ORIGINAL ARTICLE

Sediment destabilizing and stabilizing bio-engineers on tidal flats: cascading effects of experimental exclusion

Nils Volkenborn · Dylan Martin Robertson · Karsten Reise

Abstract Bioturbating lugworms (*Arenicola marina*) were excluded from 400 m² plots of intertidal sand which initiated sequences of direct and indirect changes in the structure of the benthic community. The sessile, tube-building species *Polydora cornuta* and *Lanice conchilega* took advantage of the absence of lugworms and settled preferentially on lugworm exclusion plots. The protruding tubes provided attachment for an ephemeral development of algal tufts (*Berkeleya* colonies and *Enteromorpha* thalli) which in turn enhanced settlement of the juvenile drifting clams *Mya arenaria* and *Macoma balthica*. This causal chain of enhanced bivalve settlement in the presence of above-ground structures, like animal tubes and algae, on lugworm exclusion plots occurred in 2 years at different tidal zones with different tube builders, algae and juvenile clams. A significant response of *L. conchilega* in a year with relatively low lugworm abundances at the entire site suggests that not only the actual absence of large bioturbators was responsible for the establishment of tube-dwelling species, but also a cumulative change of the sediment in exclusion plots since the onset of the experiment. While the sediment on lugworm plots remained permeable, fine particles and organic matter accumulated at exclusion plots. It is suggested that these differences in sediment characteristics were the product of divergent benthic engineering by sediment destabilizing lugworms on control plots and sediment stabilizing species on exclusion plots. Cumulative changes of the sedimentary habitat and cascading effects in the benthic community may explain the persistence of patches that are dominated by either sediment stabilizing or destabilizing species in the assemblage mosaic of intertidal sediments.

Keywords Ecosystem engineering · Arenicola marina · Bioturbation · Sediment stabilizers · Sediment destabilizers

N. Volkenborn (✉) · K. Reise
Alfred Wegener Institute for Polar and Marine Research,
Wadden Sea Station Sylt, Hafenstrasse 43, 25992 List, Germany
e-mail: nils.volkenborn@awi.de

D. M. Robertson
Department of Marine Science, University of Otago,
P.O. Box 56, Dunedin, New Zealand

Present Address:
N. Volkenborn
Department of Biological Sciences,
University of South Carolina, Columbia, SC 29208, USA
e-mail: nils@biol.sc.edu

Introduction

Ecosystem engineers in marine soft sediments may be classified into two fundamental functional categories: bioturbators loosen the sedimentary fabric and destabilise sediments (Rhoads 1974; Brenchley 1981) while sedentary species, e.g. tube-builders or seagrasses, stabilise sediments (Woodin 1981; Gallagher et al. 1983). Both, sediment destabilizing and sediment stabilizing engineers may have profound effects on the sedimentary habitat and the structures of benthic communities (Reise 2002), often making the environment less suitable for the ecologically different form (Woodin and Jackson 1979; Thayer 1983). As a result of these mobility-mode interactions, natural soft-bottom communities are often dominated by either mobile or sedentary species (review by Posey 1987). Numerous examples indicate this mutual exclusion of one mobility group by the other: dense aggregations of thalassinidean shrimps were found to exclude several sedentary species, such as bivalves (Peterson 1977), tube-building

polychaetes (Posey 1986) or seagrasses (Siebert and Branch 2006). The same is true for bioturbating lugworms which inhibit tubicolous worms (Wilson 1981; Volkenborn and Reise 2007), amphipods (Flach 1992) and rooted plants (van Wesenbeeck et al 2007). On the other hand, dense aggregations of tube-building species or seagrasses may considerably reduce the abundances of burrowing species (e.g. Woodin 1981), while other sedentary species may be facilitated (Brenchley 1982; Bolam and Fernandes 2003). Furthermore, the size of individuals needs to be taken into account when evaluating the influence of relative mobilities on the composition of benthic communities. Large, active burrowers may considerably affect small sedentary species, but not necessarily large ones (Wilson 1981), while sedentary species may reduce the abundances of intermediate-sized burrowers but not necessarily the abundance of smaller and larger species (Posey 1987).

