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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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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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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

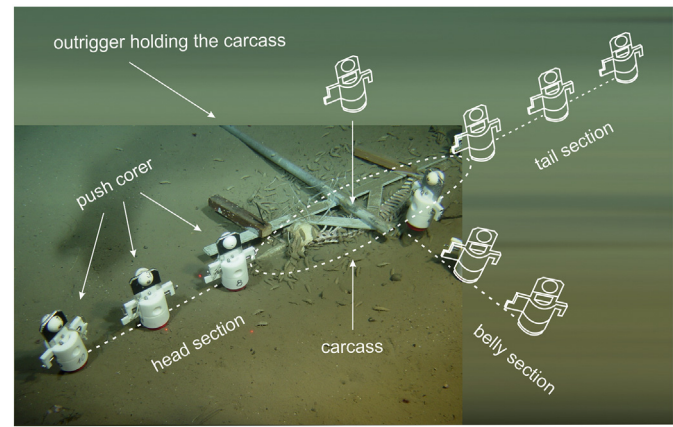


Fig. 1. Sediment sampling using ROV-handled push corers beneath the artificial food-falls and along short transects at different distances from the corpses.

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.

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 phytodetrital 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 $\mu\text{mol P g}^{-1}\text{C}$ (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 $10^{-13}\text{ g C cm}^{-3}$, as given by Børshiem et al. (1990). Chloroplastic pigments, exo-enzymatic activities, and bacterial cell numbers and biomasses were analyzed from subsamples taken with 5 ml disposable syringes.

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