Ecosystem engineering in intertidal sand by the lugworm *Arenicola marina*

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Intertidal sand bioturbated by lugworms (*Arenicola marina*) and by a backhoe to prepare the exclusion experiment in spring 2002.

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SUMMARY

Large-scale permanent experimental exclusion of the abundant bioturbating lugworm *Arenicola marina* from intertidal sand revealed manifold implications of this polychaete for ecosystem functioning. Sediment properties, biogeochemical processes and the benthic community were analysed over a three year period on six lugworm exclusion plots, each 400 m^2, and corresponding control areas with lugworm densities of 20 to 40 ind. m^{-2}. The large-scale lugworm exclusion experiment served to provide two contrasting sandy habitats in order to study a wide spectrum of direct and indirect effects linked to the presence/absence of this dominant worm.

Effects of ecosystem engineering by lugworms on sediment properties turned out to be spatially variable. Fine sand in the low intertidal was more susceptible to ecosystem engineering effects than medium sand in the mid intertidal. Modulated by hydrodynamics and sediment mediated processes, lugworms reduced microphytobenthic biomass and prevented a clogging of the sediment with fine particles and associated organic material. In the presence of lugworms sediment permeability remained high, facilitating advective pore-water exchange by waves and currents, and enlarging the oxic, metabolically most active sediment layer. Increased pore-water exchange by bioirrigation and advection in the presence of lugworms furthermore impeded an accumulation of reduced inorganic nutrients and toxic metabolites in the porewater.

Regarding the sediment properties it was found that

- metabolites accumulate in the porewater in the absence of lugworms. Average concentrations increased with depth and attained 250 µmol L^{-1} ammonia, 250 µmol L^{-1} silicate, 18 µmol L^{-1} phosphate, and 200 µmol L^{-1} sulphide in the porewater in 20 cm depth in summer. In the presence of lugworms, maximum concentration were 50 % lower and were found within the uppermost 10 cm of the sediment.
- chlorophyll content in the uppermost cm increased by a factor of up to 1.7 during summer months on lugworm exclusion plots when compared to surface sediment of lugworm plots and attained average chlorophyll concentration of 25 µg g^{-1} dry sediment.

On lugworm exclusion plots in the low intertidal fine sand

- fine particle and organic matter accumulate in the sediment. Average fine particles content attained 2.5 % dry weight and particulate organic carbon attained 0.4 % dry

weight and had therewith doubled after two years in the uppermost 5 cm when compared with sediment of lugworm plots.

- sediment permeability was up to 8-fold lower when compared to corresponding lugworm plots and decreased below $k = 1 \times 10^{-12}$ m², inhibiting advective porewater flow
- oxygen penetration depths under calm conditions in the field were slightly lower (9.3 ± 4.9 mm) when compared to lugworm plots (13.0 ± 6.6 mm) but oxygen penetration was strongly inhibited in laboratory studies due to low sediment permeability.
- volumetric oxygen consumption rates increased with depth while they remained low in the presence of lugworms.
- lower oxygen penetration depths in combination with higher volumetric oxygen consumption rates resulted in almost similar areal oxygen consumption rates of 3 to 9 mmol m^{-2} h^{-1} when compared to lugworm plots.

Effects of lugworms were not limited to the vicinity of their burrows, but extended to the entire benthic boundary layer. Naturally occurring lugworm densities of about 30 ind. m^{-2} were found to inhibit intertidal habitat succession from permeable fine sand towards cohesive muddy flats and thereby maintaining a habitat where they are able to pump sufficient volume of water into the sediment for their respiration. Removal of toxic metabolites such as sulphides furthermore improved habitat suitability for other organisms.

Lugworm induced changes in habitat properties caused a functional shift in the benthic community from assemblages dominated by mixed suspension and surface-deposit feeding tube worms to assemblages dominated by subsurface deposit-feeding discretely motile worms. Implications for the benthic community were most conspicuous, when above ground biogenic structures such as tube caps of polychaetes established preferentially on lugworm exclusion plots. Above ground structures provided attachment for drifting and recruiting organisms.

Regarding the benthic community response it was found that

- *Nereis diversicolor* invaded lugworm exclusion plots in the first year attaining 10-times ambient abundance, presumably responding to a more stable and nutritious surface layer at lugworm exclusion plots. Abundances continuously decreased in the following years, presumably caused by efficient bird foraging.
- the free-burrowing polychaete *Scoloplos* cf. *armiger* was negatively affected by the exclusion of lugworms. It may have suffered from higher sulphide concentrations in the less irrigated and less permeable sediment where lugworms were absent.

- considering all 3 years, surface and suspension feeding tube building worms and predacious worms were most abundant on exclusion plots while subsurface deposit feeders tended to dominate in the presence of lugworms.
- the increased presence of above ground structures like tubes and algae on lugworm exclusion plots entailed enhanced bivalve settlement in two years at different tidal zones with different tube builders (*Lanice conchilega*, *Polydora cornuta*), algae (*Enteromorpha* spp., *Ulva* spp. *Berkeleya rutilans*) and juvenile clams (*Mya arenaria*, *Macoma balthica*).

The ephemeral and spatially confined character of such cascading and interacting developments in the benthos is consistent with a high temporal and spatial variability of the studied benthic community. This gives rise to multiple interactions between functional response and functional effect traits of the species involved in assemblage formation.

This study complies with the mandatory demand for scaling up *in-situ* experimental approaches to improve understanding of the relationship between functional diversity and ecosystem functioning in marine sediments. The large-scale and long-term field experiment allows to identify the importance of allogenic physical ecosystem engineering relative to exogenous factors, such as environmental vagaries or biotic propagule supply. Overall, lugworm effects are highly dependent on space and time as well as on differential recruitment success in the intertidal assemblage. Sediment mediated effects of an ecosystem engineer on associated species appear to be subtle and contingent in a variable environment. Considering the widespread distribution of *A. marina* with a high and constant population density in intertidal sand along northern Atlantic shores, even these subtle and ephemeral effects of ecosystem engineering are likely to be relevant for overall ecosystem processes on a larger scale. The study further suggests that relationships between biodiversity and ecosystem functioning in soft sediment benthos significantly depend on individual species, rather than on numerical species richness.

ZUSAMMENFASSUNG

Großflächiger und dauerhafter experimenteller Ausschluss des häufigen und das Sediment umlagernden Wattwurms *Arenicola marina* von Wattflächen deckte vielfältige Auswirkungen dieses Polychaeten auf Ökosystemprozesse auf. Sedimenteigenschaften, biogeochemische Prozesse und die benthische Lebensgemeinschaft wurden über einen Zeitraum von drei Jahren auf sechs Wattwurm-Ausschlussflächen mit einer Größe von jeweils 400 m² und zugehörigen Kontrollflächen mit einer Wattwurmdichte von 20 bis 40 Ind. m^{-2} analysiert. Das großflächige Wattwurm-Ausschlussexperiment stellte zwei verschiedene sandige Habitate bereit, um ein weites Spektrum direkter und indirekter Effekte dieses dominanten und weit verbreiteten Polychaeten zu untersuchen.

Auswirkungen des „ecosystem engineerings“ durch Wattwürmer zeigte eine deutliche räumliche Variabilität. In einem feinsandigen Gebiet im unteren Gezeitenbereich waren die Auswirkungen deutlicher als in einem gröberen Sand im mittleren Gezeitenbereich. Im Zusammenspiel mit hydrodynamischen Einflüssen und sedimentabhängigen Prozessen reduzierten Wattwürmer die mikrophytobenthische Biomasse und verhinderten eine Zusetzung des Wattbodens mit feinen Partikeln und assoziierter organischer Substanz. Wattwürmer erhielten eine hohe Sedimentpermeabilität, verstärkten den durch Wellen und Strömungen hervorgerufenen advektiven Porenwasseraustausch und vergrößerten den oxischen und hinsichtlich der Stoffumsätze aktivsten Sedimentbereich. Erhöhter Porenwasseraustausch durch die Pumptätigkeit von Wattwürmern und die Erhaltung eines permeablen Sandes verhinderte zudem eine Anreicherung reduzierter anorganischer Nährstoffe und toxischer Stoffwechselprodukte im Wattboden.

Hinsichtlich der Sedimentbeschaffenheit wurden folgende Beobachtungen gemacht:

- Stoffwechselprodukte akkumulierten im Porenwasser in Abwesenheit von Wattwürmern. Durchschnittliche Konzentrationen stiegen mit zunehmender Sedimenttiefe an und erreichten im Sommer Maximalkonzentrationen von 250 µmol L^{-1} Ammonium, 250 µmol L^{-1} Silikat, 18 µmol L^{-1} Phosphat und 200 µmol L^{-1} Sulfid im Porenwasser in 20 cm Tiefe. In der Anwesenheit von Wattwürmern waren Maximalkonzentrationen um 50% niedriger und traten innerhalb der obersten 10 cm Tiefe auf.
- Der Chlorophyllgehalt im obersten cm war in Sommermonaten in Wattwurm-Abwesenheit bis zu 1.7-fach höher als auf den Kontrollflächen mit Wattwürmern

und erreichte durchschnittliche Konzentrationen von 25 µg g^{-1} trockenem Sediment.

Auf wattwurmfreien Flächen im feinsandigen unteren Eulitoral wurden zusätzlich folgende Beobachtungen gemacht:

- Feinpartikel und organisches Material reicherten sich im Wattboden an. Der durchschnittliche Gewichtsanteil an Feinfraktion erreichte 2.5% und der an partikulärem organischem Kohlenstoff 0.4% des Sedimenttrockengewichts und damit kam es nahezu zu einer Verdopplung in den oberen 5 cm des Sediments im Vergleich zu den von Wattwürmern besiedelten Flächen.
- In Abwesenheit von Wattwürmern ergab sich eine bis zu 8-fach verminderte Sedimentpermeabilität im Vergleich zu wattwurmfreien Flächen. Die Permeabilität fiel unter einen Wert von $k = 1 \times 10^{-12}$ m² und es kam damit zu einer Einschränkung des Porenwasseraustauschs durch Advektion.
- Die Eindringtiefe von Sauerstoff in den Wattboden während Hochwasser unter windstillen Bedingungen war geringfügig kleiner (9.3 ± 4.9 mm) als auf den durch Wattwürmer besiedelten Flächen (13.0 ± 6.6 mm). In Laborexperimenten zeigte sich, verbunden mit der geringeren Sedimentpermeabilität, eine deutlich verringerte Sauerstoff-Eindringtiefe.
- Auf das Sedimentvolumen bezogene Sauerstoff-Verbrauchsraten stiegen mit zunehmender Sedimenttiefe an, während sie auf Wattwurm-Flächen geringer und im Tiefenprofil konstant waren.
- Geringere Sauerstoff-Eindringtiefe in Kombination mit höheren volumetrischen Sauerstoff-Verbrauchsraten führten zu vergleichbaren Sauerstoff-Verbrauchsraten pro Fläche von 3 bis 9 mmol m^{-2} h^{-1} auf Wattwurm- und Ausschlussflächen.

Auswirkungen von Wattwürmern waren nicht auf die unmittelbare Umgebung ihrer Wohnbauten beschränkt, sondern beinhalteten Konsequenzen für den gesamten Wattboden. Im Wattenmeer weit verbreitete Wattwurmdichten von etwa 30 Ind. m^{-2} scheinen die Entwicklung von permeablen Feinsänden zu kohesiven schlickigeren Wattflächen verhindern zu können und damit ein Habitat zu schaffen, in dem auch sie selbst ausreichend Wasser zur Deckung ihres Sauerstoffbedarfs in den Wattboden pumpen können. Die Entfernung von toxischen Stoffwechselprodukten, wie beispielsweise Sulfid, verbessert zusätzlich die Habitateignung für andere Organismen.

Die durch den Wattwurm hervorgerufenen Veränderungen des Lebensraumes führten zu einer Verschiebung innerhalb der benthischen Lebensgemeinschaft von Gemeinschaften die von Suspensionsfressern oder sich an der Sedimentoberfläche ernährenden und röhrenbauenden Arten dominiert wurden hin zu Gemeinschaften, die durch unterirdisch fressende und grabende Arten dominiert wurden. Auswirkungen auf die benthische Lebensgemeinschaft waren am deutlichsten, wenn sich überirdische Strukturen, wie z.B. Wurmröhren, in erhöhten Dichten auf Wattwurm-Ausschlussflächen etablierten. Solche aus dem Sediment herausragende Strukturen ermöglichten die Anheftung von driftenden und rekrutierenden Organismen (z.B. Grünalgen, juvenile Muscheln).

Hinsichtlich der benthischen Gemeinschaft wurden unter anderem folgende Beobachtungen gemacht:

- *Nereis diversicolor* besiedelte Wattwurm-Ausschlussflächen im ersten Jahr in 10-fach erhöhten Dichten im Vergleich zum umliegenden Watt. Vermutlich reagierte diese Art auf ein stabileres Sediment und ein erhöhtes Nahrungsangebot innerhalb der Wattwurmausschlussflächen. Die Siedlungsdichte nahm im weiteren Verlauf des Experimentes kontinuierlich ab, unter anderem verursacht durch hohe Prädation durch Watvögel.
- Der unterirdisch grabende Vielborster *Scoloplos* cf. *armiger* wurde negativ durch den Ausschluss von Wattwürmern beeinflusst. Möglicherweise leidet diese Art unter den höheren Sulfidkonzentrationen im weniger bewässerten und weniger permeablen Sediment ohne Wattwürmer.
- Betrachtet man die gesamten 3 Jahre dieser Untersuchung waren Arten mit sedimentoberflächennaher oder filtrierender Ernährungsweise und röhrenbauender Lebensweise tendenziell dominierend auf Wattwurm-Ausschlussflächen, während unterirdisch grabende, detritus-fressende Arten in Anwesenheit von Wattwürmern die Lebensgemeinschaft prägten.
- Die erhöhte Präsenz von aus dem Sediment herausragenden Strukturen wie die Enden von Polychaeten-Wohnröhren und daran befestigte Makroalgen auf Wattwurm-Ausschlussflächen führte zu einer erhöhten Rekrutierung juveniler Muscheln. Dieses Phänomen trat in zwei verschiedenen Jahren und jeweils begrenzt auf einen Gezeitenbereich auf und verschiedene Arten röhrenbauender Vielborster und anheftender Algen und Jungmuscheln waren an den Entwicklungen beteiligt.

Der vorübergehende und räumlich begrenzte Charakter solch kaskadenartiger und interaktiver Entwicklungen spiegeln die hohe zeitliche und räumliche Variabilität der untersuchten benthischen Lebensgemeinschaft wider. Zudem weist er auf die Bedeutung von wechselseitigen Interaktionen zwischen artspezifischen Reaktionen auf veränderte Umweltbedingungen und Effekten verschiedener funktioneller Gruppen auf den Lebensraum für die Zusammensetzung der benthischen Gemeinschaft hin.

Die vorliegende Arbeit entspricht der Forderung, die räumlichen und zeitlichen Dimensionen von Freilandexperimenten zu vergrößern, um Zusammenhänge zwischen Diversität und Ökosystemfunktion in marinen Sedimenten besser zu verstehen. Das großflächige und langfristige Wattwurmausschlussexperiment ermöglicht eine Einschätzung der Bedeutung eines „ecosystem engineers“ unter dynamischen Bedingungen und bei einem sich wechselnden Spektrum siedelnder Arten. Wattwurmeffekte sind variabel in Zeit und Raum und hängen zusätzlich von dem von Jahr zu Jahr unterschiedlichen Arteninventar auf den experimentellen Flächen ab. Es zeigt sich, dass die durch den Wattwurm hervorgerufenen Veränderungen des Sedimentes subtile und kontingente Auswirkungen auf assoziierte Arten in diesem variablen Lebensraum haben.

Unter Berücksichtigung der weiten Verbreitung des Wattwurms mit hoher und konstanter Individuendichte im Gezeitenbereich der nordatlantischen Küsten, könnten solch eher subtilen und räumlich wie zeitlich begrenzten Auswirkungen seiner Grab- und Pumpaktivität jedoch durchaus signifikante Konsequenzen für das übergeordnete Funktionieren von Gezeitenflächen haben. Zudem scheint der Zusammenhang zwischen Biodiversität und Ökosystemfunktion in sandigen Sedimenten eher durch das Vorhandensein einzelner Schlüsselarten beeinflusst zu werden als von der numerischen Artenzahl.

Part I: General introduction and discussion

A INTRODUCTION

1. Biodiversity and ecosystem functioning

The traditional approach in community ecology has considered species diversity as dependent variable controlled by abiotic conditions and environmental constraints. Recent approaches have broadened the perspective to species' functional characteristics and their effects on ecosystem functioning (HOOPER ET AL., 2005). Increasing alteration of communities in ecosystems via species extinctions and invasions has aroused considerable interest in the question on how these often human induced changes in species composition will affect ecosystem functioning (VITOUSEK ET AL., 1997). Thus, the interplay between organisms and ecosystem processes became the focus of a considerable research effort emphasizing the need for an integrated understanding between community and ecosystem ecology (LAWTON AND JONES, 1993; LOREAU ET AL., 2001) as well as between biodiversity and ecosystem functioning (COVICH ET AL., 2004). First experimental studies focused mainly on the effects of plant species diversity and functional diversity on primary production in grassland ecosystems as a proxy for ecosystem functioning (HOOPER AND VITOUSEK, 1997; HECTOR, 1999; TILMAN ET AL., 2001).

In many of these experiments randomly assembled communities were used and positive relationships between plant diversity and primary production were found. Certain combinations of species were thought to be complementary in their patterns of resource use and to increase average rates of production. Facilitation among species additionally may contribute to increased process rates with increasing species or functional diversity (BERTNESS AND CALLWAY, 1994; CARDINALE ET AL., 2002; BRUNO ET AL., 2003).

However, other studies revealed idiosyncratic or statistically non-significant effects of changes in species richness on ecosystem functioning (WARDLE ET AL., 1997; MIKOLA ET AL., 2002). Responses to experimental manipulations of species richness seem to vary for different processes, different ecosystems and even different habitats within ecosystems. Understanding the mechanisms and the conditions under which individual species can influence ecosystem processes, remains a major task for the development of scenarios on the consequences of species extinction and species invasion. While studies on the effects of experimentally manipulated biota were carried predominantly out in terrestrial grassland, marine systems have received less attention (EMMERSON ET AL., 2001; COVICH ET AL., 2004; GESSNER ET AL., 2004).

Marine sedimentary habitats are not only the most common habitats on earth and as such need a better understanding (WILSON, 1991; SNELGROVE, 1999), they also offer ideal testing grounds for examining the relationship between functional diversity and ecosystem functioning (ARNTZ ET AL., 1999). The aqueous medium of aquatic systems greatly affects transformation of energy and materials. Shallow coastal habitats receive massive inputs of terrestrial organic matter and nutrients and are among the most geochemically and biologically active areas in the biosphere (GATTUSO ET AL., 1998; LEVIN ET AL., 2001). Recent field studies suggest that diversity/ecosystem functioning relationships in soft-sediment benthos are complex and may depend more on functional groups than on numerical species richness (MCCANN, 2000; BOLAM ET AL., 2002). Moreover, diversity/ecosystem functioning relationships will depend not only on the functional effect traits of the species involved, but also on the traits that determine how species respond to changes in environmental conditions (HOOPER ET AL., 2005).

Identification of ecological and geochemical keystone species such as physical ecosystem engineers (*sensu* JONES ET AL., 1997) could provide valuable understanding of the relationship between biodiversity and ecosystem functioning in marine sediments. Because of the difficulties in manipulating species and measuring ecosystem functioning in a dynamic and fluid environment most studies were performed on relative small scales (Hall et al., 1994) and/or in closed systems, i.e mesocosms. While there is good evidence for the considerable and multiple effects of macrofauna activities on ecosystem functioning from confined and simplified systems, there is a need to move on to larger, more open, long-term experimental studies (BOLAM ET AL., 2002; COVICH ET AL., 2004; HOOPER ET AL., 2005). Steps in this direction are to manipulate species diversity *in-situ* (PARKER ET AL., 2001; BILES ET AL., 2003). Manipulative large-scale field experiments incorporating external drivers such as dispersal and environmental change (BELYEA AND LANCASTER, 1999) are necessary for a better understanding of the complex relationship between diverse organisms and biogeochemical processes within marine sediments. Furthermore, large-scale field experiments in marine systems where key species are excluded or added, offer the potential to detect the importance of ecosystem engineering when confronted to abiotic forces in variable and dynamic environments.

2. Ecosystem engineering in the marine benthos

Key processes between organisms and their environment which are not directly trophic or competitive and which result in the modification of habitats brought forth the concept of ecosystem engineering (JONES ET AL., 1994; LAWTON AND JONES, 1995). “Ecosystem engineers are organisms that directly or indirectly modulate the availability of resources (other than themselves) to other species, by causing physical state changes in biotic and abiotic materials. In so doing they modify, maintain and/or create habitats.” (LAWTON, 1994). *Autogenic* engineers modify a habitat by their own physical structure while *allogenic* engineers modulate resources from one physical state to another through their behaviour and activity.

Trees, corals, and giant kelps are examples of *autogenic* engineers. As they grow and become larger, their living and dead tissues create habitats for other organisms to live upon or inside. The beaver is a classical example of an *allogenic* engineer (POLLOCK ET AL., 1995). It transforms living trees into dead trees by cutting them down, and then uses them to dam streams and create ponds. Beaver engineering alters the distribution and abundance of many varied organisms and also increases biodiversity at the landscape scale (WRIGHT ET AL., 2002). JONES ET AL. (1997) argued that ecosystem engineers can regulate energy and mass flows and trophic patterns in their ecosystems via an “engineering web”, established by the interactions of diverse species of engineering organisms. Engineering webs would regulate ecosystem functioning in conjunction with the comparatively well-studied food webs. However, the exact ways in which these webs interact remains to be established. Field experiments in which a keystone species is excluded or added may contribute to a better understanding of ecosystem engineering relative to important external drivers.

Due to spatial and temporal variation of benthic environments they provide ample coordinate space to investigate the mutual interplay of ecosystem engineering, biodiversity and ecosystem functioning. Although intertidal and shallow subtidal soft-sediment habitats make up only a small areal proportion of the entire seafloor, these habitats are highly productive with high remineralisation rates (CANFIELD ET AL., 1993). While benthic communities in marine sediments generally seem to have a rather simple trophic structure, various biotic habitat transformations give rise to complex habitat webs. Biotic habitat transformation by organisms in marine environments involve amongst others (1) phototrophs generating mats, tufts and rooted vegetation, (2) suspension feeders forming beds and reefs, (3) dead hard-parts of the benthos, (4) burrow builders and (5) infauna reworking and irrigating the sediment (REISE, 2002). Ecosystem processes in the marine soft sediments have been shown to be affected especially by organisms that create above ground structures like seagrass meadows (IRLANDI, 1994; IRLANDI ET AL., 1995), mussel beds (COEN ET AL., 1996; ASMUS AND ASMUS, 1998; CROOKS, 1998; GUTIÉRREZ, ET AL., 2003) or sponges (ARNTZ ET AL., 1994). These *autogenic* engineers increase the structural complexity of the habitat with considerable consequences for hydrodynamics and sediment dynamics and providing living space and shelter for other organisms.

While *autogenic* ecosystem engineering may reveal itself rather readily, subsurface *allogenic* engineering by bioturbating and bioirrigating organisms may require an extravagant approach to become visible. Bottom dwelling benthic invertebrates can significantly affect benthic pelagic coupling of organic material and nutrients by their bioturbation and bioventilation (RHOADS 1973; ALLER, 1978; GRAF, 1992). These activities may modify the entire sedimentary budget and can have significant effects on biogeochemical processes and exchange rates between the sediment and the overlying water (KRISTENSEN, 1988; ALLER, 1988). The implications of bioturbation and bioirrigation on the character of marine sediments have been reviewed by several authors (RHOADS, 1974; CADÉE, 2001; KRISTENSEN, 2001; REISE, 2002).

Macrofauna activities affect the sediment composition (BOTTO AND IRIBARNE, 2000), porewater nutrient profiles (HUETTEL, 1990), nutrient fluxes (ASMUS ET AL., 1998; BILES ET AL., 2002), oxygen fluxes (ZIEBIS ET AL., 1996B; GLUD ET AL., 2003; WENZHOEFER AND GLUD, 2004), benthic microflora (BRANCH AND PRINGLE, 1987) and associated meio- and macrofauna (REISE, 1987; SCHAFFNER, 1990). Bioturbation is responsible for transferring labile organic matter and electron acceptors from surface sediments to microbes at anaerobic depths, while refractory carbon substrates are introduced to more efficient aerobic bacteria (VALIELA ET AL., 1978; HOWARTH AND HOBBIE, 1982; KRISTENSEN AND HOLMER, 2001). Sediment defecation at the sediment surface alters the microtopography, which has additional effects on advection and porewater chemistry (HUETTEL AND GUST, 1992; ZIEBIS ET AL., 1996a). Burrows act as hot spots of organic matter diagenesis due to a three-dimensional mosaic of oxic/anoxic interfaces associated with their walls (KRISTENSEN, 2000). Within single burrows various microhabitats for microbes and meiofauna may exist (REISE AND AX, 1979; WETZEL ET AL., 1995).

The sediment and solute movement induced by these animals – bioturbation and bioirrigation – far exceed abiotic transport processes such as burial by sedimentation and molecular diffusion. Among the most effective and probably best studied bioturbators in marine sediments are thalassinidean decapod crustaceans (ATKINSON AND TAYLOR, 2005). These shrimps or prawns often occur in high densities and can monopolize the entire sedimentary habitat with considerable effects on habitat characteristics (ALLER AND DODGE, 1974; SUCHANEK, 1983; ZIEBIS ET AL., 1996B) and other benthic infauna (POSEY, 1986; POSEY ET AL., 1991; BERKENBUSCH ET AL., 2000). The ubiquitous bioturbation of lugworms in littoral sand worldwide (WELLS, 1963) qualifies this polychaete as an important ecosystem engineer as well (RIISGÅRD AND BANTA, 1998), and as a promising object for a study of bioengineering effects in marine sediments.

3. Bioturbation and bioirrigation by the lugworm *Arenicola marina*

The lugworm, *Arenicola marina* (LINNÉ, 1758) is a dominant member of the macrozoobenthos on clean to fine intertidal and shallow subtidal sand of the north west European coasts from the Arctic to the Mediterranean Sea (WELLS, 1963). Especially intertidal areas of the Wadden Sea are ubiquitously populated by this polychaete. Adults have a body length of 15 to 25 cm, but individuals of up to 36 cm have been recorded (RIISGÅRD AND BANTA, 1998). Roughly 90% of the total 4300 km² of tidal flats of the Wadden Sea are “lugworm flats”, populated by 20 to 40 ind. m^{-2} (BEUKEMA, 1976; REISE, 1985). Abundances are low to zero in soft mud, and also low in highly unstable sand exposed to strong currents or waves near low water line and below (LONGBOTTOM, 1970). Extensive information about the population ecology of *A. marina* is given by POLLACK (1979), BEUKEMA AND DE VLAS (1979), FLACH AND BEUKEMA (1994), and REISE ET AL. (2001) and about the burrowing behaviour by KRUEGER (1971) and SEYMOUR (1971).

A. marina lives head-down in 20 to 40 cm deep J-shaped burrows completed to a U by a vertical head shaft, through which surface sediment slides down and is ingested by the worm (Fig. 1). 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. Since the residence time of sediment in the gut in short (~15 min, KERMACK, 1955) only labile organic matter can be digested. Freshly deposited material, bacteria and diatoms are thought to be the main components of the lugworm diet (GROSSMANN AND REICHARDT, 1991; RETRAUBUN ET AL., 1996a). Gardening in lugworms by trapping organic material including bacteria and detritus in feeding pits was suggested by HYLLEBERG (1975) and RETRAUBUN et al. (1996a). Since lugworms ingest sediment of low nutritive value, they must handle large

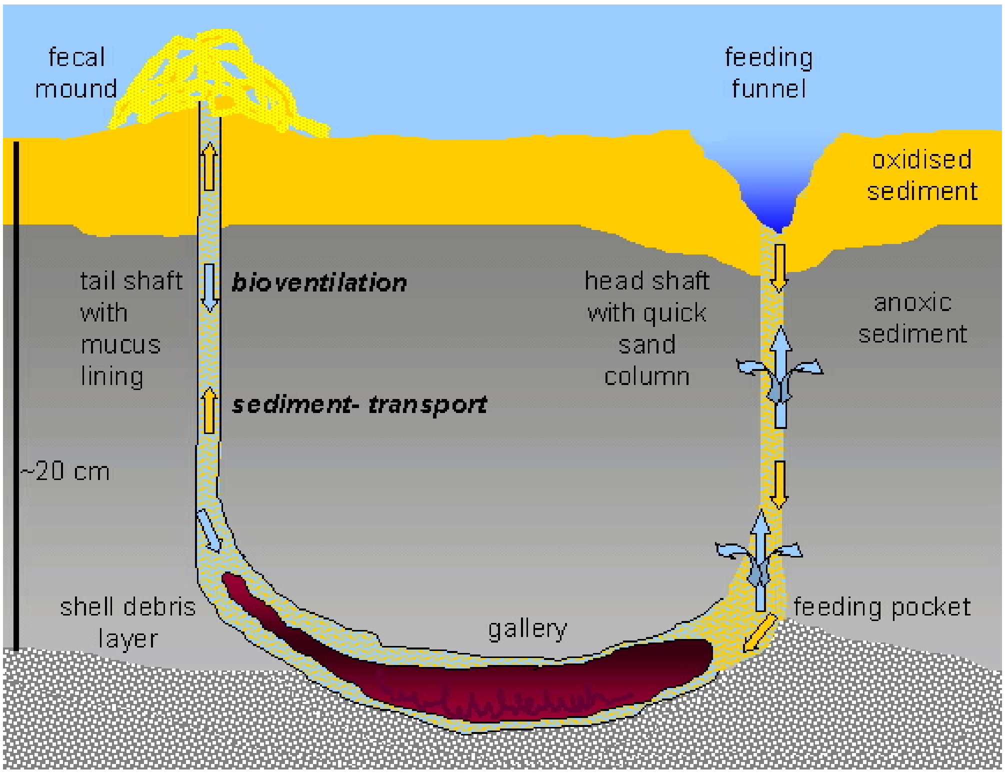

Fig. 1. The lugworm, *Arenicola marina*, in its burrow. Bioturbation and bioirrigation displace both, particles (yellow arrows) and water (blue arrows). The tail shaft and gallery constitute a permanent open tube lined with mucus and thus is relatively impermeable. Porewater exchange between burrow and surrounding sediment mainly occurs around the head shaft. Loose material of quick sand is exchanged every 2.5 to 3 h (CADÉE, 1976). Coarse particles and shell debris accumulate at feeding depth.

amounts to satisfy their metabolic need. In the course of one year the upper cm of the sediment is recycled several times (CADÉE, 1976). Highest sediment reworking activity was found in warmer months (RETRAUBUN ET AL., 1996b) but food availability additionally may affect rates of activity (CADÉE, 1976).

Burrow ventilation for respiration is done by peristaltic movements in a tail-to-head direction (RIISGÅRD AND BANTA, 1998) bringing oxygen to deeper sediment layers and flushing out nutrients rich porewater from the sediment (HUETTEL, 1990). The ventilative oxygen input has been shown to attract meiofauna and some macrofauna to distinct sections of the burrows (REISE AND AX, 1979; REISE, 1981, 1987; WETZEL ET AL., 1995; LACKSCHEWITZ AND REISE, 1998). Assuming a density of 30 ind. m^{-2}, lugworms replace a sediment layer of 15 cm per year (CADÉE, 1976) and pump 3 L of seawater per hour and m^{2} into the anoxic sediment (RIISGÅRD ET AL., 1996).

Considerable effects of lugworm bioturbation and bioirrigation were found on sediment stratification (CADÉE, 1976; BAUMFALK, 1979B), porewater nutrients (HUETTEL, 1990), biogeochemical processes (KRISTENSEN, 2001; NIELSEN ET AL., 2003), particulate and dissolved material exchange (ASMUS AND ASMUS, 1998), microorganisms

(Reichardt, 1988; Grossmann and Reichardt, 1991; Retraubun, 1996a; Goñi-Urriza et al., 1999), meiofauna (Reise and Ax, 1979; Reise, 1981, 1987; Wetzel et al., 1995), and other macrofauna (Brey, 1991; Flach, 1992a,b, 1993, 1996; Flach and de Bruin, 1993; Lackschewitz and Reise, 1998). While there is good evidence for single aspects of lugworm effects on ecosystem properties, an interdisciplinary approach may account for the complex interplay between sediment characteristics and biogeochemical and ecological processes. There is a demand for conducting measurements by *in-situ* approaches to avoid artefacts of laboratory experiments. Local sampling of lugworm burrows and adjacent sediment helped to identify small-scale interactions directly related to burrow maintenance and feeding activity of the lugworms. Accounting for the high lateral transport rates of particles and water above and within the sediment, especially in shallow coastal habitats, large-scale approaches are required to include lugworm effects beyond the immediate vicinity of individual burrows. Thus, a large-scale keystone species exclusion field experiment may considerably advance the understanding of *allogenic* engineering effects in marine sediments, their interplay, and their relevance in space and time.

4. This thesis

The primary objective of this study is to analyse ecosystem responses to large-scale experimental exclusion of the lugworm *Arenicola marina* from intertidal sand. For a better understanding of lugworm effects large-scale, long-term multi-factorial field experiments are a promising tool. With this approach not only effects of lugworm presence can be studied, but also their relative importance in time and space and the possible underlying mechanisms of ecosystem alteration. Removal experiments offer the potential to address questions regarding diversity and ecosystem functioning because they directly explore what happens to an ecosystem when a species or functional type is no longer present (Wardle et al., 1999; Symstad and Tilman 2001; Díaz et al., 2003).

4.1. Large-scale lugworm exclusion experiment

Lugworm exclusion is relatively easy to achieve. By inserting a mesh into the sediment which blocks the burrow shafts, lugworms are forced to emigrate while most of the other infauna is not affected when dwelling in the uppermost 10 cm of the sediment. This technique has been previously used to reveal significant effects of lugworms on meiofauna (Reise, 1983), macrofauna (Flach and deBruin, 1993) and seagrass (Philippart, 1994).

Exclusion plots in these studies covered areas of only a few m² and were poorly replicated. Lateral sediment transport (GRANT ET AL., 1997) and lateral porewater flow (ROCHA, 2000) typical for sandy intertidal flats may confound possible effects of lugworm exclusion. Therefore, a large-scale experimental approach is here adopted: excluding lugworms from six 20m x 20m plots. This scale of manipulation was assumed to be an appropriate compromise between effort and results when attempting to reveal effects of lugworm presence/absence on ecosystem processes.

