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Lugworm exclusion experiment: Responses by deposit feeding worms to biogenic habitat transformations

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Abstract

On six 400 m^2 plots over 3 years, we excluded the sessile subduction and conveyer-belt feeding polychaete *Arenicola marina* which generates a pit-and-mound topography at the sediment surface from intertidal sands near the island of Sylt, Germany. This experiment was used to test whether other abundant deposit feeding polychaetes (the discretely motile and surface feeding ragworm *Nereis diversicolor* and the subsurface-feeding, motile orbiniid polychaete *Scoloplos* cf. *armiger*) benefit from competitive release. Ragworms took advantage from the absence of lugworms. Presumably they responded to a more stable and nutritious surface layer at lugworm exclusion plots (relief from inhibitive bioturbation). Contrary to this, *S.* cf. *armiger* was negatively affected by the exclusion of *A. marina*. It may have suffered from higher sulfide concentrations in the less irrigated and less permeable sediment where lugworms were absent. For adult worms of both species these results were consistent in 2 out of 3 years examined. Recruitment by *N. diversicolor* was highly variable between years and occurred either irrespective of experimental treatments or the response was inconsistent. Juveniles of *S.* cf. *armiger* benefited from the presence of *A. marina* and aggregated near lugworm tail shafts where inflow of oxygen rich water was high and sulfide concentrations were low. Biogenic habitat mediated effects of lugworms on both deposit feeders were in the same order of magnitude as abundance variation in space and time. Thus, *A. marina* was one of the key factors structuring the deposit feeding community. It is suggested that arenicolids modify the composition of the associated polychaete assemblage primarily through habitat transformation.
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1. Introduction

Benthic community structure in the intertidal zone is governed by physical events and trends (Raffaelli and Hawkins, 1996; Bertness, 1999), often mitigated by an abundance of food (Beukema and Cadée, 1997; Warwick, 1982). While in this marginal zone of the sea the supply of propagules may occasionally be limiting (Underwood and Fairweather, 1989; Ólafsson et al., 1994), biotic interactions often play a key role on small spatial scales (e.g. Reise, 1985; Warwick et al., 1986; Zajac, 2004). All factors act together and vary in relative importance from time to time, place to place and over different spatial scales (Zajac et al., 1998). Long-term observations and meta-analyses over widely spaced studies may reveal general patterns, while experimental studies are needed to understand the

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underlying processes. Biotic interactions are best studied by direct observation and field experiments. However, experimental manipulation of benthic communities has mostly been executed on a scale of < 1 m^2 (Hall et al., 1994) with only few exceptions of large-scale total defaunation experiments (Beukema et al., 1999; Dittmann et al., 1999). Some interactions like predation may reveal itself rather readily, while indirect effects may be easily modified by changing circumstances and may require an extravagant approach to become visible. Therefore, we started a large-scale and long-term field experiment to investigate the potentially more subtle interactions between deposit feeding worms in organic poor sand in a sheltered tidal area. Polychaetes often dominate such environments and allocate food resources with respect to particle size and vertical feeding position (Whitlatch, 1980).

We here focus on the three largest and most abundant deposit feeding polychaetes which coexist in a bay called Königshafen, representative in habitats and biota for the Wadden Sea which is a coastal stretch in the northeastern Atlantic with the widest tidal zone in the world. We experimentally test the hypothesis that the removal of the largest of the three polychaetes, the habitat-engineering lugworm *Arenicola marina*, results in a competitive release for other deposit feeding worms. *A. marina* builds an up to 20 cm deep J-shaped semi-permanent burrow where it lives in a head-down position (Reise, 1985). Lugworms ingest sediment at depth which slides down from the surface through a funnel. After microorganisms and organics contained in the sediment have been digested, a string of sediment is defecated back to the surface, coiled up into a characteristic fecal mound above the tail shaft of the burrow. Burrow ventilation for respiration is done by piston-like movements in a tail-to-head direction (Riisgård and Banta, 1998). This ventilation has been shown to attract meiofauna and some macrofauna to distinct sections of the burrows (Reise and Ax, 1979; Reise, 1981, 1987; Lackschewitz and Reise, 1998), and to influence pore water nutrient profiles (Huettel, 1990). The pit-and-mound topography modifies flow and particulate matter distribution in the permeable sand of the upper layer (Huettel and Gust, 1992; Huettel et al., 1996) and also affects the associated fauna (e.g. Brey, 1991; Flach, 1992; Lackschewitz and Reise, 1998; Reise, 1985). At a density of 30 lugworms m^{-2}, a sediment layer of 15 cm is replaced annually and 3 l m^{-2} h^{-1} of seawater is pumped into the anoxic sediment (Cadée, 1976; Riisgård and Banta, 1998). *A. marina* qualifies as an ecosystem engineer in coastal sediments where it occurs in abundance (sensu Jones et al., 1994; Reise and Volkenborn, 2004). By inserting a mesh horizontally at 10 cm depth into the sediment, we permanently blocked lugworm burrows and thus obtained plots without *A. marina*. This method was previously used by Reise (1983) and Philippart (1994) to reveal effects on meiofauna and seagrass, respectively. However, to minimize confounding effects of lateral sediment movement caused by tidal currents and waves, a phenomenon recognized to be important in the study area by Flothmann and Werner (1991) and Zühlke and Reise (1994), we adopted a large-scale design: excluding lugworms from six plots of 20 × 20 m each. This scale of manipulation was assumed to be appropriate when attempting to reveal effects of lugworm exclusion on other deposit feeding worms. The most abundant deposit feeding polychaetes and next to *A. marina*, the most important in biomass at the site, are the ragworm *Nereis diversicolor* and the orbiniid *Scoloplos* cf. *armiger* (Reise et al., 1994). Ragworms dwell in Y-shaped semi-permanent burrows and may switch between suspension and deposit feeding (Riisgård and Kamermans, 2001), but at the site are primarily deposit feeders (Reise, 1985). *S.* cf. *armiger* is a free-burrowing subsurface feeder without a persistent burrow system (Jumars and Fauchald, 1979). Kruse and Reise (2003) showed that populations in the intertidal with holobenthic development are reproductively isolated from subtidal ones with pelagic larvae, and the taxonomic position of the intertidal populations is currently being revised (Albrecht and Kruse, in preparation). Hence, we here provisionally refer to the intertidal population as *S.* cf. *armiger*. While the early juveniles of *N. diversicolor* are highly mobile swimmers (Volkenborn, personal observations), those of *S.* cf. *armiger* hatch from egg cocoons and directly enter the sediment below the surface (Gibbs, 1968). With this study we want to test if polychaetes show compensational tendencies or if associated polychaetes respond differently to the exclusion of *A. marina* due to their different ecological traits concerning their feeding guilds (Jumars and Fauchald, 1979) and sulfide tolerance (Gamenick et al., 1996; Kruse et al., 2004). We further test whether potential effects continue over generations through differential recruitment. In particular, we speculate that the burrow building, surface-feeding omnivore and sulfide-tolerant *N. diversicolor* benefits from competitive release by lugworm exclusion, while free-burrowing and subsurface-feeding detrivore *S.* cf. *armiger* benefits from ameliorated subsurface sediment properties in the presence of bioirrigating *A. marina*. We further hypothesize that species differences concerning their mobility (very

