Experimental evidence for selective settlement of meiofauna from two distinct environments after sediment suspension

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ABSTRACT

The cosmopolitan distribution of many meiofaunal organisms raises questions about their dispersal. The small size and the lack of a planktonic life stage of most meiofauna taxa including free-living nematodes suggest that passive dispersal is a main factor determining their distribution. This study investigates the settling behaviour of meiofauna in a water column under no-flow conditions. Two ex situ settling experiments were conducted with (1) macrophyte associated meiofauna from an intertidal salt marsh and (2) meiofauna of sulphidic sediments associated with bacterial mats from the deep-sea Håkon Mosby mud volcano. Cilyndrical containers filled with sieved seawater were used as settling chambers and five different substrates, placed on the bottom of the containers, were offered to the descending meiofaunal assemblage. The substrates used in experiment 1 were agar with bacteria, agar with *Fucus spiralis*, sulphidic agar medium, bare agar and an empty Petri dish. For experiment 2 azoic sediment with algae, azoic sediment with bacteria, a sulphidic medium, bare azoic sediment and an empty Petri dish were used. The intertidal experiment revealed that nematodes and nauplius larvae showed four- to tenfold higher densities in the *Fucus* treatment compared with the controls whereas deep-sea nematode and harpacticoid copepod densities in the sulphide treatment were more than three times higher compared with all other treatments. In both experiments nematode composition did not differ from the reference samples whereas proportions of harpacticoid copepods were increased in the treatments of the deep-sea experiment compared with the reference sample suggesting a better ability to select settlement sites than nematodes. In both experiments meiofauna abundance was highest in substrates with similar characteristics as their original habitat. These findings indicate that some meiofaunal organisms can selectively settle once they are suspended in the water column in the absence of water flow and therefore actively contribute to their dispersal at small spatial scales.

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1. Introduction

Successful colonization of new suitable habitats and connectivity between populations strongly depend on the species' dispersal capacities. Benthic meiofaunal organisms lacking a planktonic larval stage (Giere, 2009) depend on resuspension from the sediment in order to disperse over larger distances by passive dispersal mechanisms (Palmer, 1988; Winston, 2012). Harpacticoid copepods and meiofaunal polychaetes can actively leave the sediment (Boeckner et al., 2009; Commito and Tita, 2002; Palmer, 1986) facilitating their dispersal considerably and allowing organisms to choose the time of dispersal while most other meiofaunal organisms depend on hydrodynamic forces or other external disturbances for resuspension into the water column. To discuss different dispersal mechanisms we need to differentiate between large (metres to kilometres) and small scale (millimetres to centimetres)

dispersal. Large scale dispersal of meiofauna is mostly ascribed to the movement of water masses (Commito and Tita, 2002; Eckman, 1983) and rafting on objects and organisms (Ólafsson et al., 2001; Thiel and Gutow, 2005). Small scale dispersal on the other hand works through a combination of suspension into the water column by sediment erosion (through hydrodynamic forces or other physical or biological disturbances) (Fleeger et al., 1984) and active processes of the organisms themselves (Armonies, 1994; Fleeger et al., 1995). Recent studies provide evidence that nematodes, the most abundant metazoan meiobenthos taxon lacking a pelagic larval stage, can actively contribute to an enhanced dispersal on a small scale in addition to advection (Lins et al., 2013; Thomas and Lana, 2011; Ullberg and Ólafsson, 2003).

Dispersal further depends on the availability of suitable habitats. These habitats can be very remote in the case of isolated and scattered sites which differ largely from the surrounding seafloor such as deep-sea chemosynthetic environments. These chemosynthetically driven habitats are often characterized by high biomass and low diversity of specific metazoan organisms as a result of high food availability provided by chemosynthetic microorganisms (Levin, 2005; Vanreusel et al.,

2010). In many cases this is accompanied by a dominance of just few species which are not present in the surrounding non-chemosynthetic sediments (Vanreusel et al., 2010). As cold seeps are distinct and isolated features in the deep sea, the question arises how these habitats were colonized and how populations interact with each other on local and regional scales.

Genetic studies suggest a repeated colonization of the deep sea from shallow water biota followed by several extinction events (Brandt et al., 2007; Wilson, 1998). Fossil evidence suggests that deep-sea colonization was followed by ecological adaptations to local environmental conditions resulting in strictly deep-sea 'endemic' lineages (Bottjer and Jablonski, 1988; Hessler and Thistle, 1975; Sepkoski, 1991) while maintaining a phylogenetic relationship with their shallow-water counterparts such as the marine nematodes *Halomonhystera disjuncta* and *Halomonhystera hermesi* (Tchesunov et al., 2014; Van Campenhout et al., 2013; Van Gaever et al., 2006). *H. disjuncta* has been identified as a cryptic species complex from the Western Scheldt estuary in the south-west part of The Netherlands (Derycke et al., 2007) and has a dominant relative *H. hermesi* in the sulphide rich bacterial mats at the Håkon Mosby mud volcano (HMMV) and Nyegga pockmarks (Portnova et al., 2010; Van Gaever et al., 2006). Phylogenetic analysis revealed that *H. hermesi* from the HMMV forms a homogeneous clade within the cryptic species complex (Van Campenhout et al., 2013). The observation of high abundances of a shallow water species in a sulphidic environment has raised questions on past connectivity between both environments (Van Campenhout et al., 2013, 2014).

