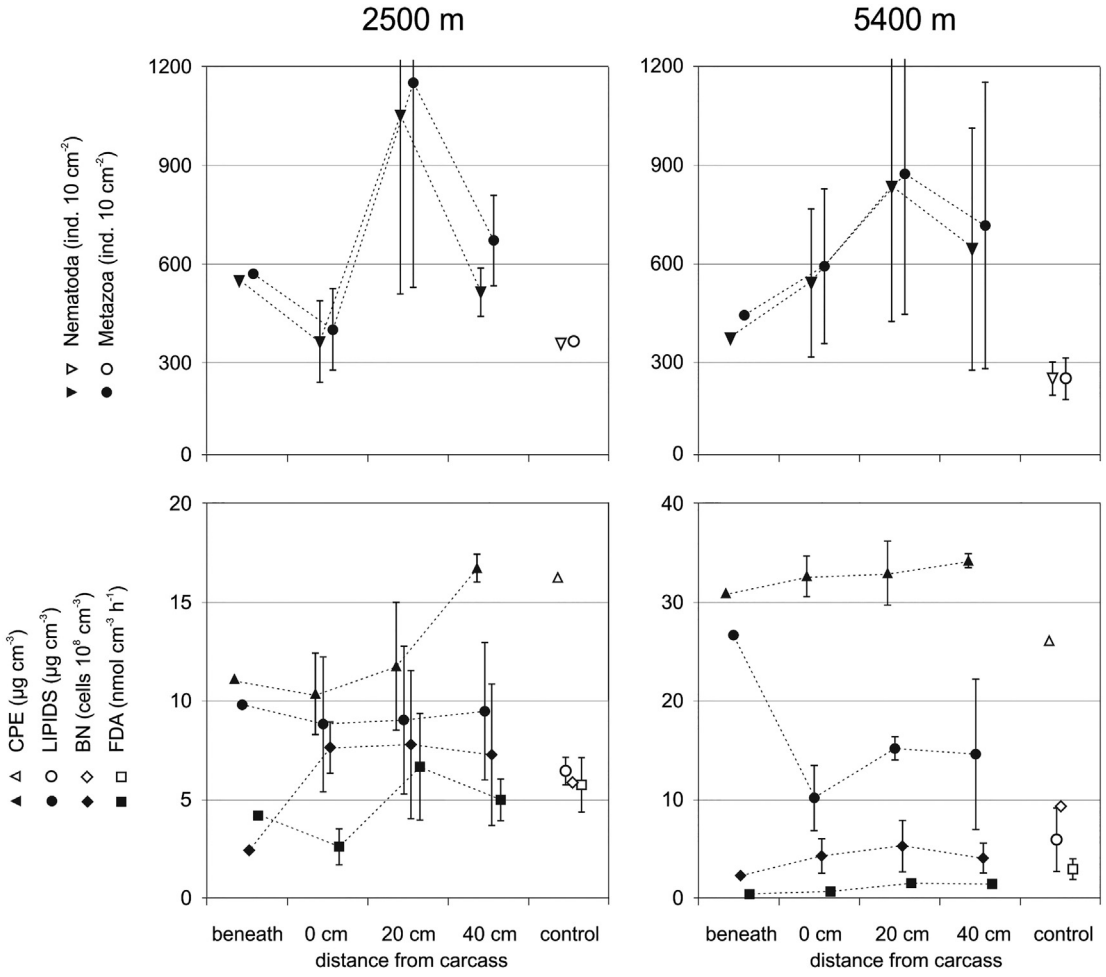


**Fig. 3.** Nematode densities and sedimentary background parameters (CPE: phytodetritial matter, LIPIDS: total microbial biomass, BN: bacterial numbers, FDA: bacterial activity) beneath the carcasses (no replicates), at different distance from the carcass (filled symbols), and in control sediments (open symbols; SDs partly indistinguishable from data points). Note the different scaling of the ordinates for background parameters (lower panel).

988, pseudo-F = 1.751). At the deeper station, the PERMANOVA revealed no significant effects for any of the selected factors.

At 2500 m water depth, selective deposit feeders with small unarmed buccal cavities (feeding type 1A) were most abundant, although in quite different proportions between the carcass and control samples. Around the carcass they accounted for ~38% of the nematode assemblage, and even for 53% in the control sediments, whereas non-selective deposit feeders (feeding type 1B) accounted only for 24% within the carcass samples and for 17% within the control samples. Non-selective deposit feeders were therefore only the third most abundant group. The second most abundant group (34% and 27%, respectively) were epigrowth feeders (feeding type 2A, small buccal cavity with teeth), whereas predators and scavengers (feeding type 2B, large armed buccal cavity) were least numerous in the communities (5% and 3%, respectively). The differences in trophic structure among carcass and control samples, in particular with regard to the selective deposit feeders, were also reflected by the ITD, which showed a higher trophic diversity for the carcass samples (ITD = 0.31) than for the control samples (ITD = 0.38).

The nematode communities at 5400 m water depth exhibited a clearly different trophic structure compared to the shallower station. Here the nematode communities were dominated by epigrowth feeders (44%), both in the samples around the carcass and the control samples. The second most important group was non-selective deposit feeders, also in nearly same proportions around the carcass and the control sediments (39% and 37%, respectively), followed by selective deposit feeding nematodes (12% and 19%, respectively). Least important were predators and scavengers, which comprised 5% of the nematode community around the carcass, but did not occur at all within the control samples. Trophic diversity of the nematode community around the carcass at 5400 m water depth (ITD = 0.36) was lower than at the shallower station, whereas the trophic diversity of the control sediments (ITD = 0.37) was roughly equal at both water depths.