The experiment was conducted on an intertidal sandflat in Königshafen, a tidal embayment at the northern end of the island of Sylt in the North Sea (55°02´ N; 8°26´ E; Fig. 2). *Arenicola*-flats with consistently more than 20 worms m^{-2} comprise 76% of this intertidal area (REISE ET AL., 2001). Sediment at the experimental site is dominated by medium and fine sand and mean tidal range is 1.8 m. A detailed description of the tidal

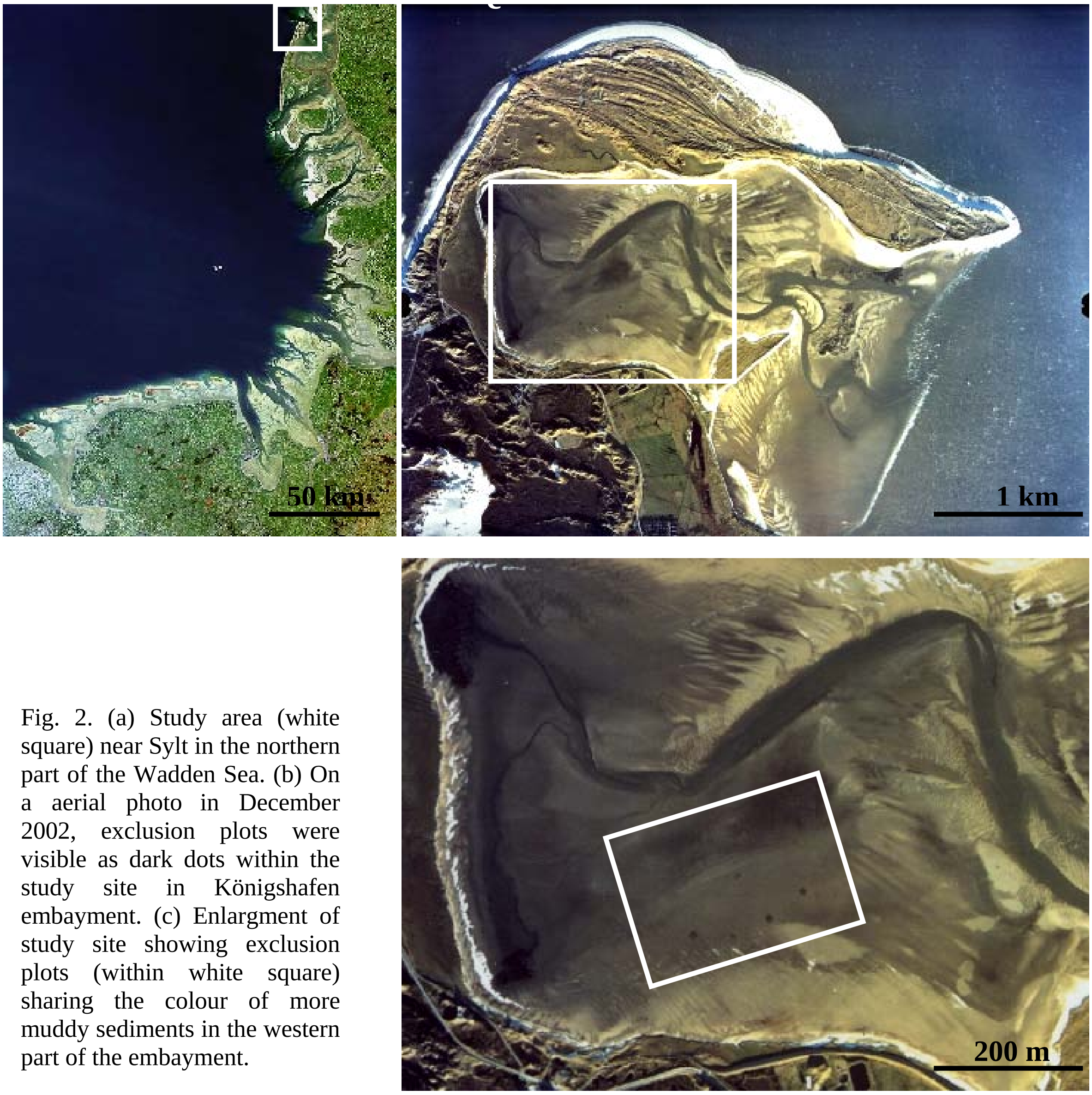

Fig. 2. (a) Study area (white square) near Sylt in the northern part of the Wadden Sea. (b) On a aerial photo in December 2002, exclusion plots were visible as dark dots within the study site in Königshafen embayment. (c) Enlargment of study site showing exclusion plots (within white square) sharing the colour of more muddy sediments in the western part of the embayment.

Fig. 3. Creating of lugworm exclusion plots (a) was achieved by excavating the upper 10 cm of the sediment with a small backhoe (b) and inserting a 1mm meshed polyethylene net (c) before returning the sediment (d).

embayment is given by REISE (1985), AUSTEN (1994), 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 spring 2002. The horizontal net prevented lugworms to maintain their burrows and effectively kept them away. An initial attempt with a 2 mm mesh failed. Surface sediment was excavated with a small backhoe (Zeppelin ZR15) to bury the net and this was also done on control plots to account for the initial disturbance (Fig. 3). Ambient plots were left untouched to represent natural conditions. To account for spatial heterogeneities, the experiment was created in a 2-factorial nested block design (Fig. 4).

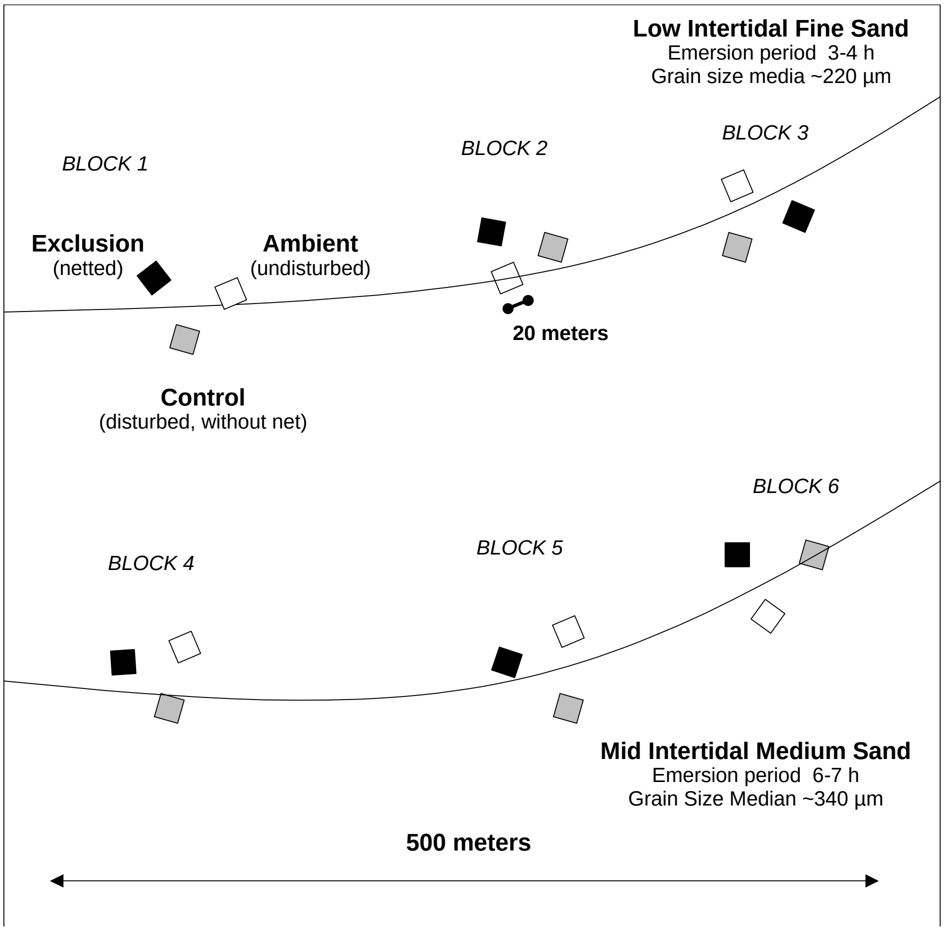

Fig. 4. Experimental set-up of the large-scale lugworm exclusion experiment in a 2-factorial nested block design. Six experimental blocks comprised three lugworm treatments and were nested within two tidal levels.

One block 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 x 20 = 400 m² in area. Six experimental blocks were nested with respect to the tidal zone: three blocks were placed within a mid intertidal medium sand (emersion period 6-7 hours per tide; grain size median 330-340 µm) and three blocks within a low intertidal fine sand (emersion period 3-4 hours; grain size median 200–220 µm). The horizontal distance between these tidal zones was about 200 m and between blocks about 100 m.

4.2. Thesis outline

The large-scale lugworm exclusion experiment served to provide two contrasting sandy habitats to study a wide spectrum of direct and indirect effects of an ecosystem engineer.

In Chapter 1 the hypothesis was tested that the large bioturbating and irrigating polychaete *Arenicola marina* inhibits succession from sandy towards muddy tidal flats.

This speculation is supported by various measurements on lugworm bioturbation and irrigation which have been conducted on individual worms, burrow structures or on small plots with and without lugworms (e.g. CADÉE, 1976; BAUMFALK, 1979B; HUETTEL, 1990; PHILLIPART, 1994; RIISGÅRD AND BANTA, 1998; GOÑI-URRIZA ET AL., 1999). However, to test this hypothesis properly one need to measure effects of lugworms on sediment properties on large replicated plots with and without lugworms over several years.

Biogeochemical key processes in sediments with and without lugworms are described in Chapter 2. Bioturbating macrofauna can strongly influence biogeochemical processes by maintaining a close coupling of particles and porewater between the sediment and the tidal water above (ZIEBIS ET AL., 1996B; BOTTO AND IRIBARNE, 2000; D`ANDEREA ET AL., 2002). In particular, oxygen and sulphide dynamics were investigated attending the most important electron acceptors in marine sediments (JØRGENSEN, 1982; CANFIELD ET AL., 1993; THAMDRUP AND CANFIELD, 2000). *In-situ* oxygen and sulphide profiling was combined with ex-situ planar optode measurements and chamber incubations for measuring oxygen consumption rates. Characterization of other sediment properties, including grain size composition, organic content, Chl *a* content, sediment permeability and porewater nutrient profiles and analysis of the benthic community allowed inferences on underlying mechanisms of biogeochemical cycling. For this multidisciplinary approach, one exclusion and the corresponding control site in the low intertidal fine sand was chosen.

In Chapter 3, 4, and 5 the response of the benthic community to lugworm exclusion is analysed in detail. Changes in the functional composition of the benthic community are described in Chapter 3. In Chapter 4 possible mechanisms how lugworm presence/absence affects deposit feeding species are discussed. In Chapter 5 positive responses of tube-building species to lugworm exclusion is reported with cascading effects on the benthic community, showing the importance of response and effect traits of the involved species and of the contingent character of intertidal assemblages within a dynamic and variable environment.

Chapter 6 gives an overview on the manifold ways how lugworms affect intertidal sediments from the micro- to the macro-scale. Implications for ecosystem characteristics include the provision of several microhabitats within the lugworm burrow but also sediment mediated effects on the macrobenthic community and finally with consequences for bird foraging behaviour. The engineering activity of lugworms is suggested to be of a higher importance than its trophic role in the intertidal food web.

The general discussion aims to synthesize the observed implications of lugworm engineering activities on the abiotic and biotic environment and to discuss the role of *allogenic* engineering in marine sediment in a more general context. Advantages and possible artefacts of the large-scale experiment are discussed. Since the experimental plots continue to exclude lugworms beyond the first three years, some further research is suggested with the highlight on three major fields which may be promising.

B DISCUSSION

1. Ecosystem engineering in intertidal sand performed by lugworms

Ecosystem engineering by lugworms in intertidal marine benthos appeared to be subtle within a dynamic environment and effects were variable in space and time. Fine sand in the low intertidal was more susceptible to ecosystem engineering effects than medium sand in the mid intertidal. Effects of lugworms were not limited to the immediate surrounding of lugworm burrows but were found to modify the entire sediment. Lugworms create and maintain their own habitat by preserving sediment permeability so that they easily can pump a sufficient volume of water down into the sediment for their respiration. Modulated by various sediment mediated processes and hydrodynamics they prevent a clogging of the sediment with fine particles and organic compounds and alter sediment and pore-water characteristics. Low sulphide concentrations in the pore-water furthermore promote habitat suitability for other organisms.

Ecosystem engineering by lugworms appeared to have considerable effects on the benthic community in individual years and/or areas, while being marginal in others. Effects on the macrobenthic community were occasionally conspicuous such as the invasion of lugworm exclusion plots by adult *Nereis diversicolor* in the first year and the almost exclusive establishment of *Lanice conchilega* in the third year. Particularly high abundances of above ground structures like sediment protruding polychaete tube caps on lugworm exclusion plots had further consequences for the benthic community, providing attachment for drifting and recruiting organisms (green algae, juvenile bivalves). The ephemeral and spatially confined character of such cascading and interacting developments reflect the high temporal and spatial variability characteristic for benthic communities (ARNTZ AND RUMOHR, 1982). This high variability in space and time of species responses to lugworm exclusion gives rise to a complex web of biogenic habitat interactions. These operate with variable strength on different spatial and temporal scales. Taking together the direct effects of lugworm presence such as the provision of microhabitats within the burrow or changes of sediment microtopography, and indirect, sediment mediated effects found within this study, lugworms are a dominant component within a biogenic habitat web of intertidal sand (Fig. 5). Due to the widespread distribution of lugworms with a high and constant population density in intertidal sand even subtle and ephemeral habitat modifications may be relevant for overall ecosystem processes and play an important role in maintaining landscape-scale ecosystem characteristics (BERLOW, 1999; CHALCRAFT AND

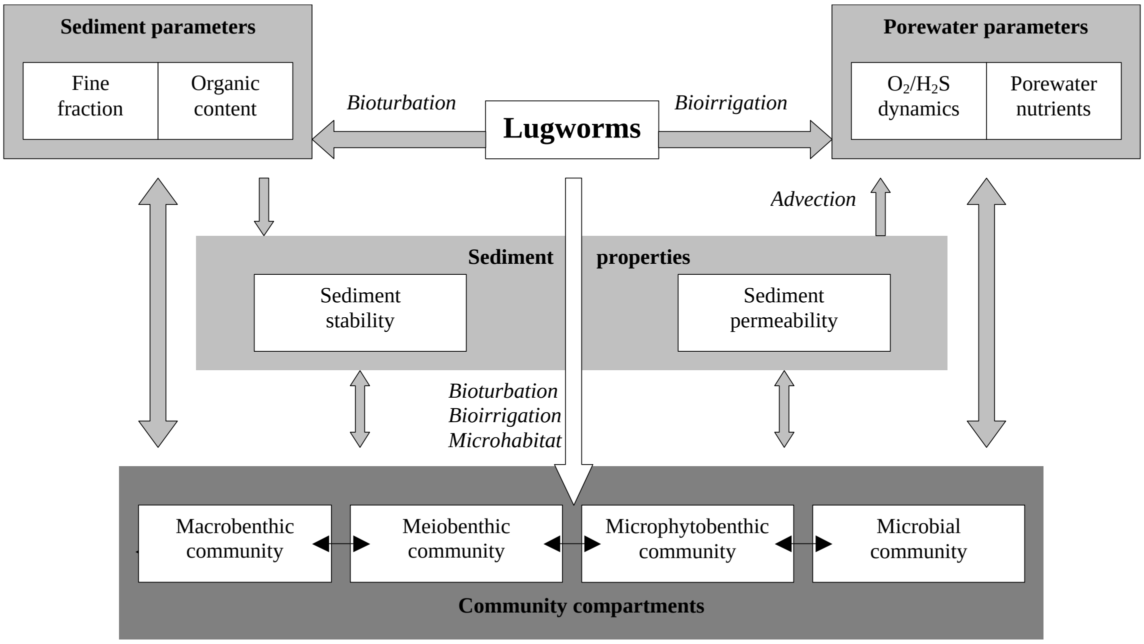

Fig. 5. Conceptual scheme of a „biogenic habitat web" in intertidal sand and the central role of the lugworm *Arenicola marina*
Lugworms not only directly affect the benthic community by their biotubation and bioirrigation (white arrow) but also indirectly, mediated by multiple sediment and porewater modifications and by sediment properties (grey arrows) modifying biological interactions (black arrows).

RESETARTIS, 2003). Accumulation of fine particles and associated organic material in the sediment and inorganic metabolites in the porewater on large-scale lugworm exclusion plots suggests, that lugworms are able to prevent a succession from sand with a low organic content towards organic enriched mud flats. The wide transition zone from permeable sand to cohesive mudflats may be significantly shifted to the former by *A. marina* (Fig. 6). Without this ecosystem engineer mud flats may considerably expand at the costs of sand flats in the Wadden Sea. Thus, *A. marina* is a biological key factor in the seascape and the geomorphological evolution of sedimentary intertidal shores.

Sandflats, densely populated by lugworms, were found to combine the filter efficiency of permeable sands with the high secondary production of more sheltered and muddy sediments (ASMUS AND ASMUS, 1985). In *in-situ* flume studies by ASMUS ET AL. (1998) and ASMUS AND ASMUS (1998) also found more efficient mineralization of particulate organic material in the presence of lugworms than in their absence. Sediments with *A. marina* were found to be sinks for particulate organic nitrogen and sources of ammonia indicating rapid turnover of organic material and effective transport of metabolites from the sediment to the water. Reduced accumulation of organic compounds and toxic metabolites and increased oxygen supply to the sediment by bioirrigation and facilitated advection in the presence of lugworms, may have further consequences for ecosystem stability. The non-accumulating character of sediment densely populated by lugworms presumably reduces the probability of oxygen depletion and the emergence of a black sulphide zone up to the surface (RUSCH ET AL., 1998). Thus, lugworms may increase the buffering capacity against organic overload in intertidal sand.

The parallel appearance of organic matter and reduced metabolite accumulation and subtle changes in the benthic community on lugworm exclusion plots show parallels to the model on fauna and sediment texture along a gradient of organic enrichment (PEARSON AND ROSENBERG, 1978). Increased organic loading will limit the sedimentary macroinfauna in anoxic mud to species which can build burrows or tubes or have other mechanisms to obtain their oxygen from the overlying water. Lugworm effects on sediment and benthic community characteristics are discussed in more detail in the following chapters without denying the mutual interactions of species response and effect traits and sediment characteristics in the marine benthos.

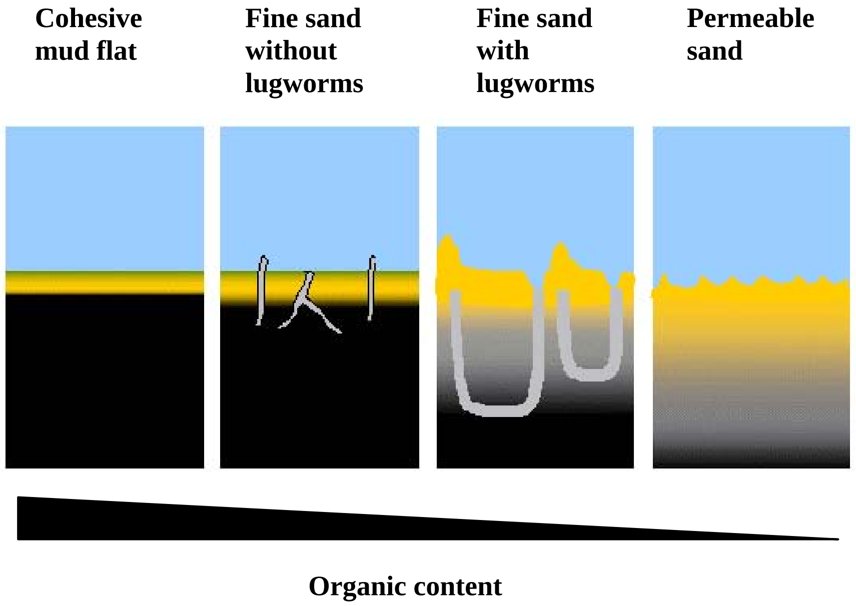

Fig. 6. Habitat shift in marine sediments induced by the lugworm *Arenicola marina*
Lugworms were found to have considerable effects on the characteristics of intertidal sand. In the presence of lugworms, sediment is provided with oxygen by lugworm bioirrigation, and by advection in a permeable sediment. Organic matter content and nutrient concentrations in the porewater remain low. Defecation on the sediment surface generate a pit-and-mound topography. In the absence of lugworms, sediment clogs with fine particles and sediment permeability decreases. Oxygen penetration depth is low and oxygen supply is limited to burrow walls of other, mainly sedentary benthic species. The sediment surface remains smooth. It is suggested that lugworm induce a habitat shift from diffusive dominated organic enriched mudflats to advective dominated permeable sand. Black colour indicates the anoxic sulphide zone, while grey shadings indicate areas which occasionally are supplied with oxygen rich, nutrient poor surface water (depending on fauna activity and hydrodynamic conditions).

2. Effects of lugworms on sediment characteristics and biogeochemical cycling

Large-scale and *in-situ* exclusion of *Arenicola marina* revealed that lugworms have profound impacts on physical, chemical and biological conditions in intertidal sediments. In addition to the abolition of the characteristic pit and mound microtopography in the absence of lugworms, successional changes in sediment properties occur, including an accumulation of fine particles and associated organic material. This entails a decrease in sediment permeability and suggests a habitat shift from permeable to diffusion dominated sediment characteristics. Exclusion of *A. marina* in the fine sand area resulted in a decrease of sediment permeability below $k = 1 \times 10^{-12}$ m² which is thought to be a critical value for advection (HUETTEL ET AL., 2003). Thus, lugworm effects are not limited to feeding and the ventilating of burrows, but also include a modification of exchange processes over the entire benthic boundary layer. Advective porewater flow in permeable sand is an effective mechanism for rapid exchange of oxygen (FORSTER ET AL., 1996, ZIEBIS ET AL., 1996A; DE BEER ET AL., 2005), dissolved and particulate organic matter (HUETTEL ET AL., 1996; HUETTEL AND RUSCH, 2000), and nutrients (MCLACHLAN ET AL., 1985; HUETTEL ET AL., 1998) which can result in high organic matter flux and turnover (D'ANDREA ET AL., 2002; HEDTKAMP, 2005). Considering the widespread and dominant occurrence of lugworms in intertidal sand along the northern Atlantic coasts, even the observed rather subtle modifications in sediment characteristics may have effects on the overall biogeochemical cycling and geomorphological evolution of sedimentary shores. Most conspicuous effects of ecosystem engineering by lugworms can be expected in intertidal areas, which are densely populated by *A. marina* and which are dominated by fine sand (Fig. 7). In these relatively impermeable sediments, bioirrigation and inhibition of fine particle accumulation may have more significant effects on exchange processes than in advective dominated, coarse grained, permeable sand.

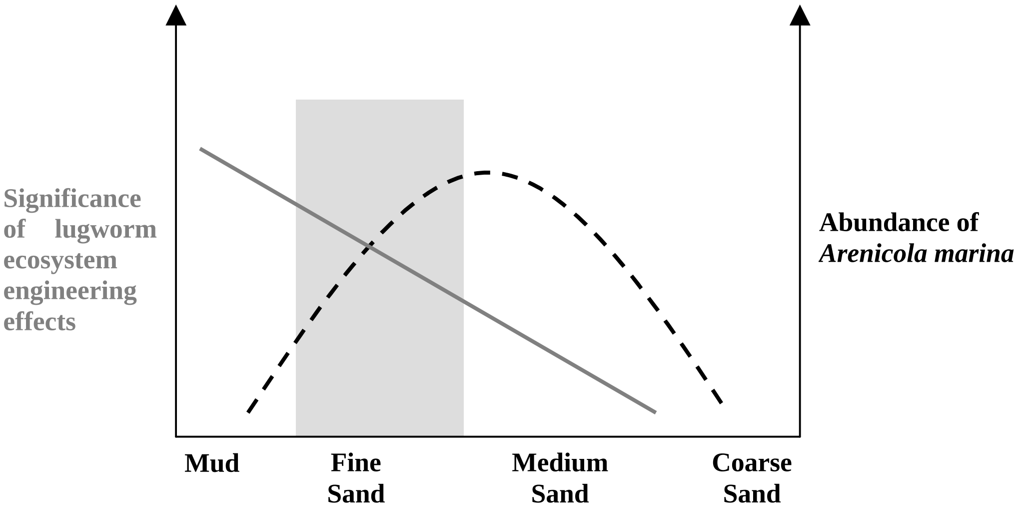

Fig. 7. Spatially variable effects of lugworm ecosystem engineering on ecosystem functioning
Importance of lugworm ecosystem engineering effects on intertidal ecosystem functioning depends on lugworm abundance, sediment type and significance of lugworm ecosystem engineering effects. Strongest effects are expected in fine sand intertidal areas with high lugworm abundances (shaded area). In finer sediments, bioturbation and bioirrigation effects may be considerable, but lugworms abundances are low to zero (Longbottom, 1970). In medium sand lugworm abundances can be high, but these sediments were found to be less suspectible to lugworm engineering effects (this study). In coarse permeable sand wave induced advection will dominate exchange processes.

Bioirrigation and bioturbation of the sediment are the main effects of lugworm pumping and feeding activity. Irrigation and sediment reworking displace both porewater and particles within the sediment (ALLER, 1982). Ventilation of the burrow is done by peristaltic movements of the lugworms and supplies them with the oxygen they need for respiration. Single lugworms were found to pump between 90 ml h^{-1} (RIISGARD ET AL., 1996) and 430 ml h^{-1} (BAUMFALK, 1979A) of water through their burrow, and pumping rates depend on temperature (BAUMFALK, 1979A). Water enters through the open tail shaft and leaves the J-shaped burrow through the sediment filled head shaft (BAUMFALK, 1979A), resulting in an upward flow of water in the sediment above the feeding pocket. Recent modelling of bioirrigative currents suggest more complex water flows which also depend on sediment characteristics (MEYSMAN ET AL., 2005). Lugworm bioirrigation was found to reduce concentrations of porewater nutrients (HUETTEL, 1990) by replacing nutrient rich and oxygen poor burrow water with nutrient poor and oxygen rich surface water at regular intervals (RIISGARD ET AL., 1996). The bioirrigative input of oxygen rich water into anoxic sediments not only supplies oxygen to animals but also results in a removal or reoxidation of toxic metabolites such as sulphides from or within the sediment. Reduced sulphide concentrations due to reoxidation of reduced compounds and attenuation of porewater by bioirrigation were observed in former studies (BANTA ET AL., 1999;

KRISTENSEN, 2001; NIELSEN ET AL., 2003). This study revealed that in the absence of lugworms pore-water sulphide concentrations may exceed 200 µmol L^{-1} and therewith lethal concentrations for other benthic infauna (GRAY ET AL., 2002). Furthermore, accumulation of inorganic porewater nutrients in the absence of *A. marina* was more conspicuous than found in comparable, but small-scale experimental studies (HUETTEL, 1990). This is possibly due to the larger scale of experimental plots of this study, reducing the impact of lateral pore-water flow (ROCHA, 2000). Overall, lugworm bioirrigation had profound effects on solute exchange between the sediment and the overlying water.

While bioirrigation affects porewater properties, bioturbation displaces particles within the sediment. Early studies on lugworm bioturbation focussed on bioturbation rates (CADÉE, 1976) and on implications of these activities for sediment stratification (BAUMFALK, 1979b). It was found that lugworms annually rework a sediment layer of 6 to 7 cm averaged over the entire Wadden Sea when assuming a lugworm density of 17 ind. m^{-2} (BEUKEMA, 1976). Feeding activity of *A. marina* results in a biogenically graded bedding in the sediment. Sediment particles smaller than 300 to 400 µm are preferentially ingested (HYLLEBERG, 1975; RETRAUBUN ET AL., 1996a) and as a result coarser particles are concentrated at feeding depth. Modifications of sediment characteristics within the large-scale lugworm exclusion plots suggest, that selective feeding by lugworms on small particles may also reduce the fine particle inventory of intertidal sediments. It may be speculated that defecation onto the sediment surface in the form of fecal mounds favours particle resuspension during high tide by waves and currents, and results in a decrease of fine particles and associated organic material at a site. If this is the main reason for the observed inhibition of sediment clogging, this mechanism of sediment cleaning may also apply for other surface defecating organisms, when fecal casts frequently are washed away by waves and currents.

However, the accumulation of fine particles in the absence of *A. marina* may be amplified by other factors. The increased fine particle fraction may provide more surface area for diatoms to attach. Additionally, this may result in a concentration of diatoms at the surface because of light limitation below. Diatoms and extracellular polymeric substances (EPS) produced by them are well known to increase sediment stability and bind fine particles (UNDERWOOD AND PATERSON, 1993; DECHO, 2000; STAL, 2003). The observed increase of microphytobenthos in the absence of lugworms may be further supported by higher nutrient availability in abolition of lugworm ventilation (FLOTHMANN AND WERNER, 1991). Thus, the most plausible explanation for the observed changes in sediment properties is a mutual interaction of several processes.

Such effects were hypothesized by GOÑI-URRIZA ET AL. (1999) from observations on a long-term accidental lugworm exclusion experiment at the French Atlantic coast. On an intertidal lugworm flat a wooden wreck was buried in 10 cm depth, excluding lugworms from 16 m^2. They found a reduced median grain size and an increased organic matter content, clay content, and total bacteria number in sediment at this lugworm exclusion site when compared with surrounding bioturbated sediment. The large scale exclusion near Sylt gave evidence from a replicated experiment that *A. marina* in fact inhibits fine particle accumulation. This process of sediment clogging was more obvious in a low intertidal fine sand when compared with mid intertidal medium sand (Fig. 7).

Changes in sediment properties had further consequences on fluid exchange processes between the sediment and the overlying water. Decreasing sediment permeability in the absence of *A. marina* result in reduced oxygen penetration depths and thus a reduction of the aerobic, metabolically most active sediment layer. On lugworm plots areal oxygen consumption originate from low volumetric oxygen consumption in an increased sediment volume, while high volumetric oxygen consumption in a thin layer occurred on lugworm exclusion plots. Thus, areal oxygen consumption rates were found to be similar on lugworm and on lugworm exclusion plots (3 to 9 mmol m^{-2} h^{-1}) but underlying processes differed (Fig. 8).

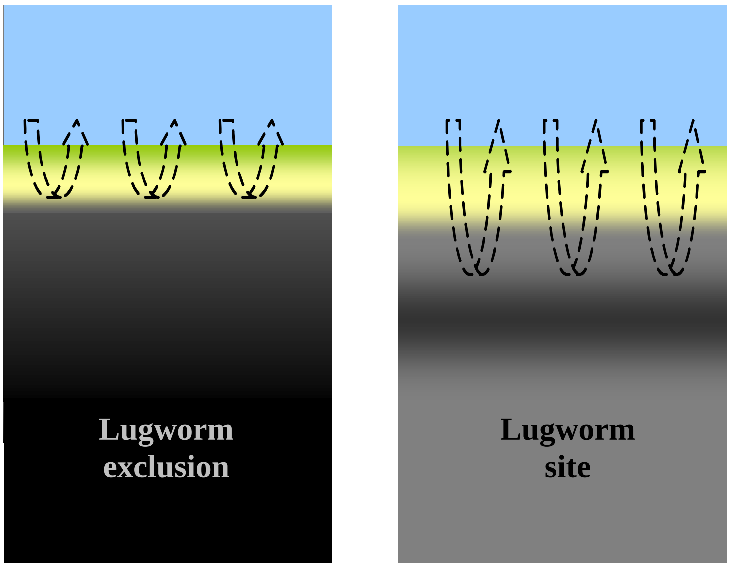

Fig. 8. Sediment properties and oxygen consumption rates
Comparable areal oxygen consumption rates in the absence and presence of lugworms are the result of low oxygen penetration depth and high volumetric oxygen consumption due to high concentrations of reduced compounds (grey shading) on lugworm exclusion plots and deeper oxygen penetration, but lower volumetric oxygen consumption on lugworm plots.

3. Effects of lugworms on the benthic community

There is good evidence for significant effects of lugworm presence on the benthic community operating within different compartments of the benthic habitat (review by RIISGÅRD AND BANTA, 1998). Two main mechanisms of benthic interactions, both directly related to lugworm activities, were suggested: (1) bioirrigation increases oxygen supply to subsurface sediments and facilitate small zoobenthos and meiofauna along the burrows (REISE AND AX, 1979; REISE, 1981, 1983, 1987; WETZEL ET AL., 1995; LACKSCHEWITZ AND REISE, 1998) and (2) bioturbative disturbance decreases surface sediment stability and inhibits other, primarily sedentary macrofauna species (BREY, 1991; FLACH, 1992; FLACH AND DE BRUIN, 1993; FLACH AND BEUKEMA, 1994; PHILLIPART, 1994; GOÑI-URRIZA ET AL., 1999; ZIPPERLE AND REISE, 2005). The results of this study give rise to a third mechanism operating on a larger scale than the creation of micro-habitats. Large-scale exclusion of lugworms gave strong evidence that sediment mediated differences in habitat properties in the presence/absence of lugworms may considerably affect other benthic species beyond the immediate vicinity of lugworm burrows, casts and funnels.

Lugworm exclusion induced changes in habitat properties including sediment texture, organic content, porewater nutrients, oxygen/sulphide dynamics and microphytobenthic inventory. There is some indirect evidence that this development from sandy towards more muddy sediment characteristics in the absence of *Arenicola marina* affected the benthic fauna. Lugworm effects on other species were more conspicuous in the low intertidal fine sand area compared with the mid intertidal medium sand area. This agrees well with the observation, that changes in sediment characteristics were also more pronounced in the fine sand area. An interesting event was the almost exclusive appearance of *Lanice conchilega* on lugworm exclusion plots in the low intertidal fine sand in the third year, when lugworm abundances at the study site happened to fall below 10 ind. m^{-2}. Considering this low lugworm abundance, small-scale disturbance alone is unlikely to have caused this pattern and stresses the relevance of sediment mediated lugworm effects and demographic aspects (ZAJAC AND WHITLATCH, 1991) for soft-sediment species assemblages. The establishment of tube building polychaetes with protruding tube caps had further consequences for the benthic community. Recruiting algal species settled on these structures and postlarval byssus drifting bivalves attached to these above ground structures and settled between polychaete tubes. Thus, conspicuous differences in the benthic community were observed, when tube-building species took advantage from the absence of *A. marina*.

Presumably, a mixture of microhabitat creation, small-scale disturbance, and sediment mediated ecosystem engineering by lugworms operate as benthic community modulator. The relative importance of each mechanism seems to vary from time to time and place to place. This variable interplay of mechanisms may partly explain inconsistencies found in former lugworm experiments and the absence of substantial lugworm effects in modelled community dynamics using long-term monitoring data (WILLIAMS ET AL., 2004). It may be speculated that the provision of oxidized subsurface micro-habitat is of a major importance in unstable sediments. There, small macrofauna species find refuge alongside lugworm burrows from physical disturbance (REISE AND LACKSCHEWITZ, 1998). Meso-scale ecosystem engineering and small-scale disturbance seem to be more relevant in fine grained, sheltered sediments, which were found to be more susceptible to lugworm induced changes and where a discretely mobile macrofauna requires stable conditions.

Changes in the benthic community were primarily reflected in species abundance rather than in the presence or absence of individual species. In part this unspecific pattern can be explained by the nature of soft sediment communities where species are adapted to the variable conditions of the intertidal zone. Thus, subtle consequences of *allogenic* ecosystem engineering may be too weak to induce considerable changes in species richness. A shift in the benthic community, where some functional groups tend to be facilitated and others tend to be inhibited seem to be a better description of the observed pattern. REISE (1987) and REISE AND LACKSCHEWITZ (1998) identified some micro-site specialists within the lugworm burrow. However, this burrow-fauna was not included in this study.