mobile and active *N. diversicolor* vs. slowly subsurface crawling *S.* cf. *armiger*) and their reproduction modes and dispersal ability (pelagic larvae and swimming juveniles in *N. diversicolor* vs. holobenthic development in *S.* cf. *armiger*) cause differences in their colonization success on experimental plots.

2. Materials and methods

2.1. Study area and experimental design

The lugworm exclusion experiment was conducted on an intertidal sand flat in Königshafen, a tidal bay at the northern end of the island of Sylt in the North Sea (55°02′N; 8°26′E). Unvegetated sand of low organic content (<1%) and densely populated by *A. marina* comprises 76% of the tidal area (Reise et al., 1994). Sediment at the experimental site is dominated by medium and fine sand. Salinity varied between 27 PSU in spring and 31 PSU in summer. Mean tidal range is 1.8 m. A detailed description of the tidal embayment is given by Reise (1985) and Reise et al. (1994). Exclusion of lugworms was achieved by inserting a 1-mm meshed polyethylene net at 10 cm depth into the sediment in March 2002. To test the effect of excavating surface sediment with a small bulldozer, sediment was dredged in the same way without inserting a net on control plots. Ambient plots were left untouched to represent natural conditions. The experiment was created in a 2-factorial (3×2 levels) nested block design (Fig. 1). One block thus consisted of three plots differing in treatment: Exclusion=buried net, Control=similarly dug up but left without a net, Ambient=untouched plot. Each plot was 20×20=400 m^2 in area. This large size was chosen to minimize effects of lateral sediment transport when sampling in the middle of the plots. 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).

2.2. Sampling of polychaetes

Densities of lugworm fecal mounds were estimated approximately monthly between March 2002 and September 2004 with 10 randomly chosen quadrates of 0.25 m^2 within each experimental plot. Number of fecal castings varies with feeding activity but may serve as a proxy for abundances of *A. marina* at least in summer (Reise et al., 2001). Casts were categorized into those of juveniles (fecal string <2 mm in diameter) and adults (>2 mm in diameter). Counts were done during

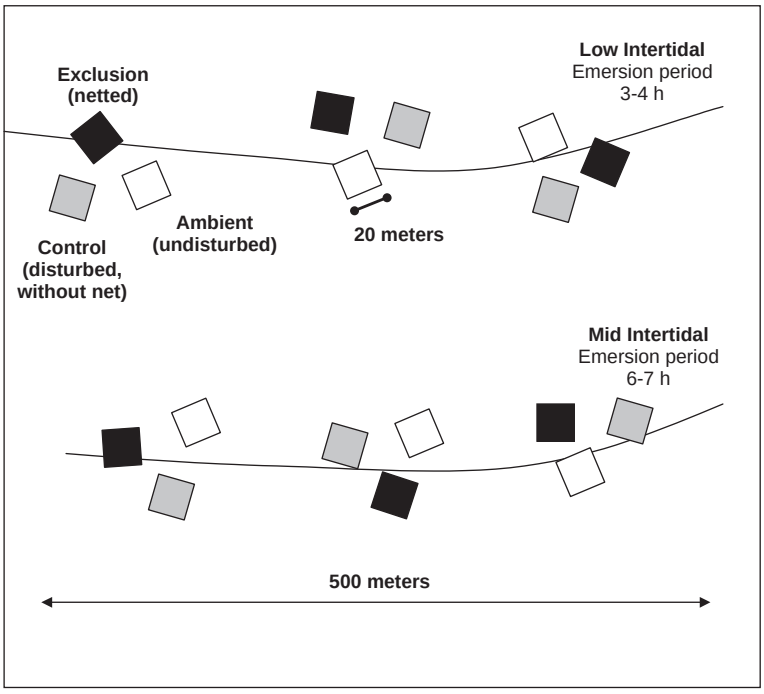

Fig. 1. Experimental set-up in a 2-factorial (2×3 level) nested block design.

the second half of tidal emergence and only on calm days with no rain drops destroying emerging casts.

Sampling of the macroinfauna on the experimental plots was done in August 2002, 2003 and 2004 by counting animals retained on a 1-mm mesh sieve from 8 pseudo-replicated cores of 100 cm^2 within each experimental plot. Sampling was done randomly excluding the outer 2 m of each plot in order to minimize possible plot edge effects. Sampling depth was 20 cm and samples were divided in upper and lower 10 cm sediment fractions. At the exclusion site only the upper layer could be sampled due to the net at 10 cm depth. Since worms were encountered only occasionally below 10 cm (mainly adult *N. diversicolor*), results are presented as individuals m^{-2} with upper and lower core sections combined for the plots without a net. Sampling was generally completed within 1 week and was done block-wise in order to include the effect of consecutive sampling into the block effect. Individuals of *N. diversicolor* and *S.* cf. *armiger* were divided into juveniles and adults by their size (*N. diversicolor* <1 mm> prostomium width; *S.* cf. *armiger* <20 mm> body length). *Scoloplos* egg cocoons were counted from late winter to early spring in 2003 and 2004 on 10 randomly chosen quadrates of 0.25 m^2 within each experimental plot. Counts were done weekly from first appearance of egg cocoons around February until abundances began to decrease in April. Maximum egg cocoon densities occurred in March in both years. Abundances of juvenile *S.* cf. *armiger* at lugworm mounds, funnels and interspaces were estimated by counting individuals from six cores of 10 cm^2 to a depth of 5 cm. These samples were taken in between the tidal zones of the experiment in July 2002. Sediment was sieved through a 250-µm mesh and juvenile *S.* cf. *armiger* were counted under a stereo microscope.

