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Effects of antagonistic ecosystem engineers on macrofauna communities in a patchy, intertidal mudflat landscape

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ABSTRACT

Ecosystem engineers are organisms that strongly modify abiotic conditions and in the process alter associated communities. Different types of benthic ecosystem engineers have been suggested to facilitate different communities in otherwise similar marine environments, partly because they alter sediment conditions in contrasting ways. However, most studies testing this hypothesis have either not manipulated the presence of engineers, or have transplanted engineers into areas already dominated by other engineers, which limits the ability to assess the relative engineering effects. Here we combined a field survey and a field experiment to investigate if two contrasting ecosystem engineers – the sediment-stabilizing seagrass *Zostera noltei* and the bioturbating lugworm *Arenicola marina* – facilitate different macrofauna communities. The study was performed in a sheltered mudflat area of the eastern Dutch Wadden Sea, where seagrasses and lugworms form a mosaic of spatially alternating seagrass-dominated elevations (hummocks) and lugworm-dominated depressions (hollows). Results showed that seagrasses facilitated some organisms (mainly attached epifauna) while lugworms facilitated others (primarily burrowing infauna), generating distinctly different macrofauna communities in hummocks and hollows. However, seagrasses had a much stronger effect on the macrofauna communities than lugworms, and competitively excluded lugworms. This contrasts with results from similar studies in hydrodynamically more exposed sand flats, where lugworms instead dominate communities and exclude seagrass. We therefore propose that effects of ecosystem engineering (acting primarily on a local scale) and variation in abiotic conditions (acting on larger scales, e.g., hydrodynamic gradients along the Dutch coastline) strongly interact to dictate the distribution and fitness of engineering species, and indirectly, the diversity and structure of associated benthic communities.

1. Introduction

Ecosystem engineers are organisms that strongly modify abiotic conditions and in the process alter natural communities (Hastings et al., 2007; Jones et al., 1994, 1997). By changing resource availability and local stress levels, they facilitate some organisms and inhibit others (Jones et al., 1997; Reise, 2002; van Wesenbeeck et al., 2007). This results in engineered ecosystem states that differ distinctly from those in surrounding areas (Donadi et al., 2013; van der Zee et al., 2012).

Ecosystem engineers are typically subdivided into 'autogenic engineers' (those that transform ecosystem properties via their presence) and 'allogenic engineers' (those that transform ecosystem properties via their movement and/or feeding activities) (Jones et al., 1994). Because autogenic and allogenic engineers often have different morphology, life history and differential effects on abiotic conditions, they can be assumed to facilitate different communities in otherwise similar environments. An archetypical example is sediment-stabilizing versus -destabilizing engineers in benthic ecosystems (Fig. 1a). It is often argued that sediment-stabilizing engineers (e.g., rooted plants) facilitate epibenthic organisms and potentially suppress some types of burrowing infauna, while sediment-destabilizing engineers (e.g., bioturbating worms) facilitate other burrowing infauna, and suppress epifauna (for review, see Bouma et al., 2009a). Most of these studies, however, merely compare areas dominated by

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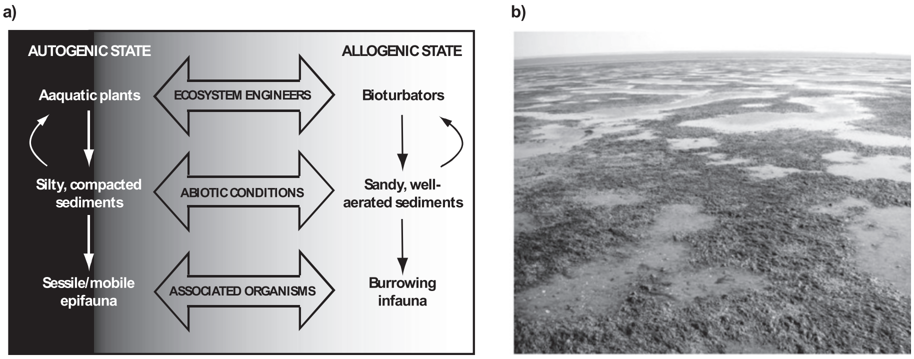