Overall, lugworm effects on the benthic community were found to be variable from year to year, stressing the importance of external factors such as environmental constraints and propagule supply (Fig. 9). Infaunal species responded differentially to changes in sediment characteristics according to their ecological response traits. While free-burrowing subsurface feeding species were facilitated in the presence of lugworms (i.e. *Scoloplos* cf. *armiger*), abundances of tube- and burrow building, surface feeding species increased in the absence of lugworms. (i.e. *Pygospio elegans*, *Polydora cornuta*, *Lanice conchilega*, *Nereis diversicolor*). Especially effects of lugworms on abundances of species which construct above ground structures had considerable effects on further developments within the benthic community. The protruding tubes provided attachment for an ephemeral development of algal tufts (*Berkeleya* colonies and *Enteromorpha* thalli) which in turn triggered settlement of the juvenile drifting clams *Mya arenaria* and *Macoma balthica* giving rise to rather complex bioengineering webs structuring the benthic community. Moreover, these developments indicate that both, response and effect traits of the involved species, are important features of assemblage formation in soft-sediment benthos.

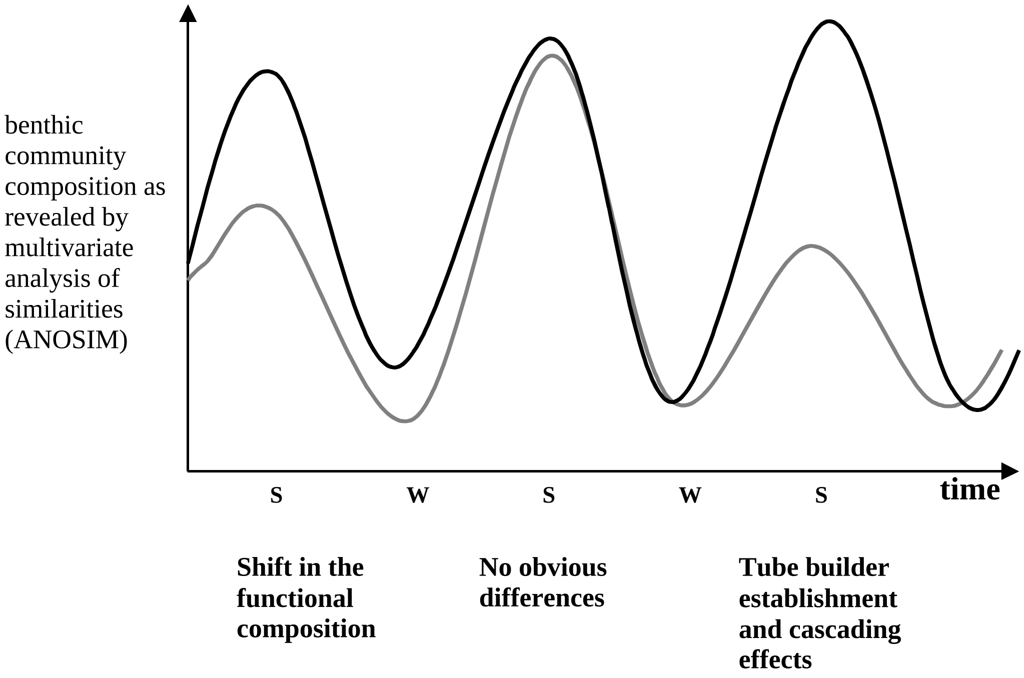

Fig. 9. Temporally variable effects of lugworm ecosystem engineering on the benthic community Benthic community dynamics with a high year-to-year variability (S=summer, W=winter) in intertidal sand were found to be variably affected by lugworm presence (black line) and absence (grey line). In one year lugworms had no obvious effects on the composition of the benthic community. A shift in the benthic community from mixed filter and surface deposit feeding tube worms to subsurface deposit feeding motile worms was obvious in another year. Most conspicuous were effects of lugworms, when tube building species took advantage from the absence of lugworms and settled preferentially on lugworm exclusion plots. Above ground structures had further cascading effects on the benthic community. High temporal variability of lugworm effects indicate the importance of environmental vagaries and biotic propagule supply.

4. Large-scale lugworm exclosures: advantages and possible artefacts

This study responds to an apparent lack of large-scale and long-term field experiments in marine sediments. These may avoid some artefacts prevalent in the frequently used manipulative laboratory and small-scale field experiments (KRISTENSEN, 2001; GOÑI-URRIZA ET AL., 1999). The approach with replicated 20 x 20 m experimental plots, however, may not only have advantages and may not be completely free of artefacts.

The *in-situ* approach allowed an incorporation of external drivers such as hydrodynamics (tidal currents and wave action), particle and advective porewater exchange, larval and recruit supply or visiting of ebb and flood predators. Based on previous studies it was concluded that effects of bioturbation on ecosystem processes from manipulative laboratory experiments cannot be directly extrapolated to *in-situ* conditions (KRISTENSEN, 2001). Field experiments are the most promising tool for detecting the importance of bioturbation relative to environmental constraints. Moreover, organisms are thought to behave differently in laboratory confinements than in their natural environment. Compared to previous field studies we adopted a large-scale approach, because lateral sediment drift (GRANT ET AL., 1997) and porewater exchange (ROCHA, 2000) may have concealed possible effects in small-scale approaches with plots of only a few m². Another advantage of 400 m² plots is that a consecutive sampling over several years was possible with a low probability of sampling the same spot twice. The scale of the experiment enhanced the chance of settling events by various species and enabled to apply different investigations within the same experimental plots simultaneously.

The permanent exclusion of lugworms furthermore enables and possibly will enable the identification of rather slow processes such as cumulative changes in sediment properties, accumulation of shell debris at the surface or invasion of seagrass from the nearby seagrass meadow. Replication of experimental plots allowed a statistical analysis of the data with different uni- and multivariate approaches. The two factorial nested design accounted for spatial heterogeneities of sediment and benthic community characteristics and allowed to identify interactive effects and to evaluate the relative importance of lugworms for ecosystem functioning in space and time.

The success of the experimental treatment was controlled by continuous counts of lugworm casts in the course of the experiment (Fig. 10). Adult lugworms were permanently excluded from meshed experimental plots. Lugworm abundances on control and ambient plots were high in the first two years, but decreased in the course of the third year. This decrease in population size of *Arenicola marina* was also evident on the scale of

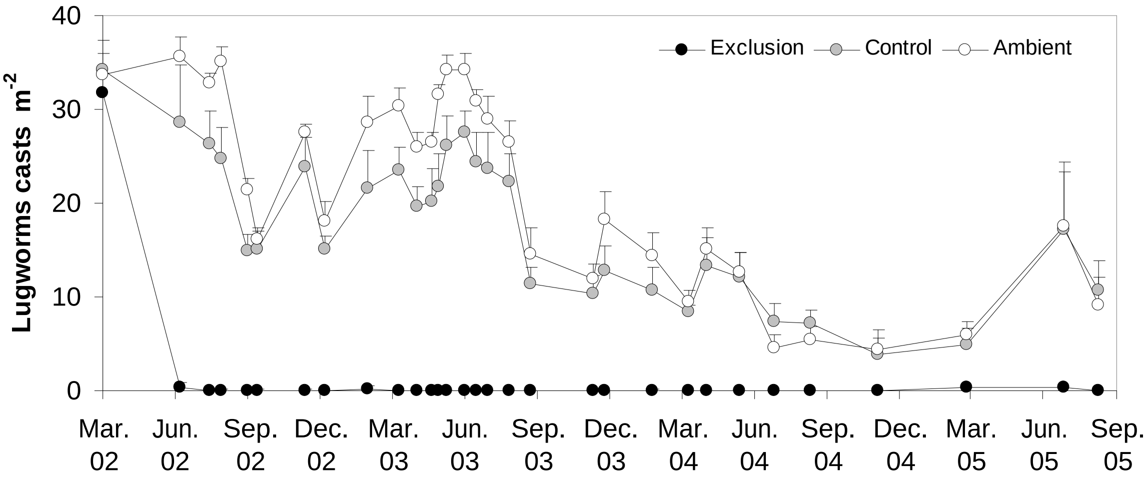

Fig. 10. Lugworm abundance on experimental plots
Abundances of lugworm casts on experimental plots over a three year period (mean of six plots and standard error). Adult lugworms (fecal strings >2 mm) were permanently excluded from experimental exclusion plots. Seasonal fluctuations in number of lugworm casts indicate variable feeding activity rather than changes in lugworm abundances. While lugworm abundances were high in the first two years, population size significantly decreased on experimental plots in the course of the third year for unknown reasons.

the entire embayment (REISE, unpublished data). This development was not expected since *A. marina* is known to have a relatively constant population size and density in time in Wadden Sea benthos in general (BEUKEMA, 1976) and at the study site except when struck by a particularly harsh winter (REISE ET AL., 2001 and pers. com.).

Disturbance of sediment stratification and infauna by initial dredging of experimental plots was minimized by flattening the surface after dredging with a shovel. However, it was not possible to preserve the surface sediment layer when excavating the sediment ruggedly with a backhoe. Thus, disturbance by initial dredging was taken into account by creating control plots subjected to identical disturbance. However, even during the first year of the experiment no significant differences regarding sediment and benthic community characteristics were found between control and ambient plots, reflecting high and fast resilience of the system from the disturbance (BOESCH ET AL., 1976). It was not possible to remove lugworms mechanically before inserting the mesh. The net was placed in the sediment as 1m wide and 20m long lanes and each day 4 to 5 consecutive lanes were put into the sediment. It may be assumed that some lugworms were able to escape horizontally from being trapped underneath the net. However, a considerable number of lugworms presumably died below the net. Before net insertion lugworm mean abundance on the plots was 30 ind. m^{-2} which approximately corresponds to a biomass of 10 to 20 g m^{-2} (BEUKEMA, 1976; REISE ET AL. 1994). Although an effect of this added dead organic material on nutrient and organic content cannot be excluded it is assumed that after the first summer months mineralization of dead lugworms was completed and all porewater was exchanged. This assumption is based on experiments on artificial organic enrichment of comparable sandy sediments which were done with much higher organic input (>100 g m^{-2}) and on a much shorter time scale (10s of days) (KRISTENSEN AND HANSEN, 1995; HANSEN AND KRISTENSEN, 1998).

Molecular diffusion was possible through the 1mm mesh allowing porewater exchange processes from below the net. Depth of the net was monitored each year at 100 locations of each exclusion plot (Fig. 11). Constant depth indicates a relatively stable sediment or at least a balanced erosion and deposition rate at the study site. Other deep burrowing infauna might have been excluded simultaneously with the lugworms by the 1 mm net at 8 to 9 cm depth. However, sampling of the sediment layer between 10 and 20 cm on lugworm plots revealed, that *A. marina* was the only abundant deep burrowing species at the study site. Only few species were occasionally found below 10 cm depth. *Nereis diversicolor* does not require this burrow depth (ESSELINK AND ZWARTS, 1989) and invaded exclusion plots in the first year irrespective of the net. However, during winter deep burrows are known for this species (MUUS, 1967). Another deep burrowing species is *Heteromastus filiformis*. This polychaete is thin enough to pass the 1mm mesh and was regularly found in samples from netted plots. Living depth of the soft clam *Mya arenaria* increases with increasing size (ZAKLAN AND YDENBERG, 1997). Thus, while no effect can be considered for the first year, the net in 8 to 9 cm depth may affect *M. arenaria* from the second year onward. The same is true for juveniles of *A. marina* which recruited in all years on experimental plots. In the course of the year they usually had left the exclusion plots, presumably because hampered from burrowing deeper. Lower burrowing depth may also increase the risk of predation (ZWARTS AND WANINK, 1991). Impeded vertical mixing of particles and porewater due to the net is thought to be minimal at the study site. Hydrodynamic disturbances were reported to maximally 4-8 cm depth at a nearby site which is more exposed to waves and currents (RUSCH AND HUETTEL, 2000).

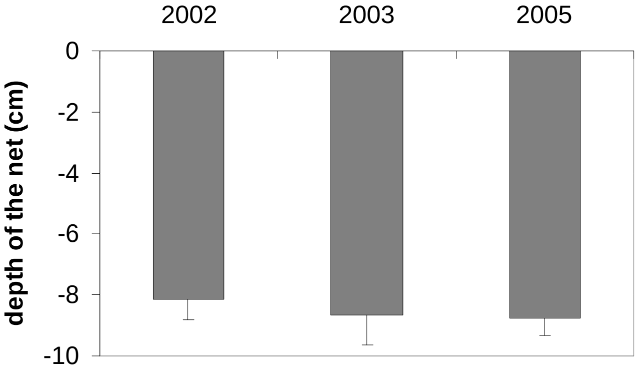

Fig. 11. Depth of the net on lugwrom exclusion plots
Depth of the net in the course of the experiment on lugworm exclusion plots indicate almost balanced erosion and deposition rates at the study site. Shown are means of the six plots and standard deviation (n=6). On each plot, the depth of the net was measured at 100 different locations.

5. Ecosystem engineering in the marine benthos

Bioturbators have been identified as classic examples of ecosystem engineers (LEVINTON, 1995). Worldwide, especially shallow coastal habitats were found to be dominated by single bioturbating macroinvertebrate species such as arenicolids (BEUKEMA, 1976; REISE, 1985; KRAGER AND WOODIN, 1993), thalassinid shrimps (ALLER AND DODGE, 1974; POSEY, 1986; ZIEBIS ET AL., 1996B, ATKINSON AND TAYLOR, 2005), or enteropneusts (FLINT AND KALKE, 1986). These soft-sediment systems are among the most geochemically and biologically active areas of the biosphere (GATTUSO ET AL., 1998) and at the same time are subject to a broad scope of anthropogenic impacts (LEVIN ET AL., 2001). Given the complexity of processes, identification of mechanisms that alter system functioning is critical to understanding mutual relationships between diversity and ecosystem functioning and maintaining living resources (LEVIN ET AL., 2001).

Although effects of various burrow-dwelling macroinvertebrate engineers on marine sediments and benthic communities were found to be variable among species and ecosystems (ALLER, 1982; MEADOWS AND TUFAIL, 1986; BOTTO AND IRIBANE, 2000; ATKINSON AND TAYLOR, 2005), there is good agreement on some fundamental implications of bioturbators for biotic, physical and chemical components comprising “ecosystem functioning”. Bioturbating and bioirrigating macrofauna maintain a close coupling of particles and porewater between the sediment and the tidal water above (RHOADS 1973; ALLER, 1978; GRAF, 1992; ZIEBIS ET AL., 1996b). Recent studies address the significant impact of bioturbating macrofauna on biogeochemical processes (ZIEBIS ET AL. 1996b; BOTTO AND IRIBARNE 2000; D`ANDEREA ET AL. 2002). A pit-and-mound topography at the sediment surface induces advective porewater exchange by creating pressure gradients within permeable surface sediments (ZIEBIS ET AL., 1996a). Mucous lined burrow walls act as “hot spots” for organic matter decay (KRISTENSEN, 2000). Burrows provide microhabitats for small infauna (FLINT AND KALKE, 1986; REISE, 1987; SCHAFFNER, 1990) and bioturbating activities inhibit other, mainly sedentary species (BRENCHLEY, 1981; POSEY, 1986; FLACH, 1992a,b).

Despite these overall similarities in effects of bioturbating and bioirrigating ecosystem engineers, studies increasingly point to the importance of species-specific behaviours (BOTTO AND IRIBARNE, 2000), architecture and longevity of burrows (KRAGER AND WOODIN, 1993) and activity rates (BOUDREAU AND MARINELLI, 1994). This study suggests that the impact of an ecosystem engineering species also varies among sediment type and hydrodynamic exposition. The observed differences in the benthic community give rise to a superior role of large bioturbators within complex interactions of diverse engineering organisms and the importance of response and effect traits of assembling species (HOOPER ET AL., 2005). Single bioturbating and bioirrigating ecosystem engineers may locally affect the benthic community structure and the entire sediment geochemistry beyond the immediate vicinity of their burrows with broad scale effects on ecosystem functioning (LEVIN ET AL., 1997). Alteration of communities in soft sediment habitats via species extinctions and invasions may considerably affect ecosystem functioning especially when large bioturbators are involved. Even natural population fluctuations as observed for *A. marina* in the course of this experiment (Fig. 10) or for enteropneusts (*Schizocardium* n. sp.) by FLINT AND KALKE in 1986 may result in an oscillating character of ecosystem functioning. Soft sediment habitats are complex associations of physical, chemical, microbial components and the larger organisms. Multidisciplinary and integrative studies are crucial to understand relationships between ecosystem engineering and ecosystem functioning in the marine benthos.

6. Implications and scope for further research

The large-scale lugworm exclusion experiment conducted in this study will be continued beyond the first three years. The size of experimental plots and the experimental design allowed to detect *in-situ* implications of lugworm activities which presumably would be concealed in small-scale approaches. Within this study, several new aspects of biogenic interactions in marine benthos and their relative importance in space and time could be assessed. However, after three years of observations, many aspects are still not investigated for which this experiment offers promising testing ground. Continuous monitoring may further detect new or accumulating effects. The identification of slow or rare processes, such as changes in some sediment properties, accumulation of shell debris at the surface, or a possible invasion of seagrass from the nearby seagrass meadow, may be expected when continuing the experiment. On the basis of the results of this study three promising major fields for future research are singled out in this chapter.

6.1. Effects of lugworms on biogeochemical processes and the microbial community

Sediment permeability and boundary layer flow characteristics control pathways and magnitude of material exchange in surface layers of aquatic sediments. Advective transport rates can exceed those of molecular diffusion by two orders of magnitude and more (HUETTEL ET AL., 2003). Decreasing sediment permeability in the absence of *Arenicola marina* therefore may considerably affect exchange processes between the sediment and the tidal water above. The results of this study revealed slightly deeper oxygen penetration on lugworm plots during calm conditions, possibly mediated by a changed benthic community. However, based on percolation experiments with sediment from lugworm exclusion and lugworm sites it can be speculated that more implications of sediment permeability will be recognized under various other hydrodynamic conditions. Single wave induced flushing events may considerably differ in both sediment types during stormy periods with further consequences for biogeochemical processes. *In-situ* microprofiles of oxygen and other chemical species under different hydrodynamic conditions may add further understanding of sediment mediated lugworm effects on ecosystem processes.

Altered distributions of oxygen, sulphide and inorganic nutrients in the presence/absence of *A. marina* not only affect habitat suitability for benthic species but also imply an altered microbiological environment regarding electron acceptor availability. Bioirrigative oxygen input allows oxidative mineralization processes and oxidation of reduced compounds along burrow walls in an otherwise anoxic environment (KRISTENSEN, 1988; ALLER, 1988; ALLER AND ALLER, 1992). Advective porewater exchange in permeable sediments also enhances oxidative processes (D'ANDREA, 2002; DE BEER ET AL., 2005). This study gives some evidence that bioirrigation and sustained sediment permeability in the presence of lugworms increase oxidative mineralization processes. Relatively refractory organic compounds, rich in aromatic structures like lignin, can be depolymerised only in the presence of oxygen due to the presence of oxygen radicals (CANFIELD, 1994). Besides organic matter remineralization, oxygen is consumed by the reoxidation of reduced inorganic metabolites such as sulphide, iron (II), and manganese (II) (CANFIELD ET AL., 1993) by chemical reactions or mediated by chemoautotrophic microorganisms (JØRGENSEN, 1989). The oxidized forms of these chemical species then become available as electron acceptors in suboxic pathways (ALLER, 1994; KRISTENSEN, 2001). Increased oxygen supply in sediments due to lugworm activities may therefore considerably affect the microbial community (KOSTKA ET AL., 2002). Further investigations on the composition of the microbial community, their distribution and biogeochemical processes on experimental plots with and without lugworms are promising. New molecular techniques like fluorescence *in-situ* hybridisation (*FISH*) allow the identification and quantification of individual cells without their cultivation (AMANN ET AL., 1995; LLOBET-BROSSA ET AL., 2002). Application of such techniques may reveal new insights in the effects of macrofauna on microbial communities and biogeochemical cycling in marine sediments.

6.2. Habitat web versus food web in soft sediment benthos

Within this study, only few investigations were done on the response of ebb and flood tide predators (i.e. birds, fish or crustaceans). Due to the size of experimental plots further investigations may considerably contribute to a better understanding of the interplay between biogenic habitat transformations and trophic interactions.

In autumn 2003, one year after the ragworm *Nereis diversicolor* had invaded lugworm exclusion plots in the low intertidal with abundances of up to 2000 ind. m^{-2}, observations on bird foraging behaviour from an observation tower build up in between the experimental blocks were done (Fig. 12). For oystercatchers a significantly higher efficiency in foraging was found on lugworm exclusion plots and the dominant prey item was *N. diversicolor* (SCHIEK, unpublished data). An abundant wader, the golden plover, also showed longer residence/foraging time on the more muddy exclusion plots. These observations suggest, that optimal foraging theory may further modulate the outcome of ecosystem engineering. Predation on *N. diversicolor* by birds conceivably resulted in the observed continuous decrease in ragworm abundance after invasion in 2002 and thus

Fig. 12. Observations on bird foraging
Bird observation tower build up in between the experimental blocks and waders foraging on a lugworm exclusion plot.

concealed this pattern in the following years. The same may be true for time-restricted consequences of increased bivalve recruitment for following years.

Investigations on meiofauna on experimental plots revealed an at least temporal increase in abundance of nematodes in the organically enriched sediment of lugworm exclusion plots in the low intertidal fine sand (SCHMIDT, 2004), potentially increasing the attractiveness of these plots for organisms which prey on meiofauna. Increased complexity of sediment microtopography in the presence of lugworm casts and funnels may further affect abundances of flood and ebb tide predators such as shrimps, fish or birds (BOTTO ET AL., 2000). Within this study changes in chlorophyll and organic content and shifts in the meiobenthic and macrobenthic community suggest also changes in benthic foodweb structure. Application of stable isotope techniques (PETERSON AND FRY, 1987; PETERSON, 1999) are promising for further investigations being targeted on the interaction of habitat and food web in intertidal sand.

6.3. Ecosystem engineering, biodiversity, and ecosystem functioning

Human activities dramatically increase alteration of communities via species extinctions and invasions and the mutual interactions between organisms and ecosystem processes has become the focus of a considerable research effort (VITOUSEK ET AL., 1997; LOREAU ET AL., 2001; COVICH ET AL., 2004). Manipulating species composition and measuring ecosystem functioning *in-situ* is an important task for a better understanding of relationships between biodiversity and ecosystem functioning, particularly in dynamic environments (HALL ET AL., 1994). The large-scale lugworm exclusion experiment provide ample testing ground for further research regarding the relationship of ecosystem engineering, biodiversity and ecosystem functioning in marine sediments and lend itself for a large variety of species transplantation experiments. First single-species transplantations have already been conducted during the last years with various species (Fig. 13) including mudsnails (*Hydrobia ulvae*, ROBERTSON, 2005) juvenile and adult cockels (*Cerastoderma edule*, ROBERTSON, 2005; THIELTGES AND VOLKENBORN, unpublished data), and seagrass (*Zostera noltii* and *Zostera marina*, KOSCHE, in prep.). These studies were focussed on growth rates and mortality of transplanted species in the presence/absence of lugworms in order to investigate the relevance of classical models of interactions such as the trophic group amensalism or mobility mode hypothesis in intertidal sand. Overall, responses of the investigated species were rather subtle, possibly indicating high adaptation of these species

Fig. 13. Species transplantation experiments
Experimental plots offer ample testing ground for transplantation experiments. First transplantations have been conducted with molluscs within cages (Thieltges and Volkenborn, unpublished data) and seagrass (Kosche, in prep.).

to a variable environment. Transplanted animals were put on experimental plots within cages and cage artefacts were found to be high, possibly concealing effects of lugworm presence/absence. Further transplantation experiments should preferentially be conducted without cages. Experiments should be focussed not only on response traits of transplanted species, but also involve their effect traits and how effects may be modified by lugworms. Transplantation of invasive species such as *Marenzelleria* cf. *vereni, Tharyx* cf. *killariensis* or *Ensis americanus* may give indications if large bioturbators may affect the resistance of ecosystems to biological invasions (ESSINK AND DEKKER, 2002; REISE ET AL., 2005). Multi-species transplantations, resembling terrestrial and mesocosm biodiversity/ecosystem functioning studies, are promising for the investigation of lugworm effects on biodiversity on intertidal sandflats. The experiment also offer ideal testing ground for the role of *Arenicola marina* on ecosystem resistance to and resilience from disturbance. Successional recolonization after defaunation or processes conjunct with artificial organic enrichment in the presence or absence of lugworms are only two examples for promising future research regarding relationships of ecosystem engineering, biodiversity and ecosystem functioning in the marine benthos.

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Part II: List of publications

This cumulative thesis includes six publications listed below. My contribution to each publication is explained. The initial idea to conduct a large-scale and long-term lugworm exclusion experiment to reveal lugworm effects on ecosystem functioning was developed by Karsten Reise and Nils Volkenborn. Choice of the experimental site and the experimental design was made by Nils Volkenborn and Karsten Reise. The realization in the field was accomplished by Nils Volkenborn.

1. **Volkenborn, N., Hedtkamp, S.I.C., van Beusekom, J.E.E., Reise, K.** Intertidal habitat succession inhibited by lugworm bioturbation
ESTUARINE COASTAL AND SHELF SCIENCE, in review
    - *concept: N. Volkenborn and K. Reise*
    - *sampling and measurements: N. Volkenborn (field work, porewater sampling and processing, sediment sampling and processing), S.I.C. Hedtkamp and J.E.E. van Beusekom (nutrient analysis)*
    - *data analysis: N. Volkenborn*
    - *writing of manuscript: N. Volkenborn, revised and improved by J.E.E. van Beusekom and K. Reise*

2. **Volkenborn, N., Polerecky, L., Hedtkamp, S. I. C., van Beusekom, J. E. E., De Beer, D.** Habitat shift from diffusive to permeable sediment characteristics in intertidal sand by the lugworm *Arenicola marina*
LIMNOLOGY AND OCEANOGRAPHY, in review
    - *concept: N. Volkenborn*
    - *sampling and measurements: N. Volkenborn in cooperation with D. de Beer (microsensor measurements), L. Polerecky (planar optode imaging), S.I.C. Hedtkamp (benthic chamber incubations and nutrient analysis) and J.E.E. van Beusekom (nutrient analysis)*
    - *data analysis: N. Volkenborn and L. Polerecky*
    - *writing of manuscript: N. Volkenborn, revised and improved by L. Polerecky, S. Hedtkamp, D. De Beer and J.E.E. van Beusekom*

3. **Volkenborn, N., Reise, K.** Cumulative sediment mediated effects of *Arenicola marina* on polychaete functional diversity revealed by large-scale experimental lugworm exclusion
JOURNAL OF SEA RESEARCH, submitted
    - *concept: N. Volkenborn*
    - *sampling and measurements: N. Volkenborn*
    - *data analysis: N. Volkenborn*
    - *writing of manuscript: N. Volkenborn, revised and improved by K. Reise*

4. **Volkenborn, N., Reise, K.** (2005) Lugworm exclusion experiment: responses by deposit feeding worms to biogenic habitat transformations
JOURNAL OF EXPERIMENTAL MARINE BIOLOGY AND ECOLOGY, accepted and in press
    - *concept: N. Volkenborn*
    - *sampling and measurements: N. Volkenborn*
    - *data analysis: N. Volkenborn*
    - *writing of manuscript: N. Volkenborn, revised and improved by K. Reise and W. Armonies*

5. **Volkenborn, N., Robertson, D.M., Reise, K.** Contingency in ecological patterns of the tidal zone: How experimental lugworm exclusion caused bivalve settlement
MARINE BIOLOGY, in review

- *concept: N. Volkenborn and K. Reise*
- *sampling and measurements: N. Volkenborn, D. Robertson*
- *data analysis: N. Volkenborn*
- *writing of manuscript: N. Volkenborn, revised and improved by K. Reise*

6. **Reise, K., Volkenborn, N.** (2004) Large worms as ecosystem engineers in intertidal sediments
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Intertidal habitat succession inhibited by lugworm bioturbation

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ABSTRACT

The hypothesis that the lugworm *Arenicola marina* inhibits the development from sandy towards muddy intertidal flats by its bioturbation has been tested with a permanent large-scale exclusion experiment in a sheltered bay of the North Sea. Results on sediment properties indicated a progressive clogging of interstices with fine particles and associated organic matter resulting in a lower permeability in exclusion plots compared to control plots. Chlorophyll content in the surface layer was consistently higher in the absence of lugworms. Lack of subsurface irrigation in the absence of lugworms combined with reduced sediment permeability resulted in increased pore-water concentrations with sediment depth for ammonium, phosphate, silicate and sulphide, while concentrations remained low where lugworms occurred. Exclusion plots became sinks for nutrients and sulphide concentrations of >100 µM indicated toxic conditions for macrofauna. This syndromatic development was more conspicuous at the zone where median grain size was low than where it was high. It is therefore concluded that *A. marina* contributes to the maintenance of permeable sand, sustaining suitable conditions for the lugworm population, and it is suggested that without this "ecosystem engineer" mud flats would greatly expand at the costs of sand flats in the Wadden Sea.

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

1. INTRODUCTION

On geological time scale, steep reflective sandy shores develop towards gentle sloping dissipative shores. With sufficient sediment supply, shores may further develop long shore bars, spits and barrier islands (Carter, 1988; Davis, 1996). These provide shelter for fine particle deposition on their leeward side similar to fine particle accumulation is estuaries. In this geomorphological succession of the shore, sandy shoals gradually accumulate more and more fine particles and finally become mud flats where wave disturbance remains low. Where sediment supply exceeds sea level rise at the upper shore, salt marsh vegetation may convert marine sediments into a terrestrial environment (Levin et al. 2001). At the lower shore, marine organisms either stabilize and destabilize the sediment with facilitating or inhibiting effects on shoreline succession (Reise, 2002).

To explore seascape effects of biogenic habitat transformations in unvegetated sand, we designed a field experiment to test the hypothesis that the large bioturbating and irrigating polychaete *Arenicola marina* inhibits succession from sandy towards muddy tidal flats. The lugworm, *A. marina*, is a prominent member of the macrobenthos on sandy sediments of the northwest European coasts. In the eastern North Sea, where the largest coherent sediment flats of the world extend between the tide marks, the lugworm maintains a rather stable population with densities of 20 to 40 adult worms m^{-2} over most of the tidal zone (Flach and Beukema, 1994) and dominates deposit feeder biomass (Beukema, 1976; Reise, 1985). In the entire Wadden Sea with about 4300 km² of tidal flats, roughly 90% are 'lugworm flats' composed of sand to silty sand, and only 7% are mud flats unsuitable for a high density of *A. marina* (Beukema, 1976). Abundances are also low in clean unstable sand exposed to strong currents or waves near low water line and below (Longbottom, 1970). In our study area, a sheltered bay with 4.8 km² of tidal flats at the leeward side of the island of Sylt, also about 90% are densely populated by lugworms (Reise et al., 1994; 2001). *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. Due to the burrowing activity of *A. marina* a seascape surface topography develops dominated by lugworm funnels and fecal castings. Burrow ventilation for respiration is done by piston-like movements in a tail-to-head direction (Riisgård and Banta, 1998). Assuming a density of 30 ind. m^{-2}, lugworms replace a sediment layer of 15 cm per year (Cadée, 1976) and pump 3 l of seawater per hour and m^2 in the anoxic sediment (Riisgård et al., 1996). We hypothesize that *A. marina* by its effects on sediment properties is responsible for the large areal share of sandy flats in this coastal region. In the absence of lugworms, sandy flats in sheltered positions would give way to muddy flats.

The areal ratio between sandy and muddy sediment bottoms may be in part a product of lugworm activities. This speculation is based on measurements on bioturbation and bioirrigation of *A. 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; Phillipart, 1994; Riisgård and Banta, 1998). However, we assume to test properly our hypothesis one need to measure effects of lugworms on sediment properties on large plots with and without lugworms over several years. We here report results from replicated experimental plots of 400 m² one to two years after the exclusion of lugworms commenced. Because of lateral sediment transport across such plots in the tidal zone, size and time may still not be sufficient to quantify all effects but we expect some indications whether this approach may lead towards an answer to what extent the proportion of sand flats versus mud flats is affected by *A. marina*. The question whether and where permeable sand or cohesive mud prevails in a coastal area has cascading effects on the food web and ecosystem functions.

A shift in sediment properties from permeable sand in the direction of cohesive mud upon the exclusion of lugworms will be considered to support our hypothesis of lugworms inhibiting succession from sand to mud flats. We here focus 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 *A. marina*. In detail we expect that exclusion plots show

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

As these variables are not independent of each other we do not regard each as separate evidence but as necessary parts of a syndromatic development leading from sand towards mud flats, and that lugworms have the potential to maintain suitable habitat conditions against the geomorphological evolution of sedimentary shores.

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 are low organic sandy flats densely populated by *Arenicola marina*, compromising more than 90% of the total intertidal area (Reise et al., 1994). Sediment at the experimental site is dominated by medium and fine sands. Salinity varies on average between 27.5 in spring and 31.0 in summer and freshwater up-welling is negligible. Mean tidal range is 1.8 m. A detailed description of the tidal embayment can be found in Wohlenberg (1937), Reise (1985) and Reise et al. (1994). Exclusion of *A. marina* was achieved by inserting a 1 mm meshed polyethylene net in 10 cm depth into the sediment (Reise, 1983; Huettel, 1990; Phillipart, 1994). This was done on six 20 x 20 m experimental plots by the use of a backhoe. To test the effect of dredging, control plots were created in which the sediment was dredged in the same way without inserting the net. In a third treatment (ambient), plots were left untouched, constituting natural conditions.

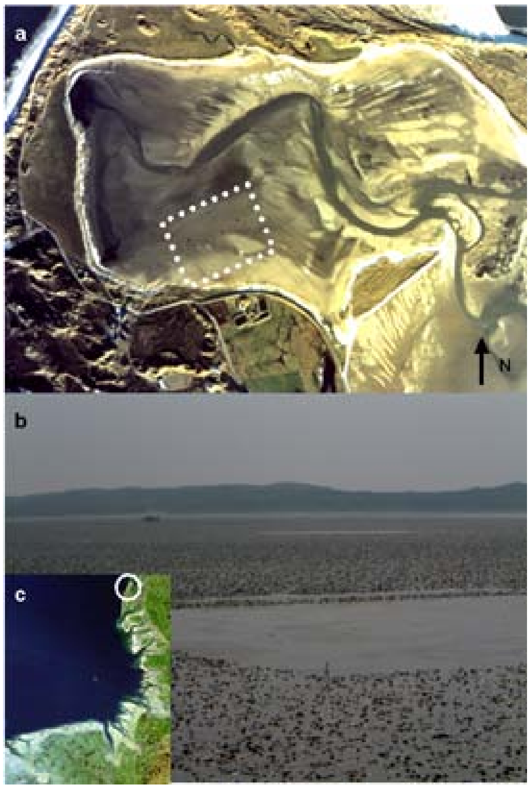

Fig. 1. (a) On a aerial photo of the embayment in December 2002, exclusion plots were visible as dark dots within the study site in Königshafen embayment, sharing the colour of more muddy sediments in the western part of the bay. (b) Experimental plot, where lugworms were excluded from 400 m² areas, by inserting a 1 mm meshed net in 10 cm depth. (c) Study area in northern part of the Wadden Sea.

