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Effects of bioturbation and bioirrigation by lugworms (*Arenicola marina*) on physical and chemical sediment properties and implications for intertidal habitat succession

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Abstract

Sediment destabilization by sediment-reworking organisms is common in coastal aquatic environments, but the potential of bioturbation to inhibit shoreline succession has not been suggested previously. The lugworm *Arenicola marina* is a widespread and dominant large burrower at European Atlantic shores, and a major source of bioturbation and bioirrigation on the extensive intertidal flats in the Wadden Sea (eastern North Sea). The hypothesis that lugworm activities inhibit the successive development from sandy to muddy sediments in depositional embayments has been tested by a large-scale exclusion field experiment. Changes in sediment properties indicate a progressive clogging of interstices with fine particles and organic matter, resulting in lower sediment permeability in exclusion areas compared to lugworm inhabited control areas. Chlorophyll content in the surface layer was consistently higher in the absence of lugworms. Lack of sub-surface irrigation in the absence of lugworms combined with reduced sediment permeability resulted in increased concentrations of ammonium, phosphate, silicate, and sulphide in the pore-water. Concentrations >100 μM of sulphide gave rise to toxic conditions for macrofauna. The effects of lugworms on sediment characteristics were more conspicuous in fine than in medium sand. It is concluded that *A. marina* contributes to the maintenance of permeable sand and thereby sustaining suitable conditions for the lugworm population itself. Without this "ecosystem engineer" mud flats would greatly expand at the expense of sand flats in the Wadden Sea.

Keywords: *Arenicola marina*; bioturbation; bioirrigation; ecosystem engineering; intertidal sand; sediment properties; Wadden Sea

1. Introduction

Nearshore soft sediments support large populations of burrowing and bioirrigating macroinfauna, such as arenicolid polychaetes (Beukema, 1976; Reise, 1985), crabs and thalassinidean shrimps (Botto and Iribarne, 2000), or enteropneusts (Flint and Kalke, 1986). As "ecosystem engineers" (*sensu* Jones et al., 1994) these organisms can alter the physical state of the sedimentary environment, thereby improve their own living conditions and affect those of other organisms (Levinton, 1995). In the eastern North Sea, where the largest coherent sediment flats of the world extend between the tide marks, the deposit-feeding lugworm (*Arenicola marina)* is the dominant sediment reworking species of unvegetated intertidal sand (Reise, 1985). Lugworms maintain a rather stable population with densities of 20 to 40 adults per square metre over most of the tidal zone (Flach and Beukema, 1994). In the entire Wadden Sea with about 4300 km^2 of intertidal flats, up to 90% are "lugworm flats" composed of fine to medium sand, and only 7% are mud flats unsuitable for a high density of *A. marina* (Beukema, 1976; Dijkema et al., 1989). Abundances are also low in clean unstable sand exposed to strong currents or waves near low water line and below (Longbottom, 1970; Lackschewitz and Reise, 1998).

The areal ratio between sandy and muddy sediment bottoms in the Wadden Sea may be in part a product of lugworm

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activities. This speculation is based on measurements on bioturbation and irrigation of *Arenicola marina* which have been conducted on individual worms, burrow structures or on small plots with and without lugworms (e.g. Cadée, 1976; Baumfalk, 1979; Huettel, 1990; Philippart, 1994; Goñi-Urriza et al., 1999; Timmermann et al., 2006; Papaspyrou et al., 2007). *A. marina* lives in 20 to 40 cm deep J-shaped burrows completed to a U by a vertical head shaft, through which surface sediment slides down to become ingested by the worm and defecated as a mound of coiled faecal strings at the sediment surface above the tail shaft (review by Riisgård and Banta, 1998). Burrow ventilation for respiration is achieved by piston-like movements in a tail-to-head direction. Water-pumping into the blind ending burrows induces an advective water flow into the surrounding sediment (Meysman et al., 2006; Timmermann et al., 2006). Assuming a lugworm density of 30 ind. m^{-2}, sediment turnover corresponds to a sediment layer of 15 cm $year^{-1}$ (Cadée, 1976) and 3 L h^{-1} m^{-2} of seawater are pumped into the anoxic sediment (Riisgård et al., 1996).

Despite this detailed knowledge of lugworm bioturbation and bioirrigation, the potential of these activities to control the characteristic of the inhabited sediment is poorly understood. Results from laboratory studies may considerable deviate from what is observed in the field (Biles et al., 2002; Papaspyrou et al., 2007) and small scale experimental *in situ* approaches may alleviate possible effects, due to lateral particle and pore-water exchange between manipulated plots and the surrounding sediment, especially in dynamic environments like intertidal sand flats. In order to properly test the hypothesis that lugworms control sedimentary habitat characteristics it is therefore necessary to measure effects of lugworms on sediment properties *in situ* and on large plots with and without lugworms over several years. The present study presents results from replicated experimental lugworm exclusion areas and corresponding lugworm populated control areas of 400 m^2 each, 1 and 2 years after the exclusion commenced. Because of lateral sediment and pore-water transport across such plots in the tidal zone, size and time may still not be sufficient to quantify all effects but some indications are expected to what extent the sediment character is affected by *Arenicola marina.*

A shift in sediment properties from permeable sand in the direction of cohesive mud upon the exclusion of lugworms will be considered to support the hypothesis that lugworms inhibit the succession from sand to mud flats in depositional embayments, which may eventually progress into salt marsh vegetation. The present study focuses on grain size, organic content, chlorophyll and permeability of the sediment as well as on vertical solute profiles of nutrients and sulphide to infer flushing rates on experimental plots with and without *Arenicola marina*. It is expected that exclusion plots show

- an accumulation of fine sediment particles and associated organic matter,
- an increase in microphytobenthos on the sediment surface,
- a decrease in permeability in the sediment column, and
- an increase in pore-water solutes characteristic of anoxic conditions below the sediment surface.

As these parameters are not independent of each other, each variable is not regarded as separate evidence but as necessary parts of a progressive development leading from sand towards mud flats.

2. Methods

2.1. Sampling site and experimental design

A large-scale lugworm exclusion experiment was conducted on a sandy tidal flat in Königshafen, a tidal bay at the northern end of the island of Sylt in Germany (Fig. 1). The major intertidal habitat type in this embayment is low organic medium to fine sand, densely populated by *Arenicola marina* (Reise et al., 1994). Salinity varies on average between 27.5 in spring and 31.0 in summer and freshwater seepage into the marine environment is negligible. Mean tidal range is 1.8 m. A detailed description of the tidal embayment and its biota is provided by Wohlenberg (1937), Reise (1985) and Reise et al. (1994). Exclusion of *A. marina* was achieved by inserting a 1 mm meshed polyethylene net at 10 cm depth into the sediment (Reise, 1983; Huettel, 1990; Philippart, 1994). This was done on six 20 × 20 m experimental plots by the use of a shovel excavator. The net was placed in the sediment as 1 m wide and 20 m long lanes. The horizontal net prevented lugworms from maintaining their burrows and effectively kept them away. It was not feasible to remove lugworms mechanically before inserting the mesh. Lugworms near the edges were potentially able to escape horizontally from being trapped underneath the net, while others presumably died below the net. Before net insertion lugworm mean abundance on the plots was 30 ind. m^{-2}, which corresponds approximately to a biomass of 10–20 g m^{-2} (Beukema, 1976; Reise et al., 1994). Although a temporary effect of this added dead organic material on nutrient and organic content was inevitable, it is assumed that after several months the mineralization of dead lugworms was completed and that the pore-water had been exchanged. This assumption is based on artificial organic enrichment experiments of comparable sandy sediments which were done with much higher organic input (>100 g m^{-2}) and on a shorter time scale (tens of days) (Kristensen and Hansen, 1995; Hansen and Kristensen, 1998). To test the effect of the initial dredging, control plots were created in which the sediment was dredged in the same way but without inserting a net. In a third treatment (ambient), plots were left untouched constituting natural conditions. The initial disturbance of the sediment did not significantly affect sediment properties or the benthic community (Volkenborn and Reise, 2006, 2007).