Functional group interactions may go far beyond direct sediment disruption through burrowing and binding of sediment by animal tubes or plant roots as suggested in the mobility-mode hypothesis (Brenchley 1982). Indirect, sediment-mediated effects of engineering activities may also affect the outcome of localised mobility-mode interactions. Bioirrigating infauna facilitates microbial degradation of organic material (Kristensen and Blackburn 1987) and decreases porewater nutrient concentrations (Huettel 1990) and microphytobenthic growth (Volkenborn et al. 2007a, b). Dense aggregations of tube-dwelling species may stabilise the sediment and increase the organic and fine particle content (Luckenbach 1986) and even dead biogenic structures, such as shell debris, may significantly alter habitat characteristics (Gutierrez et al. 2003). Sediment-mediated effects may thus considerably affect both, the food availability, and the sedimentary habitat characteristics for other benthic species.

Integration of mobility-mode interactions into the concept of ecosystem engineering (*sensu* Lawton and Jones 1993) will account for the complexity of benthic habitat transformations. Cumulative engineering of the sedimentary habitat may be a slow process, and many effects possibly are conditional, depending upon environmental constraints, such as sediment type or hydrodynamic exposure (Norkko et al. 2006). Large-scale, long-term field experiments thus may be the most appropriate tool to investigate under which environmental constraints spatial competition between alternate ecosystem engineers may unfold and if so, what are the consequences for the functioning of benthic communities.

This study focussed on intertidal benthic community dynamics induced by the permanent exclusion of the bioturbating polychaete *Arenicola marina* (L.), which is a widespread and abundant destabiliser of intertidal sandy sediments at northwest European coasts (Beukema 1976; Reise 1985, Cadée 1976). *Arenicola marina* lives in 20–40-cm deep J-shaped burrows completed to a U by a vertical head shaft. Bioirrigation by the lugworm fluidises the sediment in the head shaft so that surface sediment slides down, is ingested by the worm, and defecated as a mound of coiled faecal strings at the sediment surface above the tail shaft (Riisgård and Banta 1998).

In 2002, a large-scale lugworm exclusion experiment was initiated. On six 400 m² lugworm exclusion plots and corresponding lugworm populated plots, the sediment characteristics and the benthic community were monitored in subsequent years. Investigations of sediment and porewater properties in the presence/absence of *A. marina* revealed significant changes in habitat characteristics at lugworm exclusion plots (Volkenborn et al. 2007a, b). In summary, microphytobenthic biomass and the proportion of fine particles and associated organic material almost doubled on lugworm exclusion plots, sediment permeability decreased, and inorganic porewater nutrients and sulphide accumulated within the sediment. Benthic community response was variable in space and time, but the overall effect was that tube-building and burrow-constructing species (e.g. *Pygospio elegans* and *Nereis diversicolor*) took advantage of the absence of lugworms, while free burrowing species (e.g. *Scoloplos* cf. *armiger*) were not affected or even decreased in abundance (Volkenborn and Reise 2006, 2007).

Results from the large-scale lugworm exclusion experiment support the mobility mode hypothesis of mutual exclusion of functional different forms (Brenchley 1982). It is hypothesised that the underlying mechanisms go far beyond local and direct disturbance through burrowing and binding of sediment by animal tubes. Moreover, changes of the benthic habitat, originally induced by the exclusion of sediment destabilizing lugworms, may have been amplified by the bio-engineering of sediment stabilizing species. This paper will focus on developments in the benthic community on experimental plots one and 2 years after the experiment was started. Based on the observed species responses to the manipulative experimental treatments and on relevant literature, the mutual exclusion of sediment stabilizing and destabilizing bio-engineers on intertidal flats is proposed. Divergent trajectories may unfold, which contribute to the longevity of patches which are dominated by either mobility-mode. On a larger scale, these may generate a dynamic mosaic of assemblages in the marine benthos (Reise 1991).