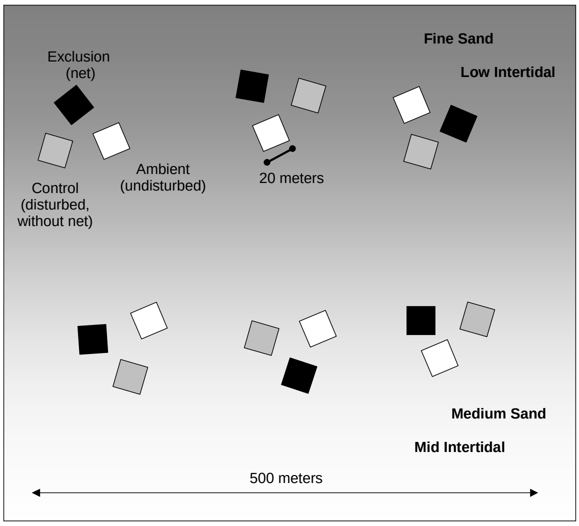

Fig. 2. Experimental set-up in a 2-factorial nested block design. Six experimental blocks comprehended three lugworm treatments and were nested within two different sediment types.

The experiment was created in 2002 in a 2-factorial (3x2 levels) nested block design (Fig. 2). Each block comprehended three lugworm treatments (exclusion, control, ambient), each experimental plot with an area of 400 m². 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 relevance of the regnant sediment composition, experimental blocks were nested with respect to two different sediment types: three blocks were conducted within an area of medium sand (grain size median 330-340 µm) and three blocks within an area dominated by fine sand (grain size median 200–220 µm). Emersion period of these different sediment type areas was 6-7 and 9-10 hours per tide, respectively. Due to aeolian sand input from surrounding 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 of up to 5 cm and height of up to 2 cm. To control the effect of lugworm treatment, lugworm densities were estimated approximately monthly on the experimental plots by counting the fecal castings within the experimental plots on 10 randomly chosen areas of 0.25 m². The number of fecal castings varies with feeding activity of lugworms but can be taken as an approximation for abundance of *A. marina* (Flach and Beukema, 1994). Lugworms were effectively excluded from experimental exclusion plots. While almost no adult lugworms could be found on the exclusion plots, lugworm cast densities on the control and ambient plots where high. Over the whole investigation period of 2.5 years mean density was 17.8 casts m^{-2} on the control plots and 22.0 casts m^{-2} on the ambient plots. Maximum cast densities were reached in early summer with densities of 30 casts m^{-2} averaged over all control plots and 35 cast 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 with at least 10 cm distance to lugworm casts or funnels. Apart from this, samples within the experimental plots were taken randomly, excluding a border area of 2 meters in order to minimize possible edge effects. Pseudo-replicate samples were taken within each experimental plot and pooled in order to achieve reliable mean values for the 400 m² areas. Sampling of sediment and pore-water was done between 2002 and 2004.

2. 3 Grain size composition

Sediment samples were taken randomly with 10 cm² cores from 10 different locations within each experimental plot in August 2002 and August 2003 and divided into 3 intervals (0-1 cm, 1-5 cm, 5-10 cm). 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 3 cores (10 cm², 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 of ignition (500 °C, 12 h).

2. 5 Chlorophyll content

Samples were taken with a 2 cm² core 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 with 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 (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

Sediment permeability was estimated by the constant head method (Klute and Dirksen, 1986). From each experimental plot one 10 cm² core was taken and the flow velocity of about 2 ml seawater was measured under 4 different pressure gradients (ranging from 1 to 20 cm H_2O). 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 can be collected simultaneous from 6 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 done in April and July 2004. From 4 randomly chosen spots within each experimental plot approximately 5 ml of pore-water from each depth was taken and pooled to one sample. 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 steps and pore-water from pooled slices (0-1 cm, 2-3 cm, 4-5 cm and 6 to 7 cm depth) was blown out with pressurized N_2 gas (Billerbeck, pers. com.). Processing of pore-water samples was done as described above.

2. 9 Statistical analysis

The investigated parameters were analysed with respect to three main questions: (1) Is a parameter significantly influenced by lugworm presence/absence? (2) Are possible effects of lugworm presence/absence depending on the sediment type? (3) Can a significant modification be found over the whole sediment depth or is it restricted 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 the 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 sand, 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 α=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 different sediments types in the study area. The sandy site was dominated by medium sand and had significant higher grain size median than sediment from the fine sanded site (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 sanded area. Surface sediment grain size median 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 treatment. Organic and water content were significantly higher on lugworm exclusion plots in the fine sand area indicated by significant treatment x sediment type interactions.

Table 1
Sediment characteristics of experimental plots in August 2003 and ANOVA results on factor effects (x 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).

		Medium Sand			Fine Sand			ANOVA results			
	Depth	Exclusion	Control	Ambient	Exclusion	Control	Ambient	Treatment	SedimentType	Treatment x Sediment Type	Block
Grain size median (µm)	0-1 cm	294	338	338	190	204	208	x (C, O)	x (MS)		
	1-5 cm	329	342	335	206	218	216		x (MS)		
% water content	0-5 cm	15.86	16.68	15.53	19.87	16.21	17.14	x (E)	x (FS)	x (E, FS)	
% total organic material	0-5 cm	0.55	0.65	0.51	1.24	0.59	0.68	x (E)	x (FS)	x (E, FS)	

3. 2 Fine fraction

The amount of fine particles (<63 µm) within the sand matrix was significantly different in both years and was significantly higher in the fine grained 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 sanded area revealed by a significant treatment x sediment type interaction (Table 2). In the upper centimetre of the sediment fine fraction doubled in the absence of *Arenicola marina*. For the horizon from 1 to 5 cm depth a significant time x treatment interaction (Table 1) reflects gradual silt and clay accumulation within the sub-surface sediment. In the fine sanded area these small particles compromised 2.5% weight proportion of the total sediment of the upper 5 cm on exclusion plots but only 1.0% on

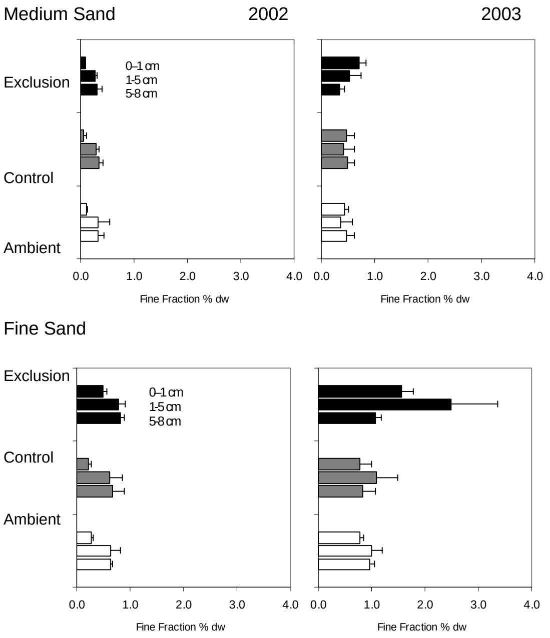

Fig. 3. Fine fraction (grains <63 µm) in sediment from different experimental treatments in August 2002 and August 2003. Shown are means (n=3) and SD.

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.

		0-1 cm			1-5 cm			5-8 cm		
	df	SQ	F	p	SQ	F	p	SQ	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 x 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 x Treatment	2	0.0613	4.36	0.053	0.1711	10.58	**0.006**	0.0080	5.00	0.039
Year x Sediment type	1	0.0000	0.00	0.979	0.1625	20.09	**0.002**	0.0077	9.61	**0.015**
Year x Treatment x Sediment type	2	0.0018	0.13	0.879	0.0515	3.18	0.096	0.0058	3.62	0.076
Year x Block(Sediment type)	4	0.0054	0.19	0.935	0.0183	0.56	0.695	0.0039	1.22	0.374
Residual	8	0.0563			0.0647			0.0064		

control and ambient plots. The sediment layer of 5 to 10 cm was not significantly affected by lugworm absence/presence.

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 upper cm and decreased with depth. A significant impact of lugworm presence was restricted to the upper 5 cm. This upper sediment layer was characterized by a significant treatment x sediment type interaction ($F_{2,8}$=7.80; p=0.013) due to more pronounced POC accumulation in exclusion sites at the fine sanded site. Organic accumulation in 1 to 5 cm depth was generally higher on the exclusion plots (Tukey Kramer $p<0.01$). The organic content within the upper 5 cm of the sediment was significantly correlated with the fine fraction (Fig. 4). The strongest correlation was found for the surface sediment but relatively more organic material was associated with the fine fraction in 1-5 cm depth.

3. 4 Sediment permeability

Permeability of the sediment at the study site depended strongly on the grain size composition of the sand matrix (Fig. 5), reflected in a significant sediment type effect (Table 3). The composition of the sand matrix explained more than 70% of permeability variance in both years. In average sediment in the fine sanded area was 5 times less permeable than sediment from the medium sanded area (k=2x10^{-12} m²) compared to k=9x10^{-12} m²). While the effect of lugworm treatment showed no significant effect on permeability in autumn 2003, data from summer 2004 revealed a significant impact. Sediment from control plots showed an up to 8-fold higher permeability compared with

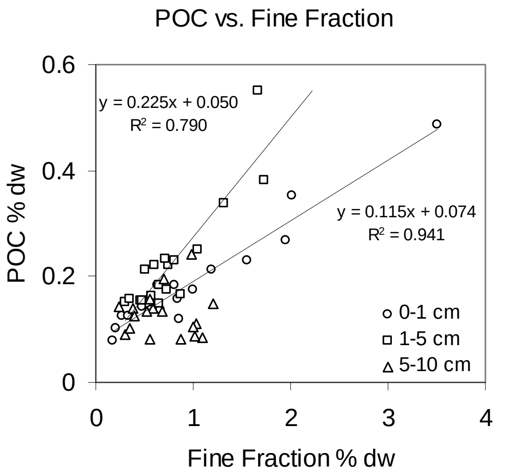

Figure 4. Correlation between fine fraction and POC in sediment samples from 0 to1 cm depth (circles), 1 to 5 cm depth (squares) and 5-10 cm depth (triangles) from the 18 experimental plots. For samples from 5-10 cm depth no correlation was found.

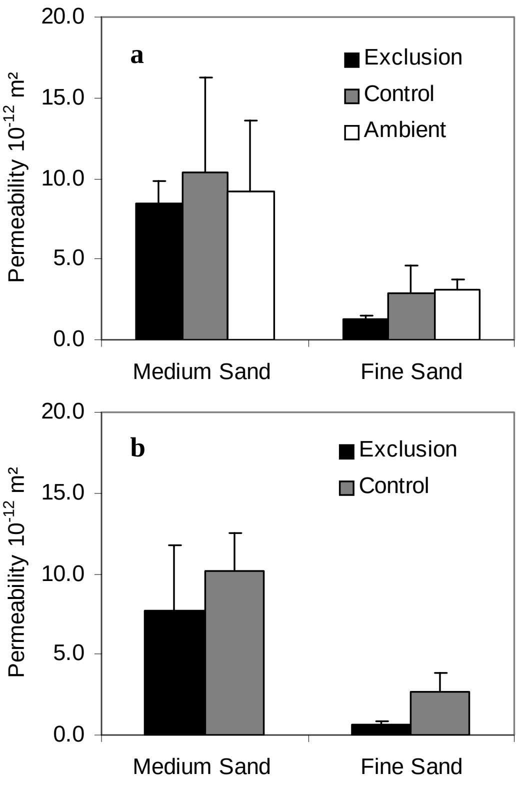

Fig. 5. Sediment permeability of experimental plots in (a) November 2003 and (b) July 2004 (mean and SD; n=3)

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.

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

sediment of the exclusion plots from the same experimental block. Beneath the general composition of the sand matrix, the amount of incorporated fine particles was found to have significant impact on sediment permeability (Fig. 6). With increasing fraction of fine material sediment permeability decreased indicating a clogging effect of fine particles. The 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 amount of fine particles (~1%) the sediment matrix was clogged and sediment permeability 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.

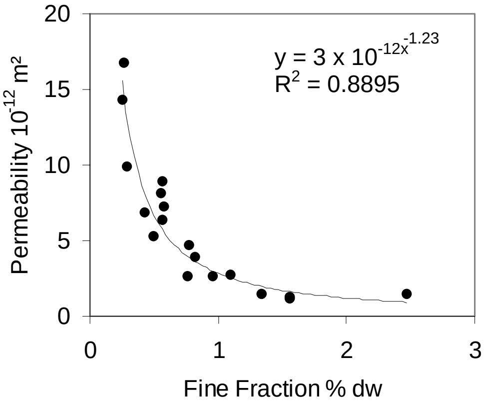

Fig. 6. Correlation between silt fraction of the upper 10 cm (in % of the dry weight) and sediment permeability (in 10^{-12} m²) for all 18 experimental plots.

3.5 Chlorophyll concentration

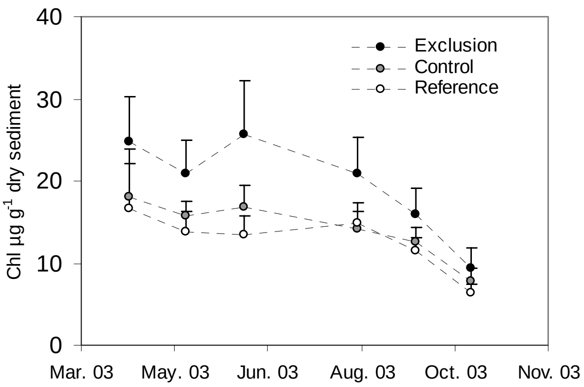

Figure 7. Chlorophyll content of the upper sediment cm in µg g^{-1} dry sediment. Shown are mean (n=6) and standard deviation.

The chlorophyll content of the surface sediment was significantly reduced by lugworm presence (Table 4). Most pronounced chlorophyll concentration differences could be observed in summer (Fig. 7). 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 sanded area and in repeated measures ANOVA treatment x sediment type interaction over all months only slightly fails significance (Table 4). Seasonal variation in chlorophyll content was much more conspicuous in the absence than in the presence of lugworms. Highest impact of *A.*

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

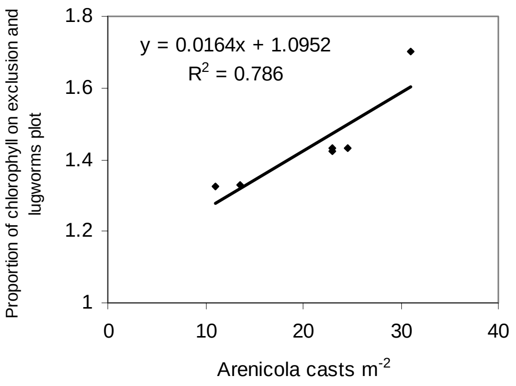

Fig. 8. Correlation between *Arenicola* casts (feeding activity) and proportion of chlorophyll concentration on exclusion and lugworm plots. For lugworm plots, chlorophyll concentration was averaged over control and adjacent ambient plots.

marina presence on the chlorophyll content was observed in month with highest feeding activity (Fig. 8). Lugworm feeding activity therefore seemed to be an important factor controlling chlorophyll concentration in the sediment.

3.6 Pore-water nutrient profiles

Nutrient profiles were strongly influenced by the presence of *A. marina*. Ammonia, phosphate and silicate showed a similar pattern of profile modification (Fig. 9). On the exclusion plots inorganic nutrient concentrations were almost linear increasing with depth reaching concentrations of up to 25 µM phosphate, 300 µM ammonia and 250 µM silicate in a depth of 20 cm. In the presence of *A. marina* ammonia, 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 $p<0.05$).

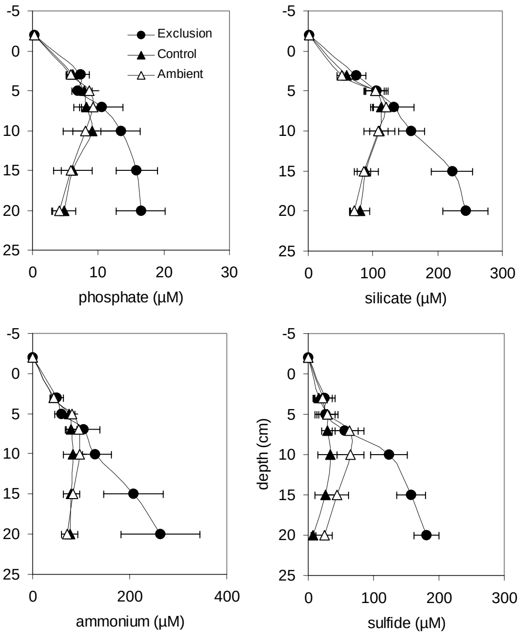

Fig. 9. Phosphate, silicate and ammonium and sulphide profiles from experimental plots July 2004. Shown are means and SE (n=6). Samples taken within a nearby tidal channel in the same week were added and represent nutrient concentrations in the overlying water.

High sulphide concentration could only be found in pore-water from the exclusion plots. In the absence of *A. marina* sulphide concentrations of more than 150-200 µM could be measured in samples from 15 and 20 cm depth. In the presence of lugworms sulphide concentrations stayed far below 100 µM. Nitrogen relevant profiles indicate nitrification in the presence of lugworms (Fig. 10). While nitrate concentrations on the exclusion plot were low over the whole investigated depth, nitrate concentrations increased in the presence of lugworms from 15 cm downwards and reached up to 20 µM at a depth of 20 cm. 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 *A. marina* on nutrient concentrations was not restricted to deep sediment layers. Ammonia concentrations increased with depth on all plots but with almost doubled concentrations on the exclusion plots (Fig. 11). Additionally, lugworm presence inhibited the formation of sub-surface peaks of phosphate in the upper cm and of silicate in 2-3 cm depth. ANOVA revealed significant treatment effects on concentrations of ammonia 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

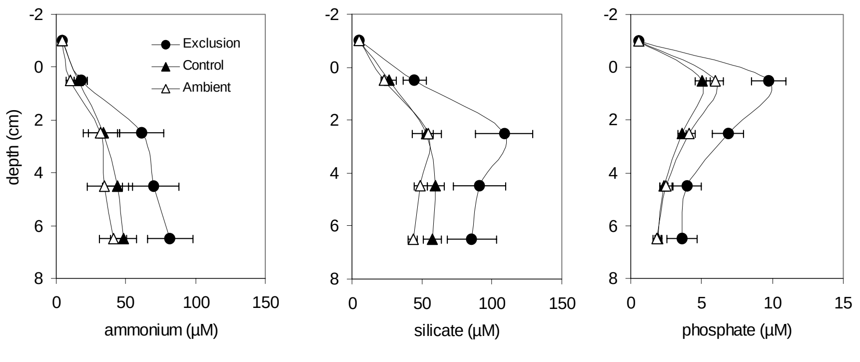

Fig. 10. Ammonium, nitrite and nitrate profiles from experimental plots in April 2004. Shown are means and SE (n=6). Samples taken within a nearby tidal channel in the same week were added and represent nutrient concentrations in the overlying water.

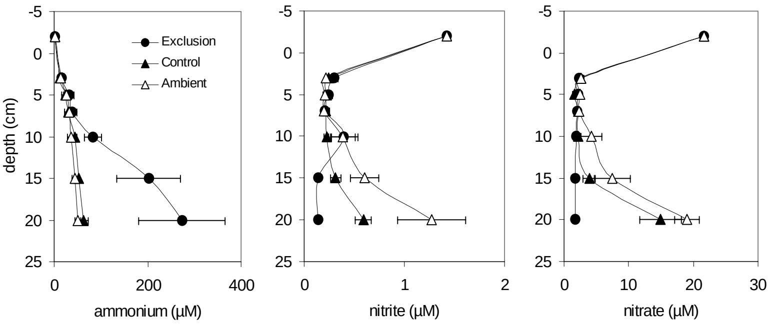

Figure 11. Ammonium, silicate and phosphate profiles from experimental plots in October 2003. Porewater was retrained by flushing 1 cm slices of 3 pseuedoreplicate cores with nitrogen gas. Shown are means and SE (n=6). Samples taken within the tidal channel in the same week were added and represent nutrient concentrations in the overlying water.

upper cm ($F_{2,8}$=11.941; p<0.01) with significant higher concentrations on exclusion plots (Tukey Kramer p<0.01). The effect of lugworms on nutrients was the same in both sediment types.

4. DISCUSSION

4. 1 Ecosystem engineering by *Arenicola marina*

This experiment revealed a manifold effect of lugworms on the solid and pore-water phase of intertidal sandflats. These effects were not restricted to the vicinity of individual burrows but affected the characteristic of the entire tidal flat. The observed changes in sediment characteristics are not independent of each other. Thus, we do not regard each as separate evidence but as necessary parts of a syndromatic development leading from sand towards mud flats. The most obvious change was the accumulation of fine particles and associated organic matter (POM) in the upper 5 cm in the absence of *A. marina* conjunct with a decrease in sediment permeability. Lugworm surface defecation, followed by resuspension of fine material from washed away casts is presumably one important mechanism for the observed lower fine fraction inventory in the presence of lugworms. According to Cadée (1976), sediment reworking by *A. marina* on the lugworm plots of this study corresponds to a sediment layer of approximately 10 cm yr^{-1}. Small particles have a greater chance to be swallowed than large ones (Baumfalk, 1979) and are deposited on the sediment surface within the faecal casts. In shallow waters tidal currents and wave action are the dominating forces for particle fluxes between the sediment water interface (Miller and Sternberg, 1988; de Jonge and van Beusekom, 1995). Fecal casts of *A. marina* may persist several tidal cycles under calm conditions but can be washed away by waves and currents within minutes after submersion (personal observation). Thereby especially fine particles are resuspended and get removed from the sediment. The increased roughness of the seabed due to lugworm mounds and pits can additionally enhance erosion and resuspension of material (Graf and Rosenberg, 1997) and solutes (Huettel and Gust, 1992). Lowered chlorophyll concentrations (due to abolition of feeding activity and reduced nutrient concentrations in the pore-water) may be additionally responsible for the observed low amount of fine particles in surface sediments of lugworm tidal flats, since diatom films are able to accumulate fine particles and stabilize the sediment (Mayer et al., 1985; Brouwer et al., 2000; Yallop et al., 2000). Differences in sediment chlorophyll content between lugworm dominated and exclusion plots were highest in periods of intensive lugworm feeding activity in summer. Grazing of microalgae by deposit feeding infauna was assumed as mechanism controlling their abundance in former studies (Davis and Lee, 1983). High rates of disturbance and burial additionally can reduce sediment chlorophyll concentrations (Webb and Eyre, 2004). Increased microphytobenthic growth on lugworm exclusion plots may have been additionally facilitated by higher nutrient supply in the less bioirrigated sediment (Flothmann and Werner, 1991).

The effect of lugworm absence/presence was not restricted to the sediment surface. The accumulation of organic material and reduced pore-water solutes in the absence of *A. marina* presumably indicate a less effective degradation of organic material (Kristensen, 2001). 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 spinoid polychaete *Pygospio elegans* during all years of this study, especially on the exclusion sites, 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 additionally explain the downward transport of fine particle and organic material (Sun et al., 1991). Temporally increased accumulation of fine material at the sediment surface had therefore lasting consequences for deeper sediment layers. It could be shown that the incorporation of fine particles and associated organic material into the sand matrix significantly reduced sediment permeability by clogging the sediment matrix. Exclusion of *A. marina* in the fine sanded area resulted in a decrease of sediment permeability below $k = 1 \times 10^{-12}$ m² which is thought to be a critical value for advective pore-water flow (Huettel et al., 2003).

The analysis of the pore-water revealed a strong effects of *A. marina* on nutrient profiles and in contrast to most of the sedimentary 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 studies by Huettel (1990) the results from this study indicate a much stronger accumulation of nutrients within experimental lugworm exclusion plots. This may be due to the larger scale of experimental plots reducing the impact of lateral pore-water exchange (Rocha, 2000). Higher nutrient concentrations in surface sediments of exclusion plots might be a combined effect of abolition of bioirrigation and the decreased sediment permeability which may inhibit advective pore-water exchange.

Changes in sediment permeability are also important for *A. marina* itself, since lugworms need to pump water through the sediment for respiration. A standard lugworm (0.5 g dry weight) needs to pump 1.5 ml min^{-1} oxygen rich water through its burrow (Riisgård et al., 1996). This is done with a maximum pressure corresponding to a water column of 20 cm H_2O and normal operating pressure of 5 cm H_2O. The permeability measurements revealed, that water flow through the sediment from exclusion areas in the fine sanded area decreased to rates, which would be critical for lugworm survival (0.5 ml min^{-1} through a sediment column of 7.5 cm with a pressure head of 20 cm H_2O). Sediment from lugworm plots showed minimum flow rates of about 2 ml min^{-1} (pressure head 15 cm H_2O) allowing sufficient oxygen supply. Therefore lugworms create suitable conditions for the lugworm population by maintaining high sediment permeability.

Stimulation of nitrification through oxygen supply via lugworm ventilation was not restricted to the lugworm burrow but could be found in the entire sediment in depth of 15 to 20 cm. Reduced sulphide concentrations due to reoxidation of reduced compounds by bioirrigation was observed in former studies (Banta et al., 1999; Kristensen, 2001; Nielsen et al., 2003). However, 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).

4. 2 Implications of ecosystem engineering by *Arenicola marina* for intertidal habitat succession

Ecosystem engineering by the lugworm *A. marina* had significant effects on sediment and pore-water characteristics. Overall, sedimentary effects were much more conspicuous in the intertidal area where median grain size was low than where it was high, while effects on pore-water chemistry did not differ between sediment types. Coarse grained sediments with a median above 300 µm were less efficient in accumulating fine particles and less susceptible for sediment clogging. For the geomorphological development of coarse grained sands *A. marina* seemed to be of minor importance. However, in fine sands lugworm activity significantly decreased accumulation of fine particles and associated organic material. Chlorophyll concentrations were reduced and sediment permeability was maintained. Especially fine grained sands, which typically occur in between sandflats in the low intertidal and mudflats near the high water line, are therefore susceptible for ecosystem engineering effects of *A. marina*.

It should be mentioned that processes at the sediment surface were temporally very dynamic, which has been shown to be typical for intertidal sandflats (Miller and Sternberg, 1988). Enhanced accumulation of fine material on lugworm exclusion plots was observed during periods of calm conditions while under higher hydrodynamic forces accumulated material started to erode from the sides of the experimental plots and resulted in a mosaic of elevated and eroded patches. Single storm events sometimes even eroded most of the deposited material. Thus, the size of experimental exclusion plots (in combination with high sediment resuspension during stormy periods) may still not be sufficient to allow a successful development from sandy towards muddy sediments. However the at least temporally 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 suggests, that *A. marina* inhibits the intertidal habitat succession from sandy towards more muddy flats and contributes to the maintenance of permeable sands, at least on a geological time scale.

4. 3 Conclusions

By its bioturbation and bioirrigation activity lugworms alter sediment and pore-water characteristics and maintain their own habitat. This habitat is characterized by high sediment permeability where they easily can pump sufficient water volume for their respiration. At least during times of suspended matter import, lugworms prevent a clogging of the sediment with fine particles and organic compounds, especially in areas where the sand matrix is fine grained (grain size median below 300 µm). They reduce the storing capacity of organic compounds and inorganic nutrients within the sediment. Low sulphides concentrations in the pore-water furthermore affect habitat suitability for other organisms. Due to their widespread distribution with a high and constant population density on intertidal sands, *Arenicola marina* can be entitled as an ecosystem engineer of soft bottom marine habitats. The syndromatic development of large-scale lugworm exclusion plots suggests that lugworms are able to prevent a succession from sand towards mud flats and the smooth transition from permeable sands to cohesive mudflats is significantly shifted to the former by *A. marina*. Accounting for their prominent role in the Wadden Sea ecosystem we conclude, that without this ecosystem engineer mud flats would greatly expand at the costs of sand flats in the Wadden Sea.

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Habitat shift from diffusive to permeable sediment characteristics in intertidal sand by the lugworm *Arenicola marina*

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ABSTRACT

Ecosystem engineering in marine benthos by the lugworm *Arenicola marina* has sweeping consequences for biogeochemical processes in intertidal sands and is not restricted to the vicinity of individual burrows. Large scale experimental exclusion of lugworms resulted in an increased sediment clogging with fine particles, leading to approximately a 8-fold decrease in sediment permeability. High sulfide and ammonium concentrations in the porewater of the exclusion plots indicated a more reduced environment with higher nutrient and organic storing capacity in sediment without the lugworm. Lugworms maintain a close coupling of solutes and particles between marine sediments and the tidal water above. They increase the depth of the sediment where aerobic microbial processes take place directly by burrow ventilation but also indirectly by increasing sediment permeability and by improving the habitat for other burrowing infauna. Sandflats densely populated by *A. marina* share characteristics with more exposed sands, where advective processes dominate and combine the filter efficiency of permeable sands with high secondary production of more cohesive sediments.

1. INTRODUCTION

Sandy sediments cover approximately 70% of North Sea coastal zones. Their relevance for mineralization processes capacity has become a focus of interest over recent years (Cammen, 1991; De Beer et al., 2005). There is an increasing evidence for high metabolic activity in organic-poor, sandy sediments facilitated by porewater advection, especially in shallow coastal waters (Malcolm and Sivyer, 1997). Sediment permeability in combination with small-scale pressure gradients induced by hydrodynamic forces enable high exchange rates of oxygen (Forster et al., 1996; Ziebis et al., 1996), dissolved and particulate organic matter (Huettel et al., 1996) and nutrients (McLachlan, 1985; Rocha, 1998).

While processes in permeable sediments are thought to be driven by current and wave induced advective porewater flow (Rusch and Huettel, 2000), bioturbating organisms are of major relevance in more cohesive sediments. Macrofauna activities can have significant effects on biogeochemical processes and exchange rates between deeper sediment layers and the overlying water (Kristensen, 1988; Aller, 1998) especially in cohesive sediments where advective porewater flow and oxygen supply are confined to a thin top sediment layer. The implications of bioturbation and bioventilation on the character of marine sediments have been reviewed by several authors (Rhoads, 1974; Cadée, 2001; Reise, 2002). These processes affect the sediment composition (Botto and Iribarne, 2000), porewater nutrient profiles (Huettel, 1990), oxygen fluxes (Ziebis et al., 1996; Glud et al., 2003; Wenzhoefer and Glud, 2004), benthic microflora (Branch and Pringle, 1987), and associated meio- and macrofauna (Reise, 1987; Schaffner, 1990). Bioturbation additionally alters sediment surface microtopography, which has effects on advection and porewater chemistry (Ziebis et al., 1996). Burrows act as hot spots of organic matter diagenesis due to a three-dimensional mosaic of oxic/anoxic interfaces associated with their walls (Kristensen, 2000).

In intertidal sands of the Wadden Sea (North Sea, Europe), the world's largest coherent system of tidal flats, the lugworm *Arenicola marina* is a dominant member of the macrobenthos in medium to fine sand. Roughly 90% of the total 4300 km² of tidal flats are "lugworm flats", populated by 20 to 40 ind. m^{-2} (Beukema, 1976; Reise, 1985). Abundances are low to zero in soft mud, and also low in clean, unstable sands exposed to strong currents or waves near low water line and below (Longbottom, 1970). *A. marina* lives in 20 to 40 cm deep J-shaped burrows, completed to a U-shape by a vertical head shaft through which surface sediment slides down, is ingested by the worm and defecated as a fecal mound at the sediment surface above the tail shaft. Burrow ventilation for respiration is done by piston-like movements in a tail-to-head direction. At the study site lugworms replace a sediment layer of 15 cm per year and pump 3 L m^{-2} h^{-1} of seawater into the anoxic sediment (Riisgård and Banta, 1998).

In our study area, a sheltered bay with 4.8 km² of tidal flats at the leeward side of the island of Sylt, about 90% are densely populated by lugworms (Reise et al., 2001). In this intertidal flat, a large-scale long-term lugworm exclusion experiment with six exclusion areas, each with an area of 400 m², was started in 2002. This experiment revealed that *A. marina* has a significant effect on habitat characteristics of an intertidal sandflat by preventing sediment clogging and preserving a high sediment permeability (Volkenborn et al., in prep.). A comprehensive approach was initiated to investigate the significance of lugworm activity for biogeochemical processes in marine sediments after 2 years of lugworm exclusion. Parallel investigations at the experimental site and at in a nearby permeable sand in the shallow subtidal zone were conducted to compare a sheltered intertidal system with and without a large bioturbator and an hydrodynamic exposed permeable system. In particular, in-situ oxygen and sulfide profiling was combined with ex-situ planar optode measurements and stirring chamber incubations for measuring oxygen consumption rates, since oxygen uptake is the most widely used measure of sediment mineralization rates (Thamdrup and Canfield, 2000). Oxygen and sulfide dynamics were analyzed in-situ on experimental plots. Investigations on the sediment, porewater, and macrobenthic community characteristics were done at all sites (Exclusion, Lugworm, Subtidal). Characterization of other sediment properties, including grain size composition, organic content, Chl *a* content, sediment permeability and porewater nutrient profiles, allowed inferences on underlying mechanisms of oxygen and sulfide dynamics.

2. METHODS

2.1. Study site and lugworm exclusion area

The study was conducted on a sandflat in Königshafen (55°02´N, 08°26´E; Fig.1A, B) near the island of Sylt, Germany. Sediments at the experimental site are moderately sorted fine to medium sand with a median particle size of 230 µm. Due to aeolian sand input from surrounding dunes, medium sands dominate the edges and grain size median decreases towards the centre of the embayment (Austen, 1994). Tidal currents are the dominant hydrodynamic force, but wave action becomes important when winds blow from northern and eastern directions, forming sand ripples with an amplitude of up to 5 cm and height of up to 2 cm. In 2002 a large scale,

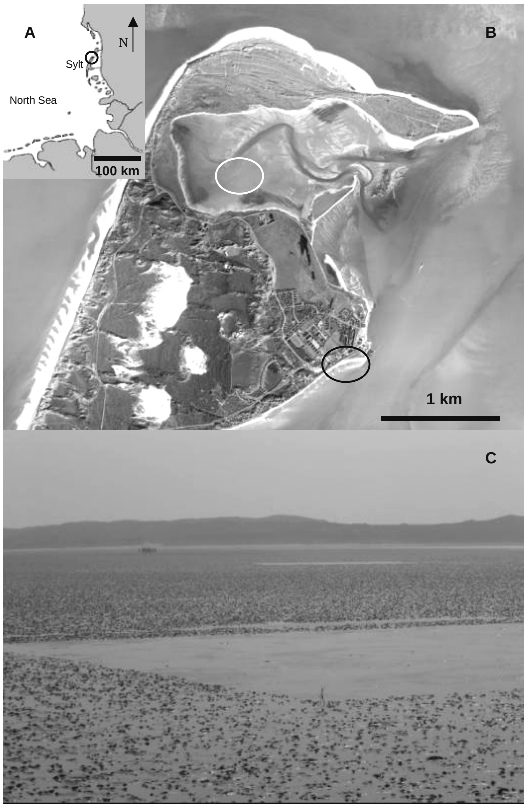

Figure 1: (A) Study area in the northern part of the Wadden Sea. (B) Experimental sites on a sheltered tidal flat (white oval) and in a shallow subtidal located at a more exposed sandflat (black oval). (C) Experimental plot, where lugworms were excluded on 400 m^2 areas by inserting a 1 mm meshed net in 10 cm sediment depth.

long-term lugworm exclusion experiment was commenced by inserting a 1 mm meshed net 10 cm deep into the sediment, blocking the burrows of *Arenicola marina* on six areas of 400 m^2 each (Fig. 1C). For control, areas of the same size next to each exclusion plot were disturbed with a backhoe in the same way, but without inserting the net. The large size of the experimental plots (20 by 20 m) was chosen to minimize effects of lateral sediment transport typical for sandy intertidal flats (Grant et al., 1997).