The experiment was created in 2002 in a 2-factorial (3 × 2 levels) nested block design (Fig. 2). Each block comprised three lugworm treatments (exclusion, control, ambient) with each experimental plot being 400 m^2 in area. This large size was chosen to minimize effects of lateral sediment transport when sampling in the central region of experimental plots. In order to account for the dominant sediment types at the study site, experimental blocks were nested: three blocks

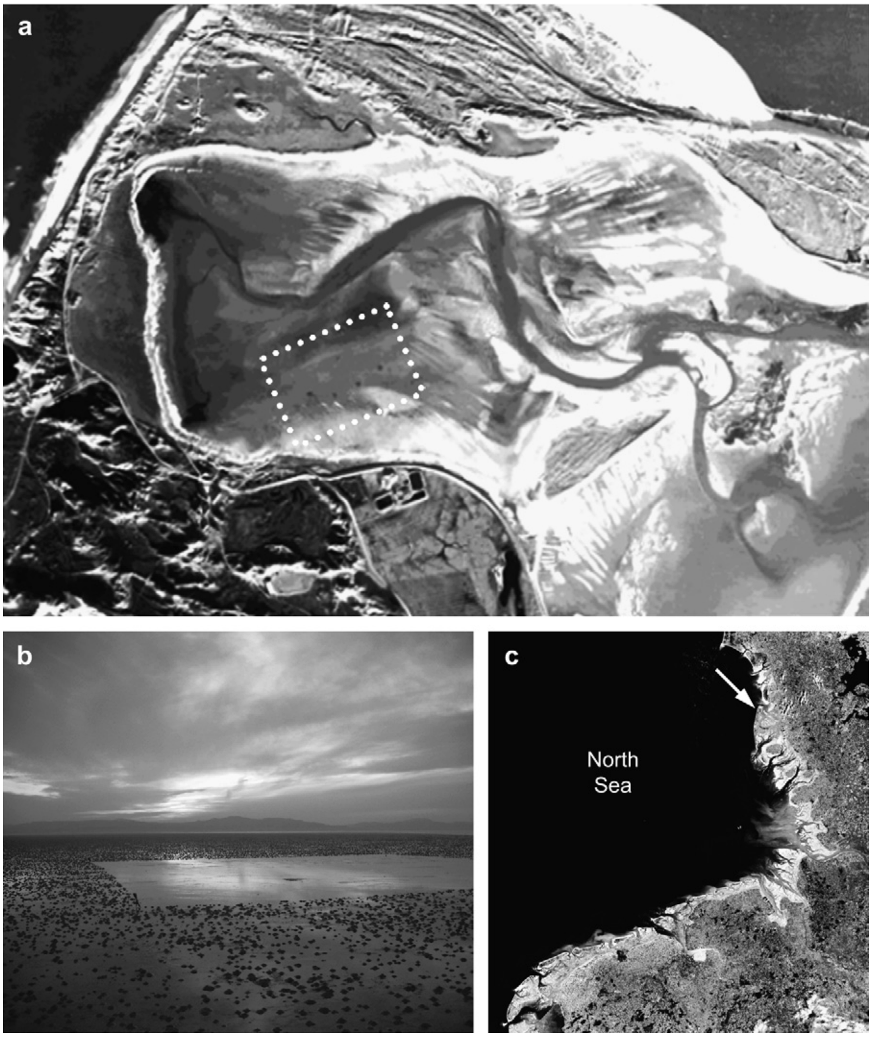

Fig. 1. (a) On an aerial photograph in December 2002, exclusion plots were visible as dark dots within the study site in Königshafen embayment, sharing the dark colour of more muddy sediments in the innermost part of the bay. (b) Experimental plot, where lugworms were excluded from 400 m^2 areas, by inserting a 1 mm meshed net at 10 cm depth. (c) Study area in the northern Wadden Sea.

were conducted within an area of medium sand (grain size median 330–340 μm) and three blocks within an area of fine sand (grain size median 200–220 μm). Emersion period was 6–7 and 9–10 h per tide, respectively. Due to aeolian sand input from adjacent dunes medium sands dominate the edges of the embayment and grain size median decreases towards the centre of the bay (Austen, 1994). Tidal currents are the dominant hydrodynamic force at the study site, but wave action becomes important when winds blow from northern and eastern directions, forming sand ripples with an amplitude and height of up to 5 cm and 2 cm, respectively.

To control the success of lugworm exclusion, lugworm densities were estimated almost monthly by counting faecal castings within each experimental plot on 10 randomly chosen areas of 0.25 m^2. The number of faecal castings varies with feeding activity of lugworms but can be taken as a proxy for the abundance of *A. marina* (Flach and Beukema, 1994). While almost no adult lugworms could be found on exclusion plots, *Arenicola* cast densities on control and ambient plots remained high (Volkenborn and Reise, 2006). Over the entire investigation period of 2.5 years mean density was 17.8 casts m^{-2} on control plots and 22.0 casts m^{-2} on ambient plots. Maximum cast densities were reached in early summer with densities of 30 casts m^{-2} averaged over all control plots and 35 casts m^{-2} averaged over all ambient plots.

2.2. Sediment and pore-water sampling

The aim of the study was to investigate the impact of *A. marina* on habitat scale rather than on the scale of individual burrows. Therefore samples for sediment and pore-water analysis were taken $\geq$10 cm apart from the nearest lugworm cast or funnel. Samples were taken randomly from 16 × 16 m central areas, excluding border zones of 2 m to minimize possible edge effects. Pseudo-replicate samples, taken within each experimental plot were pooled in order to achieve reliable mean values. Sampling of sediment and pore-water was done between 2002 and 2004.

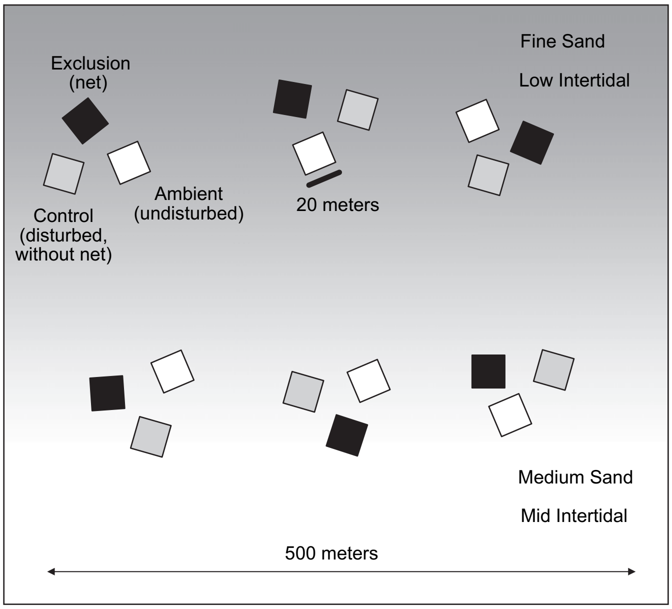

Fig. 2. Experimental set-up in a 2-factorial nested block design. Six experimental blocks comprised three lugworm treatments and were nested within two sediment types.