2.3. Statistical analyses

Monthly counts of lugworm casts were analyzed by two-factorial repeated measures (RM) nested block ANOVA to control treatment success and analyze lugworm population dynamics. Two-factorial repeated measures (RM) nested block ANOVA was used to test for inter-annual population dynamics of *N. diversicolor* and *S.* cf. *armiger* and effects of lugworm treatment and tidal height on abundances of juveniles and adults. Additionally, treatment and tidal height effects on both polychaetes and *Scoloplos* egg cocoons were tested separately for each year by two-factorial nested block ANOVA. Fixed-factor ANOVA was used to test for differences in abundances of juvenile *S.* cf. *armiger* at lugworm casts, funnels and interspaces. For ANOVA results, relative effect sizes were calculated as percentage variance explained (Howell, 1992). Post-hoc multiple means comparisons were performed using the Tukey–Kramer procedure at $\alpha = 0.05$ significance level. Prior to analysis data were tested for homogeneity of variances (Cochran's Test) and log-transformed if required.

3. Results

3.1. Lugworm exclusion

Adult *A. marina* were effectively excluded by the buried net and did not recolonize exclusion plots. On control and ambient plots fecal mound densities were high (mean 18 and 22 casts m^{-2}, respectively) and similar to each other (Fig. 2). Slightly but not statistically significant ($F_{1,4} = 3.24$; $p = 0.15$) lower cast densities on control plots may be due to mortality and migration caused by the initial dredging. In early summer of 2003 and 2004 juvenile *A. marina* also settled on the exclusion plots but left again after a few weeks (Fig. 2). In both years recruitment by juvenile *A. marina* was significantly higher on the exclusion plots in the high intertidal zone indicated by significant time × tidal height interaction (Table 1; 2003: $F_{2,16} = 14.13$; $p < 0.01$; 2004: $F_{2,16} = 4.71$; $p < 0.05$). Adult lugworms showed seasonal variability in cast production with highest activity during spring and summer and lowest activity in autumn and winter. High month-to-month variability (e.g. in winter 2002/2003) presumably indicates variation in feeding activity rather than lugworm immigration and emigration. The third year was unusual with relatively low numbers of fecal mounds (<10 casts m^{-2} compared to ~30 casts m^{-2} in the first 2 years). Population size of *A. marina* in the entire bay had generally decreased in 2004 (Reise, unpublished data).

3.2. Effects on Nereis

Overall, lugworm treatment and tidal height had significant effects on abundances of adult *N. diversicolor*, while responses of juveniles to lugworm treatment were significantly different between years, indicated by a significant time × treatment interaction (Table 2). Adult *N. diversicolor* invaded lugworm exclusion plots in the first year and reached densities of almost 500 adults m^{-2} averaged over all plots. The densities were about 10 times the ambient abundance (Fig. 3). This invasion only occurred once and in the following 2 years abundances gradually declined until densities on exclusion and lugworm plots were not significantly different in 2004. However, over the 3 years the significant treatment effect

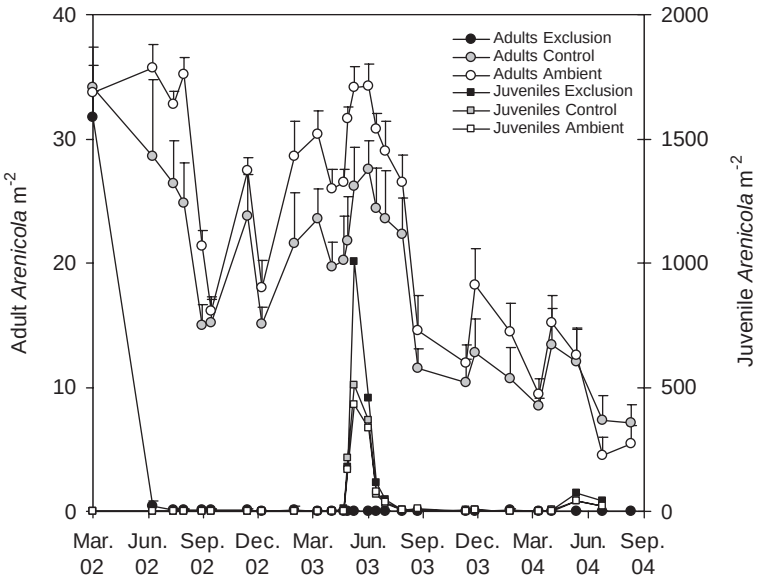

Fig. 2. Abundances of adult (circles) and juvenile (squares) *A. marina* inferred from fecal mounds on experimental plots (mean from 6 plots and SE) from March 2002 to September 2004. On each experimental plot 10 quadrants of 0.25 m^2 were counted (note differences in *y*-axis scales).

explained more than 30% of the total variance (Table 2). Responses of juvenile ragworms were inconsistent (Fig. 3). When ragworm recruitment was high in 2003, no effect of treatment could be detected. Experimental plots were recruited by 1500 juveniles m^{-2} averaged over all plots. With densities of more than 4000 juveniles m^{-2} recruitment at mid-intertidal was significantly higher than at low intertidal. This was the reverse of the invasion by adults in 2002, which occurred preferentially in the low intertidal. In 2002 and 2004, recruitment was low with

Table 1
Two-factorial ANOVA results on treatment and tidal height effects on abundances of *N. diversicolor*, *S.* cf. *armiger*, *Scoloplos* egg cocoons and juveniles of *A. marina* (x for significant effect)

	Date	Treatment	Tidal height	Treatment × Tidal height	Block
N. diversicolor					
Adults	Aug. 02	x (E)			
	Aug. 03		x (L)		
	Aug. 04		x (L)		
Juveniles	Aug. 02	x (E/C)			
	Aug. 03		x (M)		x
	Aug. 04	x (C)	x (M)	x (C/O, M)	
S. cf. *armiger*					
Adults	Aug. 02	x (C/O)			
	Aug. 03		x (L)		x
	Aug. 04	x (C/O)	x (M)		
Juveniles	Aug. 02	x (E)		x	
	Aug. 03				
	Aug. 04				x
Egg cocoons	March 03	x (C/O)	x (M)		
	March 04		x (L)		x
A. marina					
Juveniles	May 03			x (E, M)	x
	May 04			x (E, M)	

Treatment with significant higher abundances are indicated in parentheses (Tukey post-hoc). Prior to analysis data were (log + 1)-transformed (E: exclusion; C: control; O: ambient; M: mid-intertidal; L: lower intertidal).