Fig. 1. a) Conceptual model of how autogenic and allogenic ecosystem engineers in theory could facilitate two different ecosystem states in otherwise similar benthic sediment habitats. b) Photo of part of the Western study site at low tide, displaying a conspicuous 'checkerboard' pattern of seagrass-dominated elevations (hummocks) next to lugworm-dominated depressions (hollows). Photo: JS Eklöf.

the different engineers (e.g., Berkenbusch and Rowden, 2003; Berkenbusch and Rowden, 2007; Pillay et al., 2011). Importantly, the lack of experimental manipulation makes it impossible to separate potential engineering effects from differences in underlying abiotic conditions — which we know affect the distribution, fitness and function of engineers themselves (e.g., Needham et al., 2011; Philippart, 1994).

To our knowledge, only two studies have experimentally compared the relative effects of sediment-stabilizing aquatic plants and bioturbators on associated organisms, in both cases using reciprocal transplantations between areas dominated by each engineer. Interestingly, both studies found that while the engineers indeed facilitated different communities, the effects were much weaker and diminished over time when the engineers were transplanted outside their normal habitat (Berkenbusch et al., 2007; Siebert and Branch, 2007). This suggests that the engineering effects were highly context-dependent. However, both studies transplanted the engineers into the new areas *without* first removing the locally dominating engineer. This may have underestimated actual differences in engineering effects for at least two reasons. First, contrasting engineering species often compete for resources (e.g., space) via their habitat modification; so called 'biomechanical warfare' (Harrison, 1987; Philippart, 1994; Siebert and Branch, 2006; van Wesenbeeck et al., 2007). This competition may negatively impact the transplanted engineer, and thereby reduce their effects on associated organisms. Second, if the two engineering species have opposing effects on abiotic conditions (e.g., stabilizing or de-stabilizing sediments), the effect(s) of an already established engineer could reduce the effect of the transplanted engineer.

Against this background, we experimentally tested whether two antagonistic intertidal ecosystem engineers facilitate different macrofauna communities; the sediment-stabilizing seagrass *Zostera noltei* Hornemann (from here on 'seagrass') and the bioturbating lugworm *Arenicola marina* L. (lugworms). Seagrasses are a polyphyletic group of marine flowering plants that are typical autogenic ecosystem engineers (sensu Jones et al., 1994). Their leaf canopy reduces hydrodynamic energy, their roots and rhizomes stabilize sediments (Eklöf et al., 2011), and by spatially concentrating resources like food and shelter, they can increase the density and diversity of both epi- and in-faunal organisms compared to vegetation-free bottoms (Arrivillaga and Baltz, 1999; Bostrom and Bonsdorff, 1997; Eklöf et al., 2005). Lugworms, in contrast, are allogenic engineers; as bioturbators they destabilize sediments by burrowing and feeding, which in combination with strong water motion increases sediment grain size (Montserrat et al., 2011). As a consequence, lugworms can alter the diversity and distribution of invertebrates (Flach and Debruin, 1993; Reise, 1983; Volkenborn and Reise, 2006) and rooted vegetation (van Wesenbeeck et al., 2007), including seagrass (Philippart, 1994; Reise, 1983; Suykerbuyk et al., 2012).

Our study was conducted in an intertidal mudflat area in the eastern Dutch Wadden Sea, characterized by a conspicuous small-scale checkerboard-like mosaic of seagrass-dominated 'hummocks' (elevations exposed during low-tide) alternating with lugworm-dominated 'hollows' (depressions waterlogged during low-tide) (Fig. 1b). In two previous papers we have shown that this spatially patterned landscape is created and maintained by a dynamic interplay between ecosystem engineering, competition, and waterfowl herbivory on seagrass. The elevated hummocks are the result of local net sediment accretion, driven by seagrasses that stabilize fine sediment particles and competitively exclude the bioturbating lugworms. Meanwhile, the waterlogged hollows are created and maintained by local net sediment erosion, which is partly caused by lugworm bioturbation, and partly by the mechanical disturbance caused by waterfowl herbivory on seagrasses (Eklöf et al., 2011; van der Heide et al., 2012). In the present study, we combined a field survey and a seagrass removal/lugworm addition experiment in this mosaic landscape, to answer the following three questions;