The functional structure of the nematode communities in terms of life history traits also showed significant differences between the shallow and the deep experimental site. Carcass associated sediments at 2500 m water depth were dominated by general opportunists (c–p = 2; 46%), whereas more K-selected genera (c–p = 4; 44%) prevailed the control sediments. Persisters with a c–p value of 3 were the second most abundant category in both sample groups with abundances of 29% in each, followed by persisters with a c–p value of 4 around the carcass and general opportunists with a c–p value of 2 within the control sediments, accounting for almost equal shares of 24% and 26%, respectively. At 5400 m water depth nematodes described as persisters with a c–p value of 3 dominated both the carcass associated sediments as well as the control sediments (51% and 45%, respectively). Nematodes classified as general opportunists with a c–p value of 2 were ascribed in nearly equal abundances in the background (43%) and enriched (41%) sediments. Compared to the shallower experimental site, persisters with a c–p value of 4 occurred in a clearly lower dominance, accounting for 7% of total nematodes around the carcass, and 11% within the control

**Table 2**
Nematode abundances per genera with their c–p values (CP) and feeding types (FT) in sediments around the carcasses and nearby control sites at 2500 m and 5400 m water depth.

| | | | 2500 m | | 5400 m | |
|---|---|---|---|---|---|---|
| Family<br>*Genus* | CP | FT | Control<br>ind. 10 cm$^2$ | Carcass<br>ind. 10 cm$^2$ | Control<br>ind. 10 cm$^2$ | Carcass<br>ind. 10 cm$^2$ |
| Aegialoalaimidae | | | | | | |
| *Aegialoalaimus* | 4 | 1A | | 0.3 | | 0.3 |
| Anticomidae | | | | | | |
| *Anticoma* | 2 | 1A | | 0.6 | | |
| Camacolaimidae | | | | | | |
| *Camacolaimus* | 3 | 2B | | 0.3 | | |
| *Procamacolaimus* | 3 | 2A | | 1.0 | | |
| Ceramonematidae | | | | | | |
| *Pselionema* | 3 | 1A | | | 1.1 | |
| Chromadoridae | | | | | | |
| *Acantholaimus* | 3 | 2A | 6.4 | 10.8 | 41.4 | 57.0 |
| *Chromadora* | 3 | 2A | 1.1 | 0.3 | | |
| *Dichromadora* | 3 | 2A | 1.1 | | | |
| *Neochromadora* | 2 | 2A | | 1.6 | | |
| *Rhips* | 3 | 2A | | 0.3 | | |
| *Spilophorella* | 2 | 2A | | 0.6 | | |
| Comesomatidae | | | | | | |
| *Cervonema* | 2 | 1A | 1.1 | 1.9 | | |
| *Paramesonchium* | 2 | 2A | | 0.3 | | |
| *Pierrickia* | 2 | 1A | 1.1 | 2.5 | | |
| *Sabatieria* | 2 | 1B | | 4.5 | | |
| Cyartonematidae | | | | | | |
| *Cyartonema* | 3 | 1A | | 0.6 | | 0.6 |
| Desmodoridae | | | | | | |
| *Molgolaimus* | 3 | 2A | 9.5 | 13.6 | | 0.6 |
| *Spirinia* | 3 | 2A | 1.1 | 0.6 | | |
| Desmoscolecidae | | | | | | |
| *Desmoscolex* | 4 | 1A | 1.1 | 3.5 | 7.4 | 6.0 |
| *Tricoma* | 4 | 1A | 38.2 | 25.8 | 1.1 | |
| Diplopeltidae | | | | | | |
| *Campylaimus* | 3 | 2A | 6.4 | 5.7 | | 2.2 |
| *Diplopeltula* | 3 | 1A | | 0.3 | | 0.3 |
| *Southerniella* | 3 | 1B | | 9.5 | | 0.6 |
| Diplopeltoididae | | | | | | |
| *Diplopeltoides* | 3 | 1A | 3.2 | 1.9 | | 1.9 |
| Draconematidae | | | | | | |
| *Cephalochaetosoma* | 4 | 1A | | | | 0.3 |
| *Draconematidae* sp. | 4 | 1A | | 0.3 | | |
| Enchelidiidae | | | | | | |
| *Eurystomina* | 4 | 2B | | 0.3 | | |
| Ironidae | | | | | | |
| *Syringolaimus* | 4 | 2B | | 9.5 | | |
| Leptolaimidae | | | | | | |
| *Antomicron* | 2 | 1A | | 0.3 | | |
| *Leptolaimoides* | 3 | 1A | | 0.3 | | |
| *Leptolaimus* | 2 | 1A | 2.1 | 11.5 | 5.3 | 3.2 |
| Linhomoeidae | | | | | | |
| *Anticyathus* | 2 | 1B | | 0.3 | | |
| *Eleutherolaimus* | 2 | 1B | | 9.5 | 1.1 | 9.5 |
| *Metalinhomoeus* | 2 | 1B | 2.1 | 1.6 | 1.1 | |
| Microlaimidae | | | | | | |
| *Calomicrolaimus* | 2 | 2A | 1.1 | | | |
| *Ixonema* | 4 | 2A | | | | |
| *Microlaimus* | 2 | 2A | 1.1 | 12.7 | | |
| Monhysteridae | | | | | | |
| *Amphimonhystrella* | 2 | 1B | 2.1 | 0.3 | 2.1 | 11.1 |
| *Monhystrella* | 1 | 1B | 1.1 | | 1.1 | |
| *Thalassamonhystera* | 2 | 1B | 7.4 | 13.4 | 1.1 | 25.8 |
| Oxystominidae | | | | | | |
| *Halalaimus* | 4 | 1A | 5.3 | 3.2 | 2.1 | 3.2 |
| *Oxystomina* | 4 | 1A | 1.1 | 0.3 | | |
| Pandolaimidae | | | | | | |
| *Pandolaimus* | 2 | 1B | | 0.3 | | |
| Selachinematidae | | | | | | |
| *Halichoanolaimus* | 3 | 2B | | 0.6 | | |
| Sphaerolaimidae | | | | | | |
| *Sphaerolaimus* | 3 | 2B | 1.1 | 2.5 | | 7.0 |
| Thoracostomopsidae | | | | | | |
| *Fenestrolaimus* | 5 | 2B | 1.1 | 9.5 | | |
| *Mesacanthion* | 3 | 2B | | 1.6 | | |
| *Paramesacanthion* | 2 | 2B | 1.1 | | | |