Table 2
Repeated measures ANOVA on treatment and tidal height effects on the abundances of adult and juvenile *N. diversicolor* and *S.* cf. *armiger*

	Nereis adult					*Nereis* juvenile			
	df	MS	*F*	*p*	% *V*	MS	*F*	*p*	% *V*
Treatment	2	2.57	5.77	**0.028**	30.6	1.00	6.40	**0.022**	41.0
Tidal height	1	3.82	8.58	**0.019**	22.7	0.36	2.31	0.167	7.4
Treatment × Tidal height	2	0.72	1.61	0.259	8.5	0.03	0.19	0.833	1.2
Block (tidal height)	4	0.72	1.61	0.262	17.1	0.30	1.94	0.197	24.8
Residuals	8	0.45			21.2	0.16			25.6
Year	2	0.45	1.49	0.254	5.9	19.74	107.33	**0.000**	72.2
Year × Treatment	4	0.52	1.76	0.187	13.8	1.15	6.24	**0.003**	8.4
Year × Tidal height	2	1.26	4.23	**0.034**	16.6	1.35	7.35	**0.005**	4.9
Year × Treatment × Tidal height	4	0.85	2.85	0.058	22.4	0.35	1.92	0.157	2.6
Year × Block (tidal height)	8	0.19	0.64	0.735	10.0	0.45	2.42	0.063	6.5
Residuals	16	0.30			31.4	0.18			5.4
	Scoloplos adult					*Scoloplos* juvenile			
	df	MS	*F*	*p*	% *V*	MS	*F*	*p*	% *V*
Treatment	2	2.20	7.00	**0.017**	42.5	0.32	1.86	0.218	5.9
Tidal range	1	0.10	0.33	0.583	1.0	0.00	0.00	0.997	0.0
Treatment × Tidal height	2	0.16	0.51	0.619	3.1	0.15	0.85	0.464	2.7
Block (tidal height)	4	0.75	2.39	0.137	29.1	2.14	12.31	**0.002**	78.6
Residuals	8	0.31			24.3	0.17			12.8
Year	2	7.31	45.93	**0.000**	50.8	9.16	69.95	**0.000**	60.5
Year × Treatment	4	0.59	3.73	**0.025**	8.2	0.82	6.27	**0.003**	10.8
Year × Tidal height	2	2.80	17.56	**0.000**	19.4	0.35	2.69	0.099	2.3
Year × Treatment × Tidal height	4	0.02	0.10	0.982	0.2	1.83	0.173	3.2	
Year × Block (tidal height)	8	0.45	2.82	**0.037**	12.5	0.62	4.72	**0.004**	16.3
Residuals	16	0.16			8.8	0.13			6.9

Data were log-transformed ($n=6$). Bold *p* values indicate significant effects (% V = variance explained calculated as: $(SS_{factor}/SS_{total}) \times 100$).

average densities below 200 juveniles m^{-2} (Fig. 3). In the first year juveniles were significantly less abundant on ambient plots (Tukey–Kramer, $p<0.05$; Table 1) where lugworms were most abundant. In 2004 the significant treatment × tidal height interaction (Table 1) was mainly generated by low *N. diversicolor* recruitment on exclusion plots in the low intertidal zone while abundances were not affected by lugworm presence/absence at mid-intertidal where most of the juveniles recruited.

3.3. Effects on Scoloplos

Exclusion of *A. marina* negatively affected *S.* cf. *armiger* (Fig. 3). In repeated measurement ANOVA, lugworm treatment explained more than 40% of total variance ($F_{2,8}=7.0$; $p<0.05$; Table 2). Abundances of adult *S.* cf. *armiger* were significantly higher at control and ambient plots in 2002 and 2004, but remained indifferent in 2003 (Table 1), when overall abundance of *S.* cf. *armiger* was low. Responses of juvenile *S.* cf. *armiger* were inconsistent. In the first year juveniles were significantly more abundant on the exclusion plots, while they were not significantly affected by treatment in the following years (Table 1). However, abundances were doubled on the plots with lugworms in 2003 (Fig. 3). With up to 20,000 juveniles m^{-2} *S.* cf. *armiger* showed highest densities around lugworm fecal mounds (Fig. 4). Abundances at lugworm pits and at interspaces were much lower (3000 to 8000 juveniles m^{-2}). Due to the aggregated distribution of juvenile *S.* cf. *armiger*, abundances in lugworm plots might have been underestimated in randomly taken samples. *Scoloplos* egg cocoons were more abundant in control and ambient plots in 2 years (Fig. 5), but were significantly facilitated by lugworm presence only in 2003, when lugworms were most abundant (Table 1). On plots with lugworms 15–20 egg cocoons m^{-2} were found compared to 5 egg cocoons m^{-2} on exclusion plots. Egg cocoons were mainly found in low tide puddles of irregularly occurring sediment depressions. On lugworm plots egg cocoons occurred in addition at lugworm funnels.

4. Discussion

A competitive equilibrium between deposit feeding worms in intertidal sand may not exist. High between-