The measurements presented here were conducted on one of these exclusion and its corresponding control plots in the intertidal region. Additional investigations were done at a nearby (2 km) subtidal station, where the sediment is permeable, composed of moderately- well to well sorted, medium sand with a median grain size of 340 µm and characterized by a high metabolic activity (De Beer et al., 2005; Hedtkamp, pers. comm.). Salinity at both sites varies on average between 27.5 psu in spring and 31 psu in summer and freshwater up-welling is negligible. Mean tidal range is 1.8 m. Emersion time of experimental plots is about 3-4 h per tide. Further details of the study site are provided by Austen (1994), Reise (1985), and Gätje and Reise (1998).

2. 2 Macrofauna sampling

Lugworm abundance was estimated by counting *A. marina* casts within ten randomly chosen 0.25 m^2 quadrates. The number of fecal castings varies with feeding activity of lugworms but can be taken as a reliable proxy for lugworm abundance (Flach and Beukema, 1994). Counting casts was done 2 hours after exposure on calm days without rain. Macrofauna sampling at the intertidal sites was done by counting animals retained with a 1 mm sieve from 8 randomly chosen cores (area of 100 cm^2, depth of 10 cm). Sampling at the subtidal station was done from a ship using a 14 x 14 cm Box-core. Six parallel cores to a depth of about 15 cm were taken and sieved through a 500-µm mesh. Animals from all stations were divided into four groups: tube or burrow building worms, free burrowing worms, mollusks, and others. Biomass was determined from the combined samples as ash free dry weight (AFDW).

2. 3 Sediment and porewater sampling

Since the aim of the study was to investigate the impact of *A. marina* on habitat scale rather than on the scale of single burrows, samples for sediment and porewater analyses at the lugworm site were taken at least 10 cm away from lugworm casts or funnels. Apart from this, samples were taken randomly, excluding a 2 m wide region on both experimental plots to minimize possible edge effects. Samples at the subtidal station were taken randomly.

2. 4 Solid phase analysis

From each site four parallel cores (10 cm^2) were taken for sediment analysis. For the first 10 cm, sediment was sampled in 1 cm slices. On the lugworm and subtidal site one additional sample was taken from 15 cm depth. After homogenizing the 1 cm slices from parallel cores, three sub-samples of about 3 g were taken from each depth, freeze dried and kept at –20 °C until further handling. The rest of the sediment was used for the porewater extraction by blowing with nitrogen gas (see following). Two of the freeze dried sub-samples were used for the determination of POC/PON and Chl *a* content, which was done in triplicates. For the determination of particulate organic matter, 75 mg homogenized sediment samples were treated with 1 N HCl to remove carbonates, dried (1 h, 70 °C) and analyzed with a C:N analyzer (Thermo-Finnigan Flash EA 1112). Chlorophyll *a* was extracted from 1 g samples with 10 mL acetone (90%) overnight at 4 °C and centrifuged for 5 min at 4000 rpm. Concentrations of Chl *a* were measured spectrophotometrically according to Lorenzen (1967). The third freeze dried sub-sample was used for grain size analysis with a laser particle sizer. This was done with the sediment from the exclusion and lugworm site. Prior to the analysis, samples were treated with acetic acid (30%) to remove carbonate particles and with hydrogen peroxide (30%) to remove organic compounds. Samples were treated with ultrasonic to separate associated particles. The proportion of the fine fraction was additionally estimated by dry sieving of pooled samples from 20 locations within each plot taken with a 2 cm² core to 5 cm depth. The sediment was washed with freshwater to remove salt and freeze dried. Sediment permeability was estimated by the constant head method (Klute and Dirksen, 1986). From each site three 10 cm² cores were taken and the time needed for the passage of 1 mL seawater was measured under 4 different pressures, ranging from 5 to 30 cm of water column (0.5–3.0 kPa).

2. 5 Porewater extraction and analysis

Two different techniques were used to extract porewater from the sediment. In the first technique, which was used to test the effect of *A. marina* on porewater chemistry in deep sediment layers, a porewater sampling device was modified after Huettel (1990). With this “porewater-lance” multiple porewater samples were collected simultaneously from 6 different depths (3, 5, 7, 10, 15, 20 cm) while maintaining anaerobic conditions. A PVC-plate at the sediment surface was used to prevent intrusion and mixing with overlying water. The steal tip allowed penetration of the net to sample sediment layers deeper than 10 cm. From each of four randomly chosen positions within one experimental plot about 5 mL of porewater were retrieved. The first 2 mL were discarded to rinse the tygon tubing. The pooled 20 mL samples were filtered (0.45 µm nylon filter) and frozen at –20 °C (for phosphate and ammonium analysis) or put in the fridge at 4 °C (silicate analysis) until measurements with an autoanalyser (AA_3, Bran & Luebbe). Sampling was done in October 2003 and April and July 2004. In July 2004 sulfide concentrations in the porewater were measured with the colorimetric methylene blue method (Fonselius, 1983). Sampling with the porewater lance was only successful in the intertidal area (exclusion and lugworm plots).

A second porewater extraction method was based on blowing out porewater with pressurized N_2 gas (Billerbeck, pers. comm.). This method was applied for all sites and enabled the measurement of nutrient concentrations in porewater with higher spatial resolution. One centimeter slices from four parallel cores (10 cm²) from each site were pooled. The obtained porewater samples of about 5 mL were handled as described previously.

2. 6 Microsensor measurements (in-situ)

In-situ microsensor measurements were done with an autonomous profiler (Gunderson and Jørgensen, 1990). Day and night profiles from exclusion and lugworm plots were measured continuously during the submersion period (approximately 10 hours) in April 2004. For daytime measurements the autonomous profiler was equipped with 2 Clark-type oxygen microelectrodes (Revsbech, 1989). During the night a sulfide microsensor was added (Jeroschewski et al., 1996). The sulfide sensor is too light-sensitive for daytime use. Profiling was done in 150 µm steps to a depth of 10 cm. On the lugworm plot measurements were carried out approximately 10 cm away from *Arenicola* casts and funnels. Approximately 20 profiles were obtained with each microsensor during one submersion period. Oxygen penetration depths (z_P) and sulfide distributions were determined as a function of time.

2. 7 Planar optode measurements (ex-situ)

Depth profiles of volumetric oxygen consumption rates in the sediment were determined by the flow-through method (Polerecky et al., 2005). The employed planar oxygen optodes (Glud et al., 1996) and the luminescence lifetime measuring system (Holst and Grunwald, 2001) allowed the determination of oxygen concentrations and consumption rates with high spatial resolution and in 2D.

In June 2004 five parallel cores from the exclusion and four parallel cores from the lugworm plot were investigated with the flow-through technique. The sampling cores, equipped with planar oxygen optodes, had a surface area of 7.5 x 7.5 cm and were taken to a depth of 10 cm. Cores were percolated with in-situ seawater under pressures ranging from 0 to 50 cm water column (0-5 kPa). Due to low permeability, especially at the exclusion plot, a vacuum pump was used to suck water through the sediment core in order to reach deeper oxygen penetration. After a steady state of oxygen distribution was reached, percolation was stopped, oxygen images were recorded every 10 s and an image of volumetric oxygen consumption rates (OCR_v) was calculated as described in Polerecky et al. (2005). OCR_v were averaged in a horizontal direction, resulting in depth profiles of potential volumetric oxygen consumption rates (denoted as $OCR_v(z)$). Using the oxygen penetration depth, z_p, measured in-situ by the microprofiler (see above), areal oxygen consumption rates (OCR_a) were calculated as

$$(1) \qquad OCR_a(z_p) = \int_0^{z_p} \phi OCR_v(z)dz.$$

The sediment porosity, ϕ, was estimated from 1 cm sediment slices taken from sampling cores to a depth of 5 cm by determining the weight loss after drying the sediment at 60° C.

2. 8 Benthic chamber incubation (ex–situ)

Independent measurements of areal oxygen consumption rates in the sediment were done using benthic chambers. Chamber incubations were carried out in April 2004 with four cores from the exclusion site and three cores from the lugworm and subtital site. Chambers with a diameter of 8.3 cm were taken to a depth of about 10 cm. Cores were brought to the nearby lab and left overnight in a water bath (150 L) with site water at in-situ temperature (12° C). Chambers were submerged with 0.8 L of site water and a magnetically coupled stirring system in each Plexiglas chamber was suspended about 6 cm above the sediment surface, rotating at 50–60 rpm in the closed chambers. To determine areal oxygen consumption rates, sediment cores were incubated in darkness for about 5 hours and oxygen concentrations were measured in the overlying water. Samples of 50 mL were taken from each chamber with a syringe at the start and approximately 1, 3, and 5 hours after the incubation started. The sample volume was replaced by air saturated site water. Photosynthetic activity was measured in the same chambers. For light measurements, cores were illuminated with 20 to 30 µmoles photons m^{-2} s^{-1} (measured 1 cm above the sediment surface). Since it was not possible to create exactly the same light conditions in each chamber, daytime oxygen fluxes were normalized to 30 µmol photons m^{-2} s^{-1}, assuming a linear relationship between the light intensity and oxygen production for the used intensity range. Oxygen concentrations were measured by Winkler titration immediately after sampling. At the end of incubation, samples for the estimation of the Chl *a* content were taken and cores were sieved through a 500 µm mesh for the identification of macrofauna species. Their biomass was determined as ash free dry weight.

2. 9 Statistical analysis

Macrobenthic community response was tested by ANOSIM using the PRIMER v5 software

Table 1
Functional composition of the macrobenthic community at the exclusion, control and subtidal sites (mean and standard deviation, Exclusion and Lugworm n=8, Subtidal n=6).

	Exclusion ind.m^{-2}		Lugworm ind.m^{-2}		Subtidal ind.m^{-2}		ANOVA statistics of log transformed data	
	mean	sd	mean	sd	mean	sd	F	p
Arenicola marina	0.0		23.6	8.1	0.0			
tube / burrow building worms	2100.0	1282.9	937.5	465.8	42.5	59.6	6.34	**0.025**
free burrowing worms	775.0	712.6	1312.5	247.5	739.8	288.2	6.73	**0.021**
molluscs	312.5	290.0	200.0	256.3	51.0	79.0	1.07	0.319
others	0.0	0.0	0.0	0.0	17.0	41.7		
biomass (g m^{-2})	5.3		6.7		-			

package (Primer-E Ltd). Similarity matrix, based on Bray-Curtis coefficients of square root transformed data was used for ANOSIM global and pair-wise tests and for MDS plotting. For chamber incubations one factorial ANOVA was used to test for the effect of experimental site on oxygen fluxes, Chl *a* concentration and macrofauna biomass. Prior to analysis data were square root transformed to achieve homogeneity of variance. Post-hoc tests were done performing the Tukey HSD procedure on a $p<0.05$ level.

For this study only one out of six exclusion and corresponding lugworm areas were chosen to allow the implementation of time consuming methods. In a strict sense, samples taken within one of the experimental sites were not statistically independent. The outcome of the statistical analyses should therefore be regarded as likely trends and the large size of the experimental plots (each 400 m²) should not belie the indispensable need of independent parallels. However, it should be noted that the chosen experimental plots were not exceptional in any way when compared to the others and were chosen for logistical reasons.

3. RESULTS

3. 1 Macrofauna

The placement of the 1 mm mesh net 10 cm deep into the sediment resulted in a complete exclusion of *Arenicola marina* from the experimental plot. Lugworm casts were only found on the lugworm site with densities of about 24 casts m^{-2}. Functional group response was tested by dividing macrobenthic species into four groups depending on their living mode. Comparing the functional benthic community at the three sites (Table 1), it becomes apparent that free burrowing species without a permanent burrow system (mainly *Scoloplos* cf. *armiger* and *Spio martinensis*) were the dominating functional group at the subtidal site, while tube building species (mainly *Pygospio elegans* and *Hetromastus filiformis*) were the dominant group at the exclusion site. At the lugworm site most individuals were free burrowing species (*Scoloplos* cf. *armiger* and the oligochaete *Tubificoides benedii*) but tube builders were also abundant. Multivariate analysis of the functional group composition revealed a significant functional community discrimination for the three sites (ANOSIM global test) and significantly different functional communities in pair-wise tests (Table 2). The functional composition at the

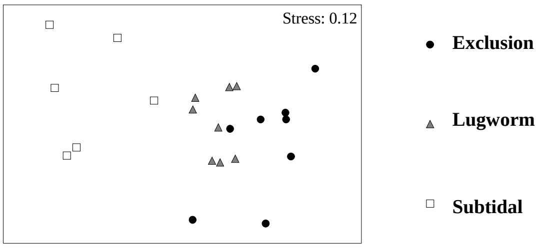

Fig. 2. MDS plots of macrofauna community based on Bray Curtis similarity of root transformed data (species were grouped into free burrowing worms, tube builders, molluscs, and others).

Table 2. Analysis of similarities (ANOSIM) of the macrofauna community at the three different sites.

ANOSIM			R	p
global	-	-	0.609	0.001
pairwise tests	Exclusion	Lugworm	0.384	0.001
	Exclusion	Subtidal	0.869	0.001
	Lugworm	Subtidal	0.835	0.002

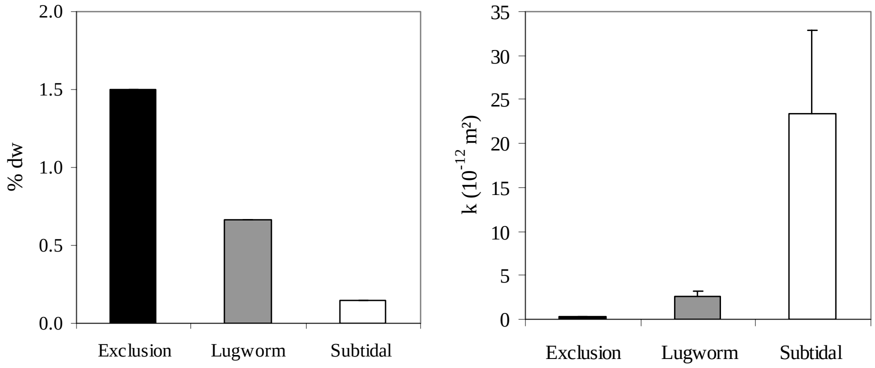

Fig. 3. (A) Proportion of the fine fraction (dry sieving) of the sediment in the top 5 cm layer and (B) sediment permeability at the exclusion, lugworm and subtidal sites.

lugworm site was intermediate, showing characteristics from both the subtidal and exclusion communities (Fig. 2).

3. 2 Solid phase analysis

Sediment characteristics significantly differed between sites (Fig. 3). Dry sieving of the sediment revealed that the amount of fine particles (<63 µm) in the top 5 cm of the sediment was highest at the exclusion (1.5 weight %), medium at the lugworm (0.66%) and lowest at the subtidal station (0.14%). Sediment permeability differed fundamentally between the three sites. Sediment permeability at the lugworm plot ($k = 2.6 \times 10^{-12}$ m²) was 8-fold higher than at the exclusion plot (0.3×10^{-12} m²). The highest permeability was found in the subtidal sand (23.4×10^{-12} m²), 9-times more permeable than the sediment at the lugworm plots and about 70 times more permeable than the sediment from the exclusion site.

Regarding the proportion of the fine fraction, laser particle size measurements revealed the same differences between the exclusion and lugworm areas (Fig. 4A). On the exclusion plot 17.1% (330 mg cm^{-3} sediment) of particles in the upper 10 cm were smaller than 63 µm but only 8.8% (175 mg cm^{-3} sediment) on the lugworm plot. In this fine fraction the grains sizes were homogenously distributed over the different size classes from coarse silt (32-63 µm) to clay (<2 µm). At the intertidal sites highest concentrations of fine particles were found at the sediment surface, indicating high

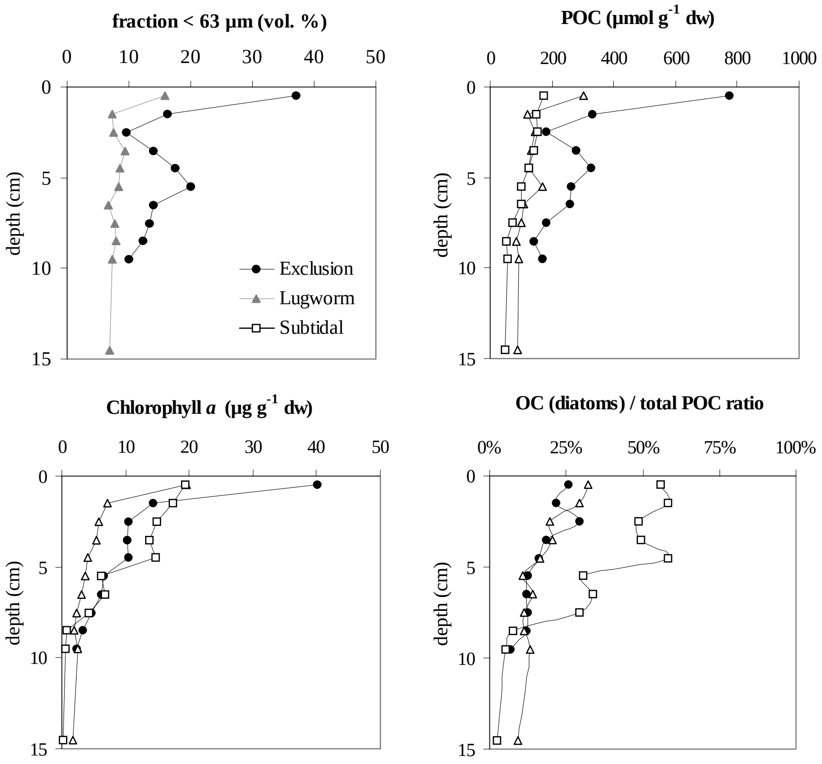

Fig. 4. (A-D) Solid phase characteristics of the sediment from exclusion, lugworm, and subtidal sites. The fraction <63 µm was determined by laser particle sizing.

deposition rates during the investigation time, which was not the case at the subtidal site. On the exclusion plot a second subsurface layer with a high amount of fine particles was found at 4-7 cm. In this layer the amount of fine particles was doubled compared with lugworm plot sediment and formed a “sticky” subsurface sediment horizon.

The distribution of particulate organic carbon (Fig. 4B) was significantly positively correlated with the distribution of the fine fraction (r^2=0.933; $p<0.001$). While the organic matter on the lugworm and the subtidal plot was about 0.2% dry weight and rather homogenously distributed over the top 15 cm, slowly decreasing with depth, sediment from the exclusion plot showed a clear horizontal stratification with maximum values at the surface (almost 1 % dry wt) and between 4 and 6 cm depth (0.4% dry wt).

C:N ratios were between 7 and 9.5 and showed no trend with depth or between sites. Chl *a* concentrations were highest in surface sediment of the exclusion plot (~ 40 µg g^{-1} dry sediment), compared to less than 20 µg g^{-1} dry weight on the lugworm and the subtidal plots (Fig. 4C). In the sediment from the subtidal station high concentrations of Chl *a* were found to a depth of 5 cm while Chl *a* concentrations in the intertidal were concentrated in the upper cm. Assuming a POC:Chl *a* - ratio of 60, diatoms made up about 25% of the total POC in the upper cm of the exclusion and lugworm site, but more than 50% at the subtidal site (Fig. 4D).

3. 3 Porewater analysis

Nutrient concentrations were strongly affected by the presence of lugworms (Fig. 5). The profiles obtained by the porewater-lance sampling technique indicated a deep flushing by *A. marina*. On the lugworm plot maximum concentrations of ammonium, phosphate and silicate were found in 5-7 cm depths. In contrast, nutrient profiles on the exclusion plot showed an almost linear increase from 7 cm downwards reaching several times higher concentrations than in the lugworm site. Maximum concentrations of ammonium, phosphate, and silicate in 20 cm depth were 400 µmol L^{-1}, 30 µmol L^{-1}, and 270 µmol L^{-1}, respectively. This exclusion effect was obvious during all seasons. While sulfide concentrations on the lugworm site were below 20 µmol L^{-1} at all depths, high sulfide concentrations were encountered on the exclusion plot below 7 cm, reaching concentrations of more than 200 µmol L^{-1} below 10 cm depth.

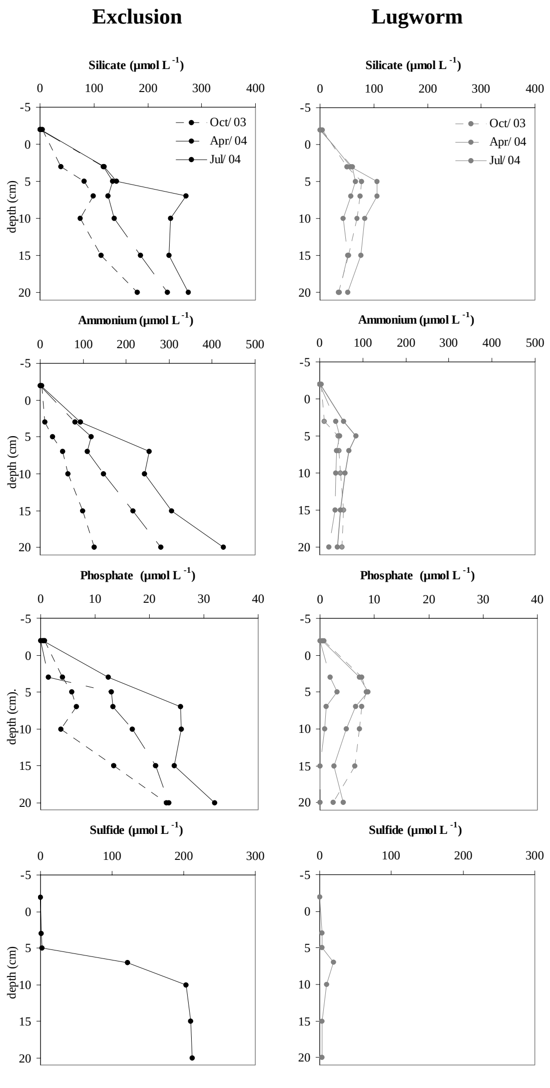

Fig. 5. Nutrient profiles in different seasons obtained by the method using a porewater lance. Values represent averages from samples taken at 4 different locations within each site. At each location about 5 mL porewater was taken from each horizon.

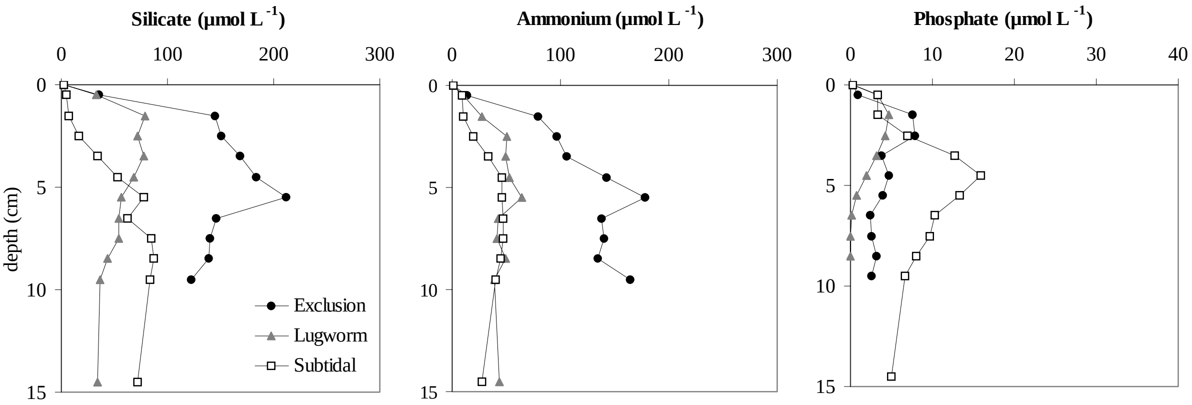

Fig. 6. Porewater nutrient profiles at the three sites in April 2004 extracted from 1 cm slices by a method based on flushing by pressurized N_2.

Porewater extraction with pressurized N_2 resulted in nutrient profiles with higher vertical resolution for the top 10 cm. While the trends in the profiles were consistent with those observed by the porewater-lance based method (see previously), this method additionally allowed a comparison between all the three sites (Fig. 6). The impact of lugworms on nutrient profiles was clearly not limited to deep horizons. On the lugworm plot lower concentrations were observed than on the exclusion plot. Silicate concentrations were more than twofold lower below 2 cm. On the exclusion plot an additional peak at 6 cm depth was observed. At the subtidal station silicate concentrations were low in the upper centimeters and stayed rather constant (~80 µmol L^{-1}) below 6 cm. Ammonium concentrations were low at the lugworm and subtidal sites, while they increased with depth at the exclusion site reaching concentrations of more than 150 µmol L^{-1}. Phosphate concentrations were higher at the subtidal station than in intertidal sediments. Phosphate subsurface concentration peaks were observed between 2 to 3 cm depth on the exclusion plot (8 µmol L^{-1}) and in 4 cm depth on the lugworm plot (5 µmol L^{-1}).

3. 4 Oxygen dynamics in chamber incubations

Oxygen consumption rates measured by chamber incubations were done at both experimental sites as well as at the subtidal site. Results are summarized in Table 3. During night oxygen uptake rates were significantly different at all three sites ($F_{2,9}$=11.46; p<0.01). Dark flux at the subtidal

Table 3
Oxygen fluxes across the sediment-water interface in the light (at 30 mmol photons m-2 s-1) and in the dark based on chamber incubation measurements. Gross photosynthetic oxygen production was calculated as light flux – dark flux. Negative values indicate fluxes from the water into the sediment. Mean values and standard deviations (SD) were obtained from n=4 (Exclusion), n=3 (Lugworm) and n=3 (Subtidal) replicate measurements. Values of the macrofauna biomass (AFDW) and Chlorophyll a content in the sediment in the chambers are also shown.

		Exclusion		Lugworm		Subtidal	
		mean	sd	mean	sd	mean	sd
Light flux	mmol m^{-2} h^{-1}	0.83	0.57	1.24	0.59	1.57	0.36
Dark flux	mmol m^{-2} h^{-1}	-1.38	0.26	-1.15	0.09	-0.79	0.04
Gross photosynthesic oxygen production	mmol m^{-2} h^{-1}	2.21	0.46	2.40	0.55	2.36	0.35
AFDW	g m^{-2}	11.4	6.4	12.4	8.8	1.4	1.9
Chl *a*	µg g^{-1}	29.9	7.2	16.5	0.6	16.5	1.2

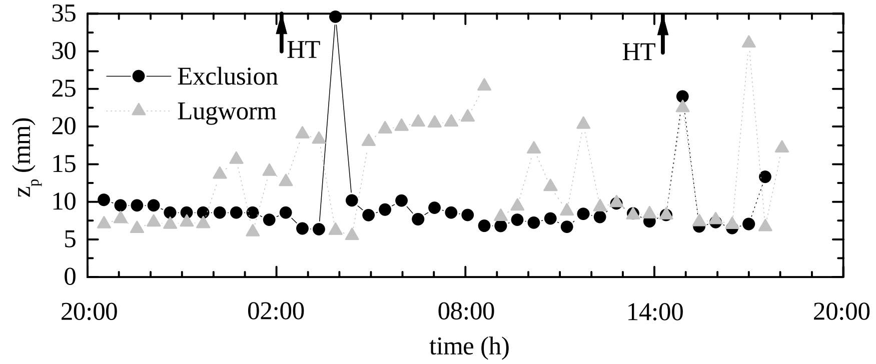

Fig. 7. Oxygen penetration depth on the exclusion and lugworm sites as a function of time determined from in-situ microprofiles measured during night and daytime (April 2004). Arrows indicate the time of the high tide (HT).

site (0.79 ± 0.04 mmol m^{-2} h^{-1}) was significantly lower than at the exclusion site (1.38 ± 0.26 mmol m^{-2} h^{-1}; Tukey HSD-Test, $p<0.01$), but not significantly different from the flux at the lugworm site (1.15 ± 0.09 mmol m^{-2} h^{-1}; Tukey HSD-Test, $p>0.05$). Oxygen fluxes during daytime were much more variable than dark fluxes, leading to no significant differences observed between the sites. Gross photosynthetic oxygen production was very similar in all plots (2.21 - 2.40 mmol m^{-2} h^{-1}). Significantly higher Chl *a* content in surface sediment of the exclusion site (Tukey HSD-Test, $p<0.05$) did not result in significantly different gross photosynthetic rates. Macrofauna biomass in the subtidal site was almost 10-fold and significantly lower than in the intertidal sites (Tukey HSD-Test, $p<0.05$).

3. 5 In-situ oxygen and sulfide dynamics

In-situ oxygen and sulfide microprofiles were measured in April 2004 at the exclusion and lugworm sites during a period of calm and sunny days. When the profiles were not influenced by bioirrigation, no clear differences in oxygen penetration depth were observed between day and night, nor between ebb and flood measurements at both sites (Fig. 7). On many occasions, however, the shape of profiles indicated bioirrigation events, resulting in subsurface oxygen concentration peaks and increased oxygen penetration depths. These events were more frequent on the lugworm plot, where about 48% of the profiles had increased oxygen penetration depth up to 20 mm, whereas only 7% of profiles from the exclusion plot were affected. Taking into account all measured profiles, oxygen penetration depth was higher on the lugworm plot (13.0 ± 6.6 mm) than on the exclusion plot (9.3 ± 4.9 mm).

Sulfide dynamics fundamentally differed between the experimental plots. While no sulfide signal was detected on the lugworm plot (data not shown), on the exclusion plot high sulfide concentrations (up to 150 µmol L^{-1}) were found below 6 cm depth directly after submersion (23:00 h) and below 8 cm during high water (02:00 h) and thereafter (Fig. 8). Over the entire tidal cycle moderate sulfide concentrations (20–50 µmol L^{-1}) were additionally detected at depths between 2-8 cm.

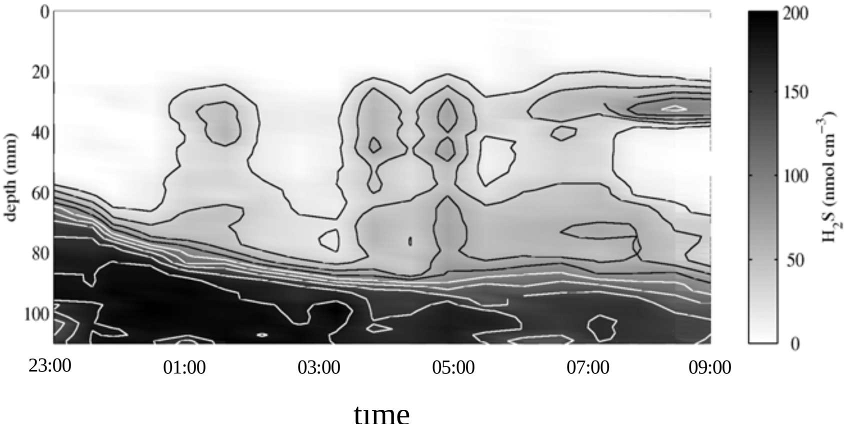

Fig. 8. Sulphide dynamics at the exclusion site during night (high tide at 02:00 h) revealed by in-situ microsensor time series measurements (April 2004).

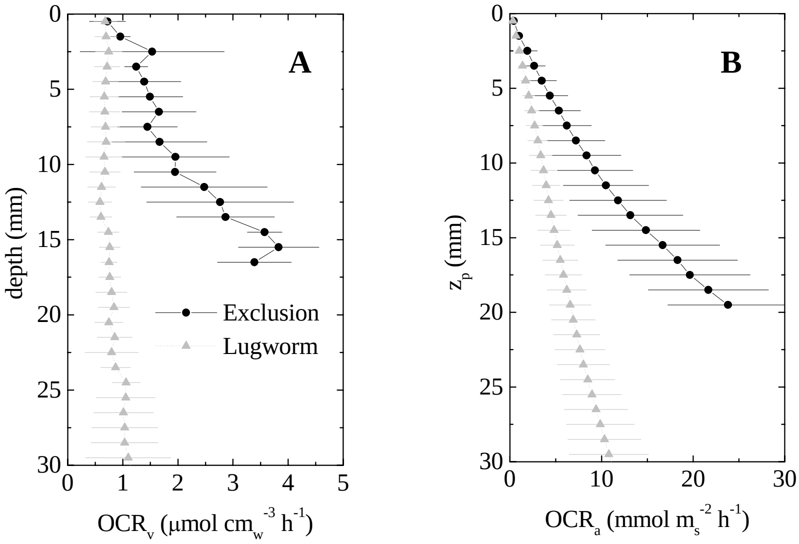

Fig. 9. (A) Depth profiles of volumetric OCR expressed per cm^3 of porewater. (B) Areal OCR as a function of oxygen penetration depth calculated from (A) using Eq. 1.

3. 6 Oxygen consumption rates measured by planar optodes

Depth profiles of potential volumetric OCR, obtained by averaging of OCR images (images not shown) in the horizontal direction, are shown in Fig. 9A. The rates on the lugworm plot ranged from 0.6 to 1.5 µmol cm^{-3} h^{-1} and were almost constant in the top 20 mm. In the sediment from the exclusion site OCR$_v$ rapidly increased with depth. In the top 2 mm average OCR$_v$ were about 0.6 µmol cm^{-3} h^{-1} and comparable to OCR$_v$ on the lugworm site, but reached rates of up to 4.2 µmol cm^{-3} h^{-1} at a depth of 15 mm. Much higher standard deviations indicate a much higher horizontal variability of OCR$_v$ on the exclusion site.

Using the depth profiles of OCR$_v$ and Eq. 1, potential areal oxygen consumption rates (potential OCR$_a$) were calculated and are shown as a function of oxygen penetration depth in Fig. 9B. The increase of potential OCR$_a$ with oxygen penetration depth was much stronger on the exclusion plot than on the lugworm plot. For oxygen penetration depths lower than 10 mm there were no significant differences in the potential OCR$_a$ between the two plots. However, for z_p >10 mm the exclusion plot showed significantly higher potential OCR$_a$.