Materials and methods

Study area and experimental design

A lugworm exclusion experiment was conducted on a sheltered, unvegetated intertidal sandflat in Königshafen, a tidal embayment at the northern tip of the island of Sylt in the North Sea (55°02′ N; 8°26′ E). Details of the experimental

set-up can be found in Volkenborn et al. (2007a) and Volkenborn and Reise (2006) and details of the study site are provided by Reise (1985) and Austen (1994). Exclusion of lugworms on replicated ($n = 6$) 400 m^2 plots was achieved by inserting a 1-mm meshed net at 10 cm depth into the sediment in spring 2002. The experiment was arranged in a 2-factorial (3×2 levels) nested block design. Six experimental blocks were nested with respect to tidal height: three blocks around mid-tide level (emersion period 6–7 h per tide) with medium sand (grain size median 330–340 μm) and three blocks near low-tide level (emersion period 3–4 h) with a finer sediment (grain size median 200–220 μm). Each experimental block consisted of three plots differing in treatment: exclusion = buried net, control = similarly dredged but left without a net, ambient = untouched plot.

Sampling of macrofauna and algae

Sampling of macroinfauna was done by counting invertebrates retained on a 1-mm mesh sieve from eight cores of 100 cm^2 and 10 cm depth randomly taken within each of the 18 experimental plots. Sampling was done every fourth month between April 2003 and August 2004. In August 2003, eight additional subsamples of 10 cm^2 from all experimental plots were sieved through a 250-μm mesh to include small, juvenile polychaetes. Sampling was generally completed within one week and was done block-wise in order to include the effect of consecutive sampling into the block effect. Abundances of *Lanice conchilega* were additionally estimated by counting tube caps within one sub-quadrate of 10×10 cm of eight quadrates of 0.25 m^2. Colonies of the diatom *Berkeleya rutilans* (Trentepohl ex Roth) were counted in eight quadrates of 0.25 m^2 on each experimental plot in April 2003. Abundances of algal strings of *Enteromorpha* spp. were not estimated, since it was not possible to identify individuals. As a measure of algal cover, the frequency in 25 sub-quadrates of 10×10 cm in six randomly chosen quadrates of 0.25 m^2 were determined in August 2004. Only green algal *Enteromorpha* strings that were anchored within sub-quadrates were considered. Additionally, green algal biomass was estimated from three representative samples of 100 cm^2 within each plot as ash-free dry weight.

Statistical analyses

Abundances of macrofauna on experimental plots were analysed using two-factorial ANOVA. The effect of lugworm presence/absence was used as fixed factor (three levels: exclusion, control, ambient). Tidal position as second fixed factor was used to test the effect of tidal height (two levels: low intertidal, mid intertidal) and accounting for the significance of interaction effects of tidal height and

lugworm presence/absence. Experimental blocks, nested in the tidal heights, were assessed as random factor to incorporate the spatial heterogeneity of the study site into the statistical analysis. Prior to analysis, data were tested for homogeneity of variances (Cochran's test) and log-transformed if required. Post hoc multiple means comparisons were performed using the Tukey–Kramer procedure at $\alpha = 0.05$ significance level. In 2004, algae and *Lanice* frequency data were not homogenous. Due to the fact that *L. conchilega* and green algae almost exclusively occurred on lugworm exclusion plots in the low intertidal, statistical tests on factor effects were not performed in this case. In 2004, *L. conchilega* tubes and juvenile bivalves where counted within the same samples, allowing to test for localised species interactions by regression analysis. This was possible for the 2003 data since *Polydora cornuta* abundances were estimated from 10 cm^2 samples while abundances of juvenile *Macoma balthica* were estimated from (different) 100 cm^2 samples.

Results

Seasonal developments in the benthic community 2003

In spring 2003 colonies of the tuft-forming diatom *B. rutilans* developed mainly on experimental lugworm exclusion plots in the mid intertidal zone (Fig. 1a, b). Most of these diatom colonies were attached to tubes of the spinoid *P. cornuta* (Bosc). In April 2003 abundances of *P. cornuta* were threefold on lugworm exclusion plots compared to control and ambient plots in the mid intertidal zone (Fig. 2a) but overall, this polychaete was not significantly affected by the experimental treatment ($F_{2,8} = 0.41$; $P = 0.68$) nor by treatment × tidal height interaction ($F_{2,8} = 2.03$; $P = 0.19$). In August 2003, when samples where sieved with 250 μm mesh a significant treatment effect was found on abundances of *P. cornuta* ($F_{2,8} = 7.37$; $P = 0.015$) with significant higher abundances of *P. cornuta* on lugworm exclusion plots (Tukey $P < 0.05$; Fig. 2b). The tuft-forming diatom *B. rutilans* appeared in March 2003, and until April algal tufts had reached a size of up to 10 cm and densities up to 50 colonies m^{-2} (Fig. 2c). Colony abundances were significantly affected by treatment × tidal height interaction ($F_{2,8} = 28.76$; $P < 0.001$) indicating significant higher abundances of *Berkeleya* colonies on exclusion plots in the mid intertidal zone compared to other experimental treatments (Tukey $P < 0.01$). In spring 2003 juveniles of *M. balthica* (L.) recruited to the study site. In August, they also reached highest densities on lugworm exclusion plots in the mid intertidal area (significant treatment × tidal height interaction, $F_{2,8} = 4.53$; $P < 0.01$). In the mid intertidal area average abundance of *M. balthica*