2.3. Grain size composition

Sediment samples were taken randomly with 10 cm^2 corers from 10 different locations within central parts of each experimental plot in August 2002 and August 2003. Cores were divided into 3 consecutive layers (0–1, 1–5, 5–10 cm depth). Samples were washed three times with 1500 ml freshwater to deplete salt. Sediment was freeze dried and separated into grain size fractions by dry sieving.

2.4. Water and total organic material content

From each experimental plot three cores (10 cm^2, depth 5 cm) were taken in August 2003. After siphoning the overlying water, water content was obtained as the difference between wet and dry weight (after being dried at 70 °C for 72 h). Total organic matter content was determined by loss at ignition (500 °C, 24 h), expressed as percentage of sediment dry weight.

2.5. Chlorophyll content

Samples were taken with a 2 cm^2 corer from 20 randomly chosen locations within each experimental plot almost monthly from April 2003 until October 2003. Each sample was divided into three depth horizons (0–1 cm, 1–5 cm, 5–10 cm) and samples from the same depth and experimental plot were pooled. Samples were freeze dried and homogenized. Chlorophyll was extracted from triplicate samples of about 1 g dry weight with 10 ml acetone (90%) overnight at 4 °C and centrifuged for 5 min at 400 rpm. The chlorophyll content was measured spectrophotometrically after Lorenzen (1967).

2.6. POC and PON

Sediment samples for chlorophyll extraction from June 2003 were used to measure particulate organic carbon and nitrogen. From each sample, three sub-samples (75 mg) were taken, treated with 1 N HCl to remove carbonates and dried subsequently (1 h at 70 °C). Estimation of POC and PON was done with a C/N analyser (Thermo-Finnigan Flash EA 1112).

2.7. Sediment permeability

Permeability describes how easy a fluid medium flows through a porous medium. It is a key factor for sedimentary processes, such as exchange rates and penetration depths of solutes (Forster et al., 1996; Huettel et al., 1996). Sediment permeability was estimated by the constant head method (Klute and Dirksen, 1986). Different hydrostatic pressures were applied to sediment cores and the volume of water that flows through a core at a given hydraulic pressure was recorded. The hydraulic conductivity was calculated with eq. (1).

$$K = (V \times L)/(h \times A \times T) \tag{1}$$

where K is the hydraulic conductivity (m s^{-1}), V is the volume of water collected (m^3), L is the length of the sediment core (m), h is the pressure head of the water column (m), A is the surface area of the core (m^2), and T is the time interval of water flow (s).

The hydraulic conductivity was transformed to permeability with eq. (2).

$$k = (K \times m)/(d \times g) \tag{2}$$

where k is the permeability (m^2), K is the hydraulic conductivity (m s^{-1}), m is the viscosity (g m^{-1} s^{-1}), d is the density (g m^{-3}), and g is the gravity (9.81 m s^{-2}).

From each experimental plot one 10 cm^2 and 10 cm deep core was taken and the flow velocity of 2 ml seawater was measured under 4 different pressure gradients (ranging from 1 to 20 cm of water column). Permeability measurements were done in November 2003 on all plots and in July 2004 on exclusion and control plots.

2.8. Pore-water profiles

Pore-water sampling was done using two different extraction methods. A pore-water sampler modified after Huettel (1990) was used to analyse deep profiles. With this sampling device multiple pore-water samples were collected simultaneous from six different depths (3, 5, 7, 10, 15, 20 cm) while maintaining anaerobic conditions. Due to a steel tip it was possible to penetrate the net on the exclusion plots and to get samples from deeper sediment layers. Pore-water sampling was carried out in April and July 2004. From four randomly chosen locations within each experimental plot approximately 5 ml of pore-water from each depth was taken and pooled. These 20 ml samples were filtered (0.45 µm nylon filters) and inorganic nutrients (NH_4, PO_4, SiO_2, NO_3, NO_2) were measured with an autoanalyser (AA_3, Bran & Luebbe). Sulphide concentrations were measured with the colorimetric methylene blue method described by Fonselius (1983).

Sampling with the pore-water lance has the disadvantage of disturbance when penetrating the sediment. To get undisturbed pore-water samples with higher spatial resolution a second pore-water extraction technique was used for the upper sediment layer in October 2003. From each experimental plot four 10 cm^2 cores were sliced in 1 cm layers and pore-water from pooled slices (0–1, 2–3, 4–5 and 6–7 cm depth) was blown out with pressurized N_2 gas (Billerbeck et al., 2006). Processing of pore-water samples was carried out as described above.

2.9. Statistical analysis

The investigated parameters were analysed with respect to three main questions:

- Is a parameter significantly influenced by lugworm presence/absence?
- Are effects of lugworm presence/absence dependent upon the sediment type?
- Is a significant modification confined to distinct sediment layers?

Results of the nested block designed experiment were analysed using different types of ANOVA. Two-factorial nested block ANOVA was used to test for effects of lugworm presence/absence, sediment type and their interaction on total organic material, water content, permeability and nutrient concentrations in distinct depths. The effect of lugworm absence/presence was used as first factor (3 levels: exclusion, control, ambient). Sediment type was used as second factor to test the effect of sediment characteristic (2 levels: medium and fine sand) and accounting for the significance of interaction effects of sediment type and lugworm presence/absence. The blocked design of the experiment was used to incorporate the spatial heterogeneity of the study site into the statistical analysis. Therefore experimental blocks were nested in the sediment type. Repeated measures ANOVA was used to test factor effects on the amount of fine particles in 2002 and 2003 and on monthly estimated chlorophyll concentrations. Post hoc multiple means comparisons were performed using the Tukey–Kramer procedure at $\alpha = 0.05$ significance level. When necessary, data were square-root transformed prior to analysis in order to achieve homogeneity of variance (Cochran's test).

3. Results

3.1. Sediment composition

Traditional sediment parameters clearly discriminate two sediment types in the study area. The upper site was dominated by medium sand and had significantly higher median grain size than the lower site with fine sand (Table 1). Water content ($F_{1,8} = 61.22$; $p < 0.001$) and total organic content ($F_{1,8} = 36.14$; $p < 0.001$) were significantly higher in sediment from the fine sand area. Surface sediment median grain size was significantly affected by the lugworm treatment ($F_{2,8} = 10.38$; $p < 0.01$) and significantly lower on lugworm exclusion plots (Tukey $p < 0.01$), while grain size median of the sub-surface sediment was not affected by lugworm presence. Organic and water content were significantly higher on lugworm exclusion plots in the fine sand area indicated by significant Treatment × Sediment type interactions (Table 1).

3.2. Fine fraction

The proportion of fine particles (<63 μm) within the sand matrix was significantly different in both years and was significantly higher in the fine sand area (Table 2). In 2002, weight percentage of the fine fraction was low, especially in surface sediments. From 2002 to 2003 an increase in fine fraction could be observed on all experimental plots (Fig. 3). Lugworm presence significantly inhibited the accumulation of fine particles in surface and sub-surface sediments. The potential of binding fine particles in the upper sediment layer was highest on lugworm exclusion plots in the fine sand area revealed by a significant Treatment × Sediment type interaction (Table 2). In the top 1 centimetre of the sediment, the fine fraction doubled in the absence of *Arenicola marina*. For the horizon from 1 to 5 cm depth a significant Time × Treatment interaction (Table 2) indicate gradual silt and clay accumulation within the sub-surface sediment. In the fine sand area these small particles comprised 2.5% by weight of the total sediment in the upper 5 cm on exclusion plots but only 1.0% on control and ambient plots. The sediment layer of 5 to 10 cm was not significantly affected by lugworm absence/presence.

