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Sediment-mediated effects of lugworms on intertidal meiofauna

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ABSTRACT

Based on a large-scale, long-term lugworm exclusion experiment established on an intertidal sand flat in Königshafen (Sylt, North Sea), the effect of ecosystem engineering by the lugworm *Arenicola marina* on the meiofaunal community was studied. Samples for sediment and meiofauna analyses were taken from a lugworm exclusion plot three years after lugworms were excluded, a disturbed control plot and a pristine ambient plot. Statistical analyses revealed significantly higher concentrations of total organic matter and chloroplastic pigments at the lugworm exclusion site. The median abundance of total meiofauna was 21–29% higher at the lugworm-free site as compared to the lugworm-inhabited sites. Copepoda and Nematoda were distributed homogeneously over all experimental plots while Ostracoda and copepod nauplii reached their highest abundances in the absence of lugworms. Univariate and multivariate analyses revealed significant differences between the copepod species composition of the experimental sites. While the harpacticoid copepod *Arenosetella germanica* reacted with a decline in individual numbers to lugworm exclusion, *Halectinosoma gothiceps* and *Asellopsis intermedia* benefited from the induced changes in the sediment characteristics. Overall, a higher copepod species diversity and evenness was observed at the lugworm exclusion site. The results of this study indicate that sediment-mediated effects of bioturbating organisms influence the abundance and diversity of surface-living meiofauna.

1. Introduction

Meiofauna is a highly diverse and abundant component of the marine benthic infauna, inhabiting all varieties of marine and estuarine sediments. Meiofauna significantly contributes to the processing of organic material (Giere, 1993) and plays a key role in the functioning of benthic ecosystems (Coull, 1988). With high metabolic turnover rates, rapid generation times and diverse functional traits meiofaunal communities are highly suitable for studies of recovery and colonization mechanisms in pristine or impacted habitats (Schratzberger et al., 2004; Veit-Köhler et al., 2008 and references therein). Meiofaunal assemblages are characterized by high species diversity and are thus an ideal group for biodiversity studies in marine systems (e.g. Schratzberger et al., 2000). The distribution of meiofaunal organisms is dependent on sediment factors, including grain size composition, organic content and pore water characteristics (Coull, 1988). The greatest meiobenthic diversity and abundances can be found in the oxygenated and sulfide-free zones of the sediment, whereas zones of anoxia are avoided. In intertidal sands, where oxygen typically penetrates only a few millimeters, high meiobenthic diversity and abundances are restricted to the uppermost sediment layer (Coull, 1988). However, as "ecosystem engineers" (sensu Jones et al., 1994) macrobenthic organisms can alter the availability of resources to other organisms, provide biogenic structures and alter the sedimentary habitat through their bioturbating activities (Reise et al., 2009). For example, burrows of bottom-dwelling macrobenthic organisms provide additional attractive small-scale habitats where meiofaunal organisms benefit from bioirrigation that supplies oxygen at depth (Reise and Ax, 1979; Reise, 1981, 1983; Wetzel et al., 1995). The effects of macrobenthic organisms on meiobenthic communities may well go beyond the provision of suitable habitats at depth on the micro-scale. Bioturbating organisms alter the sediment characteristics and the sediment stability which may have considerable implications for the habitat suitability of marine sediments for benthic meiofauna. A dominant bioengineer of the Wadden Sea is the lugworm *Arenicola marina* (Linné, 1758), an abundant member of the macrozoobenthos in intertidal and shallow subtidal sandy sediments of northwestern European coasts (Wells, 1963; Riisgård and Banta, 1998). So-called "lugworm flats" are populated by 20 to 40 ind. m^{-2} (Beukema and de Vlas, 1979; Reise, 1985) that live in 15 to 20 cm deep J-shaped burrows. Through a vertical head shaft surface sediment is subducted to depth where it is ingested by the lugworm and defecated as characteristic fecal mounds at the sediment surface. The dominating role of lugworms on tidal flats in the Wadden Sea has aroused considerable interest in their role for the functioning of benthic systems and it has been shown that the

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bioturbating activities fundamentally affect the characteristic of inhabited intertidal sand flats (Volkenborn et al., 2007a,b). Lugworms were found to affect sediment stratification (Cadée, 1976; Baumfalk, 1979), pore water nutrients (Huettel, 1990), biogeochemical processes (Kristensen, 2001; Nielsen et al., 2003), particulate and dissolved material exchange (Asmus and Asmus, 1998), microorganisms (Reichardt, 1988; Grossmann and Reichardt, 1991; Retraubun et al., 1996; Goñi-Urriza et al., 1999) and benthic macrofauna (Brey, 1991; Flach, 1992a,b, Flach, 1993; Flach and de Bruin, 1993; Lackschewitz and Reise, 1998).

Recently a large-scale, long-term lugworm exclusion experiment was initiated at the island of Sylt (German Bight, North Sea; Volkenborn and Reise, 2005) with experimental plots of 400 m² in area. Over the following years the benthic community (with a focus on macrofauna) and sediment properties were studied to reveal the effects of *A. marina* on the functioning of intertidal sand flats (Volkenborn et al., 2007a,b, Volkenborn et al., 2009). A first meiofauna study carried out on these large experimental plots revealed a temporal increase of meiofauna on the lugworm exclusion plots. Especially copepods and ostracods preferred the organically enriched lugworm-free sites in the low-intertidal fine-sand zone (Schmidt, 2004). This was contradictory to the studies of Reise (1983) where effects of lugworms on small zoobenthos were restricted to subsurface sediments while taxa restricted to the sediment surface were not affected. The aim of this study was to determine the effects of a long-term absence of the ecosystem engineer *A. marina* and the related sediment changes (1) on surface-living meiofauna communities in general and (2) copepod assemblages in particular.