i) To what extent and in what way(s) do macrofauna communities differ between seagrass-dominated hummocks and lugworm-dominated hollows?
ii) Are those differences in macrofauna communities caused by the two ecosystem engineers?
iii) Are potential effects of the two engineers caused by the engineers directly (e.g., that they constitute a novel substrate and/or consume other organisms), and/or their indirect engineering effects on abiotic sediment conditions?

2. Materials and methods

2.1. Study area

The study was conducted on the intertidal mudflats at Emmapolder, Netherlands (53° 28′ 0 N, 6° 45′ 0 E). This is one of a few areas in the Dutch Wadden Sea where seagrass still occurs (Eklöf et al., 2011; Philippart, 1995). The field survey and the experiment were conducted in two 100 × 50 m sites situated ~350 m apart and ~400 m from the highest shoreline.

2.2. Field survey

First, we assessed to what extent and in what way(s) macrofauna communities differ between two naturally occurring habitat types in the study area; seagrass-dominated hummocks and lugworm-dominated hollows. This was done using a field survey conducted in June and August 2009, corresponding roughly to the start and peak of seagrass growth, respectively (Philippart, 1995).

2.2.1. Macrofauna

Sediment cores (diameter: 10.5 cm, depth: 20 cm) were extracted from the center of randomly selected hummocks and hollows ($n = 3$ per habitat type and site, respectively). The width of the hollows changed from ca. 2.0 m in June to ca. 0.5 m in August, as the seagrasses expanded from hummocks into hollows (Eklöf et al., 2011). The six hummocks sampled in early August were also used as 'control' plots in the Field experiment (see below). Following wet sieving, all macrofauna – here defined as living invertebrates retained on a 1 mm sieve (which is sufficient for community-level studies, see James et al., 1995) – were fixated in 70:30% isopropanol:seawater solution stained with Rose Bengal Red (following Thrush et al., 1996). In the lab, all organisms were identified (mostly to species level, see Table S1) and counted under a 10 × magnification stereo lens. We then calculated taxa diversity (Shannon index, H′) and the three components that together influence this index; taxa richness, evenness (Pilou's J), and total abundance (pooling all taxa).

2.2.2. Statistical analyses

The effects of 'patch type' (hummock vs. hollow) and 'month' on macrofauna diversity, richness, evenness and density were estimated using linear mixed-effects models with 'site' (two levels) as a random offset, using the *nlme* package (Pinheiro et al., 2014) for R v. 2.15.1 (CRAN, 2012). Since all samples came from different hummocks and hollows, 'site' was a crossed factor. Since we only wanted to account for differences between the two sites, we do not report the estimates for the site factor. The assumption of homoscedasticity was assessed by plotting fitted versus raw residuals, and the assumption of normal error distribution by plotting theoretical versus observed quantiles (QQ-plots). If necessary, data was transformed (square root or log) until assumptions were met. We started with the full model (including 'patch type', 'month' and their interaction), and then identified the minimal adequate model using the 'dredge' function in the MuMIn package (Barton, 2013). Selection was based on Akaike's Information Criterion corrected for small sample size (AICc) (Burnham and Anderson, 2002).

To assess if there were differences in macrofauna species composition between patch types and months, we first visualized macrofauna community composition using non-Metric Dimensional Scaling ordination (nMDS) plots based on the Bray–Curtis similarity index, using PRIMER v.6 for Windows (Clarke and Warwick, 2001). To down-weigh the influence of the most common species, we transformed the abundance data to the 4th root prior to analyses. We then tested for statistical differences between 'patch type', 'month' and 'site' (random factor with two levels), using a three-factor permutated mixed-model analysis of variance (PERMANOVA) (Anderson, 2005), based on the Bray–Curtis dissimilarity index and 9999 permutations (using PERMANOVA v.1.6 for Windows). To identify the species contributing to most of identified differences, we used the SIMPER (SIMilarity PERcentages) routine in PRIMER v.5 (Warwick and Clarke, 1993).