Table 1
Sediment characteristics of experimental plots in August 2003 and ANOVA results of factor effects (× for significant effect). In parentheses, treatment with significant (Tukey–Kramer post-hoc test) higher value is indicated (E: exclusion; C: control; O: ambient; MS: medium sand; FS: fine sand)

	Depth	Medium sand			Fine sand			ANOVA results			
		E	C	O	E	C	O	Treatment	Sediment type	Treatment × Sediment type	Block
Grain size median (μm)	0–1 cm	294	338	338	190	204	208	× (C, O)	× (MS)		
	1–5 cm	329	342	335	206	218	216		× (MS)		
% Water content	0–5 cm	15.9	16.7	15.5	19.9	16.2	17.1	× (E)	× (FS)	× (E, FS)	
% Total organic material	0–5 cm	0.6	0.6	0.5	1.2	0.6	0.7	× (E)	× (FS)	× (E, FS)	

Table 2
Repeated measures ANOVA of treatment and sediment type effects on fine fraction in different sediment depths. Prior to analysis data were square root transformed. Bold values indicate significant factor effects

	df	0–1 cm			1–5 cm			5–8 cm		
		SS	*F*	*p*	SS	*F*	*p*	SS	*F*	*p*
Treatment	2	0.2959	45.75	**0.000**	0.2632	3.89	0.066	0.0032	0.18	0.842
Sediment type	1	0.7005	216.64	**0.000**	1.5464	45.77	**0.000**	0.7840	86.38	**0.000**
Treatment × Sediment type	2	0.0736	11.38	**0.005**	0.1617	2.39	0.153	0.0549	3.02	0.105
Block (nested in Sediment type)	4	0.0546	4.22	**0.040**	0.2118	1.57	0.272	0.0913	2.51	0.124
Residuals	8	0.0259			0.2703			0.0726		
Year	1	1.7531	249.03	**0.000**	0.5296	65.48	**0.000**	0.1028	128.80	**0.000**
Year × Treatment	2	0.0613	4.36	0.053	0.1711	10.58	**0.006**	0.0080	5.00	**0.039**
Year × Sediment type	1	0.0000	0.00	0.979	0.1625	20.09	**0.002**	0.0077	9.61	**0.015**
Year × Treatment × Sediment type	2	0.0018	0.13	0.879	0.0515	3.18	0.096	0.0058	3.62	0.076
Year × Block (Sediment type)	4	0.0054	0.19	0.935	0.0183	0.56	0.695	0.0039	1.22	0.374
Residuals	8	0.0563			0.0647			0.0064		

3.3. Organic content

Analysis of POC and PON revealed a close relationship between the organic material and the fine fraction for the upper 5 cm of the sediment. Highest organic content was found within the top 1 cm and decreased with depth. A significant impact of lugworm presence was restricted to the upper 5 cm. The organic content in the top 1 cm of the sediment was characterized by a significant Treatment × Sediment type interaction ($F_{2,8} = 7.80; p = 0.013$) due to more pronounced POC accumulation on exclusion areas at the fine sand area. Organic accumulation in 1 to 5 cm depth was generally higher on the exclusion plots (Tukey–Kramer $p < 0.01$).

3.4. Sediment permeability

Permeability of the sediment strongly depended on grain size composition (Fig. 4), reflected in a significant sediment

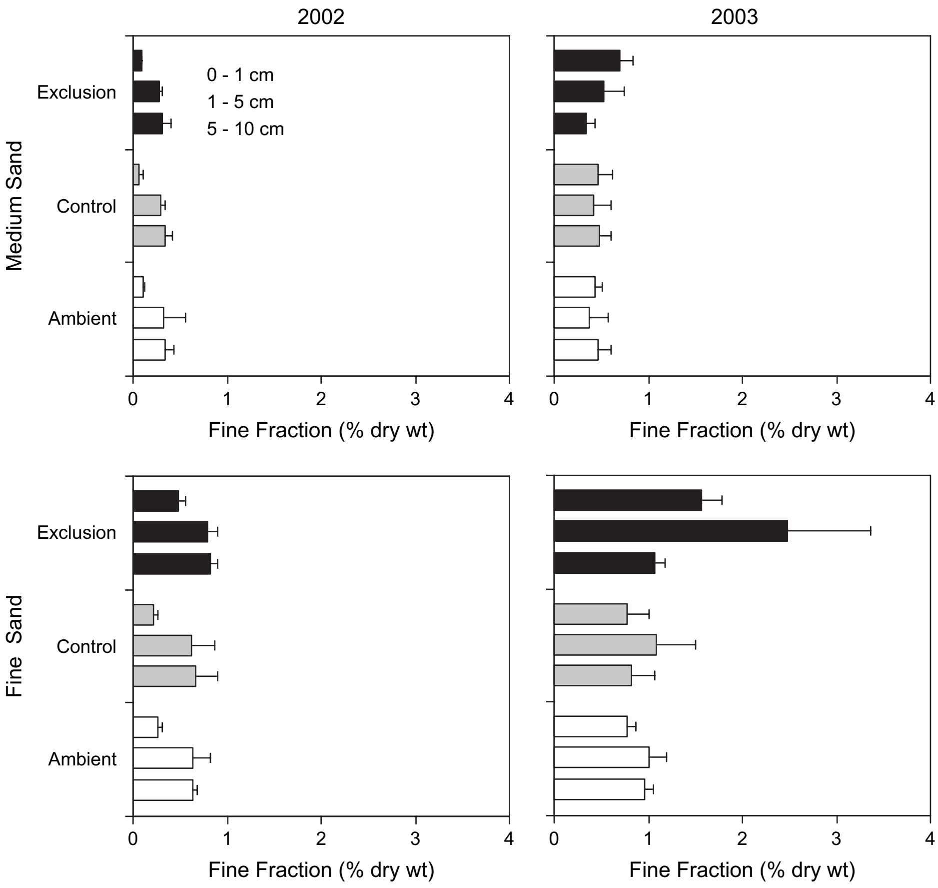

Fig. 3. Fine fraction (grains <63 μm) in sediment from experimental treatments in August 2002 and August 2003. Shown are means ($n = 3$) and SD.

type effect (Table 3). The composition of the sand matrix explained more than 70% of permeability variance in both years. In general, sediment in the fine sand area was five times less permeable than sediment from the medium sand area ($k = 2 \times 10^{-12}$ m^2 compared to $k = 9 \times 10^{-12}$ m^2). The lugworm treatment showed no significant effect on permeability in autumn 2003, while data from summer 2004 revealed a significant impact. Sediment from control plots showed an up to eight-fold higher permeability compared to sediment from exclusion plots of the same experimental block. Besides the general composition of the sand matrix, the proportion of incorporated fine particles was found to have a significant impact on sediment permeability (Fig. 5). With increasing fraction of fine particles, permeability decreased, indicating a clogging effect. This relationship between fine fraction and permeability was exponential. Small changes in the amount of fine particles had dramatic consequences for sediment permeability. Above a critical proportion of fine particles (~1%) the sediment matrix was clogged and water flow through the sediment remained low. The effect of lugworm absence on sediment permeability was much more pronounced in the fine grained area than in the medium sand area.