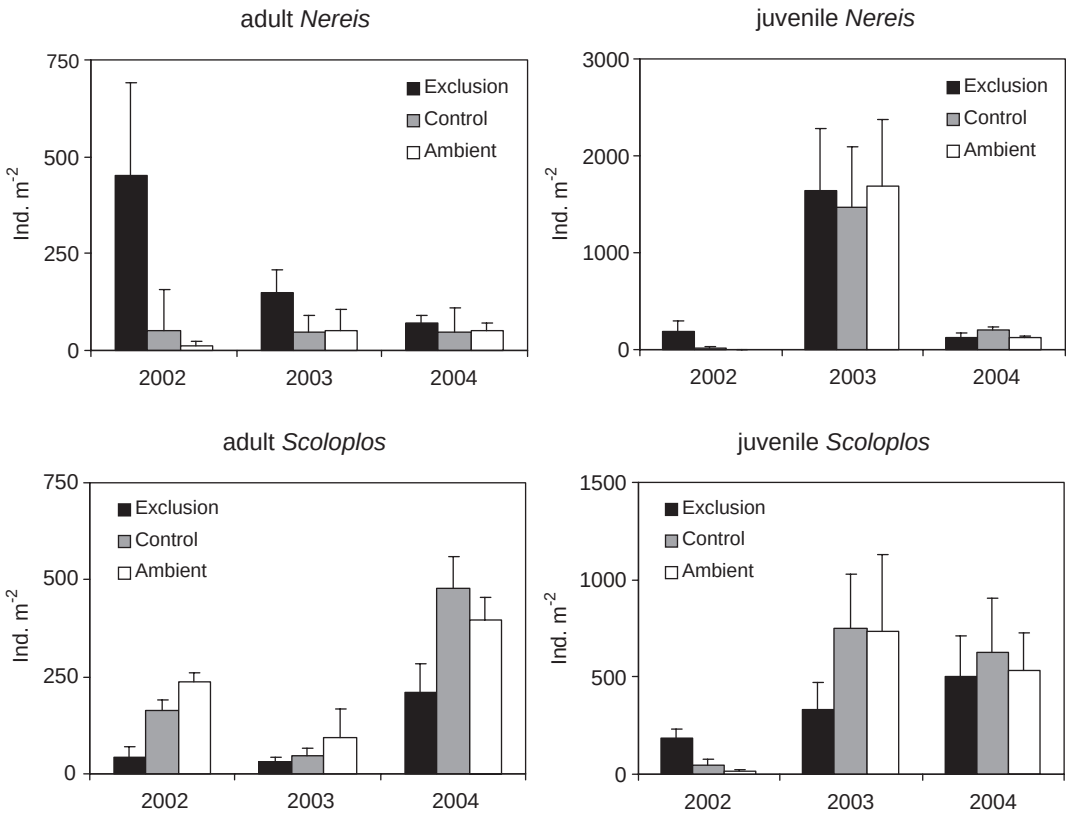

Fig. 3. Abundances of adult and juvenile *N. diversicolor* and *S.* cf. *armiger* in August of 2002, 2003 and 2004. Shown are mean abundances of six experimental plots and SE. On each experimental plot 8 subsamples of 100 cm^2 were taken.

year variability of adult and recruit densities of the polychaetes *A. marina*, *N. diversicolor* and *S.* cf. *armiger* showed no compensational tendencies. These species differ in feeding mode: lugworms are head-down subduction and conveyer-belt sediment swallowers, ragworms are head-up bulk feeders of organic matter at the sediment surface, and the orbiniid is a head-straight selective feeder on small organic particles at the oxic/anoxic boundary layer in the sediment (Jumars and Fauchald, 1979; Reise, site specific observations). Although all species exploit dead and alive organic carbon in the sediment, overlap in

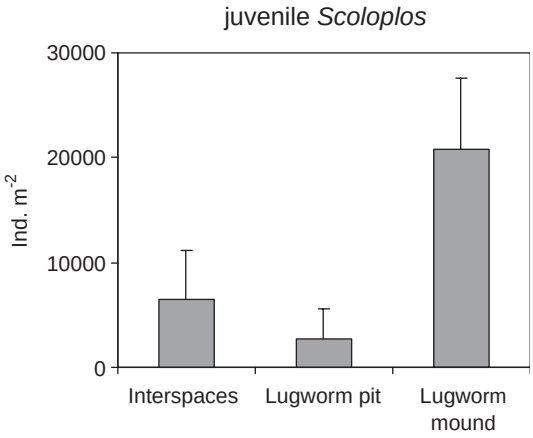

Fig. 4. Abundances of juvenile *S.* cf. *armiger* at mid-intertidal in samples from lugworm pits, mounds and the sediment in between not directly affected by *A. marina* in July 2002 (mean and S.D.; $n=6$).

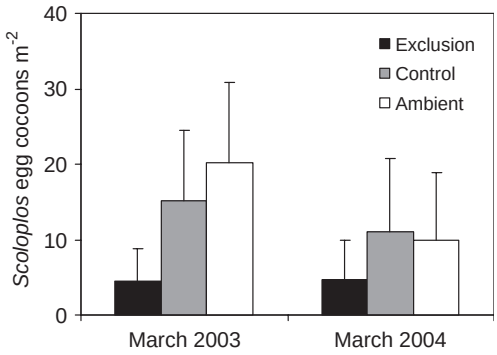

Fig. 5. Abundances of *Scoloplos* egg cocoons in March 2003 and March 2004 on experimental plots (mean and S.D.; $n=6$). On each experimental plot 10 subsamples of 0.25 m^2 were taken.

resources is mitigated by differential use of particle size and vertical position (Whitlatch, 1980). Hence, removal of lugworms may not immediately be followed by increasing numbers of the other two deposit feeders as a consequence of competitive release. Nevertheless, this was the case with adult ragworms and juvenile *A. marina* while the orbiniid decreased in abundance. We assume that the experimental results cannot be sufficiently explained by competition for food. Facilitation and inhibition of associated polychaetes induced by lugworm habitat transformations seem to overshadow trophic interactions.

4.1. Lugworms inhibit ragworms

Exclusion plots were conspicuous by their smooth sediment surface contrasting with the pit-and-mound topography of the lugworm flat. Because of sheltered position, ripple marks were generally absent, at least in summer. Pits and mounds became leveled during tidal flooding but reappeared during low tide exposure. This indicates stability of the surface layer to be higher at lugworm exclusion plots than on the lugworm flat, as was reflected in smaller median grain size, higher silt fraction, higher particulate organic carbon and chlorophyll content compared to plots where lugworms were present (Table 3; Volkenborn unpublished data). These biogenic effects of *A. marina* were more pronounced in the finer sediments of the low intertidal zone where ragworms invaded the exclusion plots. Thus, the invasion of adult *N. diversicolor* in the first summer may have been triggered by a combination of sediment stability and food availability. Nereids dwell in vertical burrows and were observed to feed on the sediment surface in the vicinity of burrow openings. Out of burrows, they readily crawl across the sediment or may actively swim to change locality (Lambert et al., 1992) which enabled adult *N. diversicolor* the fast initial response to experimental lugworm exclusion. Adjacent to the experimental site, natural patches with a smooth sediment surface similar to the exclusion plots occurred in the upper tidal zone, also contrasting with the pit-and-mound topography of the surrounding lugworm flat (Zipperle and Reise, 2005). These are patches with discrete freshwater seepage, are avoided by *A. marina* but are densely populated by nereids (up to 1000 ind. m^{-2}). This constitutes a natural analogue to the experimental removal of lugworms using a horizontal net. The response of nereids is the same, and supports the generality of the experimental results. Apparently, ragworms seek refuge from unstable conditions in bioturbated sediments. When a strong recruitment event occurred in summer 2003, juvenile nereids settled irrespective of experimental treatments. In contrast to the adults, juveniles are freely crawling on or just below sediment surface, they frequently swim, and do not yet establish permanent burrows (Bartels-Hardege and Zeeck, 1990; Volkenborn, unpublished data). Consequently, juveniles are not affected by sediment instability inflicted by the lugworms as are the discretely motile adults of *N. diversicolor*. The amensalism only operates between adult lugworms and adult ragworms, and it should be noted that adult *N. diversicolor* may bite juvenile *A. marina* to occupy their burrow shafts (Witte and de Wilde, 1979).