*(continued on next page)*

**Table 2** (*continued*)

| Family *Genus* | CP | FT | 2500 m Control ind. 10 cm$^2$ | 2500 m Carcass ind. 10 cm$^2$ | 5400 m Control ind. 10 cm$^2$ | 5400 m Carcass ind. 10 cm$^2$ |
|---|---|---|---|---|---|---|
| Xyalidae | | | | | | |
| *Ammotheristus* | 2 | 1B | 2.1 | 9.5 | 1.1 | 0.3 |
| *Amphimonhystera* | 2 | 1B | | | 1.1 | |
| *Daptonema* | 2 | 1B | | 1.3 | 17.0 | 9.9 |
| *Elzalia* | 2 | 1B | | 9.5 | | |
| *Enchonema* | 2 | 1A | 2.1 | | 1.1 | |
| *Manganonema* | 2 | 1A | | 0.3 | | |
| *Paramonhystera* | 2 | 1B | | 0.3 | 2.1 | |
| *Promonhystera* | 2 | 1B | | 0.3 | | 0.3 |
| *Theristus* | 2 | 1B | 3.2 | 7.0 | 6.4 | 4.8 |
| *Xyalidae* sp. | 2 | 1B | | 0.3 | 1.1 | |

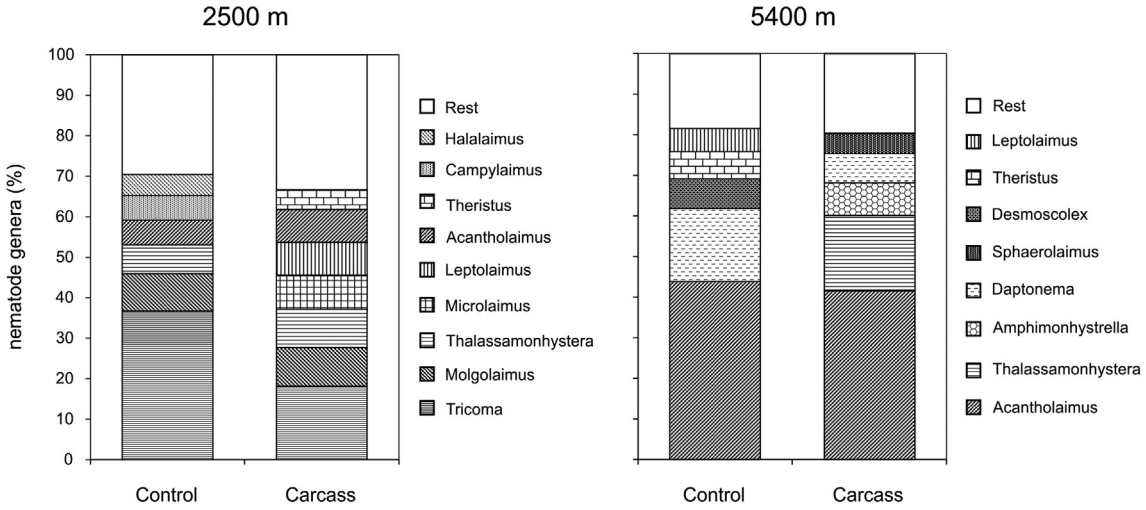


**Fig. 4.** Proportions of the dominant nematode genera (≥5%) below and around the carcasses, and in control sediments at 2500 m and 5400 m water depth.

communities. Extreme colonizers (c–p = 5), though also only very rarely observed within the shallower sediments (~1%), were completely absent at 5400 m water depth.

The MI of the nematode community in the enriched sediments at 2500 m water depth (2.80) was lower compared to the control sediments (MI = 3.18). In contrast, at 5400 m water depth, although slightly dominated by persisters (c–p = 3), enriched and control sediments support communities of colonizers, showing the same relatively low MI (2.66) compared to the shallow experimental site.

### 3.4. Background parameters

Parameters indicating organic matter availability, total microbial biomass, bacterial numbers and biomass, as well as bacterial exo-enzymatic activity in the sediments showed no clear trends, neither between sites nor with increasing distance to the carcasses (Table 1).