3.5. Chlorophyll concentration

The chlorophyll content of the surface sediment was significantly reduced by lugworm presence (Table 4). Most pronounced chlorophyll concentration differences were observed in summer months (Fig. 6). In June, mean chlorophyll concentration on the exclusion plots was 25.6 μg g^{-1} dry sediment, while concentrations on control (16.8 μg g^{-1}) and ambient plots (13.4 μg g^{-1}) were significantly lower. This effect of lugworm absence was more conspicuous in the fine sand area, and in repeated measures ANOVA Treatment × Sediment type interaction over all months only slightly fails significance (Table 4). Seasonal variation in chlorophyll content was more conspicuous in the absence than in the presence of lugworms. The highest impact of *Arenicola* presence on the chlorophyll content was observed in months with highest feeding activity (Fig. 7). Lugworm feeding activity therefore seemed to be an important factor controlling chlorophyll concentration in the sediment.

Table 3
ANOVA results of treatment and sediment type effects on sediment permeability in 2003 and 2004. Prior to analysis data were square root transformed. Bold values indicate significant factor effects

	df	2003			2004		
		SS	*F*	*p*	SS	*F*	*p*
Treatment	2	0.52	2.17	0.176	1.28	8.47	**0.044**
Sediment type	1	9.89	82.26	**0.001**	9.15	60.63	**0.001**
Treatment × Sediment type	2	0.21	0.89	0.447	0.12	0.79	0.425
Block (nested in Sediment type)	4	2.31	4.81	**0.028**	1.07	1.77	0.296
Residuals	8	0.96			0.60		

3.6. Pore-water nutrient profiles

Nutrient profiles were strongly influenced by the presence of *Arenicola marina*. Ammonium, phosphate and silicate showed a similar pattern of profile modification (Fig. 8). On the exclusion plots, inorganic nutrient concentrations almost linearly increased with depth reaching concentrations of up to 25 μM phosphate, 300 μM ammonium and 250 μM silicate at a depth of 20 cm. In the presence of *A. marina* ammonium, phosphate and silicate concentration peaks were found between 3 and 10 cm depth and concentrations decreased with further depths. ANOVA revealed a significant treatment effect on all nutrients in 15 cm depth with highest nutrient concentration on exclusion plots (Tukey–Kramer $p < 0.05$).

High sulphide concentration could only be found in porewater from the exclusion plots. In the absence of *Arenicola marina* sulphide concentrations of more than 150–200 μM were measured in samples from 15 and 20 cm depth. In the presence of lugworms sulphide concentrations remained below 100 μM. Nitrate concentrations on exclusion plots were low throughout the investigated depth, while nitrate concentrations

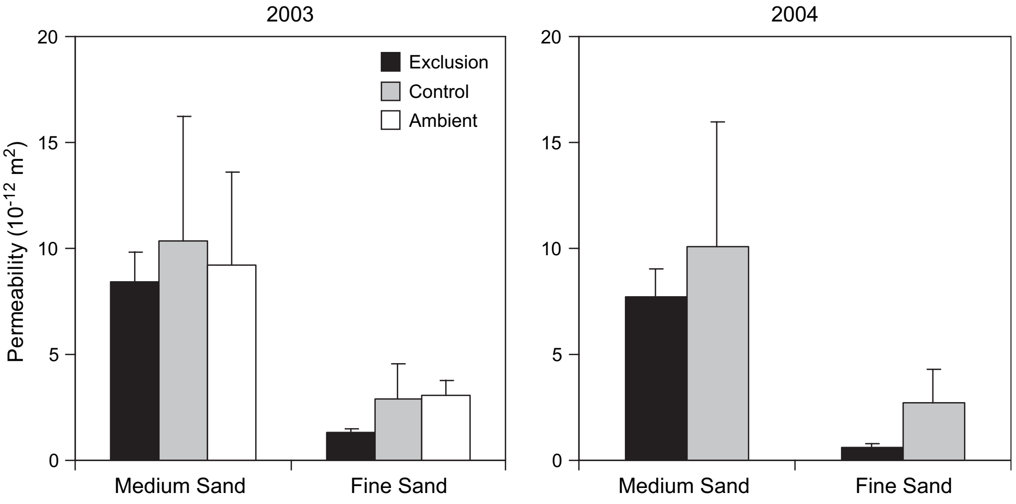

Fig. 4. Sediment permeability of experimental plots in November 2003 and July 2004 (mean and SD; $n = 3$).

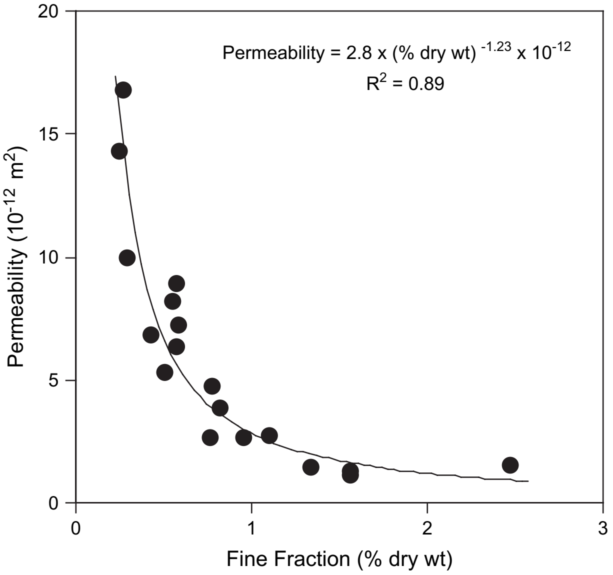

Fig. 5. Correlation between silt fraction of the upper 10 cm (in % of the dry weight) and sediment permeability (in 10^{-12} m^2) for all 18 experimental plots.

increased in the presence of lugworms below 10 cm and reached up to 20 μM at a depth of 20 cm (Fig. 9), indicating bioirrigation of deep sediment layers with overlying water and nitrification in the presence of lugworms. The sediment type had no effect on pore-water nutrient concentrations.

Extraction of pore-water with nitrogen gas from sliced cores revealed that the impact of *Arenicola marina* on nutrient concentrations was not restricted to deep sediment layers. Ammonium concentrations increased with depth on all plots but with almost doubled concentrations on the exclusion plots (Fig. 10). Additionally, lugworm presence inhibited the formation of sub-surface peaks of phosphate in the upper cm and of silicate in 2 to 3 cm depth. ANOVA revealed significant treatment effects on concentrations of ammonium in 6 to 7 cm depth ($F_{2,8} = 4.474$; $p < 0.05$), of silicate in 2 to 3 cm depth ($F_{2,8} = 7.835$; $p < 0.05$) and of phosphate in the upper centimetre ($F_{2,8} = 11.941$; $p < 0.01$) with significantly higher concentrations on exclusion plots (Tukey–Kramer $p < 0.01$). The effect of lugworms on nutrients was the same in both sediment types.