Fig. 1 Lugworm exclusion plots with ephemeral algal growth. In spring 2003, colonies of the tuft-forming diatom *Berkeleya rutilans* were growing on exclusion plots in the mid intertidal (**a**) and most colonies were attached to tubes of the spinoid polychaete *Polydora cornuta* (**b**). In summer 2004, green algal tufts were growing on lugworm exclusion plots in the low intertidal (**c**). Most algal strings were attached to sand-tubes of the polychaete *Lanice conchilega* (**d**). *Broken lines* indicate the edges of lugworm exclusion plots
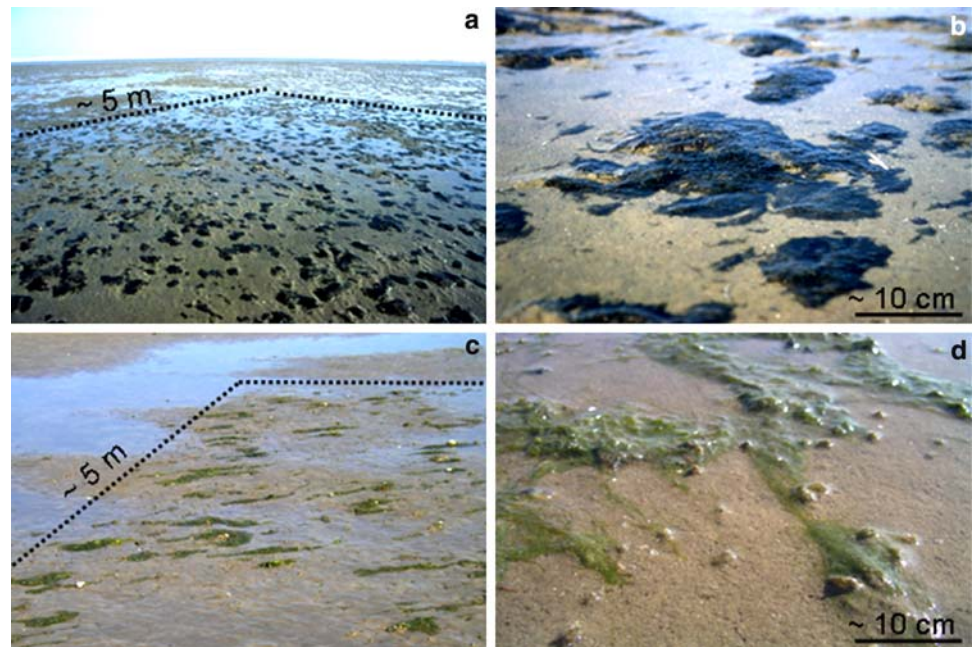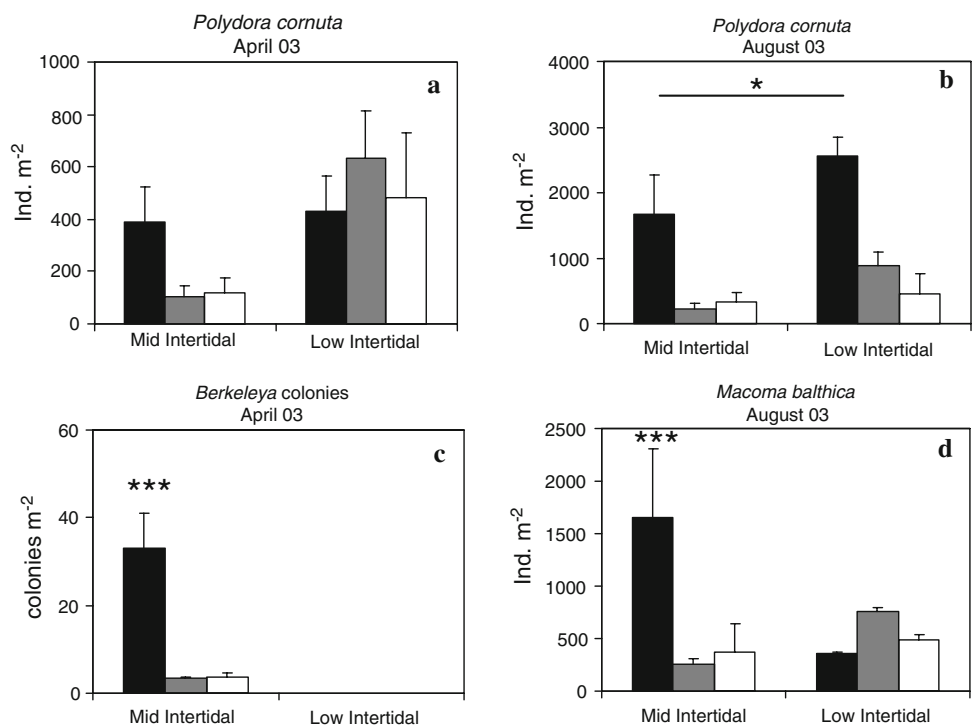