Few studies on marine nematodes have already investigated the potential of nematodes to selectively disperse through the water column (Lins et al., 2013; Ullberg and Ólafsson, 2003). Based on their results and experiment design we want to assess the settling behaviour of meiofauna from two different marine environments, intertidal (Paulina polder tidal flat, Western Scheldt, The Netherlands) and deep sea (HMMV, Barents sea), in two similar ex situ experiments. Interestingly, *H. disjuncta* occurs in both environments which allows us to compare the settling behaviour of morphologically similar and phylogenetically related organisms. With these experiments we seek to answer the following questions:

(1) Is there a differential settlement behaviour between meiofauna taxa originating from the same source environment?
(2) Do taxa preferentially or even exclusively select for the same substrate as their source?
(3) Do phylogenetically related nematode species respond similarly in their settlement behaviour?

Understanding the active settling behaviour of meiofauna and nematodes in particular may give new insights into the capacity and efficiency of these organisms to colonize new habitats, especially in patchy and low-energy environments like the Håkon Mosby mud volcano.

2. Material and methods

2.1. Study area and sampling

2.1.1. Intertidal

The studied intertidal mudflat (Paulina polder) is situated in the polyhaline part of the Western Scheldt estuary in the south-west Netherlands (at 51° 20′ 56″N, 3° 43′ 29″E). It covers an area of about 2 km^2 and is characterized by a high variability in sediment characteristics with a tidal range of approximately 4.1 m. The high heterogeneity at the site offers a variety of microhabitats for meiofaunal organisms (Moens et al., 1999). At the Paulina polder, the preferred habitat of *H. disjuncta* is decaying organic matter (Derycke et al., 2007). In order to obtain a high quantity of macroalgae associated meiofauna, a litterbag (mesh size 200 μm) was filled with *Fucus spiralis* and left at the site for one week. After retrieval the *Fucus* was washed twice in sieved (38 μm) seawater obtained from the sampling site and removed. The water was sieved through two stacked sieves with mesh sizes of 1000 μm (top sieve) and 38 μm (bottom sieve) in order to remove macrofaunal organisms and capture meiofauna. The fraction from the 38 μm sieve was retained in 3 L of sieved seawater.

2.1.2. Deep-sea

The HMMV is a methane venting cold seep located at the continental slope of the Southwest Barents Sea (72°00.3′N and 14°44.0′E) at 1265 m depth (Jerosch et al., 2007). The nematode *H. hermesi* is found in high densities (up to 11 000 ind. 10 cm^{-2}) at bacterial mat sites at the HMMV (Van Gaever et al., 2006).

Deep-sea samples were collected during R/V "Maria S. Merian" campaign (MSM 16/2) on 25.09.2010 at Station MSM16-2-802-1 (72°0.17′ N, 14°43.88′ E). A TV-guided multicorer was used to obtain samples from the white *Beggiatoa* mats at the mud volcano. The sediment used in the experiment was acquired from one core (MUC A1) of a single multicorer deployment and sieved over two stacked sieves with mesh sizes of 1000 μm and 38 μm, respectively. The meiofauna fraction, retained on the 38 μm sieve, was used for the experiment. An additional sediment core (A5) of the same multicorer deployment (MUC A) was analysed to serve as a reference sample.

2.2. Experimental set-up

2.2.1. Intertidal

Three cylindrical containers (bottom diameter: 35 cm, height: 55 cm, top diameter: 45 cm) were filled with sieved (38 μm) seawater obtained from the sampling site up to a water height of 50 cm corresponding with a volume of approximately 126 L. Temperature and salinity were 8 °C and 25, respectively, according to field conditions at times of sampling. A perforated disc containing five equally spaced Petri dishes was positioned on the bottom (Fig. 1). Petri dishes
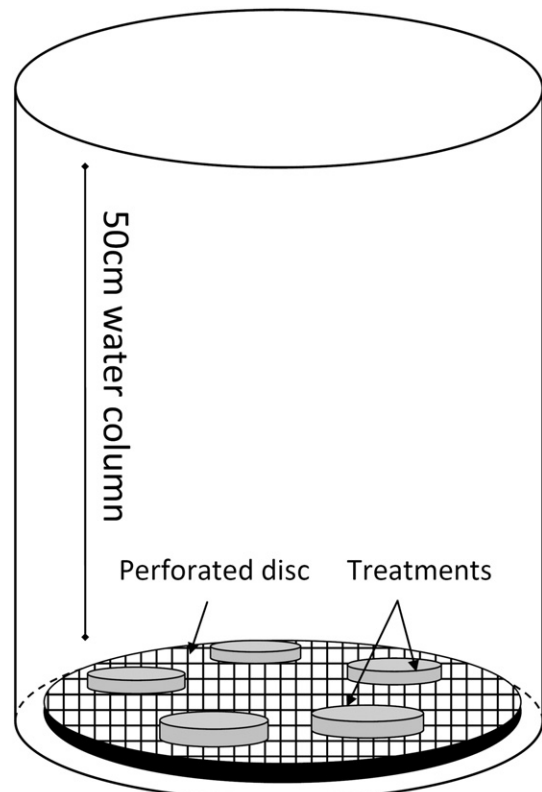

Fig. 1. Schematic drawing of the experimental set-up.