Combining the in-situ time series of oxygen penetration (Fig. 7) and the planar optode measurements of OCR$_v$ (Fig. 9A), areal oxygen consumption rates (OCR$_a$) were calculated for both experimental sites (Fig. 10). The OCR$_a$ were very variable and ranged between 4.8 – 9.0 mmol m^{-2} h^{-1} on the exclusion plot and between 2.4 – 7.2 mmol m^{-2} h^{-1} on the lugworm plot. During times of low variability, i.e., when the profiles were not affected by bioirrigation (e.g., the first 4 hours), OCR$_a$ were threefold higher on the exclusion site.

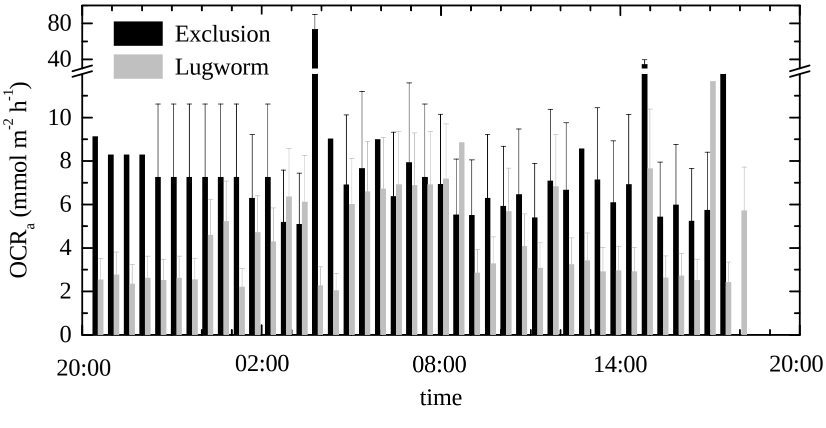

Fig. 10. Dynamics of areal OCR obtained by combining the in-situ measurements of oxygen penetration depth (Fig. 7) and the OCR measurements by a planar oxygen optode (Fig 9).

3. 7 Oxygen penetration into sediment

Steady state oxygen distributions obtained during the percolation of the sediment cores with aerated seawater under different pressure heads are shown in Fig. 11. The images demonstrate that oxygen penetration, at a given pressure head *h*, was clearly easier in the sediment from the lugworm site. This is quantitatively shown in Fig. 12A. Even though relatively lower volumetric OCR in this site (see Fig. 9A) are potentially responsible, the primary reason for this observation was the significantly higher permeability of the sediment from the lugworm site, which allowed higher flow-rates of water through the sediment (Fig. 12B) and thus more efficient delivery of oxygen by advection. Images in Fig. 11 also revealed that the pressure-induced water flow occurred preferentially in channels, indicating a possible inhomogeneity in sediment permeability caused by infauna activity. Combining the oxygen penetration values (Fig. 12A) with the depth profiles of OCR_v (Fig. 9) in Eq. 1, the obtained areal OCR_a demonstrate that, at a given pressure head, the sediment from the lugworm site has a much higher potential for oxygen uptake than the sediment from the exclusion site (Fig. 12C).

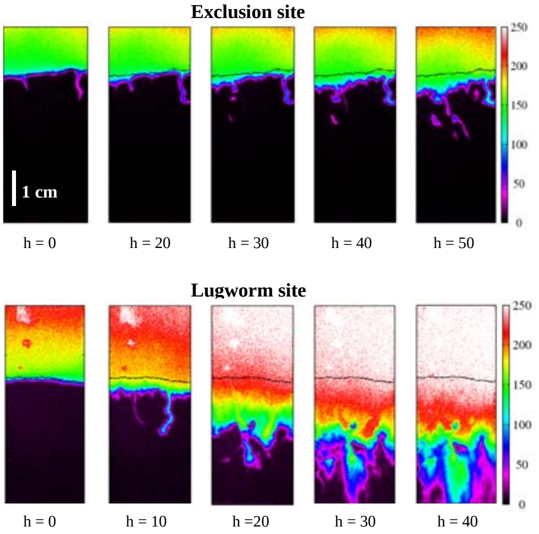

Fig. 11. Steady state oxygen distributions at different water pressure heads (h in cm) in sediment from the exclusion and lugworm plots measured in a core equipped with a planar oxygen optode. Black horizontal line indicates the sediment surface.

4. DISCUSSION

Sandy tidal flats, densely populated by the lugworm *Arenicola marina*, differ in many respects from sandflats where lugworms were excluded (Volkenborn and Reise, submitted; Volkenborn et al., in prep.; this study) and share many characteristics of permeable sands. Lugworms decrease the accumulation

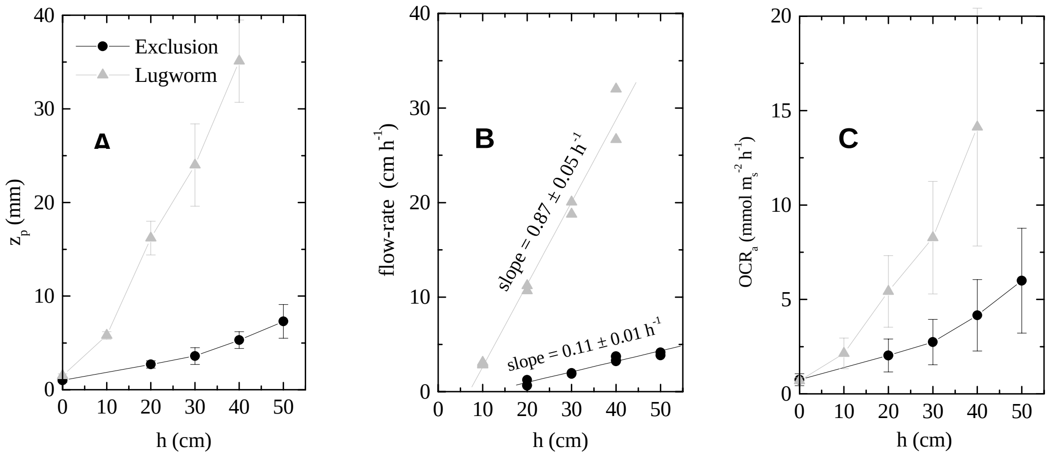

Fig. 12. (A) Oxygen penetration depth, (B) water flow-rate, and (C) areal oxygen consumption rates as a function of the pressure head revealed by planar optode imaging. Data in (A) were extracted from images in Fig. 11, while data in (C) were calculated by combining values in (A) and Fig. 9.

and consolidation of fine particles and associated organic material in the sediment and thereby maintain higher sediment permeability. Conjunct with their bioirrigation activity, they decrease nutrient and sulfide concentrations in the porewater. These changes in habitat properties had significant consequences for the macrobenthic community. Free burrowing species, being directly exposed to the sediment and porewater, benefit from ameliorated habitat characteristics mediated by the presence of lugworms, while tube building species were inhibited due to unstable conditions (Volkenborn and Reise, in press).

4. 1 Effects of lugworms on sediment and porewater characteristics

The effect of *A. marina* on sediment and porewater characteristics is manifold. Primarily, the presence of *A. marina* inhibits fine particle accumulation, presumably as a result of its bioturbation activity. Sediment reworking by *A. marina* on the lugworm plot of this study corresponds to a sediment layer of approximately 10 cm yr^{-1}. Due to their greater chance of being swallowed, small sediment particles are deposited on the sediment surface within the faecal casts. Although fecal casts of *Arenicola* may persist several tidal cycles under calm conditions, they can be washed away by waves and currents within minutes after submersion, leading to a loss of the fine fraction from the sediment.

Additionally, the increased roughness of the sea-bed due to lugworm mounds and pits can enhance erosion and resuspension of material (Graf and Rosenberg, 1997). Furthermore, lowered Chl *a* concentrations (due to abolition of feeding activity and reduced nutrient concentrations in the porewater) may also be responsible for the observed low amount of fine particles in surface sediments of lugworm tidal flats, since diatom films are able to accumulate fine particles and stabilize the sediment (Grant et al., 1986; Yallop et al., 2000).

The effects of lugworm absence/ presence were not restricted to the sediment surface. From the surface layer fine particles and associated organic material were incorporated and consolidated in the subsurface sediment. The incorporation of fine material by advective co-transport of the fine particles to several cm depths was observed by Rusch and Huettel (2000). In addition, biogenic activities of benthic organisms may have contributed to this consolidation of fine particles. High abundances of tentaculate polychaetes like *Pygospio elegans* during all years of this study, especially on the exclusion site, are capable of enhancing particle removal from the water column and their tubes may function as small sediment traps, bringing fine material to 3-5 cm depths (Bolam and Fernandes, 2003).

The incorporation of fine particles into the sand matrix clogged the sediment and significantly reduced sediment permeability from $k = 2.58 \times 10^{-12}$ m² to $k = 0.33 \times 10^{-12}$ m². This is lower than the minimum value of $k = 1\text{-}1.5 \times 10^{-12}$ m² needed for advective interfacial water fluxes (Huettel and Gust, 1992) and suggests that at the exclusion plot diffusive fluxes dominate the porewater exchange with the overlying water.

Porewater profiles of phosphate, silicate and ammonium indicate a significant flushing effect of *A. marina*. In the presence of lugworms concentrations of silicate were 5-fold lower and those of phosphate and ammonium 10-fold lower than concentrations at the lugworm exclusion site in 10 cm depth. Compared with previous studies by Huettel (1990) using the same porewater extraction method, the flushing effect of *A. marina* was considerably higher. While nutrient profiles in the presence of *A. marina* had about the same shape in both studies, large-scale, long-term exclusion of *A. marina* resulted in higher nutrient concentrations than reported previously. Additionally, the impact of lugworms on nutrients concentrations was not limited to deep (>10 cm) sediment layers. Phosphate, ammonium and silicate concentrations were reduced approximately by a factor of 2 within the upper 5 cm of the sediment. This significant decrease indicated efficient removal of degradation products from the lugworm inhabited sediment.

4. 2 Areal oxygen consumption rates

Major parameters affecting total sedimentary oxygen consumption include sediment permeability (Rusch and Huettel, 2000), organic content (Banta et al., 1999), microbial activity (Mackin and Swider, 1989), microalgae and meiofauna respiration (Schwinghamer et al., 1986), and macrofauna activity (Wenzhoefer and Glud, 2004). For most of these parameters significant impacts of *A. marina* could be detected in this large-scale long-term exclusion experiment (Volkenborn et al., in prep.; this study). The proportions of the above factors to overall oxygen consumption rates remain speculative, but overall lugworm presence decreases the oxygen consuming compartments and increase sediment permeability. Especially the accumulation of reduced compounds like sulfides and ammonia in the absence of *A. marina* is likely to increase oxygen consumption by their re-oxidation. The importance of reduced compounds for total oxygen consumption (Cook et al., 2004) is supported by an almost linear increase of volumetric OCR in the upper 15 mm of the sediment at the exclusion site.

Sediment chamber incubations revealed that the trophic sediment characteristics (heterotrophy versus autotrophy) differed between the three experimental sites (Table 3). In the subtidal and permeable sand light fluxes of oxygen from the sediment into the water were twofold compared with fluxes from the water into the sediment in the dark. At the lugworm site light and dark fluxes were approximately the same and at the exclusion site oxygen consumption of the sediment core in the dark exceeded the light flux by a factor of 1.6. We cannot give a general statement on the trophic status of the sediments at the three sites because photosynthetic oxygen production by the microphytobenthos will considerable vary with tidal height, turbidity of the water and season. What can be seen, however, is a trend from a rather heterotrophic system at the exclusion site to a rather autotrophic at the permeable site.

Oxygen consumption rates based on chamber incubations have the disadvantage of excluding large infauna (Glud et al., 2003), hydrodynamic forces and their considerable impact on in-situ exchange processes from measurements (Huettel and Gust, 1992). For the calculation of areal oxygen consumption rates (OCR_a), we therefore additionally used the combination of in-situ oxygen penetration depth measured by microsensors and volumetric oxygen consumption rates revealed by planar oxygen optode imaging. The observed total oxygen consumption rates were very variable in time but with 2.4 to 9.0 mmol m^{-2} h^{-1} well within the range found in other field studies (e.g., Wenzhoefer and Glud, 2004). Oxygen penetration depth was highly variable in time and subsurface oxygen peaks presumably indicate fauna-driven irrigation events (Wenzhoefer and Glud, 2004). This impact of infauna on the oxygen penetration depth was more frequent at the lugworm tidal flat than at the exclusion site. While infauna activity moderately, but almost continuously, affected oxygen penetration depth and OCR_a on the lugworm plot, peaks of OCR_a on the exclusion plot were high but occurred only occasionally. Fauna mediated oxygen uptake temporarilly doubled the total oxygen uptake from 3 to 6 mmol m^{-2} h^{-1} at the lugworm site while it played only a minor role at the exclusion site (Fig. 10). It seems to be unlikely that this increase of oxygen input is solely due to bioventilation by *A. marina* itself, since microsensor measurements were done with at least 10 cm distance to lugworm burrows and exchange rates between tail shaft and surrounding sediment are limited due to mucus lining. Instead, the differences in fauna mediated oxygen uptake may be due to higher sediment permeability combined with higher abundances of free burrowing worms (like *Scoloplos* cf. *armiger*). Bioventilation by these species in permeable sediments has presumably significant flushing effects since oxygen rich water is pumped directly through the sediment matrix. Tube builders (like *Pygospio elegans*) were more abundant on the exclusion site but their bioventilation impact in the less permeable sediment may be small due to limited exchange of oxygen between the tube and surrounding sediment. It is suggested that changes in the benthic community structure caused by *A. marina* facilitates bioirrigative flushing.

During times of low bioventilation activity oxygen penetration depths were between 5 and 10 mm and no obvious differences were observed between the lugworm and the exclusion plots. However, measurements were done during calm days without wind and wave action. It can be speculated that under higher hydrodynamic input sediment permeability becomes a critical factor determining the oxygen penetration depth. These conditions were mimicked by the flow-through method and higher sediment permeability at the lugworm site indeed allowed a significantly deeper oxygen penetration (Fig. 9). The 8-fold higher sediment permeability on the lugworm site facilitates advection and results in an increase in oxygen penetration depth and total oxygen uptake. At the exclusion site oxygen penetration depths were low even for high pressure heads, but volumetric OCR were significantly higher than in the presence of lugworms. Thus, OCR_a at the exclusion site can presumably be attributed to high oxygen consumption within a relatively thin aerobic metabolically active sediment layer, while oxygen consumption on the lugworm site occurs in a thicker sediment layer with a lower volumetric oxygen demand, especially under more efficient hydrodynamic input. Thus, although the in-situ overall oxygen uptake was almost the same, the underlying mechanisms of oxygen delivery and uptake differed fundamentally between the two habitats.

The discussed changes in habitat characteristics and exchange processes are not independent of each other. Thus, we do not regard each as separate evidence but as necessary parts of a syndromatic development leading to a shift from a rather cohesive sediment in the absence towards a more permeable sand in the presence of *A. marina*.

4. 3 Geochemical impacts of macrofauna on intertidal sediments

Due to their dominating occurrence, especially on intertidal sandflats, bioturbating macrofauna and their impact on the biogeochemical processes were in the focus of several studies (Ziebis et al., 1996; Botto and Iribarne, 2000; D`Anderea et al., 2002). Bioturbating and bioirrigating macrofauna maintain a close coupling of particles and porewater between the sediment and the tidal water above. A pit-and-mound topography at the sediment surface induces advective porewater exchange by creating pressure gradients within the surface sediment (Ziebis, et al. 1996). Burrow walls act as "hot spots" for organic matter decay (Kristensen, 2000) and products of organic matter degradation are efficiently transported into the overlying water (Ziebis et al., 1996). With this study we could show that the impact of burrowing macrofauna is not restricted to the vicinity of individual burrows, but can affect the entire sand characteristics by different direct and indirect processes. However, caution should be taken in generalizing the observed effects of *A. marina* on other system. The deposition of sediment at the sediment surface may not necessarily lead to higher sediment permeability by reduced accumulation of fine particles within the sediment. For the burrowing crab *Chasmagnathus granulata* it has been shown that deposition of fine cohesive sediments on the surface lead to a stabilization of the sediment (Botto and Iribarne, 2000). Feeding pits accumulate fine material which can lead to a locally clogged sediment filter (D´Andrea et al., 2002). We suggest that the impact of large burrowing macrofauna is closely linked to the hydrodynamic regime. At least at semi-exposed tidal flats where a pit-and-mound topography is frequently obliterated by water movements, fine material within deposits becomes resuspended, leading to the maintenance of higher sediment permeability in the presence of bioturbating infauna. The shift from a rather diffusive system in the absence to a rather advective system in the presence of lugworms is conjunct with a high storing capacity of reduced compounds and organic material at the lugworm exclusion site, while low organic content and rapid exchange of porewater is typical for the lugworm site.

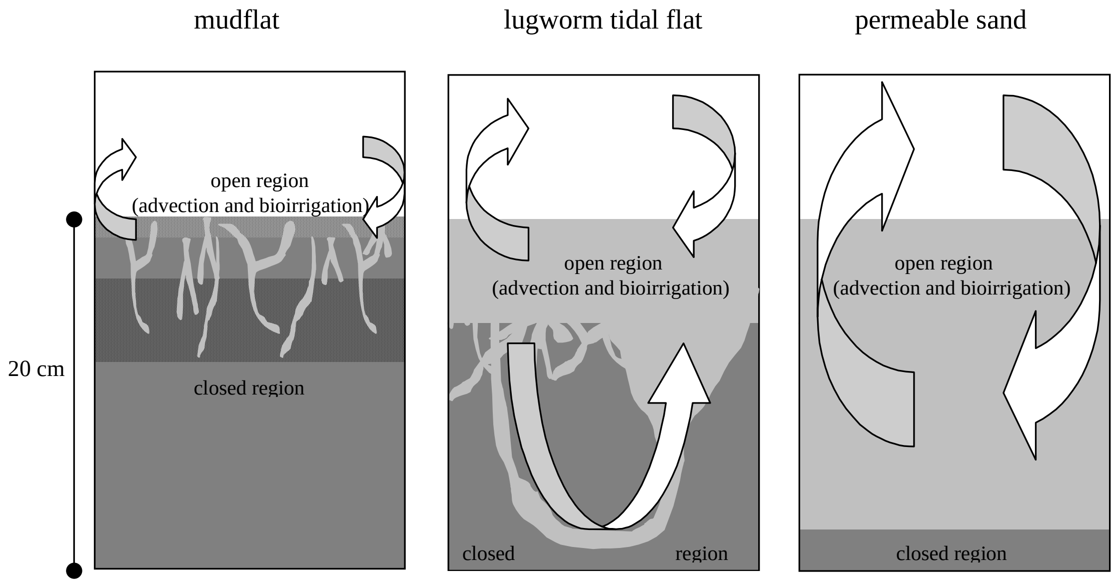

Fig. 13. Schematic diagram depicting a habitat shift induced by *Arenicola marina* from a diffusion dominated cohesive system (mudflat) to an advection dominated permeable sand. The higher contribution to the open system (light grey) in the presence of lugworms is due to higher sediment permeability (caused by preventing sediment clogging with fine particles; black dots) and more effective bioirrigation by facilitated free burrowing infauna in the presence of lugworms and by *A. marina* itself.

4. 4 Conclusions

This study stresses the relevance of macro-invertebrates to ecosystem functioning of intertidal sandflats by different interacting mechanisms. Apart from direct effects of bioturbation and bioventilation, such as porewater flushing and reduction of the organic inventory, long-term changes in sediment characteristics preserve sediment permeability. Assuming a smooth transition between diffusive dominated mudflats, with a relatively small open region, and advective dominated permeable sands, it can be concluded that lugworms are capable of shifting the habitat to the latter system (Fig. 13). The increase of the open system region is conjunct with an accelerated remineralization of organic material and an efficient removal of degradation products from the sediment. *Arenicola marina* increases the volume of the open system (1) by its own bioventilation, (2) by facilitating other bioirrigating infauna, and (3) by inhibiting sediment clogging. The effect of bioturbating animals on biogeochemical processes is not limited to the adjacency of their burrows but may affect the characteristics of the entire sediment (at least of the top 15 cm investigated in this study) with sweeping consequences for ecosystem functioning. These effects involve changes in sediment properties interacting with changes in the functional benthic community composition. Sandflats, densely populated by lugworms combine the filter efficiency of permeable sands and high secondary production of more muddy sediments. Due to its widespread distribution along the northwest European coasts, *A. marina* is a key factor in biogeochemical cycling in fine sanded intertidal sediments.

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Cumulative sediment mediated effects of *Arenicola marina* on polychaete functional diversity revealed by large-scale experimental lugworm exclusion

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ABSTRACT

The lugworm *Arenicola marina* was excluded from sandy sediment in the mid and low intertidal zone of the Wadden Sea. Exclusion, control and ambient plots were 400m² each, replicated 6 times and sampled in August of three consecutive years. Responses were analysed with respect to functional trait groups in the associated polychaete assemblage. Using uni- and multivariate statistical techniques, a paradoxical result was obtained. In the third year, when lugworm density had decreased 4-fold on control and ambient plots, the polychaete functional group composition on lugworm exclusion plots differed more strongly from that on control and ambient plots than in the two previous years. Tube building worms and predacious worms were most abundant on exclusion plots while subsurface deposit feeders tended to dominate in the presence of lugworms. Lugworm effects were stronger in a low intertidal fine sand than in a mid intertidal medium sand. Apparently, the permanent exclusion of lugworms initiated a cumulative change in sediment properties on the exclusion plots. Overall, lugworm effects were highly dependent on space and time as well as differential recruitment success in this intertidal polychaete assemblage. Sediment mediated effects of an ecosystem engineer on associated species appear to be subtle and contingent in variable environments.

Keywords: *Arenicola marina*, Benthic Assemblage, Bioturbation, Functional Groups, Intertidal, Polychaetes, Wadden Sea

1. INTRODUCTION

Tidal flats in the Wadden Sea are widely populated and strongly bioturbated by the lugworm *Arenicola marina* (Beukema, 1976; Cadée, 1976; Reise, 1985). Its dominant appearance aroused interest on the effects of lugworms on other sediment dwelling organisms and on implications of their bioturbating and bioirrigating activity for habitat properties (review by Riisgård and Banta, 1998). While lugworms were found to facilitate small zoobenthos in the immediate vicinity of ventilated burrows by supplying oxygen to an otherwise anoxic subsurface sediment (Reise, 1981, 1983; Lackschewitz and Reise, 1998) disturbances at the sediment surface by their reworking activity was found to inhibit some other, primarily sedentary species (Brey, 1991; Flach, 1992a,b, 1993, 1996; Flach and de Bruin, 1993). These results were either based on sampling of burrow structures, on small scale field experiments (<2 m²) where lugworms were excluded or added, and on correlative studies on a km-scale. The assumed mechanisms are small-scale interactions directly related to burrow maintenance and feeding activity of the lugworms. Given the small size of most infauna and their limited motility, it is assumed that such biotic interactions are confined to small distances at the surface (Zajac et al., 1998; Zajac, 2004) as well as below (Lackschewitz and Reise, 1998). Much less is known about sediment mediated biotic interactions on a meso-scale (Zajac et al., 1998) arising from ecosystem properties modified by populations of habitat engineering species (sensu Jones et al., 1994). This can be partly explained by the fact that most experimental studies of assemblage formation in soft sediment habitats have been conducted at small scales (<1m², Hall et al., 1994). However, biogenic habitat transformations (sensu Reise, 2002) are well known to structure benthic assemblages and these may extend over wider spatial scales.

Indirect effects may be easily modified by changing boundary conditions and may require an extravagant approach to become visible. In fact, experimental exclusion of *A. marina* from replicated 400 m² plots induced significant changes in habitat properties including an increase in microphytobenthic biomass, an accumulation of sulphide, inorganic nutrients, fine particles and associated organic matter and a decrease in sediment permeability (Volkenborn et al., 2005a, submitted). With this study we test whether ecosystem engineering by *A. marina* affects the benthic community on the scale of our experimental plots.

We here focus on the response of polychaete species to experimental lugworm exclusion since polychaetes are the most diverse group in the benthic macrofauna and comprise a variety of feeding and mobility modes (Fauchald and Jumars, 1979; Reise, 1985). The presence of different trophic and mobility traits at the study site allows to test predictions for functional modes. Furthermore, functional groups eased comparisons between years because inter-annual fluctuations of individual species are high in temperate intertidal sediments (Beukema, 1991). Other abundant macrofauna species on the experimental plots, the gastropod *Hydrobia ulvae* and the juvenile bivalves *Macoma balthica* and *Mya arenaria* were omitted to analyse their dynamics separately (Volkenborn at al., 2005b, submitted).

The response of polychaete species and functional groups to lugworm exclusion was analysed in three consecutive summers between 2002 and 2004 on 6 lugworm exclusion and corresponding control and ambient plots, each of 400 m². Experimental plots were located in a low intertidal fine sand and a mid intertidal medium sand. We tested if lugworm presence/absence affected total abundances, different functional groups and the functional composition of the polychaete assemblage. Furthermore we tested if effects are consistent in time and space or if effects vary from year to year and/or site to site. Effect variation might be an important hint for the importance of endogenous biogenic effects relative to exogenous processes.

With univariate und multivariate statistical techniques we address the question: Does *A. marina* affect the macrofauna community beyond the immediate vicinity of individual burrows? If so, (a) are there any differential inhibitive and promotive effects on polychaete functional groups?, and (b) are such effects consistent in space and time? This may reveal the role of the most widespread ecosystem engineer of the Wadden Sea in structuring benthic assemblages relative to external drivers.

2. MATERIALS AND METHODS

2. 1 Study area and experimental design

A large-scale lugworm exclusion experiment was conducted on an intertidal sandflat in Königshafen, a tidal embayment at the northern end of the island of Sylt in the North Sea (55°02´ N; 8°26´ E). *Arenicola*-flats with consistently more than 20 worms m^{-2} comprise 76% of the intertidal area (Reise et al., 2001). Sediment at the experimental site is dominated by medium and fine sand and mean tidal range is 1.8 m. Due to aeolian sand input from surrounding dunes medium sand dominates the edges of the embayment and grain size median decreases towards the centre of the bay (Austen, 1994). This is in contrast to most other tidal flats of the Wadden Sea where high intertidal zones are often muddy and grain size increases towards low tide line (Beukema, 1976). 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 spring 2002. The horizontal net prevented lugworms to maintain their burrows and effectively kept them away. Surface sediment was excavated with a backhoe to bury the net and this was also done on control plots to account for the initial disturbance. Ambient plots were left untouched to represent natural conditions. The experiment was created in a 2-factorial nested block design. One block 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 x 20 = 400 m² in area. The large size of the experimental plots was chosen to minimize effects of lateral sediment transport typical for sandy intertidal flats (Grant et al., 1997) and known from previous experiments at the study site (Flothman and Werner, 1992; Zühlke and Reise, 1994). Six experimental blocks were nested with respect to the tidal zone: three blocks were conducted within a mid intertidal medium sand (emersion period 6-7 hours per tide; grain size median 330-340 µm) and three blocks within a low intertidal fine sand (emersion period 3-4 hours; grain size median 200–220 µm). Emersion time and sediment type were always interrelated in the area and thus could not be kept separate in our experimental design.

2. 2 Macrofauna sampling

Analysis of macrofauna on experimental plots was done in three consecutive summers between 2002 and 2004. Sampling was done by counting polychaetes retained on a 1-mm mesh sieve from 8 randomly chosen pseudo-replicate cores of 100 cm² within each experimental plot. Sampling depth was 20 cm and samples were divided in upper and lower 10 cm. At the exclusion site only the upper layer could be sampled due to the net in 10 cm depth. Since polychaetes 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 two weeks and was done block-wise, thus including possible effects of consecutive sampling into the block effect. Polychaete species were grouped regarding their trophic and mobility guilds, based on published information (Fauchald and Jumars, 1979) and own site specific observations. Accounting for the plasticity of feeding and motility traits in single species (i.e. feeding guilds of tube worms or motility of surface deposit feeders) we decided to use a bi-functional characterization of species combining trophic and motility traits as these are the most fundamental attributes in functional group ecology (Pearson, 2001). This multifunctional approach (Bremner et al., 2003) enabled a clear classification without ambiguity and a comparison of years with different species composition. Within the polychaete community four functional groups were classified: (a) mixed suspension and surface deposit feeding tube worms (*Pygospio elegans*, *Polydora cornuta*, *Spio martinensis*, *Lanice conchilega*), (b) surface deposit feeding discretely motile worms (*Nereis diversicolor*, *Nereis virens*, *Tharyx killariensis*, *Malacoceros fuliginosus*, juvenile *Arenicola marina*), (c) subsurface deposit feeding discretely motile worms (*Scoloplos* cf. *armiger*, *Capitella capitata*, *Heteromastus filiformis*) and (d) carnivorous motile worms (*Eteone longa*, *Phyllodoce mucosa*, *Nephtys hombergii*). Adults of the lugworm *A. marina* were not included in the response analysis because it constituted the experimental treatment.

Densities of lugworm fecal mounds were estimated on calm days without rain within 10 randomly chosen quadrates of 0.25 m² on 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).

2. 3 Statistical analysis

To test effects of lugworm presence/absence on the functional composition of the polychaete assemblage with respect to time and space we used univariate and multivariate techniques. Two-factorial repeated measurement ANOVA with experimental blocks nested in the tidal zones as additional factor was used to test the effects of

1. lugworm presence/absence and disturbance by initial dredging (exclusion, ambient and control plots),
2. tidal zone (low intertidal fine sand and mid intertidal medium sand),
3. experimental blocks (accounting for spatial heterogeneities on a scale of 10´s to 100´s of meters),
4. year-to-year variability (accounting for temporal heterogeneities),
5. and possible factor interactions
   on polychaete and functional group abundances.

All ANOVA´s were calculated with the General Linear Model (GLM) procedure of STATISTICA (StatSoft, Inc.). Prior to analysis abundance data were log+1-transformed to achieve homogeneity of variances (Cochran´s Test). Relative effect sizes were calculated as percent variance explained (Howell, 1992). Post-hoc multiple means comparisons were performed using the Tukey-Kramer procedure at $\alpha = 0.05$ significance level.

Temporal, spatial and lugworm treatment effects on the functional assemblage composition were explored with non-parametric ANOSIM procedures (PRIMER software, Plymouth Marine Laboratory). Multivariate analysis and multi-dimensional scaling (MDS) were based on Bray-Curtis similarity index of square-root transformed abundance data. To test for general effects consistent over all years, 2-way crossed ANOSIM was applied combining year as first factor and lugworm treatment, tidal zone or experimental block as second factor. To test for general effects of lugworm presence/absence on benthic assemblages within both tidal zones we used 2-way crossed ANOSIM (Year x Treatment) separated for both tidal zones.

To test for factor effects on the functional composition and to assess their relative importance within single years we used (a) 2-way crossed ANOSIM 2 (treatment x experimental blocks) without replication within experimental blocks (Clarke and Warwick, 2001) for the effects of lugworm presence/absence and (b) nested ANOSIM (blocks nested in tidal zones) for the effects of spatial factors. With these statistical techniques we analysed (1) whether there were lugworm treatment effects while allowing experimental block effects, (2) whether there were assemblage differences between the low intertidal fine sand and the mid intertidal medium sand and (3) whether there were assemblage differences among experimental blocks within both tidal zones. Due to the low number of replicates (i.e. only three blocks within both tidal zones) and low numbers of possible permutations we will focus on the R values rather than on their statistical significance.

To identify which species or functional group primarily account for assemblage differences SIMPER procedures were applied. With this exploratory technique we analysed the relative contribution of individual species or functional groups to within treatment Bray-Curtis similarities and to factor induced assemblage dissimilarities between treatments.

3. RESULTS

3. 1 Control of experimental treatment

Lugworms were permanently excluded from all six plots by the inserted mesh (Figure 1A). Lugworm abundances on ambient and control plots were high in the first two years but significantly lower in the third year (RM ANOVA; factor year: $F_{2,8}$=438,2; $p<0.001$; Tukey $p<0.001$). This decrease in population

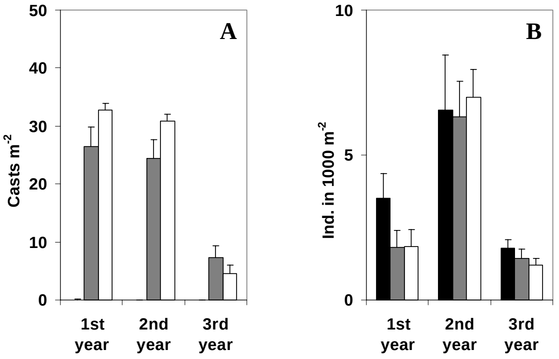


Fig. 1. Abundances of *Arenicola marina* estimated by cast counts (A) and total polychaete abundances on experimental plots (B) over the three year period (black=exclusion; grey=control; white=ambient). Shown are means (n=6) and SE.

size of *Arenicola marina* was also evident on the scale of the entire embayment (Reise, unpublished data). Lugworm abundances were slightly reduced on control plots compared to ambient plots, presumably caused by increased mortality conjunct with the dredging process. However, total polychaete abundances did not differ between control and ambient plots, which suggests that the initial dredging of the sediment in early spring 2002 had no lasting effect on the polychaete assemblage (Figure 1A and B).

3. 2 Polychaete total abundance and species composition

During the three years of this study 15 polychaete species were encountered on the experimental plots (Table 1). Some species were abundant in all years (*Scoloplos* cf. *armiger*, *Nereis diversicolor*, *Pygospio elegans*) while others occurred in abundance only in one year (*Polydora cornuta*, *Spio martinensis*, *Lanice conchilega*). Total polychaete abundance was highest in 2003 when *Pygospio elegans* compromised with ~ 4000 ind. m^{-2} about 50 % of all individuals (Figure 1B). Total polychaete abundance was significantly higher in the mid compared to the low intertidal zone ($F_{1,8}$=12.3; p<0.01) and spatially heterogeneous as indicated by a significant block effect ($F_{4,8}$=7.4; p<0.01). The assemblage was dominated by different species each year. In 2002 the three species *Polydora cornuta*, *Scoloplos* cf. *armiger* and *Pygospio elegans* together contributed 74.4 % to an overall within-year assemblage similarity of 41.4 %. In 2003 and 2004 the assemblage was characterized by single species: in 2003 by *Pygospio elegans* (57.0 % contribution to 53.6 % overall similarity) and in 2004 by *Scoloplos* cf. *armiger* (70.0 % contribution to 55.4 % overall similarity).

Table 1
Abundances of polychaetes (ind. m^{-2}) at mid and low intertidal zone on exclusion (E), control and ambient plots (lumped as C,A) in August 2002, 2003 and 2004.