Fig. 2 Abundances of *Polydora cornuta* in April 2003 (**a**; sieved with 1,000 μm mesh) and August 2003 (**b**; sieved with 250 μm mesh), *Berkeleya* colonies (**c**) and juvenile *Macoma balthica* (**d**) on experimental plots in spring and summer 2003 (shown are means and SE ($n = 6$); *Black* = exclusion; *Grey* = control; *White* = ambient; *asterisks* indicate significant different treatments)

was 1,600 ind. m^{-2} on lugworm exclusion plots while abundances were below 500 ind.$^{-2}$ in all other experimental treatments (Fig. 2d).

Seasonal developments in the benthic community 2004

In summer 2004 green and red algae (*Enteromorpha* spp., *Ulva* spp., *Polysiphonia* spp.) developed on experimental plots in the low intertidal zone (Fig. 1c, d). Most of these

algal strings were attached to tubes of the terebellid polychaete *L. conchilega*.

Lanice conchilega was first recorded on experimental plots in summer 2003. Until winter, abundances remained low (<5 m^{-2} averaged over all plots), but were already significantly affected by lugworm treatment ($F_{2,8} = 12.47$; $P < 0.01$) and tidal height ($F_{2,8} = 16.36$; $P < 0.01$) with higher densities on lugworm exclusion plots and on plots in the low intertidal area (Tukey $P < 0.01$ for both effects).

Densities significantly increased from spring to summer 2004. In summer, *L. conchilega* was found almost exclusively on lugworm exclusion plots in the low intertidal area (Fig. 3a). In August 2004, *L. conchilega* reached average densities of 500 ind. m^{-2} on these plots. Algae occurred also almost exclusively on the lugworm exclusion plots (Fig. 3b). In the 10×10 cm grid used to estimate algal cover, green algal frequency was about 90% and algae biomass was up to 20 g dry weight m^{-2}. Two bivalve species (*Mya arenaria* (L.) and *M. balthica*) recruited to the low intertidal area of the experimental site in spring 2004. For both species, highest abundances were found within lugworm exclusion plots in the low intertidal area (Fig. 3 c, d). Within all 144 samples of 100 cm², abundances of both species were significantly and positively correlated with the number of protruding *Lanice* tubes (*M. arenaria* $r^2 = 0.755$; $P < 0.001$; *M. balthica* $r^2 = 0.395$; $P < 0.001$; Fig. 4a, b).