Table 4
Repeated measures ANOVA of treatment and sediment type effects on chlorophyll content in the upper sediment centimetre. Samples were taken monthly between April and October 2003, (except July). Bold values indicate significant factor effects. Data were square root transformed

	df	SS	*F*	*p*
Treatment	2	13.61	23.05	**0.0005**
Sediment type	1	1.71	5.79	**0.0428**
Treatment × Sediment type	2	2.41	4.09	0.0598
Block (Sediment type)	4	1.45	1.23	0.3711
Residuals	8	2.36		
Time	5	30.76	61.92	**0.0000**
Time × Treatment	10	1.91	1.92	0.0706
Time × Sediment type	5	0.74	1.49	0.2149
Time × Treatment × Sediment type	10	1.40	1.41	0.2123
Time × Block (Sediment type)	20	2.09	1.05	0.4300
Residuals	40	3.97		

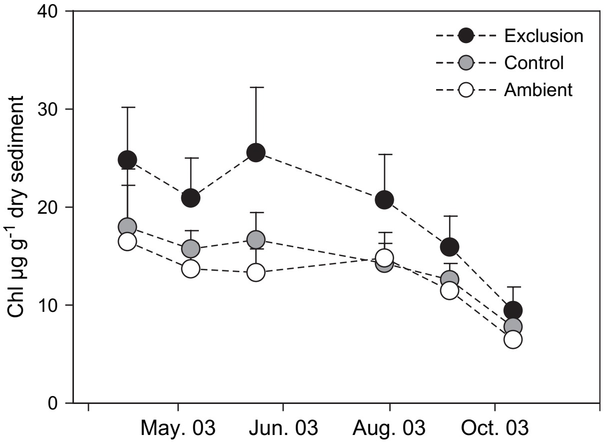

Fig. 6. Chlorophyll content of the upper sediment cm in μg g^{-1} dry sediment. Shown are mean ($n = 6$) and SD.

4. Discussion

4.1. Intertidal habitat succession and the role of lugworms

On the geological time scale, steep reflective sandy shores may develop towards gentle sloping dissipative shores. With sufficient sediment supply, shores may further develop longshore bars, spits and barrier islands (Carter, 1988; Davis, 1996). These provide shelter for fine particle deposition on their leeward side. In this geomorphological development of the shore, sandy shoals gradually accumulate more and more fine particles and finally may become mud flats when wave

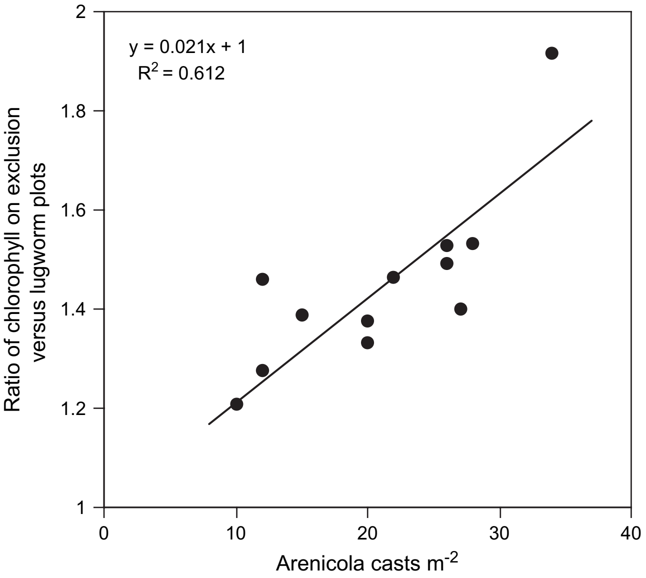

Fig. 7. Correlation between *Arenicola* casts (feeding activity) on lugworm plots and ratio of chlorophyll concentration on exclusion plots versus lugworm plots. Ratios are calculated by dividing chlorophyll concentrations at exclusion plots by the respective concentrations at the lugworm plots (averaged over control and ambient plot). Microphytobenthic biomass was consistently higher in the sediment of the exclusion plots (proportion > 1.0). This difference was most pronounced in the summer months, when lugworms were most active.

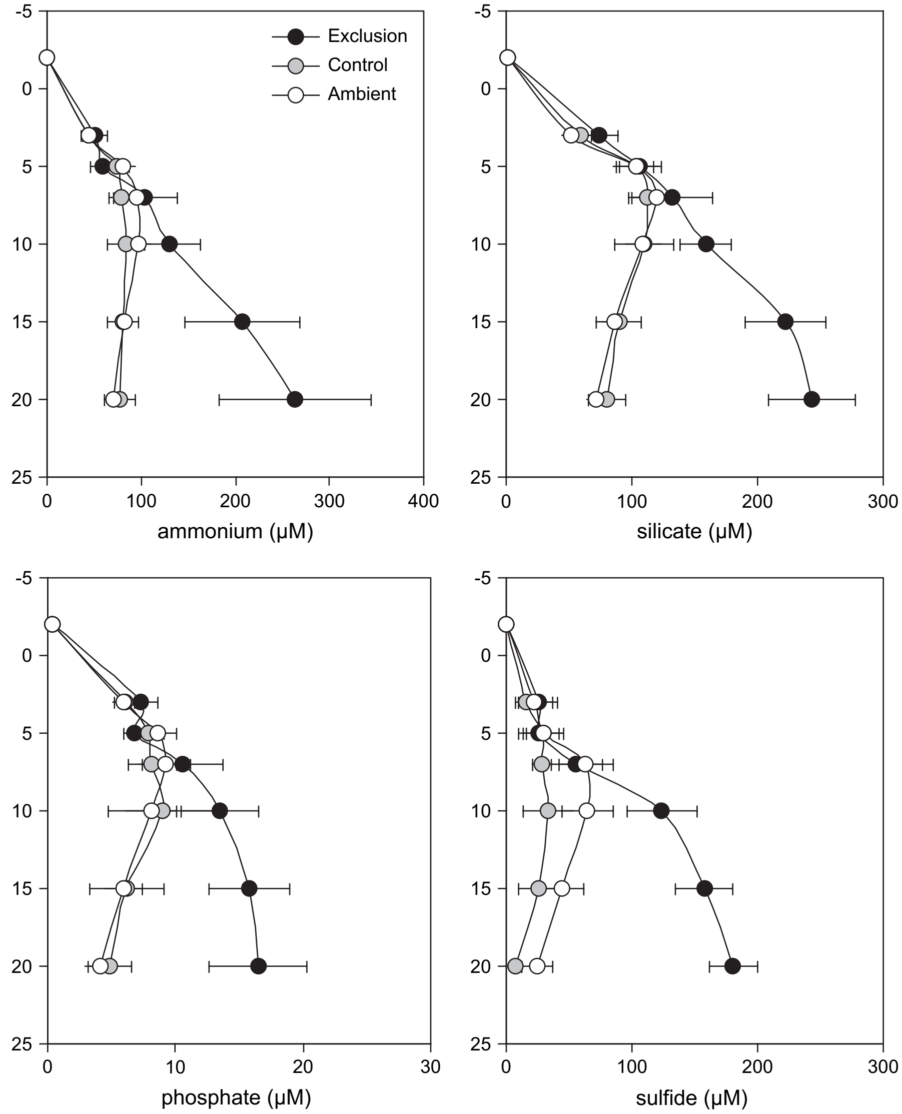

Fig. 8. Ammonium, silicate and phosphate, and sulphide pore-water profiles from experimental plots in July 2004. Shown are means and SE ($n = 6$). Samples taken from a nearby tidal channel in the same week were added and represent nutrient concentrations in the overlying water.

disturbance remains low. Where sediment supply at the upper shore exceeds sea level rise, salt marsh vegetation may arise on marine sediments and succession proceeds into a terrestrial environment (Levin et al., 2001). This succession of habitats commonly occurs in the Wadden Sea (Reise, 1985) and is schematically shown in Fig. 11. Marine organisms either stabilize or destabilize the sediment with facilitating or inhibiting effects on shoreline succession (Reise, 2002). This study provides experimental evidence that lugworms have the potential to maintain a sandy habitat against geomorphological evolution towards muddy flats in a depositional coastal environment. It is suggested that the prevalence of sandy tidal flats in the Wadden Sea is in part the result of lugworm bioturbation and bioirrigation.