Continuous decrease of adult ragworm abundances on lugworm exclusion plots following fast initial response may have been caused by bird predation. Investigations on bird foraging in autumn 2003 from an observation tower build up in between the experimental plots revealed higher foraging efficiency of oystercatchers (*Haematopus ostralegus*) on exclusion than on lugworm plots and *N. diversicolor* as the principal prey item (Volkenborn and Schiek, unpublished data). Infaunal predation, on the other hand, was presumably minor and not affected by lugworm presence/absence.

Table 3
Habitat properties of lugworm flats and lugworm exclusion plots at mid and low intertidal zone

		Lugworm tidal flats		Lugworm exclusion	
		Lower intertidal	Mid-intertidal	Lower intertidal	Mid-intertidal
Grain size median (μm)	Upper 8 cm	221	340	209	334
Fraction <63 μm	Upper 8 cm	0.96%	0.43%	1.86%	0.47%
POC	Upper 5 cm	0.18%	0.13%	0.38%	0.16%
Chlorophyll content (μg g^{-1})	Upper 1 cm	14.2	14.9	24.1	17.5
Sulfide in pore water (μmol L^{-1})	10 cm depth	83	15	170	78
Permeability k (m^2)	Upper 7.5 cm	2.7×10^{-12}	10×10^{-12}	0.6×10^{-12}	7.7×10^{-12}

Given are means from 3 experimental plots. For lugworm flats values of control and corresponding ambient plots were averaged. Solid phase analysis was done in August 2003, sulfide and permeability in July 2004. Data from Volkenborn (unpublished data).

Abundances of the predacious polychaete *Nephtys hombergii* (Schubert and Reise, 1986) and the nemertean *Lineus viridis* (Nordhausen, 1988) were generally low (<10 ind. m^{-2}) in all years and their abundances were not affected by lugworm presence/absence.

4.2. Lugworms facilitate orbiniids

Juveniles and adults of *S.* cf. *armiger* stay permanently below the sediment surface, and freely move without establishing burrows. While juveniles are only found a few millimeters below surface, adults may retreat to 10 cm depth or more (Reise, 1979). Tolerance against hypoxia and sulfide is low (Kruse et al., 2004), and worms may ascend into the oxic layer during low tide (Schoettler and Grieshaber, 1988). Consequently, the orbiniid may benefit from irrigation and bioturbation activity of lugworms, which is known to lower the level of total sulfide in the sediment (Nielsen et al., 2003). The observed high density of juveniles at fecal mounds is similar to observations by Lackschewitz and Reise (1998) on the amphipod *Bathyporeia sarsi* which also aggregates at lugworm mounds on shoals with clean sand. These responses may be explained by enhanced advective pore water flow around the fecal mounds (Huettel and Gust, 1992; Huettel et al., 1996; Reise, 2002) and enhanced water inflow due to bioirrigation by *A. marina*. Sulfide concentration in pore water had strongly increased in the absence of lugworms, and permeability of the sediment had decreased (Table 3). Thus, we assume that irrigation and bioturbation by the lugworms create subsurface conditions beneficial to *S.* cf. *armiger* on the intertidal sand flat, with more oxygen, less sulfide, and possibly more bacteria in the subsurface layer due to burrow ventilation and enhanced advective pore water flows (Huettel, 1990; Huettel and Gust, 1992; Huettel et al., 1996; Reichardt, 1988). This engineering of subsurface biogeochemistry by the lugworms may be less relevant to juvenile *S.* cf. *armiger* outside fecal mounds because they reside close to the sediment surface. However, higher densities of egg cocoons on lugworm plots and aggregation of juveniles near lugworm tail shafts indicate a facilitation process by creating the pit-and-mound topography forming low tide puddles and by enlarging the oxidative zone. The effect of lugworm presence on the abundance of juveniles *S.* cf. *armiger* might have been underestimated due to their aggregated distribution and under-representation of samples from lugworm casts when sampling randomly. Interestingly, differences of *Scoloplos* egg cocoon abundances between exclusion and lugworm plots were most obvious in 2003, when lugworm abundance was high and the sediment micro-topography was dominated by lugworm casts and pits. In 2004, when the sediment surface was less structured due to lower lugworm abundances, egg cocoon abundances in the presence of *A. marina* were only slightly and not significantly higher.

5. Conclusions

The negative effects of *A. marina* on *N. diversicolor* and its own juveniles by destabilizing the sandy surface layer resemble trophic group amensalism between bioturbating deposit feeders inhibiting suspension feeders by producing easily resuspended mud (Rhoads and Young, 1970). The positive effect of *A. marina* on *S.* cf. *armiger* by ameliorating the subsurface layer corresponds to promotive or facilitating processes between large tube or burrow builders and deep burrowers shown to be prevalent in estuarine macrobenthic communities (Schaffner, 1990). Large-scale experimental defaunated intertidal sands in the Dutch Wadden Sea were only slowly recolonized by adult *A. marina* (full recovery after 4 years; Beukema et al., 1999) and thus resemble a lugworm exclusion experiment. Settlement of several species was thought to be favored by initial low abundances of lugworms on these plots and recolonization was much faster by juvenile stages of macrofauna and small opportunistic species than by adults of long-lived species. In general we found the same colonization patterns in our study, but responses were clearly not limited to juvenile stages. Furthermore, we could show that both facilitative and inhibitive mechanisms play an important role in structuring benthic intertidal assemblages on a mesoscale (1 m^2–1 ha; see Zajac et al., 1998). For adult *N. diversicolor* subsurface habitat modifications by lugworms may be less relevant because ragworms create their own oxic burrow environment by ventilation and remove sulfide (Davey, 1994; Miron and Kristensen, 1993a,b) while *S.* cf. *armiger* is directly exposed to sediment and pore water conditions. The opposite effects of lugworms on associated polychaetes contribute to the maintenance of deposit feeder diversity, and demonstrate the importance of a habitat-mediated interaction web bioengineered in marine sediments (Reise, 2002). Furthermore, the experimental evidence for inhibition of juvenile *A. marina* is consistent with density dependence of recruitment in the *A. marina* population in this area (Reise et al., 2001). However, responses of other polychaetes to the removal of lugworms showed considerable variability during 3 years of experiment and variance explained by lugworm treatment was