Discussion

In the absence of *A. marina*, increased abundances of tube-building polychaetes and decreased abundances of burrowing species confirm the mobility-mode hypothesis in soft-bottom communities, suggested by Brenchley (1982) and Posey (1987). Increased abundances of sessile species had further consequences for the benthic community, as protruding tube caps provided attachment for macroalgae and above-ground structures, like animal tubes and algae, in
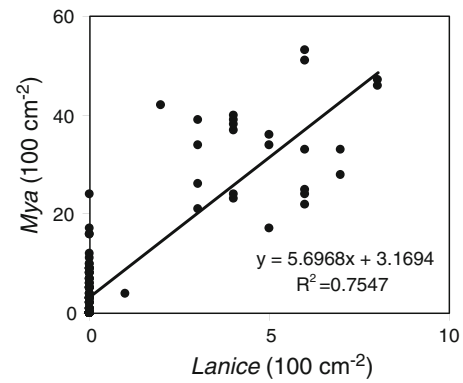

$$y = 5.6968x + 3.1694$$
$$R^2 = 0.7547$$

Fig. 4 Regression analysis between *Lanice conchilega* and spat of *Mya arenaria* (**a**) and *Macoma balthica* (**b**) within 144 samples from all experimental plots in summer 2004

turn triggered settlement of juvenile benthic species. The separate aspects of these cascading processes have already been described in the literature (lugworms inhibit tube builder, e.g. in Flach 1992; tube builder anchor algae, e.g. in Thomsen and McGlathery 2005; above-ground structures facilitate bivalve recruitment, e.g. in Cummings et al. 1996). In this study the consecutive pattern of these interactions has been triggered by the experimental large-scale and long-term exclusion of a dominant sediment destabilizing bio-engineer. It is proposed that mobility-mode interactions may go far beyond localised sediment disturbance or stabilization and involve manifold aspects of bio-engineering. In the first part of the discussion, the benthic community

Fig. 3 Abundances of *Lanice conchilega* (**a**), green algal frequency (**b**) and abundances of *Mya arenaria* (**c**) and *Macoma balthica* (**d**) on experimental plots in summer 2004 (shown are means and SE ($n = 6$); *Black* = exclusion; *Grey* = control; *White* = ambient; *asterisks* indicate significant different treatments)
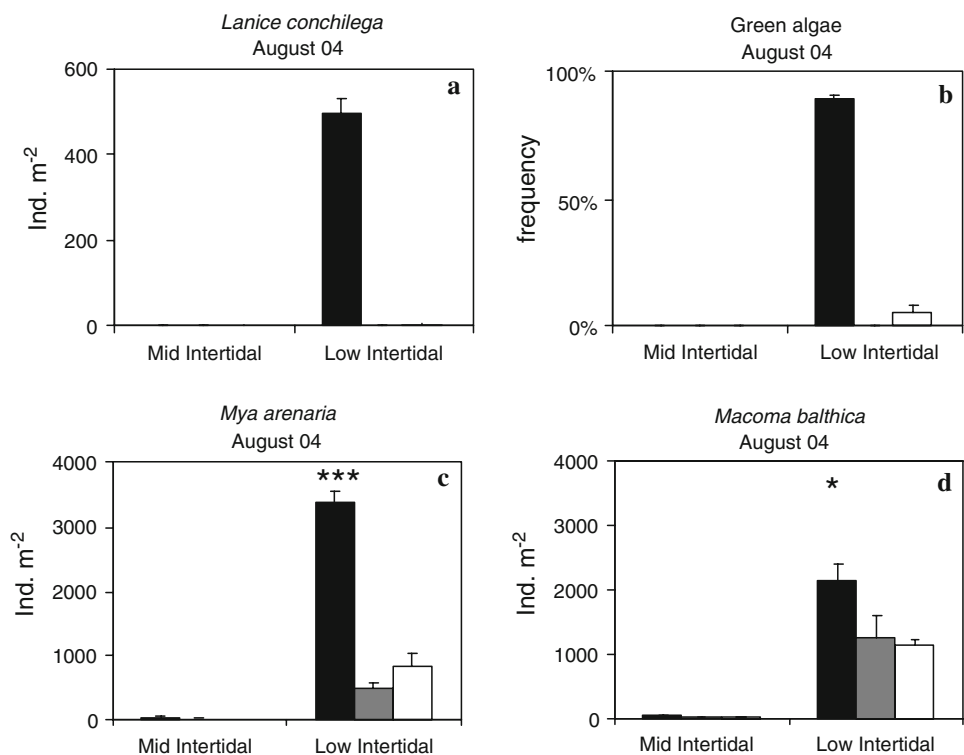
developments on experimental plots in the course of the experiment will be discussed separately. In order to assess the underlying mechanisms this part is augmented by additional information on the ecology and the engineering effects of involved species from the literature. In the second part of the discussion these findings are put into a wider ecological context. It is suggested that spatial competition of sediment stabilizing and destabilizing bio-engineers is a characteristic element of benthic community dynamics.