**Table 3**
Number of genera (G), identified specimens (N per 10 cm$^2$), and univariate diversity indices (J′, $EG_{(30)}$, $H'_{(log2)}$) for nematode assemblages around the carcasses at 2500 m and 5400 m water depth.

| | *G* | *N* | *J′* | $EG_{(30)}$ | $H'_{(log2)}$ |
|---|---|---|---|---|---|
| Food fall 2500 m | 49 | 45 | 0.77 | 12.39 | 4.31 |
| Control 2500 m | 26 | 33 | 0.76 | 12.34 | 3.59 |
| Food fall 5400 m | 21 | 43 | 0.65 | 9.50 | 2.85 |
| Control 5400 m | 18 | 30 | 0.68 | 8.00 | 2.85 |

Concentrations of chloroplastic pigments from phytodetritial matter in the sediments were up to 3-times higher at 5400 m, compared to the shallower site. At 2500 m, pigment concentrations increased with increasing distance from the carcass, whereas CPE concentrations at 5400 m stayed at comparable values around the carcass, but showed significantly lower values in the controls (Fig. 3). Total microbial biomass estimates from PL concentrations were roughly twice as high at

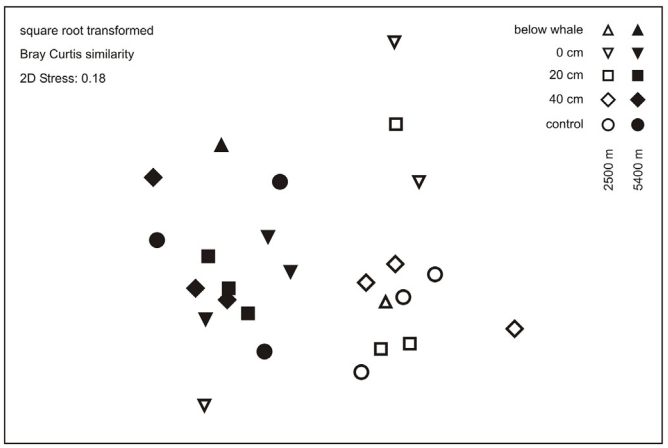


**Fig. 5.** MDS plot showing similarities in nematode community compositions at different positions around the carcasses and in control sediments at 2500 m and 5400 m water depth.

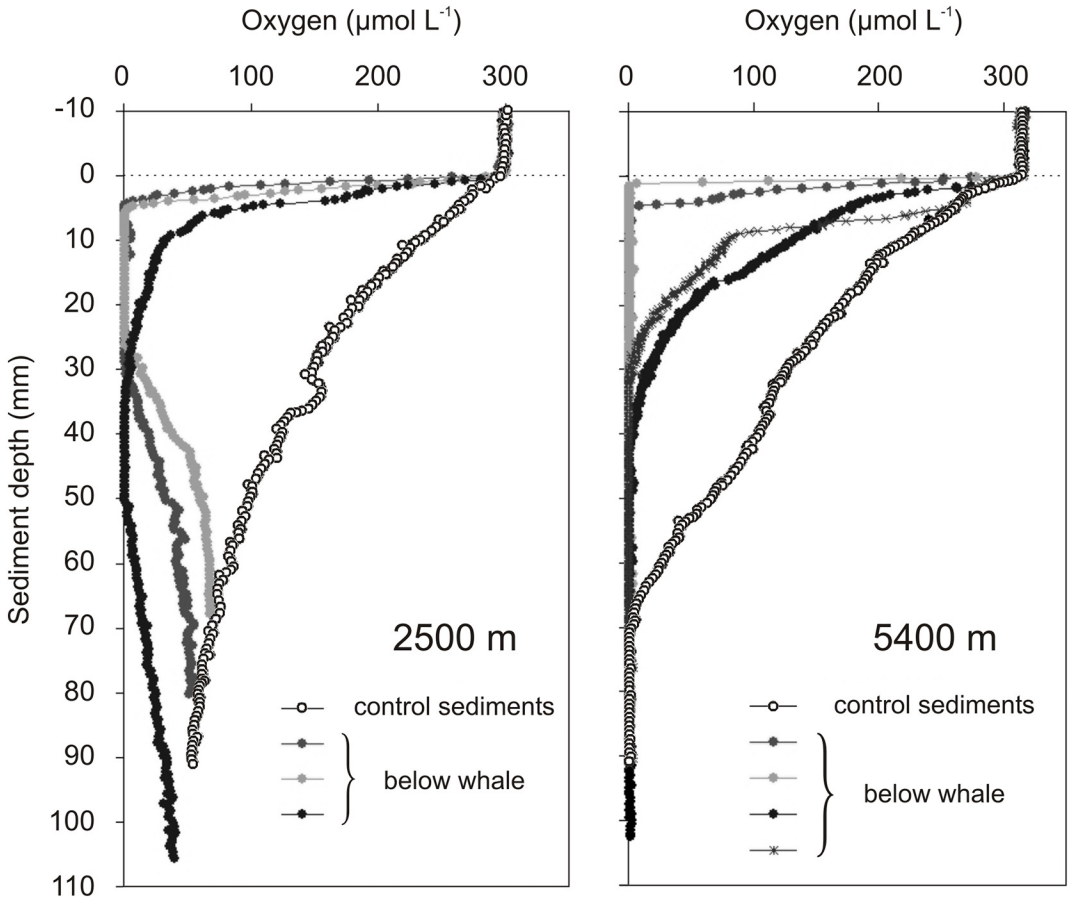


**Fig. 6.** Oxygen profiles from *in situ* measurements below the carcasses and in control sediments at 2500 m and 5400 m water depth.