generally below 50%, implying the importance of other factors for observed patterns. Several Time × Factor interactions in repeated measurement ANOVA on polychaete abundances (Table 2) indicate high temporal variability in species abundances in combination with spatial factors, which presumably operate on larger scales (Zajac et al., 1998). Only in the first summer did adult *N. diversicolor* invade the exclusion plots in high numbers but then declined in the subsequent years, possibly caused by predation. Sediment disturbance caused by lugworms was found to initiate emigrations of *Corophium volutator* which exposed them to epibenthic predators (Flach and de Bruin, 1994). Juvenile recruitment was highly variable between years and responses to experimental treatments were either inconsistent or not significant in both species. This suggests that differential abundances of adults mainly result from immigration of adults as response to actual conditions on the plots. However, in spring 2003 more egg cocoons of *S.* cf. *armiger* were found in the presence of lugworms compared to exclusion plots. Correspondingly, higher juvenile densities were recorded in the following summer and higher adult densities in the next year on plots with lugworms than without. This causal chain resembles the slow recovery of long-lived species on defaunated plots (Beukema et al., 1999) and stresses the need of long-term experiments (>1 year) to reveal possible effects. Response of deposit feeding polychaetes to experimental lugworm exclusion was of a similar magnitude as the variability of abundances in space and time on the ambient sand flat. Therefore we suggest that the influence on the dynamics of the associated polychaete assemblage by *A. marina* is similar to other key factors in the tidal zone and that consequences of the presence of lugworm for other species are not limited to disturbing activities but also include more subtle biogenic habitat transformations.

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References

Bartels-Hardege, H.D., Zeeck, E., 1990. Reproductive behaviour of *Nereis diversicolor* (Annelida: Polychaeta). Mar. Biol. 106, 409–412.

Bertness, M.D., 1999. The Ecology of Atlantic Shorelines. Sinauer Associates Inc, Sunderland, MA, p. 416.

Beukema, J.J., Cadée, G.C., 1997. Local differences in macrozobenthic response to enhanced food supply by mild eutrophication in a Wadden Sea area: food is only locally a limiting factor. Limnol. Oceanogr. 42, 1424–1435.

Beukema, J.J., Flach, E.C., Dekker, R., Starink, M., 1999. A long-term study of the recovery of the macrozoobenthos on large defaunated plots on a tidal flat in the Wadden Sea. J. Sea Res. 42, 235–254.

Brey, T., 1991. The relative significance of biological and physical disturbance: an example from intertidal and subtidal sandy bottom communities. Estuar. Coast. Shelf Sci. 33, 339–360.

Cadée, G.C., 1976. Sediment reworking by *Arenicola marina* on tidal flats in the Dutch Wadden Sea. Neth. J. Sea Res. 10, 440–460.

Davey, J.T., 1994. The architecture of the burrow of *Nereis diversicolor* and its quantification in relation to sediment–water exchange. J. Exp. Mar. Biol. Ecol. 179, 115–129.

Dittmann, S., Günther, C.-P., Schleier, U., 1999. Recolonization of tidal flats after disturbance. In: Dittmann, S. (Ed.), The Wadden Sea Ecosystem: Stability, Problems and Mechanisms. Springer, Berlin, pp. 175–192.

Flach, E.C., 1992. Disturbance of benthic infauna by sediment-reworking activities of the lugworm *Arenicola marina*. Neth. J. Sea Res. 30, 81–89.

Flach, E.C., de Bruin, W., 1994. Does the activity of cockles, *Cerastoderma edule* (L.) and lugworms, *Arenicola marina* L., make *Corophium volutator* Pallas more vulnerable to epibenthic predators: a case of interaction modification? J. Exp. Mar. Biol. Ecol. 182, 265–285.

Flothmann, S., Werner, I., 1991. Experimental eutrophication on an intertidal sandflat: effects on microphytobenthos, meio- and macrofauna. In: Colombo, G., et al. (Ed.), Marine Eutrophication and Population Dynamics. Proceedings of the 25th EMBS. Olsen & Olsen, Fredensborg, Denmark, pp. 93–100.

Gamenick, I., Jahn, A., Vopel, K., Giere, O., 1996. Hypoxia and sulphide as structuring factors in a macrozoobenthic community on the Baltic Sea shore: colonization studies and tolerance experiments. Mar. Ecol. Prog. Ser. 144, 73–85.

Gibbs, P.E., 1968. Observations on the population of Scoloplos armiger at Whitstable. J. Mar. Biol. Assoc. U. K 48, 225–254.

Hall, S.J., Raffaelli, D., Thrush, S.F., 1994. Patchiness and disturbance in shallow water assemblages. In: Giller, P.S., Hildrew, A.G., Rafaelli, D.G. (Eds.), Aquatic Ecology: Scale, Pattern, and Process. Blackwell, Oxford, pp. 333–375.

Howell, D.C., 1992. Statistical Methods for Psychology. Duxbury Press, Belmont, CA, p. 816.

Huettel, M., 1990. Influence of the lugworm *Arenicola marina* on porewater nutrient profiles of sand flat sediments. Mar. Ecol. Prog. Ser. 62, 241–248.

Huettel, M., Gust, G., 1992. Impact of bioroughness on interfacial solute exchange in permeable sediments. Mar. Ecol. Prog. Ser. 89, 253–267.

Huettel, M., Ziebis, W., Forster, S., 1996. Flow-induced uptake of perticulate matter in permeable sediments. Limnol. Oceanogr. 41, 309–322.

Jones, C.G., Lawton, J.H., Shachak, M., 1994. Organisms as ecosystem engineers. Oikos 69, 373–386.

Jumars, P.A., Fauchald, K., 1979. The diet of the worms: a study of polychaete feeding guilds. Oceanogr. Mar. Biol. Ann. Rev. 17, 193–284.

Kruse, I., Reise, K., 2003. Reproductive isolation between intertidal and subtidal *Scoloplos armiger* (Polychaeta, Orbiniidae) indicates sibling species in the North Sea. Mar. Biol. 143, 511–517.

Kruse, I., Strasser, M., Thiermann, F., 2004. The role of ecological divergence in speciation between intertidal and subtidal *Scoloplos armiger* (Polychaeta, Orbiniidae). J. Sea Res. 51, 53–62.

Lackschewitz, D., Reise, K., 1998. Macrofauna on flood delta shoals in the Wadden Sea with an underground association between the lugworm *Arenicola marina* and the amphipod *Urothoe poseidonis*. Helgol. Mar. Res. 52, 147–158.