Lugworms inhibit tube-building polychaetes

Arenicola marina was found to have significant positive effects on the abundance of several other meio- and macro-benthic species around the burrow (Reise and Ax 1979; Lackschewitz and Reise 1998), while sedentary species near the surface were negatively affected (Flach and de Bruin 1993; Zipperle and Reise 2005). Negative effects of this bioturbator on tube-building species were mainly attributed to unstable conditions in the presence of lugworm feeding activity (Brey 1991; Flach 1992). This is generally supported by observations on the experimental plots in this study: species with permanent tubes or burrows were more abundant on lugworm exclusion plots, while abundances of free-burrowing species decreased (see also Volkenborn and Reise 2007). However, it is suggested that also other factors than direct and localised disturbance by bioturbation need to be considered to explain the differential abundances on experimental plots.

Polydora cornuta was not significantly affected by lugworm presence/absence in April, though abundances at mid intertidal were threefold in the absence of *A. marina*. When sampled later with a finer mesh in August, abundances of *P. cornuta* were significantly higher on lugworm exclusion than on lugworm plots. Presumably, juvenile *P. cornuta* had settled near the adults in early summer. Protruding tubes of *P. cornuta* were composed of very fine material (personal observation). *A. marina* was found to inhibit the accumulation of fine particles in surface sediments on experimental plots (Volkenborn et al. 2007a, b). Thus, *P. cornuta* may have taken benefit from a higher availability of fine particles in the absence of *A. marina*. Overall, lugworm effects on abundances of *P. cornuta* were moderate and a combined effect of direct disturbance and biogenic habitat transformations is suggested.

Lanice conchilega became established almost exclusively on lugworm exclusion plots in the low intertidal zone. Lugworm abundances were generally low on lugworm plots in 2004 (5–10 ind. m^{-2} on experimental plots in the low intertidal area; for details see Volkenborn and Reise 2006), when *L. conchilega* settled on experimental plots. Thus, disturbance by lugworm feeding activities is unlikely to be the only reason for the establishment of the

tube-dweller. A plausible explanation for the observed pattern is a cumulative change in sediment properties in the course of 2 years. It is left to speculation which characteristics actually attracted *L. conchilega*, but a combined effect of increased organic matter, more fine particles and more microphytobenthos on lugworm exclusion plots (Volkenborn et al. 2007a, b) is very likely. Since colonisation of *L. conchilega* was found to be facilitated by the presence of already existing *Lanice* tubes (Strasser and Pieloth 2001; Callaway 2003), abundances of *L. conchilega* may continue to increase on lugworm exclusion plots in the low intertidal.

Polychaete tubes anchor algal tufts

In both years of this study, ephemeral growth of tuft-forming algae was found on experimental plots. Most of these diatom, green and red algal tufts were attached to protruding polychaete tubes. On dynamic intertidal sands, where substrate for algal attachment is scarce, polychaete tube caps may significantly facilitate algal growth by providing anchorage (Woodin 1977; Thomsen and McGlathery 2005). On lugworm exclusion plots algal biomass reached values of up to 20 g dry weight m^{-2}. During and after the growth season, algae were partly buried in the sediment. This incorporation of organic material presumably contributed to the organic enrichment of lugworm exclusion plots.