	Mid Intertidal Medium Sand		**Low intertidal Fine Sand**	
1st year	**E**	**C,A**	**E**	**C,A**
Arenicola marina (juveniles)	0	0	4	0
Capitella capitata	123	117	208	70
Eteone longa	8	15	25	0
Heteromastus filiformis	4	15	72	15
Nepyhts hombergii	0	0	17	20
Nereis spec.	106	68	1167	17
Phyllodoce mucosa	21	28	8	6
Polydora cornuta	1345	1248	815	620
Pygospio elegans	382	189	1545	267
Scoloplos cf. *armiger*	195	282	263	178
Spio martinensis	119	127	552	361
Tharyx killariensis	0	11	34	6
Total individuals	2305	2099	4711	1560
2nd year				
Arenicola marina (juveniles)	13	13	0	0
Capitella capitata	296	38	21	35
Eteone longa	17	40	29	42
Heteromastus filiformis	4	29	50	21
Lanice conchilega	0	0	17	0
Malacoceros fuliginosus	4	2	0	0
Nepyhts hombergii	0	0	8	19
Nereis spec.	2708	2596	879	667
Phyllodoce mucosa	0	2	13	19
Polydora cornuta	658	125	567	148
Pygospio elegans	5958	4042	958	3479
Scoloplos cf. *armiger*	492	944	225	681
Spio martinensis	0	2	42	333
Tharyx killariensis	0	2	117	27
Total individuals	10150	7833	2925	5471
3rd year				
Arenicola marina (juveniles)	42	10	13	4
Capitella capitata	0	0	4	8
Eteone longa	0	2	96	10
Heteromastus filiformis	8	8	29	31
Lanice conchilega	0	0	496	2
Nepyhts hombergii	0	0	63	19
Nereis spec.	242	192	142	225
Phyllodoce mucosa	4	2	142	2
Pygospio elegans	0	0	817	88
Scoloplos cf. *armiger*	1013	1313	413	721
Tharyx killariensis	0	0	33	6
Total individuals	1308	1527	2246	1117

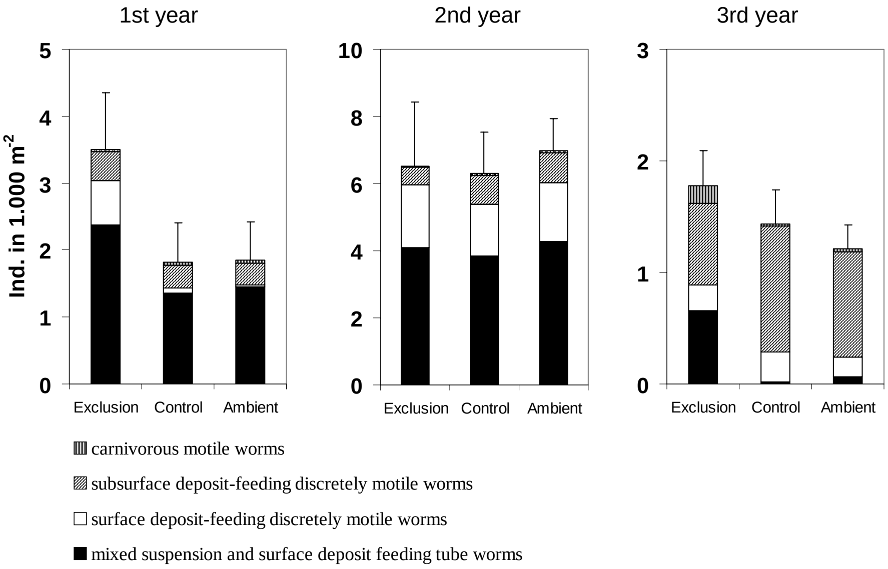


Fig. 2. Functional group composition of polychaete assemblages in relation to experimental treatments during three years of observation. Shown are mean abundances (n=6) for each group. Error bars represent SE of total polychaete numbers (note different scale of y-axis).

3. 3 Response of functional groups: univariate approach

Treatment effects on functional groups were not consistent over space and time (Figure 2). Repeated measurement ANOVA revealed significant lugworm effects on tube worms and discretely motile surface deposit feeding worms, with higher abundances of both groups on lugworm exclusion plots, but these effects were variable in time and space as indicated by significant time x treatment x tidal zone interactions (Table 2). Subsurface feeding and carnivorous worms were not affected by lugworm treatment nor by an interaction with temporal and spatial factors. In the abundances of two functional groups, tube worms and discretely motile surface deposit feeding worms, the factor time explained 70% and 65% of overall variance, while abundances of subsurface deposit feeders and carnivorous worms where less variable between years (variance explained 30% and 15%, respectively). Tube worms and discretely motile surface and subsurface deposit feeders were heterogeneously distributed over the tidal flat as indicated by significant time x block interaction effects (Table 2).

3. 4 Response of functional groups: multivariate approach

Multivariate SIMPER analysis revealed that

Table 2

Repeated measures ANOVA of treatment and tidal height effects on the abundances of polychaete functional groups. Data were log - transformed (n=6). Bold p values indicate significant effects.

		mixed suspension and surface deposit feeding tube worms			surface deposit feeding discretely motile worms			subsurface deposit feeding discretely motile worms			carnivorous motile worms		
	df	MS	F	p	MS	F	p	MS	F	p	MS	F	p
Treatment	2	0.53	7.74	**0.013**	0.58	5.00	**0.039**	0.09	1.58	0.265	0.03	0.11	0.900
Tidal Zone	1	7.28	106.62	**0.000**	0.06	0.53	0.486	0.16	2.70	0.139	4.01	12.33	**0.008**
TR x TZ	2	0.15	2.26	0.167	0.46	3.98	0.063	0.01	0.10	0.907	1.12	3.45	0.083
Block	4	0.47	6.86	**0.011**	0.15	1.27	0.358	0.49	8.41	**0.006**	0.22	0.66	0.635
Residuals	8	0.07			0.12			0.06			0.33		
Time	2	27.94	560.34	**0.000**	8.84	74.24	**0.000**	0.53	18.14	**0.000**	1.23	4.61	**0.026**
Time x TR	4	0.31	6.14	**0.003**	0.31	2.61	0.075	0.07	2.50	0.084	0.71	2.67	0.071
Time x TZ	2	8.40	168.43	**0.000**	0.73	6.16	**0.010**	0.05	1.88	0.185	2.51	9.40	**0.002**
Time x TR x TZ	4	0.54	10.83	**0.000**	0.49	4.16	**0.017**	0.07	2.49	0.084	0.11	0.41	0.798
Time x Block	8	0.24	4.87	**0.004**	0.41	3.45	**0.017**	0.14	4.82	**0.004**	0.23	0.86	0.569
Residuals	16	0.05			0.12			0.03			0.27		

Table 3
ANOSIM analysis of the functional benthic community for each year of investigation. ANOSIM was based on Bray Curtis Similarities of square-root-transformed functional group abundance data.

	1st year		2nd year		3rd year	
	R	p	R	p	R	p
Treatment groups averaged across all Block groups	**0.433**	**0.06**	0.1	0.25	**0.733**	**0.007**
Tidal zone groups using Block groups as samples	-0.111	0.7	0.37	0.2	**0.963**	**0.1**
Block groups averaged across all tidal zone goups	**0.436**	**0.08**	**0.444**	**0.007**	0.206	0.1

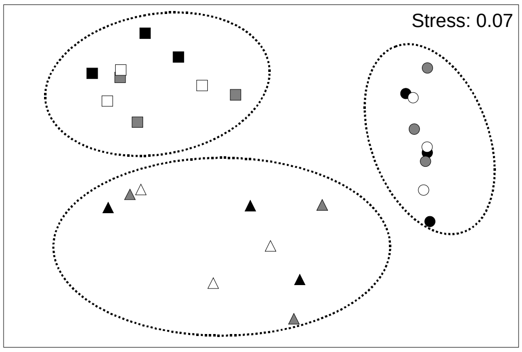
different functional groups dominated the polychaete assemblage each year. Tube worms contributed most to the observed assemblage similarity in the first two years while subsurface feeding polychaetes were dominant in the third year. The three investigated factors (lugworm exclusion, intertidal zone, experimental block) contributed in changing proportions to functional assemblage separation over the three years of investigation (Table 3). The effect of lugworm exclusion was moderate in the first year and highly significant in the third year, but played no role in the second year. The moderate effect of lugworm treatment in the first year was mainly based on lower abundances of tube worms in the presence of lugworms (50 % contribution to average dissimilarities between treatment groups). In the third year, higher abundances of tube and predacious worms and lower abundances of subsurface deposit feeders in the absence of lugworms accounted for more than 90 % to overall dissimilarities between assemblages in the presence and absence of lugworms. In the first and second year the functional composition was significantly separated regarding experimental blocks indicating a high spatial heterogeneity. The functional composition strongly differed between tidal zones in 2004. Mid range and even high values of R were not significant in some cases which can be mainly attributed to low number of replicates and thus low numbers of possible permutations (i.e. only 3 block samples within both tidal zones).

Over all years and experimental blocks lugworm treatment had no consistent effect on the functional composition of the polychaete assemblage (time x treatment two-way crossed ANOSIM: R=0.013; p=0.35). Mid intertidal medium sand and low intertidal fine sand assemblages differed significantly, but separation was weak (R=0.133; p <0.01). Differentiation improved when experimental blocks were used as second factor (R=0.378; p <0.001). Pair-wise comparison of block assemblage dissimilarities revealed that the assemblage of the three blocks in the low intertidal fine sand were not different while the functional composition in the mid intertidal medium sand were very heterogeneous and clearly separated (R >0.512 for all pair-wise tests). Multivariate statistical analysis was therefore applied separately for both tidal zones (Table 4). Significant treatment effects on the functional composition were restricted to the low intertidal fine sand. Pair-wise ANOSIM comparisons revealed that the functional composition clearly differed between exclusion plots and control or ambient plots, while assemblages of control and ambient plots were indistinguishable. On exclusion plots tube worms contributed 44% to within treatment assemblage similarity, while subsurface deposit feeding species were characteristic for control and ambient plots (38 % contribution to overall similarity). Over the three years of observation assemblage similarity in the low intertidal fine sand was higher on lugworm exclusion plots (78 % similarity within treatment) compared to control and ambient plots (~65 %), indicating a decline in the year-to-year variation of the polychaete assemblage in the absence of *A. marina*. MDS plots also indicate a much

Table 4
ANOSIM and SIMPER analysis of the functional benthic community on experimental plots in the mid and low intertidal between 2002 and 2004. ANOSIM was based on Bray Curtis Similarities of square-root-transformed data (E=exclusion, C=control, A= ambient)

ANOSIM					**SIMPER**			
			R	p		similarity within treatment	dominating funtional group	contribution to similarities within treatments
Mid Intertidal Medium Sand	**Global**	Year	0.86	**0.001**				
		Treatment	-0.251	0.99				
Low Intertidal Fine Sand	**Global**	Year	0.756	**0.001**				
		Treatment	0.429	**0.002**				
	Pairwise	E-C	0.543	**0.008**	E	78.20%	mixed suspension and surface deposit feeding tube worms	44%
		E-A	0.654	**0.001**	C	63.81%	subsurface deposit feeding discretely motile worms	38%
		C-A	0.123	0.178	A	66.51%	subsurface deposit feeding discretely motile worms	38%

Mid Intertidal Medium Sand



Low Intertidal Fine Sand

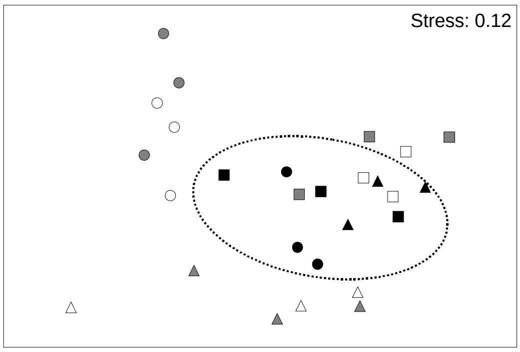


Fig. 3. MDS plots of functional polychaete composition in mid intertidal medium sand and the low intertidal fine sand. Shading indicates lugworm treatment (black=exclusion; grey=control; white=ambient) and symbols indicate years (triangle=1st year; square=2nd year; circle=3rd year). Plots are based on Bray Curtis Similarities of square-root-transformed functional group abundance data. Dotted line indicate the significantly different polychaete functional composition revealed by ANOSIM (Table 4).

higher variability of functional group composition on lugworms plots (Figure 3). A stress value of 0.12 aroused from functional group heterogeneities on lugworm plots which were not visualized in a two-dimensional MDS plot but became visible in a three-dimensional MDS plot (not shown). In the mid intertidal medium sand the functional composition clearly differed between individual years and was not consistently affected by lugworm treatment.

4. DISCUSSION

Lugworms do affect the polychaete assemblage beyond the immediate vicinity of burrows in intertidal soft sediments, but effects vary in time and space. The impact of lugworms was found to be significant in single years and within one intertidal zone while it was marginal in others. Time consistent effects were restricted to the low intertidal fine sand, with strongest effects in the last year.

Small-scale experiments have revealed that lugworms negatively affect juvenile densities of various worm and bivalve species with different trophic and motility traits and that these effects increase with increasing lugworm abundance (Flach, 1992a,b,1993; Flach and deBruin, 1993). Negative response was found for tube worms (i.e. *Pygospio elegans*), surface deposit feeding worms (i.e. *Nereis diversicolor*) as well as for subsurface deposit feeding worms (i.e. *Scoloplos armiger*) and small-scale disturbance of infauna by lugworm bioturbating activity was suggested to be the main mechanism responsible for lower abundances of infaunal species. In our study polychaete functional groups responded differentially to lugworm exclusion. While abundances of mixed suspension and surface deposit feeding tube worms and surface deposit feeding discretely motile worms tended to increase in the absence of lugworms, subsurface deposit feeding worms were not affected but became the characteristic functional group in the presence of lugworms. Lower abundances of sedentary species in the presence of lugworms (Brey, 1991; Flach, 1992, this study) correspond to the mobility group hypothesis based on small scale disturbance of infauna by a large bioturbator (Brenchley, 1981; Wilson, 1981). However, in the second year high lugworm abundances did not result in a changed functional composition of polychaetes suggesting that the assemblage was highly adapted to lugworm bioturbating disturbance. Within-year assemblage dissimilarities between lugworm and exclusion plots were moderate in the first, low in the second and highly significant in third year, when overall lugworm abundances happened to be low. Considering the relatively low abundances of *A. marina* in the third year, small-scale disturbance alone is unlikely to cause the assemblage separation on lugworm exclusion and control/ambient plots and give rise to sediment mediated effects of large bioturbators for benthic assemblage composition (Flint et al., 1986; Posey, 1986; Posey et al., 1991; Botto and Iribane, 1999). The coinciding low lugworm abundances on control and ambient plots in 2004 and strongest separation in the polychaete assemblage in the presence/absence of lugworms in the same year suggest that changes in sediment properties cumulating in the course of three years due to lugworm exclusion might have been responsible for the conspicuous shift in the functional diversity of the polychaetes assemblage. Assemblage differentiation on exclusion plots occurred in the low intertidal fine sand where changes in sediment properties were also most significant (Volkenborn et al., 2005a, submitted). Surface deposit feeding worms may have been attracted by the higher availability of microphytobenthos and organic material in the sediment of lugworm exclusion plots (Volkenborn and Reise, 2005). Higher abundances of potential prey in the organic enriched sediment may have been responsible for abundant motile predacious worms on exclusion plots in 2004. Subsurface deposit feeding worms like *Scoloplos* cf. *armiger* were found to take advantage from ameliorated sediment properties in the presence of lugworms (Volkenborn and Reise 2005). Indirect sediment mediated effects may therefore be more important than direct small-scale disturbance by *A. marina* alone in influencing the functional composition of the assemblage on this larger scale.

The functional composition of the polychaete assemblage at our study site seems to be driven by the variable and contingent interplay of external factors, such as dispersal and environmental constraints (Belyea and Lancaster, 1999) and endogenous ecosystem engineering effects of the lugworm *A. marina*, operating on different spatial scales. Moreover, the polychaete assemblage seems to be highly adapted to the dynamic and unstable conditions of intertidal sand. Dredging of experimental plots at the start of the experiment had no obvious effect on species composition and abundance. This reflects high resilience after disturbance (Boesch et al., 1976) and may apply to the small-scale disturbances caused by lugworm bioturbation as well. Our results clearly indicate that widely occurring lugworm densities in the Wadden Sea of 20 - 40 lugworms m^{-2} (Beukema 1976) do not necessarily result in a conspicuous change in the endobenthic assemblage. Direct disturbance of infauna may become important as lugworm abundances increase above these typical densities but a generally negative effect of lugworms on other benthic infauna, as it was assumed by Flach (1992), may not exist. Overall community dynamics may partly explain the observed inconsistencies of lugworm effects. The abundances of single species and functional groups were highly variable in time and space, and the assemblage was dominated by different species in each year. This confounding variability caused by differential recruitment and propagule supply between years and tidal zones presumably overshadowed lugworm effects. Especially in the mid intertidal medium sand the benthic assemblage was temporally and spatially very heterogeneous and consistent effects of lugworm presence/absence on the polychaete assemblages were not detected. The high temporal and spatial variability of lugworm effects may partly explain the absence of substantial lugworm effects in modelled community dynamics using long-term monitoring data (Williams et al., 2004). However, our experimental results imply that even contingent and subtle effects of lugworm presence may be important on a large scale in structuring the benthic community, particularly in fine grained sediments of the low intertidal zone. Within this tidal zone lugworms were found to modify the functional diversity in polychaetes and increase assemblage year-to-year variability, thus maintaining the functional diversity in polychaetes on a larger time scale within the spatio-temporal mosaic of soft-bottom habitats (Johnson, 1973). The changing success of functional groups in time and space at our study site seems to be driven by a variable interplay of large-scale environmental variation, meso-scale ecosystem engineering by the lugworm *A. marina* (this study) and small-scale disturbance conjunct with lugworm activity (Brey, 1991; Flach, 1992; Lackschewitz and Reise, 1998). Their relative contribution to assemblage composition vary from time to time and site to site which stress the importance of combined biotic and abiotic variables for benthic community formation (Hagberg et al., 2003) and the importance of the spatial scale of controlling factors (Zajac et al, 1998). We conclude that the spatial and temporal contingent interplay of (1) small-scale disturbance and (2) meso-scale sediment mediated ecosystem engineering by the lugworm *A. marina* and (3) external factors should be regarded as characteristic for assemblage formation in unvegetated intertidal sediments.

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

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ABSTRACT

On six 400 m² 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 two out of three 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.

Keywords: Amensalism; Bioturbation; Deposit feeding; Facilitation; Intertidal; Polychaeta; Soft-bottom benthos

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 underlying processes. Biotic interactions are best studied by direct observation and field experiments. However, experimental manipulation of benthic communities have mostly been executed on a scale of <1 m² (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 are pumped into the anoxic sediment (Cadée, 1976; Riisgård and Banta, 1998). *Arenicola 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 20x20m 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). *Scoloplos* 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 are currently being revised (Albrecht and Kruse, in prep.). 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, pers. 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 sandflat 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 *Arenicola 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 x 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 x 20 = 400 m² 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).

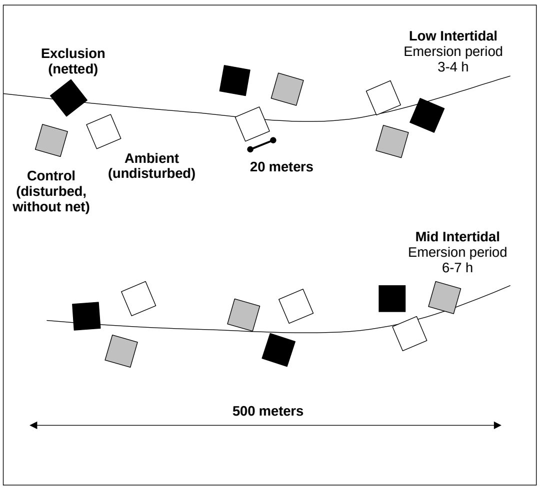

Fig. 1. Experimental set-up in a 2- factorial (2 x 3 level) nested block design.

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 m² within each experimental plot. Number of fecal castings vary 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 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 one 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 α=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 *Arenicola marina* were effectively excluded by the buried net and did not recolonise 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

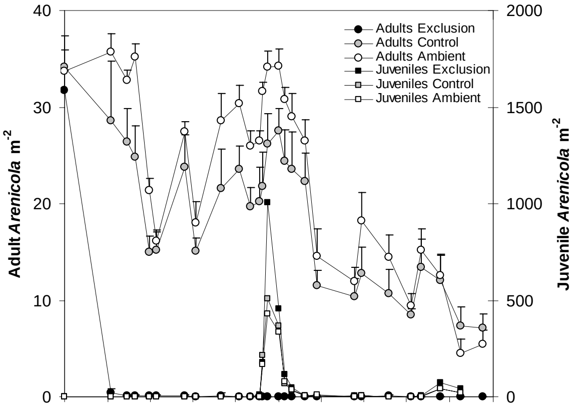

Fig. 2. Abundances of adult (circles) and juvenile (squares) *Arenicola marina* inferred from fecal mounds on experimental plots (mean from 6 plots and SE) from March 2002 to September 2004. On each experimental plot 10 quadrats of 0.25 m^2 were counted (note differences in y-axis scales).

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 x 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 two years). Population size of *A. marina* in the entire bay had generally decreased in 2004 (Reise, unpublished data).

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

	date	Treatment	Tidal Height	Treatment x 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 cocons	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)	

3. 2 Effects on *Nereis*

Overall, lugworm treatment and tidal height had significant effects on abundances of adult *Nereis diversicolor*, while responses of juveniles to lugworm treatment were significantly different between years, indicated by a significant time x 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 two years abundances gradually declined until densities on exclusion and

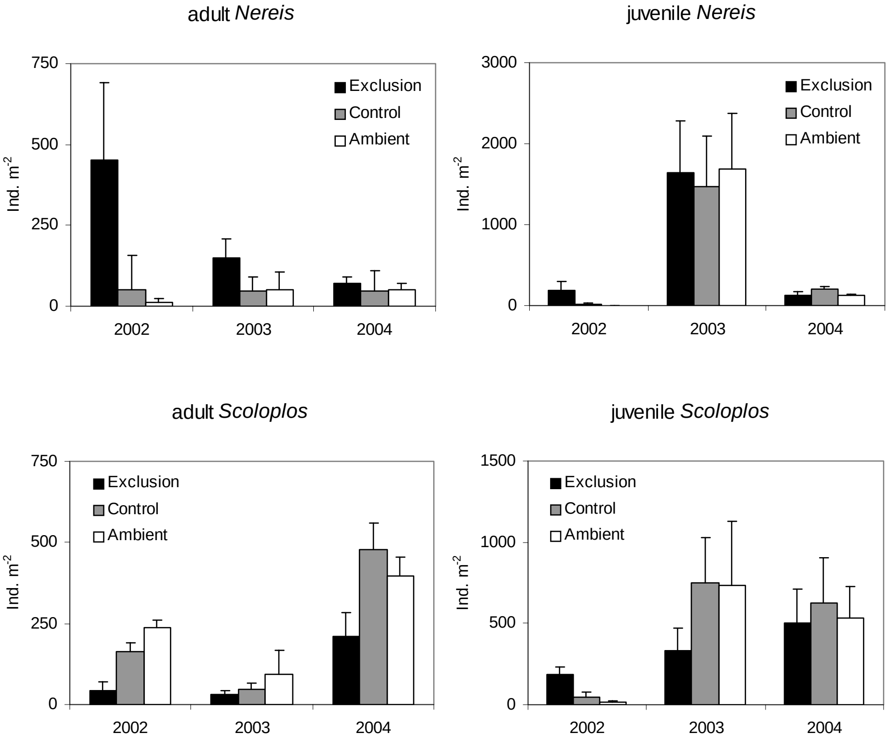

Fig. 3. Abundances of adult and juvenile *Nereis diversicolor* and *Scoloplos* cf. *armiger* in August of 2002, 2003 and 2004. Shown are mean abundances of six experimental plots and SE. On each experimental plot 8 sub-samples of 100 cm² were taken.

Table 2
Repeated measures ANOVA on treatment and tidal height effects on the abundances of adult and juvenile *Nereis diversicolor* and *Scoloplos* cf. *armiger*. Data were log - transformed (n=6). Bold p values indicate significant effects (% V = variance explained calculated as: $(SS_{factor} / SS_{total}) \times 100$).

		***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 x 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 x Treatment	4	0.52	1.76	0.187	13.8	1.15	6.24	**0.003**	**8.4**
Year x Tidal height	2	1.26	4.23	**0.034**	**16.6**	1.35	7.35	**0.005**	**4.9**
Year x Treatment x Tidal height	4	0.85	2.85	0.058	22.4	0.35	1.92	0.157	2.6
Year x 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 x 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 x Treatment	4	0.59	3.73	**0.025**	**8.2**	0.82	6.27	**0.003**	**10.8**
Year x Tidal height	2	2.80	17.56	**0.000**	**19.4**	0.35	2.69	0.099	2.3
Year x Treatment x Tidal height	4	0.02	0.10	0.982	0.2	0.24	1.83	0.173	3.2
Year x 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

lugworm plots were not significantly different in 2004. However, over the three years the significant treatment effect 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 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 x 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 *Scoloplos* 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 (3,000 to 8,000 juv. m^{-2}). Due to the aggregated distribution of juvenile *S.* cf.

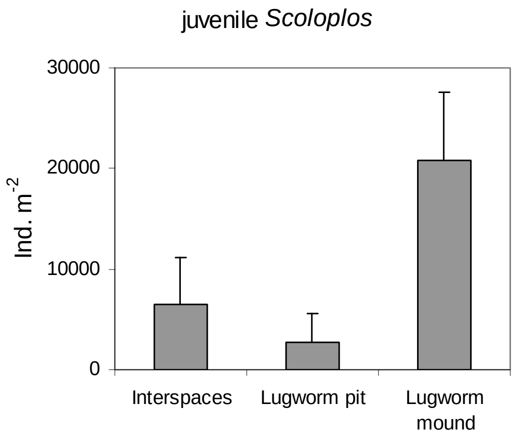

Fig. 4. Abundances of juvenile *Scoloplos* cf. *armiger* at mid intertidal in samples from lugworm pits, mounds and the sediment in between not directly affected by *A. marina* in July 2002 (mean and SD; n=6).

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 two years (Fig. 5), but were significantly facilitated by lugworm presence only in 2003, when lugworms where 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.

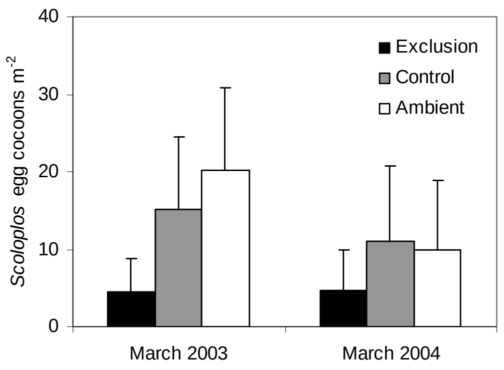

Fig. 5. Abundances of *Scoloplos* egg cocoons in March 2003 and March 2004 on experimental plots (mean and SD; n=6). On each experimental plot 10 subsamples of 0.25 m² were taken.

4. DISCUSSION

A competitive equilibrium between deposit feeding worms in intertidal sand may not exist. High between-year variability of adult and recruit densities of the polychaetes *Arenicola marina, Nereis diversicolor* and *Scoloplos* 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 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 et al., in prep.). 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, in press). 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

Table 3
Habitat properties of lugworm flats and lugworm exclusion plots at mid and low intertidal zone. 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 et al. (in prep.)

		Lugworm Tidal Flats		**Lugworm Exclusion**	
		Lower Intertidal	Mid Intertidal	Lower Intertidal	Mid Intertial
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
Sulphide in porewater (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}

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. 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 mm 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 (Schöttler 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 was 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.

4. 3 Conclusions

The negative effects of *Arenicola marina* on *Nereis 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 *Scoloplos* 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 recolonised by adult *A. marina* (full recovery after 4 years; Beukema et al. 1999) and thus resemble a lugworm exclusion experiment. Settlement of several species were 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 meso-scale (1 m² - 1 hectare; 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, 1993 a, 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 an habitat-mediated interaction web bioengineered in marine sediments (Reise, 2002). Further, 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 three years of experiment and variance explained by lugworm treatment was generally below 50 %, implying the importance of other factors for observed patterns. Several Time x 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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Contingencies and emergent patterns in intertidal soft-sediment communities

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ABSTRACT

Lugworms (*Arenicola marina*) were excluded from 400 m² plots of intertidal sand which initiated sequences of direct and indirect changes in the benthic community. The tube-building polychaetes *Polydora cornuta* and *Lanice conchilega* became established in the absence of bioturbating lugworms. The protruding tubes provided attachment for an ephemeral development of algal tufts (*Berkeleya* colonies and *Enteromorpha* thalli) which in turn triggered settlement of the juvenile drifting clams *Mya arenaria* and *Macoma balthica.* Contingent events due to the presence of above ground structures like tubes and algae in lugworm exclusion plots with enhanced bivalve settlement occurred in two years at different tidal zones with different tube builders, algae and juvenile clams. We conclude that the bioturbation of a large subsurface feeder in unvegetated sand inhibits successional developments through above ground structures with cascading effects on the benthic community. In coastal zones contingent events, such as intertidal zone and larval supply, and their interaction with biogenic habitat transformations should be regarded as characteristic elements in structuring benthic assemblages.

1. INTRODUCTION

Community dynamics are the result of internal processes (i.e. trophic interactions) (Paine, 1966; Menge and Sutherland, 1987; Wilson, 1991) and external factors (i.e. environmental variability) (Lundberg et al., 2000). On large spatial scales exogenous factors (e.g. water temperature) have been found to be of major importance for benthic community characteristics (Hagberg and Turnberg, 2000; Hagberg et al., 2003), while biotic interactions often play a key role for assemblages on small spatial scales (e.g. Reise, 1985; Flach, 1992; Zajac, 2004). In soft sediment communities the interplay between functional groups such as free burrowers and tube builders or sediment stabilizers and destabilizers create a complex biogenic habitat matrix, where facilitating and inhibiting effects occur simultaneously shaping the benthic community (Reise, 2002). Wootton (2002) emphasized the role of indirect effects, reflected in interaction chains and interaction modifications between several species giving rise to rather complex systems. Ecosystem engineering species (*sensu* Jones et al., 1994) also can indirectly affect benthic communities by physically modifying the environment.

Although the concepts of ecosystem engineering, external and internal processes or indirect and direct effects help to categorize species interactions in marine benthic systems, there is a paucity of experimental evidence regarding how these factors interact and generate observed patterns. Here we report on contingent events within an intertidal benthic community induced by the permanent exclusion of an abundant and large bioturbating polychaete.

The lugworm *Arenicola marina* (L.) is a prominent member of the macrofauna in sandy sediments and tends to dominate deposit feeder biomass (Beukema, 1976; Reise, 1985). in the intertidal zones of northwest European coasts. *A. marina* lives in 20 to 40 cm deep J-shaped burrows completed to a U by a vertical head shaft. Surface sediment slides down the shaft to become ingested by the worm and is defecated as a mound of coiled fecal strings at the sediment surface above the tail shaft. Assuming a density of 30 ind. m^{-2}, lugworms replace a sediment layer of 15 cm per year and the sediment surface topography can be dominated by lugworm fecal mounds and feeding funnels (Cadée, 1976).

In spring 2002 a large-scale lugworm exclusion experiment was initiated. On six 400 m² lugworm exclusion and corresponding lugworm plots developments in the benthos were monitored over a three year period. Parallel investigations of sediment and porewater properties in the presence/absence of *A. marina* revealed significant changes in habitat characteristics. On lugworm exclusion plots microphytobenthic biomass and the proportion of fine particles and associated organic material almost doubled and inorganic porewater nutrients and sulfide accumulated within the sediment (Volkenborn and Reise, in press; Volkenborn et al. submitted.). All this contributes to a more stable sediment in the absence of lugworms. Here we test the hypothesis that removal of a large sediment destabilizing bioturbator allows for the establishment of tube builders which rely on a stable sediment and analyse the consequences of above ground structures like protruding tube caps for benthic community characteristics. This was done by monitoring developments at the sediment surface in parallel with an analysis of the endobenthic infaunal composition on experimental plots during two years. We discuss the relative ecological importance of internal processes induced by removal of an ecosystem engineer and external processes such as colonizers supply in shaping ecological patterns in the intertidal zone.

2. MATERIALS AND METHODS

2. 1 Study area and experimental design

The 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). Sediment at the experimental site is dominated by medium and fine sand of low organic content (<1%). Mean tidal range is 1.8 m and salinity varies between 27 psu in spring and 31 psu in summer. Details of the study site are provided by Austen (1994), Reise (1985) and Gätje and Reise (1998). Exclusion of lugworms was achieved by inserting a 1-mm meshed net at 10 cm depth into the sediment in spring 2002. To account for the disturbance by dredging with a backhoe, sediment was disturbed on control plots in the same way, but without inserting a net. Ambient plots were left untouched to represent natural conditions. The experiment was arranged in a 2-factorial (3 x 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. Each plot was 20 x 20 = 400 m² in area. The large size of the experimental plots was chosen to minimize effects of lateral sediment transport typical for sandy intertidal flats (Grant et al., 1997) and known from previous experiments at the study site (Flothman and Werner, 1992; Zühlke and Reise, 1994).

2. 2 Sampling of macrofauna and algae

Sampling of macroininvertebrate and algae was conducted every fourth month between April 2003 and August 2004. Macroinfauna densities within each plot was done by counting invertebrates retained on a 1-mm mesh sieve from 8 randomly chosen pseudo-replicate cores of 100 cm² and 10 cm depth. 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. Sampling was done. In August 2003, 8 additional subsamples of 10 cm² from all experimental plots were sieved through a 250 µm mesh to include small, juvenile polychaetes. Colonies of the diatom *Berkeleya rutilans* (Trentepohl ex Roth) were counted within 8 randomly chosen quadrates of 0.25 m² on each experimental plot in April 2003. Abundances of algal strings of *Enteromorpha* spp. were estimated by their frequency. Therefore, their occurrence in 25 sub-quadrates of 10 x 10 cm in 6 randomly chosen frames of 0.25 m² were determined in August 2004. Green algal strings were only counted when they where anchored within sub-quadrates. Maximum numbers of *Lanice conchilega* tube caps within one sub-quadrate of each frame were also counted. Green algal biomass was estimated from 3 representative samples of 100 cm² within each plot as ash-free dry weight.

2. 3 Statistical analyses

Abundances of macrofauna on experimental plots were analysed using two - factorial ANOVA. The effect of lugworm presence/absence was used as first factor (3 levels: exclusion, control, ambient). Tidal position as second factor was used to test the effect of tidal height (2 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 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 α=0.05 significance level. In 2004, algae and *L. conchilega* 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, we abandon statistical tests on factor effects in this case. Instead, abundances of juvenile bivalves and abundances of *L. conchilega* within the same subsamples were investigated by regression analysis.