In fine sand lugworm activities significantly decreased the accumulation of fine particles and associated organic material. Chlorophyll concentrations were reduced by lugworm activity and sediment permeability was maintained. Fine grained sediments, which typically occur between sand flats in the low intertidal and mud flats near the high water mark, are therefore most susceptible to the ecosystem engineering effects of *Arenicola marina*. Coarse grained sediments with a median above 300 µm were less efficient in accumulating fine particles and less susceptible for sediment clogging. Processes at the sediment surface were very dynamic. This has been shown to be typical for intertidal sand flats (Miller and Sternberg, 1988). Enhanced accumulation of fine material on lugworm exclusion plots was observed during periods of calm conditions while under strong hydrodynamic forces the accumulated material began to erode again from the edging of experimental plots (personal observation). This resulted in a mosaic of elevated and eroded patches. Severe storm events in winter even eroded most of the deposited material. Thus, the size of experimental exclusion plots may still not be sufficient to allow long-term succession from sandy towards muddy sediments. Van De Koppel et al. (2001) suggested

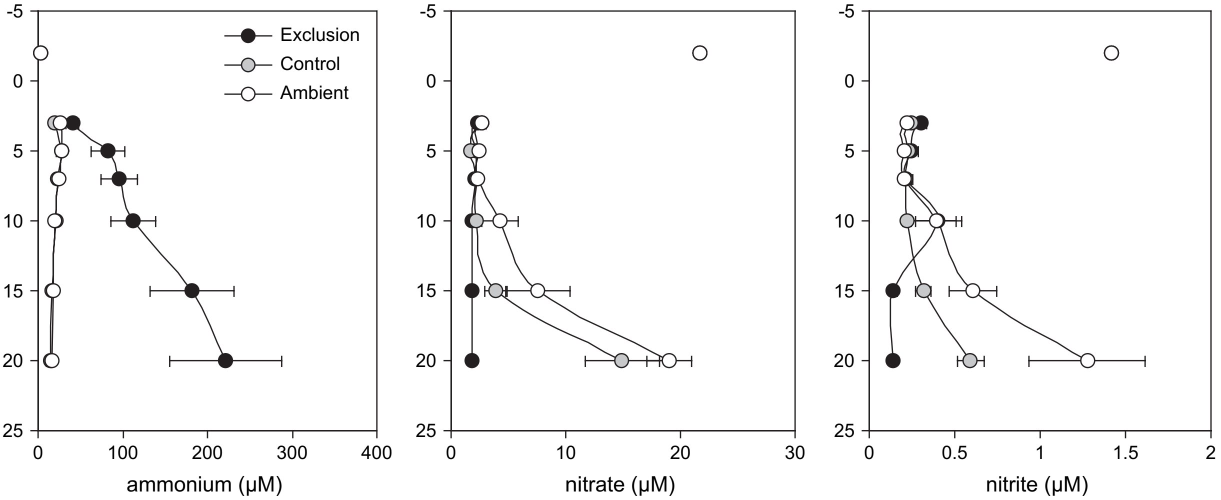

Fig. 9. Ammonium, nitrate and nitrite pore-water profiles from experimental plots in April 2004. Shown are means and SE ($n = 6$). Samples taken from a nearby tidal channel in the same week were added and represent nutrient concentrations in the overlying water.

alternate stable states for intertidal flats. One state is characterized by high diatom cover and high silt content while the other state is dominated by erosion with low diatom cover and silt content. The observed accumulation of fine material at the surface, its consolidation within the sediment and the storing of organic material and pore-water solutes in the absence of lugworms suggest that *A. marina* supports the second state and thus contributes to the maintenance of permeable sand.

4.2. Ecosystem engineering by Arenicola marina

The experiment revealed manifold effects of lugworms on the sediment and pore-water characteristics of intertidal sand flats. These effects were not confined to the vicinity of individual burrows but modified the characteristics of the entire tidal flat. The observed changes in sediment characteristics are not independent of each other, but putting all evidence together it is suggested that the sedimentary system is shifted from mud towards sand flats in the presence of lugworms. The most obvious change was the accumulation of fine particles and associated organic matter (POM) in the upper 5 cm in the absence of *Arenicola marina*, entailed by a decrease in sediment permeability. Lugworm defecation at the surface, followed by a re-suspension of fine material when casts are washed away is presumably an important mechanism preventing fine particle accumulation in the presence of lugworms. According to measurements by Cadée (1976), sediment reworking by *A. marina* on the lugworm plots at the study site corresponds to a sediment layer of approximately 10 cm year^{-1}. Small particles have a greater chance to be swallowed than larger ones (Hylleberg, 1975) and are returned to the sediment surface with the faecal casts (Baumfalk, 1979). In shallow waters, tidal currents and wave action are the main forces of lateral particle fluxes (Miller and Sternberg, 1988; De Jonge and

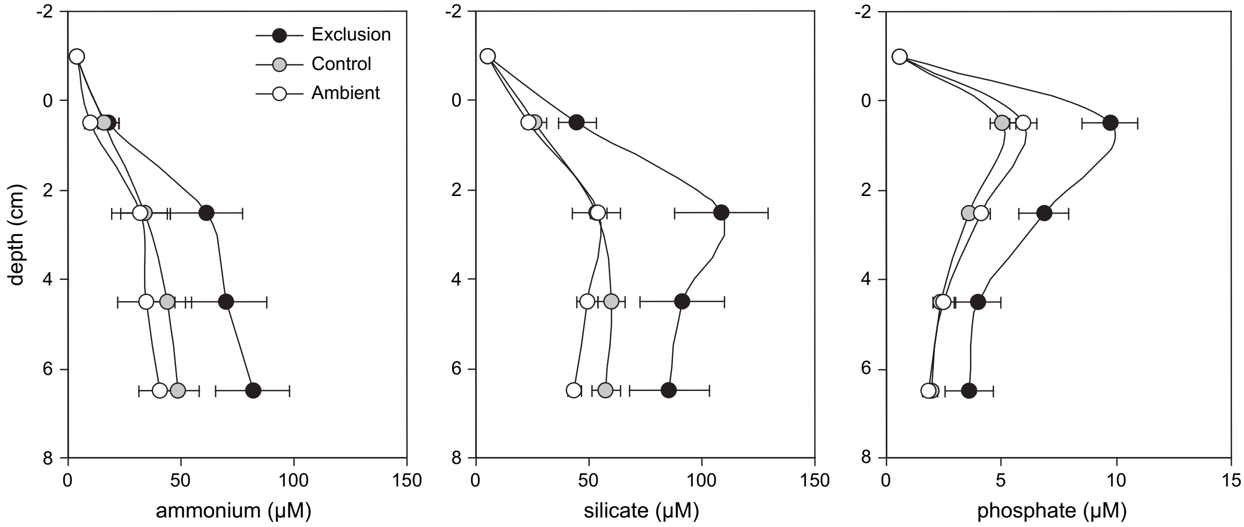

Fig. 10. Ammonium, silicate and phosphate pore-water profiles from experimental plots in October 2003. Pore-water was obtained by flushing 1 cm slices of 3 pseudo-replicate cores with nitrogen gas. Shown are means and SE ($n = 6$). Samples taken from the tidal channel in the same week were added and represent nutrient concentrations in the overlying water.