Biogenic above-ground structures increase settlement of drifting juvenile macrofauna

Juvenile abundances of *M. arenaria* and *M. balthica* were significantly higher on lugworm exclusion plots in both years and closely linked to the number of sediment protruding tube caps. Increased abundances of juvenile bivalves in the absence of lugworms may have been the product of inhibition by large bioturbators (Rhoads and Young 1970; Woodin 1976; Flach 1992) and of facilitation by sediment stabilisers and animal tubes (Cummings et al. 1996; Thomsen and McGlathery 2005; Bolam and Fernandes 2003). Strong response of juvenile bivalves in 2004, when lugworm abundances were rather low at the study site (5–10 ind. m^{-2} on control and ambient plots in the low intertidal area), suggests that inhibition by lugworm disturbance and feeding is unlikely to be the sole reason for the observed pattern. Presumably, above-ground structures, like polychaete tubes and anchored algae, provided attachment for young bivalves with byssus threads and thus facilitated their settlement. The strong correlation of juvenile bivalves numbers and protruding tube caps of *L. conchilega* within 100 cm^2 samples in 2004 does not prove this causal relationship, but based on the ecology of both bivalve species, localised increased settlement of *M. balthica* and *Mya*

arenaria in the presence of above-ground structures is very likely. Postlarval drift is a common phenomenon among many benthic species (see review by Butman 1987) and in the intertidal zone of the Wadden Sea, spat of the bivalves *M. balthica*, *M. arenaria* and others change their intertidal position by postlarval byssus drifting (Armonies 1994). In these bivalves, mucus threads several times the length of the animals enable them to become effectively transported in the water column by currents (Sigurdsson et al. 1976; Beukema and de Vlas 1989; Armonies 1996). Due to these secondary redistributions species are able to colonise habitats which are more suitable for subsequent life stages (Armonies 1994; Strasser 2002; Hiddink 2003). After having burrowed between polychaete tubes, the juvenile bivalves may additionally find shelter from predation and the likelihood of re-suspension may be reduced (Armonies and Hellwig-Armonies 1992).

Mobility-mode hypothesis and benthic bio-engineering

The results from this study resemble the mobility-mode hypothesis (reviewed by Posey 1987) that sediment destabilizing organisms (bioturbators) inhibit sedentary and tube-building species and *vice versa*. Ecosystem engineering by lugworms resulted in the maintenance of permeable, low-organic sand (Volkenborn et al. 2007a). In the course of the experiment, bio-engineering by sediment stabilizing species took over on lugworm exclusion plots and facilitated other species that rely on stable sediment or on the presence of above-ground structures. Based on relevant literature, it is suggested that bio-engineering by several species which took advantage from the exclusion of an abundant sediment destabilizer have opposite effects on the sedimentary habitat. Tube-building ploychaetes were found to increase fine particle content (Bolam and Fernandes 2003; Rabaut et al. 2007). The incorporation of algal material results in an organic enrichment of the sediment with further consequences for the benthic community (Thiel and Watling 1998). Thus, engineering by these species potentially amplified the effects of lugworm absence. In 2004, sediment permeability on experimental exclusion plots in the low intertidal had fallen below the critical value where lugworms can thrive (Volkenborn et al. 2007b). The contrasting effects of both functional types of benthic bio-engineers suggest that mutual exclusion may not only be a product of localised disturbance or sediment binding, but involve long-lasting, sediment-mediated processes. In this way, even small tube-building species, such as *P. cornuta*, may contribute to the alteration of the sediment, ultimately reducing the habitat suitability for large burrowers, such as *A. marina*.

Results from this large-scale, long-term field experiment also indicate that the effects of benthic bio-engineering are conditional, dependent upon sediment type and supply of colonisers. Similar emergent patterns occurred in the 2 years of observation but different species were involved in the processes: *P. cornuta* and *L. conchilega* as tube builders, tufts of diatoms and green algae as an epibenthic cover and juveniles of *M. balthica* and *Mya arenaria* as drifting macrofauna. Moreover, these contingent events occurred only at mid-tide level in the first year and only at low-tide level in the second year but were not observed at low-tide level in the first year or at mid-tide level in the second year. The combination of variable environmental conditions and a variable supply of colonisers may account for conditional outcome of benthic engineering in time and space (i.e. Menge and Sutherland 1987; Lotze et al. 2000; Norkko et al. 2006).

Conclusion

On intertidal flats stabilizing and destabilizing sediment-engineers have profound, but spatially and temporally variable effects on the sedimentary habitat and on benthic community dynamics. This study gives experimental evidence that spatial competition between both types of bio-engineers may exist, as both types maintain the habitat suitable for their own and the less suitable for the functionally different form. Cumulative effects of their biogenic activities and cascading effects in the benthic community may explain the persistence of patches, dominated by species of one functional group.

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