Lambert, R., Desrosiers, G., Retiere, C., Miron, G., 1992. Food searching activity of *Nereis diversicolor* (polychaete). Cah. Biol. Mar. 33, 43–54.

Miron, G., Kristensen, E., 1993a. Factors influencing the distribution of nereid polychaetes: the sulphide aspect. Mar. Ecol. Prog. Ser. 93, 143–153.

Miron, G., Kristensen, E., 1993b. Behavioural response of three nereid polychaetes to injection of sulphide inside burrows. Mar. Ecol. Prog. Ser. 101, 147–155.

Nielsen, O.I., Kristensen, E., Holmer, M., 2003. Impact of *Arenicola marina* (Polychaeta) on sediment sulfur dynamics. Aquat. Microb. Ecol. 33, 95–105.

Nordhausen, W., 1988. Impact of the nemertean *Lineus viridis* on its polychaete prey on an intertidal sandflat. Hydrobiologia 156, 39–46.

Ólafsson, E.B., Peterson, C.H., Ambrose, W.G., 1994. Does recruitment limitation structure populations and communities of macro-invertebrates in marine soft sediments: the relative significance of pre- and post-settlement processes. Oceanogr. Mar. Biol. Ann. Rev. 32, 65–109.

Philippart, C.J.M., 1994. Interactions between *Arenicola marina* and *Zostera noltii* on a tidal flat in the Wadden Sea. Mar. Ecol. Prog. Ser. 111, 251–257.

Raffaelli, D., Hawkins, S., 1996. Intertidal Ecology. Chapman and Hall, London, p. 356.

Reichardt, W., 1988. Impact of bioturbation by *Arenicola marina* on microbial parameters in intertidal sediments. Mar. Ecol. Prog. Ser. 44, 149–158.

Reise, K., 1979. Spatial configurations generated by motile benthic polychaetes. Helgol. Meeresunters. 32, 55–72.

Reise, K., 1981. Gnathostomulida abundant alongside polychaete burrows. Mar. Ecol. Prog. Ser. 6, 329–333.

Reise, K., 1983. Experimental removal of lugworms from marine sand affects small zoobenthos. Mar. Biol. 74, 327–332.

Reise, K., 1985. Tidal Flat Ecology. Springer, Berlin, p. 191.

Reise, K., 1987. Spatial niches and long-term performance in meiobenthic Plathelminthes of an intertidal lugworm flat. Mar. Ecol. Prog. Ser. 38, 1–11.

Reise, K., 2002. Sediment mediated species interactions in coastal waters. J. Sea Res. 48, 127–141.

Reise, K., Ax, P., 1979. A meiofaunal "thiobios" limited to the anaerobic sulfide system of marine sand does not exist. Mar. Biol. 54, 225–237.

Reise, K., Volkenborn, N., 2004. Large worms as ecosystem engineers in intertidal sediments. In: Tamaki, A. (Ed.), Proceedings of the Symposium on "Ecology of Large Bioturbators in Tidal Flats and Shallow Sublittoral Sediments—from Individual Behavior to their Role as Ecosystem Engineers". Nagasaki University, Japan, pp. 95–100.

Reise, K., Herre, E., Sturm, M., 1994. Biomass and abundance of macrofauna in intertidal sediments of Königshafen in the northern Wadden Sea. Helgol. Meeresunters. 48, 201–215.

Reise, K., Simon, M., Herre, E., 2001. Density-dependent recruitment after winter disturbance on tidal flats by the lugworm *Arenicola marina*. Helgol. Mar. Res. 55, 161–165.

Rhoads, D.C., Young, D.K., 1970. The influence of deposit-feeding organisms on sediment stability and community trophic structure. J. Mar. Res. 28, 150–178.

Riisgård, H.U., Banta, G.T., 1998. Irrigation and deposit feeding by the lugworm *Arenicola marina*, characteristics and secondary effects on the environment. A review of our current knowledge. Vie Milleu 48, 243–257.

Riisgård, H.U., Kamermans, P., 2001. Switching between deposit and suspension feeding in coastal zoobenthos. In: Reise, K. (Ed.), Ecological Comparisons of Sedimentary Shores. Springer, Berlin, pp. 73–101.

Schaffner, L.C., 1990. Small-scale organism distributions and patterns of species diversity: evidence for positive interactions in an estuarine benthic community. Mar. Ecol. Prog. Ser. 61, 107–117.

Schoettler, U., Grieshaber, M., 1988. Adaptation of the polychaete worm *Scoloplos armiger* to hypoxic conditions. Mar. Biol. 99, 215–222.

Schubert, A., Reise, K., 1986. Predatory effects of *Nephtys hombergii* on other polychaetes in tidal flat sediments. Mar. Ecol. Prog. Ser. 34, 117–124.

Underwood, A.J., Fairweather, P.G., 1989. Supply-side ecology and benthic marine assemblages. Trends Ecol. Evol. 4, 16–20.

Warwick, R.M., 1982. The partitioning of secondary production among species in benthic communities. Neth. J. Sea Res. 16, 1–16.

Warwick, R.M., Gee, J.M., Berge, J.A., Ambrose Jr., W., 1986. Effects of the feeding activity of the polychaete *Streblosoma bairdi* (Malmgren) on meiofaunal abundance and community structure. Sarsia 71, 11–16.

Whitlatch, R.B., 1980. Patterns of resource utilization and coexistence in marine intertidal deposit-feeding communities. J. Mar. Res. 38, 743–765.

Witte, F., de Wilde, P.A.W.J., 1979. On the ecological relation between *Nereis diversicolor* and juvenile *Arenicola marina*. Neth. J. Sea Res. 13, 394–405.

Zajac, R.N., 2004. Macrofaunal responses to pit-mound patch dynamics in an intertidal mudflat: local versus patch-type effects. J. Exp. Mar. Biol. Ecol. 313, 297–315.

Zajac, R.N., Whitlatch, R.B., Thrush, S.F., 1998. Recolonization and succession in soft-sediment infaunal communities: the spatial scale of controlling factors. Hydrobiologia 375–376, 227–240.

Zipperle, A., Reise, K., 2005. Freshwater springs on intertidal sand flats cause a switch in dominance among polychaete worms. J. Sea Res. 54, 143–150.

Zühlke, R., Reise, K., 1994. Response of macrofauna to drifting tidal sediments. Helgol. Meeresunters. 48, 277–289.