5400 m, compared to the shallower site, whereas values around the carcasses at both sites were clearly elevated when compared to the respective control samples (Fig. 3). Independent from the water depth, bacterial numbers (BN) were clearly lowest beneath the carcasses and rather stable across the sampled distances from the food-falls. Whereas control sediments at 2500 m showed cell numbers similar to values determined next to the carcass, bacterial densities in controls at 5400 m were about twice as high as within the samples taken in the vicinity of the artificial food-fall (Fig. 3). Bacterial activity (FDA) at both sites showed generally increasing values with increasing distance from the carcasses. However, FDA values at the deeper site were about 4-times lower than those recorded at 2500 m water depth (Fig. 3).

Porewater dissolved oxygen in control sediments was measured to penetrate ~7 cm into the undisturbed sediments at 5400 m, whereas it was extrapolated to penetrate 26 ± 5 cm at 2500 m water depth (Fig. 6). Compared with the respect control sites the surface gradient of the porewater oxygen concentration was found to be considerably steeper at the sediment-water interface below the food-falls at both stations. This is indicative for significantly elevated diffusive oxygen uptake rates below the carcasses. Oxygen was found to be depleted already below 4.5–35 mm at the shallower site, and below 1.5–40 mm sediment depth at the deeper site. At 2500 m, oxygen values were found to again increase within deeper sediment layers (below 3–5 cm). The concentration curves suggest that porewater oxygen concentrations reach the level of the respective control sediments below 70 mm sediment depth at that site. Unfortunately, for technical reasons, profiles in the sediments which were covered by the carcass reached down only to 7–10.5 cm sediment depth.

Marginal tests in distance-based linear modelling (DistLM) showed that none of the background factors retained for analyzes at 2500 water depth, contributed significantly to the model for the adjusted $R^2$ selection criteria. However, 23% ($p = 0.103$, pseudo-F = 3.270) of the variation in nematode diversity as $H'_{(log2)}$ is related to the variation in PL concentration alone. At 5400 m water depth, the only predictor variable contributing significantly to the model was FDA, being responsible for 36% ($p = 0.032$, pseudo-F = 6.110) of the total variation in nematode diversity. The choice of the selection criterion did not affect the results and showed comparable results for $R^2$ and AIC (An Information Criterion; Akaike, 1973).

Results of the BIO-ENV procedure indicate that the potential bacterial activity (FDA) and bacterial biomass (BB) offer the best explanation for nematode community patterns at 2500 m water depth, showing a rank correlation of $\rho = 0.927$. The single variable which best groups the sites based on faunal patterns was bacterial biomass (rank correlation $\rho = 0.794$). Significance level of the global test sample statistic was 2.9%. Although the BIO-ENV analysis also found strong correlations between environmental parameters and community patterns at 5400 m water depth, these correlations were statistically not significant (global test: $\rho = 0.855$, $p = 13.6\%$).

## 4. Discussion

### 4.1. General considerations

The potential impact of large food-falls on the local benthic fauna depends on the size of the carcass, the water depth, the availability of alternative food sources, but also to large extend on the background species assemblage (Kemp et al., 2006; Lundsten et al., 2010). Results from our experiment at the LTER observatory HAUSGARTEN in the eastern Fram Strait revealed major differences in the degradation of the artificial food-falls, thereby reflecting the distinct faunal zonation across the continental margin off Svalbard (Soltwedel et al., 2009). At bathyal

and hadal depths in the HAUSGARTEN area, lysianassoid amphipods are among the first and most abundant scavengers to arrive at the food-falls. Similar results were found for an experimental study on the California continental margin (Northeast Pacific), where a 30 t gray-whale carcass was implanted at 1675 m water depth to study the macrofaunal community succession in the surrounding sediments (Smith et al., 2014). However, while larger species of *Eurythenes gryllus* dominated the guild of scavengers at 2500 m (cf. Premke et al., 2006), small individuals of the genus *Uristes* were obviously the only scavengers at the bottom of the Molloy Hole at 5400 m water depth (cf. Klages et al., 2001). These differences in the scavenging community at the different water depths determined the degradation rate of the identical artificial food-falls, which appeared to be much faster at 2500 m water depth, mainly due to the presence of larger and more effective scavengers. Beside major differences in the necrophagous community at the different water depths off Svalbard, nematode assemblages at 2500 m and 5400 m water depth exhibited significant dissimilarities. Although nematode densities were rather similar (620 and 635 ind. 10 $cm^{-2}$, respectively), the nematode community on the Vestnesa Ridge exhibited almost twice the number of genera, compared to the nematode community in the Molloy Hole. Consequently, the response of the nematode communities to the carcasses at different water depths in our *in situ* experiment off Svalbard varied considerably. The PERMANOVA routine identified the factor depth as highly significant in explaining the variation in nematode community structure between the experimental sites. It appears reasonable that this result rather supports the assumption that differences in nematode community structure are related to differences in the scavenging community, hence different degradation rates of the carcasses, and not only related to water depths.