3. RESULTS

3. 1 Seasonal developments in the benthic community 2003

In spring 2003 colonies of the tuft forming diatom *Berkeleya rutilans* developed on experimental plots in the mid intertidal zone (Fig. 1A, B). Most of these diatom colonies were attached to tubes of the spinoid *Polydora cornuta* (Bosc) (Fig. 1C, D). In April 2003 abundances of *P. cornuta* were 3-fold on lugworm exclusion plots compared to control and ambient plots in the mid intertidal zone (Fig. 2A) but overall, this polychaete was not affected by the experimental treatment ($F_{2,8}$=0.41; p=0.68) nor by treatment x tidal height interaction ($F_{2,8}$=2.03; p =0.19). In August 2003, when samples where sieved with 250 µm mesh a treatment effect was found on abundances of *P. cornuta* ($F_{2,8}$=7.37; p=0.015) with higher abundances of *P. cornuta* on lugworm exclusion plots (Tukey p <0.05; Fig. 2B). The tuft forming diatom *Berkeleya rutilans* appeared in March 2003 and until April algal tufts reached a size of up to 10 cm and densities up to 50 colonies m^{-2} (Fig. 2C). Colonies were affected by treatment x tidal height interaction ($F_{2,8}$=28.76; p <0.001) resulting in significant higher abundances of *Berkeleya* colonies on exclusion plots in the mid intertidal zone compared with other experimental treatments (Tukey p <0.01). In spring 2003 juveniles of *Macoma balthica* (L.) recruited the study site. In August they reached highest densities on lugworm exclusion plots in the mid intertidal area (treatment x tidal height interaction, $F_{2,8}$=4.53; p <0.01). In the mid intertidal area

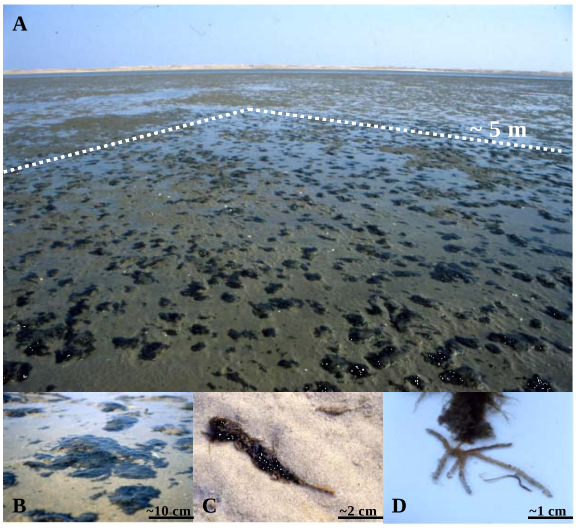

Fig. 1. Lugworm exclusion plot in the mid intertidal area in spring 2003 (A). Broken line indicate the edge of the experimental plot. Colonies of the tuft forming diatom *Berkeleya rutilans* were growing (B) and most colonies were attached to sand-tubes of the spinoid polychaete *Polydora cornuta* (C, D).

average abundance of *M. balthica* was 1600 ind. m^{-2} on lugworm exclusion plots while it was generally below 500 ind.$^{-2}$ in all other experimental treatments (Fig. 2D).

3. 2 Seasonal developments in the benthic community 2004

In summer 2003 green and red algae (*Enteromorpha* spp., *Ulva* spp., *Polysiphonia* spp.) developed on experimental plots in the low intertidal zone (Fig. 3A, B). Most of these algae strings were attached to tubes of the terebellid polychaete *Lanice conchilega* (Fig. 3C, D).

L. 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

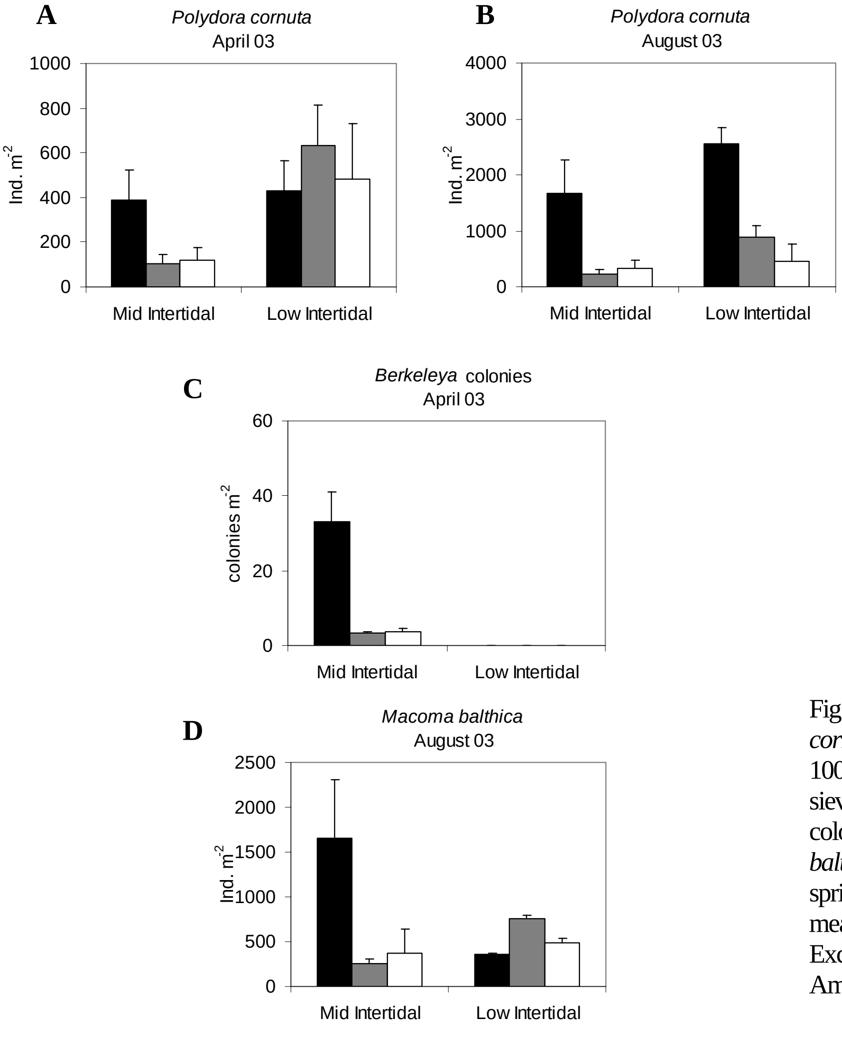

Fig. 2. Abundances of *Polydora cornuta* in April 2003 (A; sieved with 1000 µm mesh) and August 2003 (B; sieved with 250 µm mesh), *Berkeleya* colonies (C) and juvenile *Macoma balthica* (D) on experimental plots in spring and summer 2003 (shown are means and SE (n = 6); Black = Exclusion; Grey = Control; White = Ambient).

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 when *L. conchilega* was found almost exclusively on lugworm exclusion plots in the low intertidal area (Fig. 4A). In August 2004 *L. conchilega* reached average densities of 500 ind. m^{-2}. Algae occurred also almost exclusively on the lugworm exclusion plots (Fig. 4B). On the used 10 x 10 cm grid green algae frequency was about 90% and algae biomass was up to 20 g dry weight m^{-2}. Two bivalve species (*Mya arenaria* (L.) and *Macoma balthica*) recruited the low intertidal area of the experimental site in spring 2004. For both species of bivalves, highest abundances were found within lugworm exclusion plots in the low intertidal area (Fig. 4 C,D). Within all 144

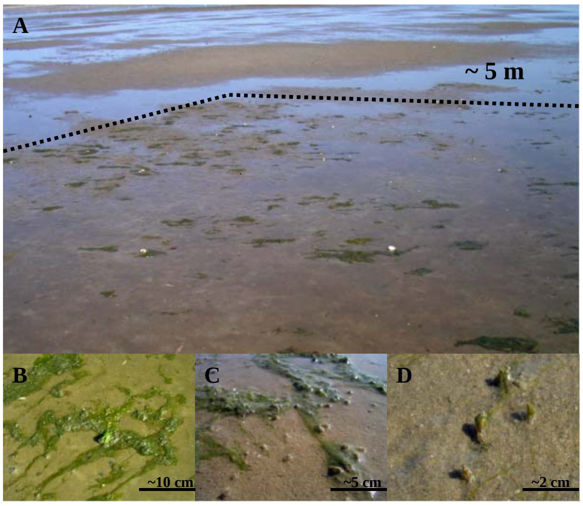

Fig. 3. Green algal tufts growing on lugworm exclusion plots in the low intertidal area in summer 2004 (A, B). Broken line indicate the edge of the lugworm exclusion field. Most algal strings were attached to sandtubes of the polychaete *Lanice conchilega* (C, D).

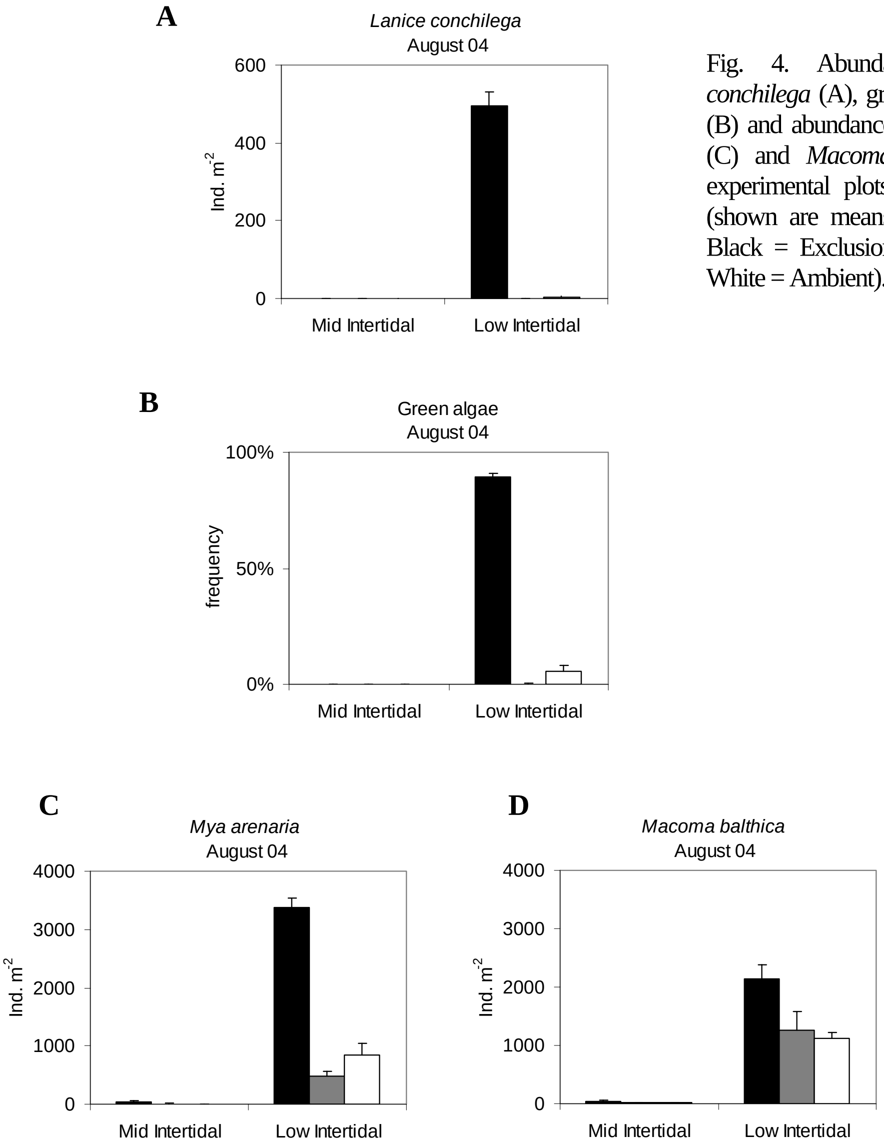

Fig. 4. Abundances of *Lanice conchilega* (A), green algal frequency (B) and abundances of *Mya arenaria* (C) and *Macoma balthica* (D) on experimental plots in summer 2004 (shown are means and SE (n = 6); Black = Exclusion; Grey = Control; White = Ambient).

samples of 100 cm^2, abundances of both bivalve 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. 5 A, B).

4. DISCUSSION

In the absence of *Arenicola marina,* increased abundances of tube-building polychaetes enabled ephemeral algal growth which in turn triggered settlement of juvenile benthic species. Changes in habitat characteristics in the absence of an ecosystem engineer had further indirect effects on the benthic community through chains of contingent events.

4. 1 Lugworms inhibit tube-building polychaetes

A. marina was found to have significant positive effects on the abundance of several other meio- and macrobenthic species around the burrow (Reise and Ax, 1979; Lackschewitz and Reise, 1998), while sedentary species near the surface were negatively affected (Brey, 1991; Flach, 1992; Flach and 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. Our observations of the experimental plots generally supported negative effects: tube- or burrow-building species were more abundant on lugworm exclusion plots, while abundances of free-burrowing species decreased (Volkenborn and Reise, in press; this study). However we suggest that other factors than direct disturbance by bioturbation activity may explain the differential benthos abundances on experimental plots at least in some of the investigated species.

Polydora cornuta was not significantly affected by lugworm presence/absence in April, though abundances at mid intertidal were 3-fold in the absence of *A. marina*. However, when sampled with a finer mesh in August abundances of *P. cornuta* were significantly higher on lugworm exclusion than on lugworm plots. Thus, juvenile *P. cornuta* might have been underestimated, when sampling was done with a 1000 µm mesh in April. Protruding tubes of *P. cornuta* were composed of very fine material. Since *A. marina* was found to inhibit the accumulation of fine particles in surface sediments (Volkenborn et al., submitted), *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 we suggest a combined effect of direct disturbance by *Arenicola* feeding activity and changes in sediment characteristics.

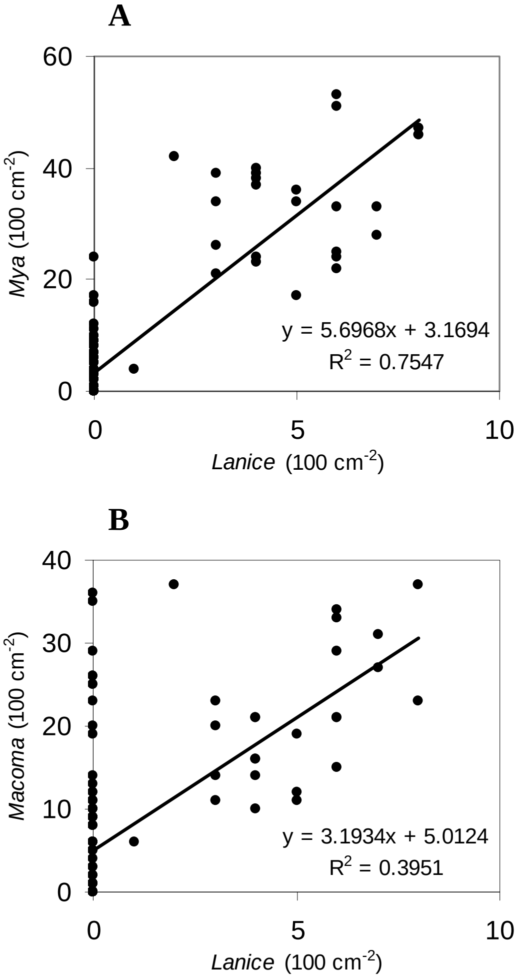

Fig. 5. Regression analysis between *Lanice conchilega* and (A) *Mya arenaria* and (B) *Macoma balthica* spat within 144 samples from all experimental plots in summer 2004.

Lanice conchilega became established exclusively on lugworm exclusion plots in the low intertidal zone. Lugworm abundances were generally low on lugworm plots in 2004 Volkenborn and Reise, in press), when *L. conchilega* settled on experimental plots. Thus, disturbances by lugworm feeding activity may have been of minor importance. A plausible explanation for the settlement exclusively on lugworm exclusion plots may be changes in sediment properties after two years of lugworm exclusion. It is left to speculation which characteristics actually attracted *L. conchilega*, but a combined effect of higher organic matter concentration, more fine particles and more microphytobenthos on lugworm exclusion plots (Volkenborn et al., in prep.) is very likely. We suggest, that long-term changes in sediment characteristics caused the abundances of tube-building polychaetes, while direct effects of lugworm feeding activity may be of minor importance. Furthermore colonization of *L. conchilega* was found to be facilitated by the presence of already existing *Lanice* tubes (Strasser and Pieloth, 2001), abundances of *L. conchilega* may continue to increase on lugworm exclusion plots in the low intertidal.

4. 2 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 found to be 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 Mc Glathery, 2005). On lugworm exclusion plots algal biomass reached values of up to 20 g dry weight m^{-2}. In the past, green algae have overgrown the entire sandflat of the study site with a dense mat of up to 100 g dw m^{-2} (Reise, 1983; Schories and Reise, 1993). However, at that time green algal strings became anchored by sliding down feeding funnels of lugworms. Thus, both processes, sediment destabilization by bioturbation as well as stabilization by tubes potentially give rise to the same pattern: algal cover on sand flats.

4. 3 Biogenic above ground structures increase settlement of drifting juvenile macrofauna

In the intertidal zone of the Wadden Sea juvenile bivalves such as *Macoma balthica*, *Mya arenaria* and others change their intertidal position by postlarval drifting (review by Butman, 1987; Armonies, 1994). Mucus threads several times the length of the animals enable them to become effectively transported in the water column by currents (Sirgurdsson et al., 1975; Beukema and deVlas, 1989; Armonies, 1996). Due to these secondary redistributions, species are able to colonize habitats which are more suitable for subsequent life stages (Armonies, 1994; Strasser, 2002; Hiddink, 2003). Juvenile abundances of *M. arenaria* and *M. balthica* were significantly higher on lugworm exclusion plots in both years and were closely linked to the number of *Lanice* tubes in 2004. Above ground structures like polychaete tubes and anchored algae provide attachment for young bivalves with byssus threads and thus facilitate settlement. After having burrowed between the polychaete tubes, juvenile bivalves may additionally find shelter from predation and the likehood of re-suspension may be reduced (Armonies and Hellwig-Armonies 1992).

4. 4 Conclusions

The experimental removal of *Arenicola marina* from intertidal sand initiated contingent events which subsequently led to enhanced settlement of drifting macrofauna. We suggest that a combination of direct and indirect effects caused the observed patterns. *A. marina* prevented these developments and thus reduced the structural diversity at the surface of the sandy intertidal flat. Similar emergent patterns occurred in the two years of observation but different species were involved in the processes: *Polydora cornuta* and *Lanice conchilega* as tube builders, tufts of diatoms and green algae as an epibenthic cover and juveniles of *Macoma balthica* and *Mya arenaria* as drifting macrofauna. Moreover, these contingent events occurred only at mid tide level in the 1st year and only at low tide level in the 2nd year but were not observed at low tide level in the 1st year or at mid tide level in the 2nd year. The combination of variable conditions and a variable supply of colonizers may account for these inconsistencies in time and space (i.e. Menge and Sutherland, 1987; Lotze et al., 2000). We conclude that *Arenicola marina* directly (by its bioturbation) and indirectly (by changes in sediment characteristics) inhibited ephemeral structural developments at the sediment surface, but realization of developments was dependent on variable external factors. This temporal interaction of biogenic habitat transformations with external factors should be regarded as an characteristic element in the emergence of benthic patterns in coastal zones.

ACKNOWLEDGEMENTS

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Large worms as ecosystem engineers in intertidal sediments

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ABSTRACT

The polychaete *Arenicola marina* increases biodiversity on sandy tidal flats by maintaining a complex burrow habitat. Occasionally, the lugworm also facilitates ecosystem disturbance by promoting green algal mass development. By reworking the upper sediment layer, it displaces some deposit feeders while promoting others. Flux rates between sediment and overlying water are increased, and this in turn decreases sediment storage capacity. Overall, the trophic role of lugworms in the tidal flat food web seems to be of lower importance than its engineering activity.

1. INTRODUCTION

Lugworms comprise eighteen species of tailed Arenicolidae (Bartholomaeus and Meyer, 1999). These polychaetes are large and abundant bioturbators in many coastal sediments, rivalling in importance the thalassinidean shrimps as ecosystem engineers (Berkenbusch and Rowden, 2003; Reise, 2001, 2002). Lugworms live in separate burrows and feed on sediment, and they may be regarded as a sluggish functional analogue to ghost shrimps. Sediment reworking rates are similar but pumping rates by lugworms are lower. The best studied lugworm species is *Arenicola marina* (L.), dwelling in nearshore sediments on both sides of the North Atlantic (Ashworth, 1904; Cadée, 1976; Riisgård and Branta, 1998).

A peculiarity of the lugworms is their tail: the abdominal segments lack appendices, and with this rear end worms approach the surface to defecate. At this very moment, worms get in the reach of predators. When these pick or bite, the last tail segments are shedded to satisfy the offender, while the lugworm retreats deep into its burrow to recover. Mainly flatfish perform this tail-end grazing, which does not seem to reduce overall growth and reproductive output of the lugworms (Bergman et al., 1988). Lugworm populations tend to be stable with adult densities often between 20 to 40 m^{-2} (Reise, 1985). Recruitment is density dependent: juveniles settle where adults have vacated space (Flach and Beukema, 1994; Reise et al., 2001). Populations seem to be food or space limited rather than regulated by predation.

The question we ultimately attempt to answer is whether the lugworm is more important for the ecosystem as a bioengineer than in its trophic role as consumer or prey. Here in a first step, we review the effect of lugworm burrows as a habitat to other sediment fauna. Then we turn to functional properties of lugworms in the tidal ecosystem, and finally present preliminary results of a large-scale lugworm exclusion experiment. Evidently, this large worm exerts a strong effect on the tidal flat community by modifying the sedimentary environment.

2. BURROWS AS HABITATS

Burrow positions last for several weeks to months, depending on the migratory ambitions of individual lugworms. Surface

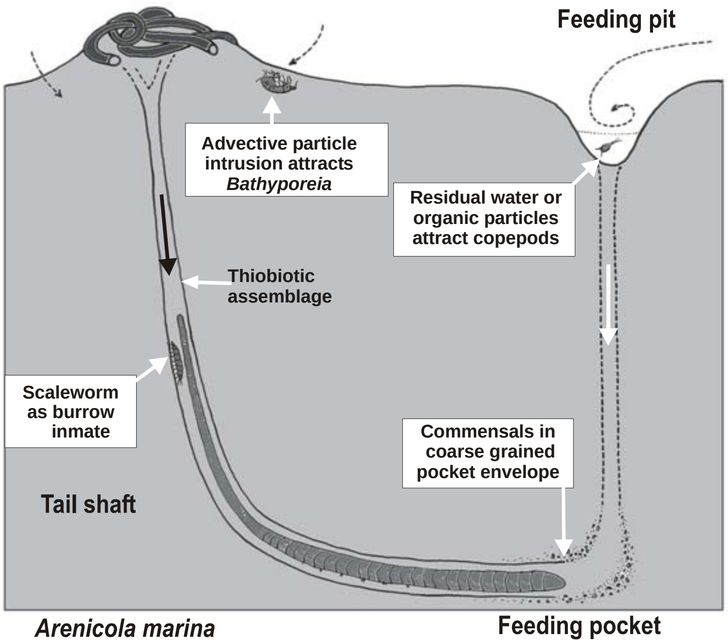

Fig. 1. Burrow of the lugworm *Arenicola marina* as a habitat for other sediment fauna. Dark arrow: water flushed into the burrow; light arrow: sediment sliding towards feeding pocket; broken arrows: deflected currents caused by mound and pit topography. Modified from Reise (2002). See also text.

sediment slides down a funnel and through a head shaft (Fig. 1).

At a depth of about 20 cm, the worm swallows the incoming surface material. It rejects particles >1mm in diameter and these tend to accumulate around the feeding pocket. From the ingested smaller particles, organic material is enzymatically removed and digested during gut passage. The cleaned sand is then recycled back to the surface above a tail shaft as coiled fecal castings (Riisgård and Banta, 1998).

For respiration, overlying water is pumped through the tail shaft, passes the gills of the worm, and then dissipates into the coarse material enveloping the feeding pocket. At the surface, feeding pits become small water reservoirs when the tide is out, and serve as refuges for swimming copepods, turbellarians and juvenile shrimp. Pits also trap suspended organic particles (Retraubun et al., 1996). On the other hand, pits are unstable and are thus avoided by small tube-building infauna such as spionid polychaetes and corophiid amphipods (Brey, 1991; Flach, 1992; Reise, 1985).

The next subhabitat is the most outstanding: the feeding pocket enveloped by coarse grained sediment particles. This coarse sand is ameliorated by the oxic respiration current enriched with nitrogen from the excretions of the worm to maintain bacterial gardens (Grossmann and Reichardt, 1991; Hylleberg, 1975; Reise, 1984; Scherer, 1985). The interstices are rich in meiofauna with a unique species composition, and several have been described as new species (Noldt and Reise, 1987; Reise, 1985, 1987; Sopott-Ehlers, 1992). In addition to the diverse meiofauna there are small capitellid polychaetes, tubificid oligochaetes and a nemertine down there, and also conspicuous aggregations of the amphipod *Urothoe poseidonis*, otherwise absent on the lugworm flats (Lackschewitz and Reise, 1998). Up to 173 of these amphipods were counted at a single burrow. They seem to complete their entire life cycle in the coarse sand surrounding the feeding pocket.

The remainder of the burrow is an open tube where the lugworm resides. Some copepods live between the bushy gills, and in the tail shaft a scale worm *Harmothoe sarsi* is a frequent inmate. More interesting as a further subhabitat is the sediment enveloping the tail shaft. Here a high density of nematodes and other slender meiofauna were encountered which apparently use the oxic burrow to tap oxygen and then feed on the sulfur bacteria at the chemocline between oxic and anoxic conditions (Ehlers et al., 1995; Reise, 1981; Wetzel et al., 1995). These tail shaft sediments are hot spots of the thiobiota, here composed of bacteria, protozoans and small metazoans with a sulfide-based trophic web (Reichardt, 1988; Reise, 1984, 1987; Reise and Ax, 1979).

There are two more subhabitats. One is a halo surrounding the fecal mound. Here currents above the surface excert pressure when confronted with a mound, and push water as advective flow into the interstitial system (Huettel and Gust, 1992; Huettel et al., 1996). Organic particles are flushed into the sediment, which are exploited by the amphipod *Bathyporeia pilosa* (Lackschewitz and Reise, 1998). It lives upside down burried in the sand and extracts suspended particles from the interstitial water.

Finally, there is the fecal mound itself. Here the scavanging turbellarian *Archiloa unipunctata* is aggregating and preys on small animals which have passed the gut of the lugworm more dead than alive. All these subhabitats together contribute considerably to the biodiversity of the sand flats by hosting species which otherwise would be rare or even absent. On the other hand, some small tube-builders are displaced.

3. FUNCTIONAL ASPECTS

By flushing its burrow, the lugworm stimulates nitrification in the sediment through oxygen supply, resulting in a net nitrogen release from the sediment (Huettel, 1990). Similarly, silicate is flushed out of the sediment. In a large double-laned flume set up in the tidal zone, more particulate nitrogen was deposited on sediment with a rough surface topography of fecal mounds and feeding pits generated by the lugworms (Asmus and Asmus, 1998). However, also the relase of dissolved nitrogen was higher than in a lane where the lugworms had been removed and where the sediment surface was smooth. Again, more silicate was exported in the presence of lugworms. Thus, in permeable sediments lugworms enhance remineralization rates. This points to a higher filtering efficiency but a lower storage capacity.

Lugworms may also contribute to ecological disaster (Reise, 1983 a,b). Green algae have taken benefit of eutrophication along many coasts, and happen to be promoted by lugworms on sandy tidal flats. Tufts of filamentous green algae, *Enteromorpha*, drift with the tidal currents, then deposit at low tide in small depressions, and many of these depressions are feeding pits of the lugworms. The green algae thus slide down the shafts together with the surface sediment and become anchored. As the algae clog the feeding shafts, lugworms are forced to make new pits and shafts, and the process is repeated over and over again. While the algae are anchored in the sediment, thalli keep on growing upon the surface. Within 2-3 weeks an entire flat becomes covered by a continuous algal mat. Mats grow thicker, anoxia arises underneath with a strong smell of sulfide. Infauna either escapes or dies, and also lugworms leave this sediment. After a month or so the algal mats are dislodged by waves, leaving an almost azoic sediment behind. This severe disturbance is made possible by the coincidental interaction between algae and worms.

4. LARGE-SCALE LUGWORM EXCLUSION

In a lugworm exclusion experiment conducted earlier (Reise 1983 b), plots were probably too small to reveal the entire spectrum of potential effects. A considerable lateral transport of surface sediment exchanges the sand of small plots every few days (Zühlke and Reise, 1994). Therefore we decided to create plots of 20 x 20 m. A bulldozer excavated the upper layer of sand. Then 1-mm gauze was placed at a depth of 10 cm, and the surface sediment was shovelled back onto the gauze. The 1-mm mesh blocks the shafts of the lugworm burrows. Plots were not recolonized from above because 10 cm are not sufficient for adult lugworm burrows. Thus, as long as this gauze remains in place, tidal flat areas without lugworm bioturbation are maintained.

We decided for six replicates arranged in two groups, one in the lower tidal zone and the other at mid tide level adjacent to a seagrass

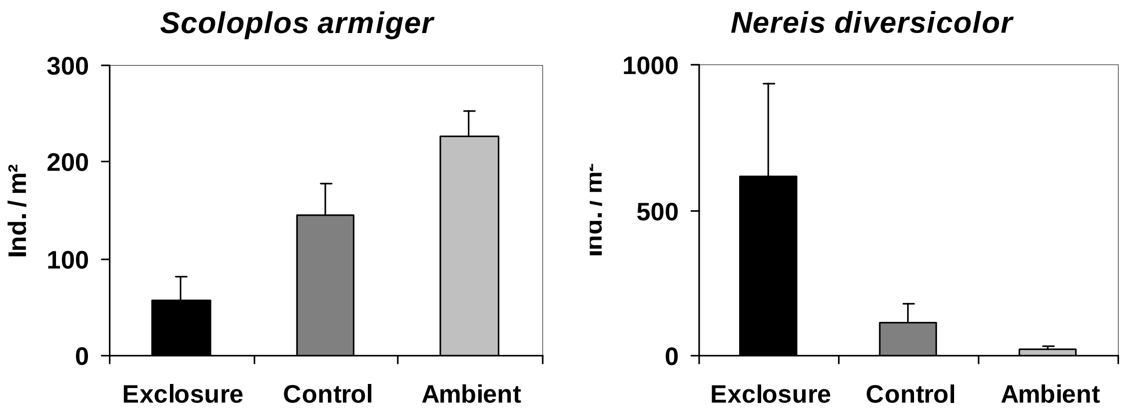

Fig. 2. Abundance of two polychaete species four months after initiating experimental exclosure of *Arenicola marina* with a fine-meshed net at 10 cm below surface, compared to control plots with a similar initial disturbance and to ambient plots left untouched. Each treatment with 6 plots of 400 m^2, each sampled with 10 cores of 100 cm^2, sieved through a 1-mm mesh in August 2002, Königshafen, island of Sylt in the North Sea.

bed. Next to each exclosure, there is a control plot which was reworked with a bulldozer in the same way as if to bury a net, and an ambient reference which was left untouched, each 400 m^2 in size. On an aerial foto from the first winter, one can spot the darker exclosure plots because of the smooth sediment surface microtopography lacking fecal mounds and pits.

In the first summer after initiating this experiment, we observed significant differences in the macrofauna (Fig. 2).

The orbiniid polychaete *Scoloplos armiger*, a free-burrowing subsurface bacterivor, prefers the ambient flat, probably because the irrigation performed by the lugworm population benefits its bacterial prey. The control plot showed intermediate densities. This indicates that the initial disturbance with the bulldozer still had an effect four months later. On the other hand, the polychaete *Nereis diversicolor*, a surface deposit feeder with deep burrows, took advantage of the absence of the lugworms and immigrated into exclosure plots. We assume that in the absence of lugworm bioturbation more food was available on the surface.

Organic carbon in the surface layer was higher at the exclosures (Fig. 3).

After one year, the controls which were initially disturbed in the same way as the exclosures, and the ambient reference plots

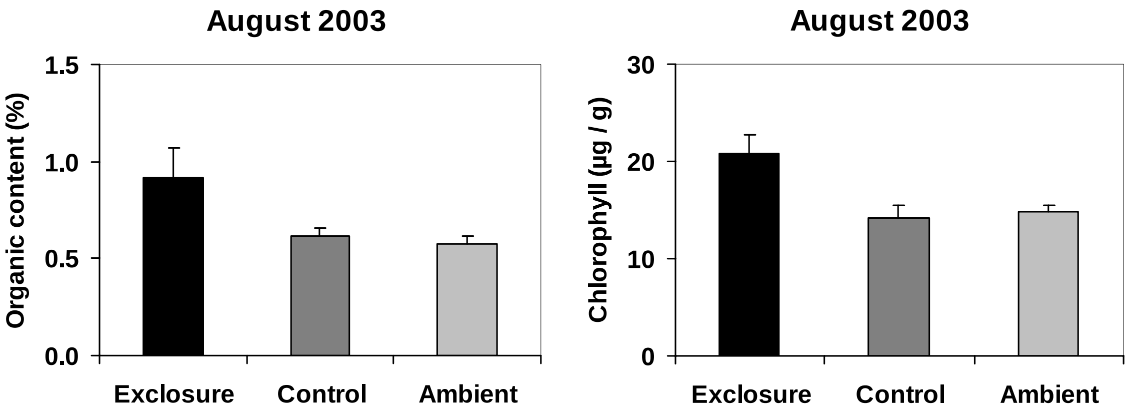

Fig. 3. Organic content as percentage of ash free dry weight in the upper 5 cm of sediment, and chlorophyll a in the upper 1 cm on *Arenicola marina* exclosure plots compared to control and ambient plots. See legend Fig. 2.

did not differ anymore. Chlorophyll concentrations were higher at the exclosures too. Interpretation of such differences must be done with caution. The ultimate cause of the higher concentration of microalgae may be the absence of lugworms. However, the actual magnitude is the outcome of interactions with other grazers such as the nereid polychaetes which preferred the exclosure plots and also feed on benthic microalgae.

In autumn, first observations on foraging birds were made to see how these respond to the exclosure plots. Gulls were more frequent on control plots. They mostly feed on epibenthic fauna like shrimp. As these tend to aggregate in feeding pits of the lugworms during low tide exposure, this may explain why gulls prefer to forage where the lugworms are still there. On the other hand, golden plovers were more frequent at exclosure plots. There they apparently foraged on nereid worms. These worms feed on the surface and then are an accessible prey for these visual hunters with a short bill. We also sampled pore water concentrations of nutrients and oxygen, and first counts have been done on bacteria. All these parameters change seasonally and in the course of time as the experiment matures. We hope to run it for 10 years or so, in order to reveal the manifold direct and indirect effects of the lugworm bioturbation and bioirrigation on the entire sediment ecosystem.

5. CONCLUSIONS

The lugworm *Arenicola marina* provides habitat for other sediment dwelling fauna which otherwise would be rare or absent. It thus increases biodiversity on the tidal flats where it abounds. Some other deposit feeders are negatively affected by the reworking of surface sediment. In addition to these sediment mediated effects, worms apparently increase remineralization rates in the sediment by flushing their burrows with oxic water. At the ecosystem level, permeable sediments with lugworms will have a higher filtering efficiency than sediment without such large worms. A chaotic element comes into play, when eutrophication favours green algal mass development. Then the coincidental anchoring of algal tufts by the lugworms leads to an intermittent disaster for the tidal flat community including the lugworm itself. More effects of lugworm populations on their environment are conceivable and need further investigations. Also their roles as consumer and prey need to be quantified and compared to that of other species dwelling in the same sediments. This may eventually allow to decide whether the conventional focus on energy flow in ecosystem models needs to be integrated with bioengineering activities in marine sediments.

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Part III: Acknowledgements and Curriculum vitae

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