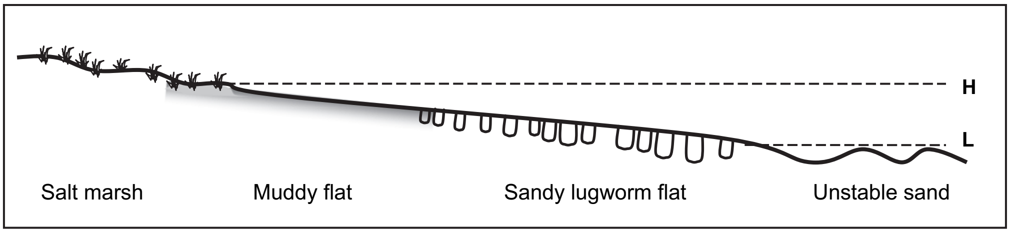

Fig. 11. Scheme of depositional shore in the Wadden Sea with accretion of fine sediment particles trapped by salt marsh vegetation and microalgal biofilms at the upper shore (H, mean high tide line). The lower shore (L, mean low tide line) is characterized by mega-ripples of coarse and clean sand. A wide middle shore is maintained as permeable sand by a bioturbating and bioirrigating population of *Arenicola marina*.

van Beusekom, 1995). Faecal casts of *A. marina* may persist several tidal cycles under calm conditions but are usually washed away by waves and tidal currents within minutes after submersion (personal observation). During this process fine particles are likely to be re-suspended and removed from the sediment.

The increased roughness of the seabed due to lugworm mounds and pits may additionally enhance erosion and re-suspension of material (Graf and Rosenberg, 1997) and solutes (Huettel and Gust, 1992). Diminished chlorophyll concentrations due to feeding activity of lugworms and the reduced nutrient concentrations in the pore-water due to lugworm irrigation may be further responsible for the observed low amount of fine particles in surface sediments of lugworm tidal flats. Diatom films are known to accumulate fine particles and to stabilize the sediment (Mayer et al., 1985; De Brouwer et al., 2000; Yallop et al., 2000). Differences in sediment chlorophyll content between lugworm and exclusion plots were highest in periods of intensive lugworm feeding activity in summer. Grazing by deposit feeding infauna was already assumed to control the abundance of microalgae in former studies (Davis and Lee, 1983), and Webb and Eyre (2004) showed that high rates of disturbance and burial can reduce sediment chlorophyll concentrations.

The effect of lugworm absence/presence was not restricted to the sediment surface. The accumulation of organic material and reduced forms of pore-water solutes in the absence of *Arenicola marina* indicates a less effective degradation of organic material (Papaspyrou et al., 2007). The incorporation and consolidation of fine particles and associated organic material in the sub-surface sediment was possibly supported by bioturbation activity of other surface deposit feeding infauna. High abundances of the spinoid polychaete *Pygospio elegans* during all years of this study, especially on the exclusion sites (Volkenborn and Reise, 2007), might contribute to this process. Tentaculate polychaetes are capable of enhancing particle removal from the water column (Frithsen and Doering, 1986) and their tubes may function as small sediment traps, bringing fine material to 3 to 5 cm depth (Bolam and Fernandes, 2003). High abundances of other surface-deposit conveyor-belt feeders may further enhance the downward transport of fine particle and organic material (Sun et al., 1991). Temporally increased accumulation of fine material at the sediment surface therefore had lasting consequences for deeper sediment layers. The incorporation of fine particles and associated organic material into the sediment matrix significantly reduced permeability by clogging the interstices of sand. Exclusion of *A. marina* in the fine sand area resulted in a decrease in sediment permeability below $k = 1 \times 10^{-12}$ m^2, which is thought to be a critical value for advective pore-water flow (Huettel et al., 2003). Thus, diffusion will prevail in vertical fluxes in the absence of lugworms, while physical and biological advection will prevail in the permeable sediment when lugworms are present.

The analysis of the pore-water revealed a strong effect of *Arenicola marina* on nutrient profiles and, in contrast to most other effects, these were independent of the sediment type. In the presence of lugworms, nutrients and sulphide were flushed out of the sediment presumably via the ventilation current. Compared to results presented by Huettel (1990), this study indicates a stronger accumulation of nutrients within experimental lugworm exclusion plots. This may be due to the larger areal size of experimental plots reducing the impact of lateral pore-water exchange (Rocha, 2000). Furthermore, the duration of lugworm exclusion was considerably longer in the present study. Higher nutrient concentrations in surface sediments of exclusion plots might be a combined effect of the elimination of bioirrigation and decreased sediment permeability, both inhibiting advective pore-water exchange.

Sediment permeability is also important for *Arenicola marina* itself. Lugworms need to pump water through the sediment for respiration. According to Riisgård et al. (1996), a "standard" lugworm (0.5 g dry weight) needs to pump 1.5 ml min^{-1} oxygen rich water through its burrow. This is done with a maximum pumping pressure of 20 cm water column and normal operating pumping pressure of 5 cm water column. The permeability measurements revealed that water flow through the sediment from lugworm exclusion plots in the fine sand area decreased to rates critical for lugworm survival (0.5 ml min^{-1} through a sediment column of 7.5 cm with a pressure head of 20 cm water column). Sediment from lugworm plots showed minimum flow rates of about 2 ml min^{-1} (pressure head of 15 cm water column) allowing sufficient oxygen supply through pumping. Therefore, lugworms generate suitable conditions for their population by maintaining high sediment permeability.

Stimulation of nitrification through oxygen supply via lugworm ventilation was not restricted to the lugworm burrow but was found in the entire sediment in depths of 15 to 20 cm. Reduced sulphide concentrations due to re-oxidation of reduced compounds by bioirrigation was observed in former studies (Banta et al., 1999; Nielsen et al., 2003). With this study it could be shown that in the absence of *Arenicola*, pore-water sulphide concentrations may exceed lethal concentrations for other infauna (Gray et al., 2002).

5. Conclusions

By their bioturbation and bioirrigation activities, lugworms alter sediment and pore-water characteristics and maintain habitat properties suitable for population persistence. Their habitat is characterized by permeable sediment where lugworms easily pump sufficient water for respiration. Lugworms prevent clogging of sediment interstices by fine particles and organic compounds, especially in areas where the sand matrix is fine grained (grain size median below 300 μm). They reduce the amount of organic compounds and inorganic nutrients. Furthermore, low sulphide concentrations in the pore-water facilitate other infaunal organisms (Volkenborn and Reise, 2006). Due to its widespread distribution with a high and constant population density on intertidal flats, *Arenicola marina* qualifies as an important "ecosystem engineer" of coastal soft bottom habitats. The experiment suggests that lugworms are able to prevent a succession from sand towards mud flats. Especially fine sand, which typically occurs between mud flats in the high intertidal and sand flats in the low intertidal, was found to be modified by lugworm activities. With respect to the prominent role of lugworms in the Wadden Sea it is suggested, that without this "ecosystem engineer" mud flats would greatly expand at the expense of sand flats.

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