### 4.2. Local effects on nematode assemblages at 2500 m water depth

Sediments influenced by the artificial food-fall at 2500 m water depth generally showed elevated nematode densities and higher relative proportions of other metazoan meiofauna taxa compared to background sediments, with (non-significantly) highest values at 20 cm distance to the carcass. Reduced meiofauna densities beneath and immediately adjacent to the carcass might reflect the feeding pressure by larger organisms, while densities at 40 cm distance to the carrion showed transition values between the densities observed at 20 cm distance and background values found at the control site. Similar results were also found for other aquatic systems (Pavlyuk et al., 2009; Fonseca et al., 2011) and it has been suggested that the density of meiofauna increased as a response to organic enrichment from the carcasses, occurring where macrofaunal abundance no longer limits meiofauna densities (Debenham et al., 2004; Premke et al., 2010). Reduced densities in the immediate vicinity of the carcass are probably also due to hypoxia and the presence of toxic sulfides beneath the carcass (Fonseca et al., 2011). High flux rates of reduced chemicals (e.g. $H_2S$, $CH_4$) appear to be a common factor influencing the sediment-dwelling fauna around various chemosynthetic ecosystems, including seeps, vents and also large organic falls (Bernardino et al., 2012). Microprofiler measurements in our experiment confirmed considerably reduced oxygen concentrations beneath the carcasses.

Although the ANOSIM routine found no significant differences between the nematode communities in sediments adjacent to the carcass compared to controls, the PERMANOVA revealed differences in community structure at the different positions around the food-fall ($p = 0.057$ for the interaction term position × distance). Compared to the deeper site, the more advanced state of degradation of the carcass at 2500 m water depth might have established the significant differences in nematode community structure at different positions around the carrion.

Beside clearly lower values for the genera number G and the heterogeneity H′, other structural diversity measures (i.e., J′, $EG_{(30)}$) for the nematode community within the control sediments were only slightly reduced compared to those within the carcass associated sediments. In contrast, Pavlyuk et al. (2009) found highest values for diversity measured as Shannon-Wiener diversity (H′) and evenness (J′) under a carcass deposited in shallow waters (30 m water depth) in the East Sea, however, they noted highest values of nematode diversity measured as the Simpson Index (D) at larger distances from the carcass (250 m and 350 m distance), compared to the sediments in which communities were influenced by the carcass.

Generally, lower nematode diversity within the sediments beneath the carcass compared to carcass sediments at greater distance from the porpoise may be due to factors such as elevated competitive exclusion rates (Rex, 1983) and challenging biogeochemical conditions (e.g., low oxygen and high sulfide levels; Bagarinao, 1992; Levin, 2003) permitting only certain genera or morphotypes to persist (Leduc et al., 2014). For instance, some of the 28 genera (out of a total of 54 genera) that occurred exclusively within the carcass-associated sediments in our experiment (e.g., *Sabatieria* and *Daptonema*) are regularly encountered in hypoxic subsurface layers of organic rich sediments (cf. Jensen, 1984; Ólafsson, 1992; Wetzel et al., 2002; Guilini et al., 2012; Leduc et al., 2014).

Compared to the background community, nematodes found around the artificial food-fall showed significant differences in the composition of feeding types. The proportion of selective deposit feeders (1A) around the carcass was clearly reduced (38%, compared to 53% in control sediments), while non-selective deposit and epi-growth feeders (1B, 2A) increased, and the share of predators (2B) stayed almost at the same, low level. Subsequently, the impact of the artificial food-fall on the nematode community at 2500 m water depth clearly increased their trophic diversity. Values calculated for the nematode assemblage around the carcass (ITD = 0.31) were similar to those found for stations at the Atacama Slope and Trench (range 0.28–0.34; Gambi et al., 2003), where a high nutrient loading was observed. Organic enrichment was up to two orders of magnitude higher than in typical oligotrophic deep-sea sediments (Gambi et al., 2003).

Affected by enhanced food availability, the nematode assemblage around the carcass shifted from a community composed of conservative colonizers (c–p value 4; 44%) to a community dominated by general opportunists (c–p value 2; 46%), which probably also multiplied in the sediments around the food-fall. Within the carcass associated sediments, typical deep-sea genera like *Microlaimus*, *Leptolaimus* and *Thalassomonhystera* are the key representatives of the dominant opportunists, whereas within the control sediments, *Tricoma* dominates the genera known as conservative colonizers.

The opportunistic colonizer *Microlaimus*, which is mainly responsible for the enhanced proportion of epi-growth feeders around the carcass (feeding type 2A), is often among the first taxa to recolonize (physically) disturbed patches (e.g., Lee et al., 2001; Raes et al., 2010). *Leptolaimus*, classified as a selective deposit feeder (feeding type 1A), is the dominant feeding type present around the carcass, and is also known to tolerate hypoxic conditions (Modig and Ólafsson, 1998). Some of the *Leptolaimus* species are also known to be very abundant at eutrophic estuarine stations (Soetaert et al., 1995).

Selective and non-selective deposit feeders like *Leptolaimus* and *Thalassomonhystera* (the latter one also occurring in increased abundances around the carcass) are the main consumers of deep-sea bacteria (Jensen, 1987, 1988; Soeteart and Heip, 1995; Ingels et al., 2011). The feeding pressure resulting from the elevated proportion of bacterial feeders might be responsible for the noticeably reduced bacterial numbers beneath the carcass. Such a negative relationship has been previously found in other studies, where the meiofauna, and especially deposit feeders, exerted a grazing pressure on the prevailing microbial community (e.g., Montagna and Bauer, 1988; Arndt, 1993; Premke et al., 2010). In fact, this interaction was shown to be important to the general (global) nutrient cycling (Schmid-Araya and Schmid, 2000).