2. Methods

2.1. Study site and experimental design

In spring 2002 a large-scale, long-term lugworm exclusion experiment was initiated on an intertidal sand flat in Königshafen (55°02′N, 08°26′E), a tidal embayment at the northern end of the island Sylt in the German Bight, North Sea (Fig. 1) (Volkenborn et al., 2007a). The area is sheltered by the “Ellenbogen” peninsula in the northern and western part of the bay as well as by the island of Uthörn in the south-east. The sediment at the study site is dominated by medium and fine sand with a median particle size of 230 µm (Gätje and Reise, 1998). The organic content is low (<1%; Reise et al., 1994). The mean tidal range is 1.8 m and the salinity varies between 27 psu in spring and 31 psu in summer. *A. marina* comprises up to 76% of the total biomass at the study site (Reise et al., 1994). Further details are provided by Austen (1994), Reise (1985), Volkenborn and Reise (2005, 2006), Volkenborn et al. (2007a,b, 2009) and Wohlenberg (1937).

Lugworms (*A. marina*) were permanently excluded from intertidal sand by placing a polyethylene net (mesh size 1 mm) 10 cm deep into the sediment. At control plots the sediment was physically reworked with a backhoe in the same way as at the exclusion plots, but without inserting the net. A third variation of plots (ambient) was left untouched in order to represent natural conditions. Each single plot (exclusion, control and ambient) had an area of $20 \times 20 = 400$ m^2 (Volkenborn et al., 2007a).

The study presented here is based on random samples from one block, including the exclusion and the corresponding control and ambient plots in the low-intertidal region with an emersion period of 3 to 4 h. In this low-intertidal fine-sand area the effects of lugworm presence were found to be more conspicuous than in the mid intertidal medium sand area (Volkenborn et al., 2007a). It should be noted that one out of three experimental blocks situated in the low-intertidal area was chosen for sampling. To counteract the normal sample variability, such as in individual numbers, more parallel samples than possible when applying strict replication according to Hurlbert (1984) were taken. We considered the randomly taken samples from each plot of the investigated block to be independent replicates because of the small size of meiofauna organisms (<1 mm) in relation to the plot areas of 400 m^2. This area is vast for animals of this size class. The results of this study should therefore be interpreted bearing in mind that the effects of lugworms may be dependent on sediment and tidal range.

To control the effect of lugworm treatment, lugworm densities were estimated by counting the fecal castings within 10 randomly chosen squares of 0.25 m^2 within each experimental area.

2.2. Sample collection

In summer 2005 (17.08.) meiofauna was sampled during low tide by means of a cut-off syringe (2.8 cm internal diameter) down to 1 cm sediment depth. Sampling was done randomly excluding the outer 2 m of each plot in order to minimize possible plot edge effects. The samples were fixed in 4% buffered formaldehyde. This fixation is appropriate for most metazoan meiofauna, except for certain soft-bodied and adhesive taxa such as flatworms. Seven replicate samples

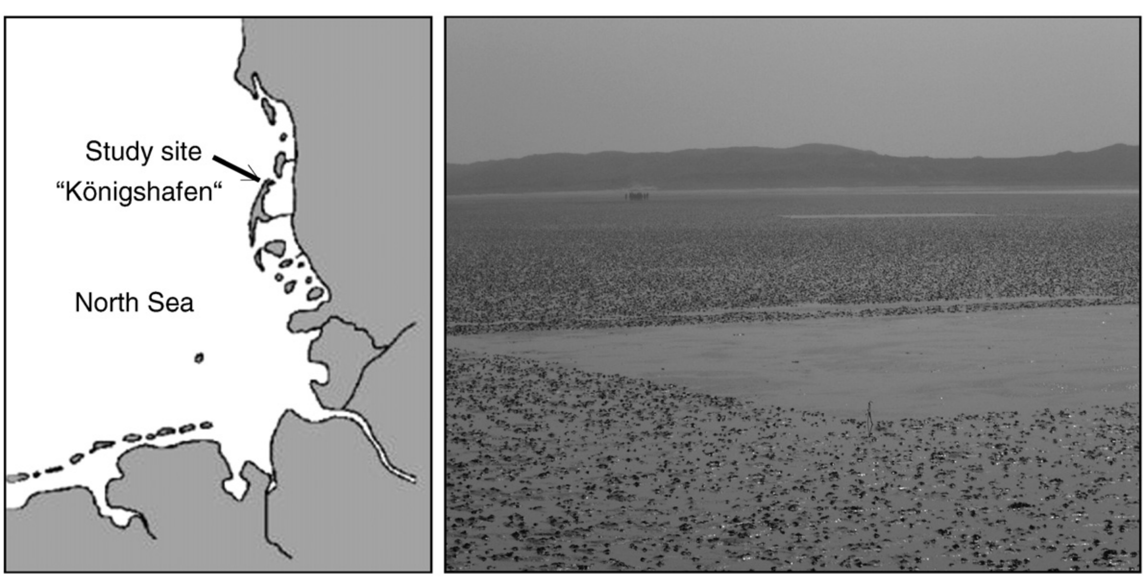

Fig. 1. Study site “Königshafen”, Sylt, Germany. The rectangular flat area lacking lugworm faeces mounds is a lugworm exclusion plot.