In general, colonizers are more abundant under eutrophic conditions, whereas the number of persisters remains constant (Singh and Ingole, 2016), but persisters (c–p values 3–4) were more often seen in deeper waters, perhaps because most deep-water nematodes are

deposit feeders, which often score 3 or 4 on the c–p scale (Bongers et al., 1991). This corresponds to the functional nematode community structure found in the more enriched sediments around the carcass compared to control sediments, where the organic content is lower.

The weighted mean of the frequencies of the c–p groups in a nematode community gives the Maturity Index (MI; Bongers, 1990), which is often used as an ecological measure of environmental disturbance, e.g., in marine pollution studies (Netto and Valgas, 2010; Moreno et al., 2011; Mirto et al., 2014). A rather high MI of the nematode community in control sediments (3.18), a value commonly indicating comparably stable environments, shifted to a (non-significantly) lower value (2.80) specifying a disturbed and/or enriched environment (Bongers, 1990). Most genera reaching high densities around the carcass are opportunistic (c–p value 2) and were responsible for the decrease of MI index. Values calculated in this study are in the same range as those found for the Hatteras Abyssal Plain and Puerto Rico Trench (range 2.8–2.9; Tietjen, 1989), where also opportunistic nematode genera with c–p values around 2 are dominant (Tietjen, 1989). It is suggested that even under deep-sea conditions carcasses of macrofauna provide niches for opportunist species and an increase in decomposition rate can result in a decreasing MI, as increasing food quantity favors fast reproducing species, with low c–p values (Bongers et al., 1991).

### 4.3. Local effects on nematode assemblages at 5400 m water depth

As with the experimental site at 2500 m water depth, sediments influenced by the artificial food-falls at 5400 m exhibited elevated nematode densities and higher relative proportions of other metazoan meiofauna taxa compared to background sediments. Again, highest densities were found at 20 cm distance to the carcass, which could be explained in the same way as for the shallower site (see above).

At 5400 m water depth, genera richness ($EG_{(30)}$) for nematode assemblages in sediments influenced by the food-fall was clearly higher, whereas the other structural diversity measures (G, J′, and H′) showed nearly no differences compared to control sediments at 5400 m water depth. As with the nematode community in close proximity to the carcass at 2500 m water depth, elevated competitive exclusion rates (Rex, 1983) and challenging biogeochemical conditions altered the dominance structure of the nematode community around the carcass (Leduc et al., 2014), and may have reduced the differences in structural diversity of the nematode communities in control and carcass associated sediments. However, during sampling, these mechanisms might (still) have had a stronger effect on the nematode communities at the deeper site compared to the shallower station, as the decaying process has not progressed as far as at 2500 m water depth. Densities of scavenging amphipods and numbers of holothurians reworking the sediment around the carcass were still high and may have led to intense biologically-induced disturbance by predation around the carcass (De Leo et al., 2010), thereby contributing to the low nematode diversity (Leduc et al., 2014). Yet, the role of biologically-induced disturbance in forming and maintaining altered diversity patterns around the carcasses remains unknown.

Based on a limited range of morphotypes compared to the shallower station, the unusual high content of phytodetritial matter within the sediments of the Molloy Hole (Soltwedel et al., 2003) supports a nematode community mainly characterized by epigrowth and deposit feeders. However, the deposit feeding nematodes are represented by different dominance patterns of genera occurring in sediments around the carcass (higher dominance of the genera *Halalaimus*, *Eleutherolaimus*, *Thalassomonhystera* and *Amphimonhystrella*) and in control sediments (higher dominance of the genera *Leptolaimus*, *Daptonema* and *Theristus*). Five deposit feeding genera exclusively occurred within the carcass samples, only two exclusively within the control samples. Together with the differing dominance patterns, these findings lead to the assumption that these manly bacterivorous nematode genera are selectively attracted to different bacterial community compositions or individual species and may respond preferentially to bacterial cues characteristic of specific stages of detritus decay (Moens et al., 1999).

Nematodes belonging to feeding type 2B (predators), were not present in the control sediments, and are exclusively represented by *Sphaerolaimus* specimens around the carcass. Our observations suggest that members of the feeding guild 2B are attracted to putrefying corpses and are able to utilize (parts of) the nutritious mixture of the body remains of dead organisms (Lopez et al., 1979; Riemann et al., 1990; Moens et al., 1999; Fonseca et al., 2011). However, these observations were mainly reported for facultative predators such as members of the family *Oncholaimidae* and the genus *Enoplus*, which were not found at 5400 m water depth. In our study the feeding type 2B around the carcass was exclusively represented by the genus *Sphaerolaimus*, considered as strictly predatory, mainly feeding on other nematodes (Lopez et al., 1979; Riemann et al., 1990; Moens et al., 1999). Although evidence suggests that some nematodes previously considered strictly predatory exhibit more widespread feeding behaviors (Moens et al., 2014), this was so far not reported for *Sphaerolaimus*. In fact, Moens et al. (2005) described the trophic position of *Sphaerolaimus* as "ambiguous". Hence, it remains unclear, whether the exclusive association of predatory *Sphaerolaimus* specimens with the carcass at 5400 m water depth is directly favored by the nutritious mixture of the porpoise remains, or whether *Sphaerolaimus* depends on the presence of prey organisms of the suitable size in the vicinity of the carcass.

Nematode assemblages at 5400 m were generally dominated by genera at intermediate c–p values and those at the lower end of the c–p scale (approx. 90% with c–p values 2 or 3). These nematodes are considered as enrichment opportunists and therefore indicate an overall resource availability, as confirmed by environmental background parameters analyzed in this study. Sediments affected by the carcass were inhabited by a nematode community with only slightly higher proportion of c–p 3 (51%) compared the community in the control sediments (45%). The c–p 3 genus *Acantholaimus* clearly dominates both communities (>40%) and is known to be abundant in deep-sea sediments (Ramalho et al., 2014). Its relative abundance usually increases with increasing water depth and hence, diminishing food availability. *Acantholaimus* is usually associated with very low amounts of phytodetritial matter in the sediments and is considered to be a persister (Bongers et al., 1991; Lee et al., 2001; De Mesel et al., 2006). In our samples, *Acantholaimus* is also more abundant at the deeper site, however, this time in an environment exhibiting high organic matter availability. Hence, generally high proportions of this genus at great water depths are probably also driven by factors other than food availability.

*Amphimonhystrella* and *Thalassomonhystera* were found to be among the subdominant genera (~25%) of the nematode community around the carcass at 5400 m water depth and contributed most to the slightly lower c–p value of the carcass associated nematode community. Opportunistic genera like *Amphimonhystrella* and *Thalassomonhystera* seem to take main advantage of the increased heterogeneous organic load associated with the carcass decaying process.

In contrast to the shallower experimental site, MI values of the nematode communities around the carcass and in control sediments at 5400 m water depth showed no difference (2.66). MI's were in the same order than those found for a station in the Puerto Rico Trench (2.68; Bongers et al., 1991) and stations from the Atacama Slope and Trench (range 2.4–2.7; Gambi et al., 2003), but still higher than the MI values found for nematode communities along a transect towards the Sandwich Trench (range 1.6–2.4; Vanhove et al., 2004).

MI's of the nematode communities in the Molloy Hole were also lower than those at the shallower experimental site, thereby specifying an enriched environment (Bongers, 1990), as confirmed by a higher organic matter availability from phytodetritus input and/or accumulation (indicated by enhanced pigment contents) and enhanced microbial biomass in the sediments (indicated by enhanced phospholipid concentrations). Generally, MI values decrease with increasing microbial activity (Bongers and Ferris, 1999), which could be confirmed by overall lower

FDA values at 5400 m water depth, indicating generally lower concentrations of free bacterial exo-enzymes in sediments due to enhanced microbial activity (Albertson et al., 1990), compared to the shallower site.

### 4.4. Concluding remarks

Our *in situ* experiment conclusively demonstrated the impact of large food-falls on the small biota at the deep seafloor. Samples retrieved five weeks after the deployment of the carcasses, provided empirical evidence for a quick response of sediment-inhabiting bacteria and the metazoan meiofauna to the carcasses at 2500 m and 5400 m water depth, thereby confirming our first hypothesis. Compared to control sediments, the substantial pulse of organic matter led to generally increased meiofauna/nematode densities around the artificial food-falls, hence validating our second hypothesis. Finally, the detailed evaluation of nematode communities in sediments affected by the carcasses in contrast with those in background sediments demonstrated shifts in the community structure and composition (especially at 5400 m water depth), and in trophic and functional diversity (mainly at 2500 m water depth), thereby also confirming our final hypothesis.

Our results convincingly confirmed the importance of environmental factors (water depth, alternative food sources) and the associated background genera composition (meiofauna/nematodes, predators/scavengers) on the assorted characteristics of the impact. The decomposition of the artificial food-falls was much more advanced at the shallower depth, which might explain the more pronounced effects of the carcass on the nematode community at 2500 m water depth, compared to the deeper site.

Microprofiler measurements revealed strong oxygen depletion beneath the carcasses, with porewater oxygen concentrations close to zero at shallow sediment depths. Hence, future experiments on the impact of large food-falls on the small benthic biota in the deep sea should include deeper sediment layers, usually inhabited by diverse nematode communities; the inclusion of nematodes from deeper layers in our study might have resulted in even stronger evidence for the direct effect of large food-falls on nematode diversity at the deep seafloor. Moreover, forthcoming studies should also include repeated sampling at specific time intervals to better follow the temporal development of changes in nematode community composition, also to determine whether the community shows a resilient behavior and falls back to its original state when the large food-fall is completely consumed.

## Acknowledgements

We would like to thank the officers and crews of RVs “Polarstern” and “L'Atalante” for their support during our expeditions in 2005. The ROV team operating “Victor 6000” during the “L'Atalante” expedition made an excellent job. The Lower Saxony State Office for Consumer Protection and Food Safety (Landesamt für Verbraucherschutz und Lebensmittelsicherheit, LAVES) provided the porpoise, found dead and stranded at the German North Sea coast near Cuxhaven. Anja Pappert and Sandra Bury are gratefully acknowledged for their assistance with the measurements of various biogenic sediment compounds, bacterial counts, meiofauna sortings, and the preparation of slides for taxonomical studies. We also gratefully acknowledge two anonymous reviewers for their valuable comments on the manuscript. This is publication e-41503 of the Alfred-Wegener-Institut Helmholtz-Zentrum für Polar- und Meeresforschung, Bremerhaven, Germany. Supplementary data are available at https://doi.org/10.1594/PANGAEA.873530. **[SW]**

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