2.3. Field experiment

Second, to test if the observed differences in macrofauna communities found on hummocks and hollows (see *Results*) were caused by the two engineers directly and/or their effects on local sediment conditions, we tested the single and joint effects of: i) removing seagrass ('control' vs. 'removal') and ii) adding lugworms ('no addition' vs. 'addition') on macrofauna and sediments in a fully crossed field experiment. This experiment was part of a larger study on the role of habitat-mediated interactions between seagrass and lugworms (Eklöf et al., 2011; van der Heide et al., 2012).

2.3.1. Experimental design

In early June, 12 1×1 m^2 squared plots were established on seagrass-dominated hummocks in each site. In 'removal' plots all seagrass (leaves, rhizomes and roots) were removed using a hand rake. Two days later, 32 adult lugworms (corresponding roughly to naturally high densities in the area) were added to each 'addition' plot (see Eklöf et al., 2011 for details). The treatments were randomly allocated to plots in a crossed manner (resulting in $n = 3$ per treatment combination and site). Since the physical disturbance imposed when removing the seagrass could itself have affected lugworms and macrofauna, we separately assessed the relative effect of this disturbance by comparing the plots treated by removing the seagrass with naturally seagrass-free hollows (see *The relative effects of engineers, abiotic conditions and physical disturbance on macrofauna*).

2.3.2. Field sampling and laboratory analyses

After two months we sampled macrofauna in the center of each experiment plot (on the same day as the *Field survey*, using the same method). To estimate treatment effects on seagrasses, we also collected and froze all seagrass leaves, roots and rhizomes found in the core samples. In the lab, the samples were thawed, cleaned, dried (60 °C, 72 h) and weighed (pooling leaves, roots and rhizomes). To estimate treatment effects on lugworm density, we counted the number of lugworm fecal casts in each plot; a good proxy for actual worm densities (see Eklöf et al., 2011). Finally, to estimate treatment effects on sediments, we collected sediments using a corer (diameter: 4 cm, depth: 5 cm) and froze the samples in the field. Following freeze-drying, median grain size was estimated using a Malvern particle counter, and sediment organic matter (SOM) content was calculated as % weight loss on ignition (LOI; 550 °C for 5 h).

2.3.3. Statistical analysis

We used linear mixed models (with 'site' as random offset) to assess the single and interactive effects of 'seagrass removal' and 'lugworm addition' on seagrass biomass, lugworm density, sediment grain size, SOM-content, and macrofauna diversity, richness, evenness and density. We started with the full model (including 'seagrass removal', 'lugworm addition' and their interaction), and identified the minimal adequate model using model selection (for more details, see *Field survey, Statistical analyses* above). For one response variable (macrofauna richness), three models fitted the data equally well ($\Delta AICc < 2$). We then used model averaging to estimate the average effect of the different predictors (Burnham and Anderson, 2002).

To assess treatment effects on macrofauna community structure, we visualized the community using an nMDS plot, and tested for single and joint treatment effects using a mixed-model PERMANOVA analysis (for more details, see *Field survey, Statistical analyses*).

2.4. The relative effects of engineers, abiotic conditions and physical disturbance on macrofauna

Experimental treatment effects could be caused by effects of the ecosystem engineers, by abiotic sediment conditions, but also by the physical disturbance imposed when removing the seagrass. Therefore, we first combined the 24 macrofauna samples from the experiment (which contained samples from undisturbed and disturbed seagrass hummocks) with 12 samples from undisturbed lugworm hollows (the six samples collected for the August field survey, plus another six samples collected simultaneously). We then used a linear mixed model (with 'site' as a random offset) to tease apart the effect of the categorical factor 'physical disturbance' ('no clearing' vs. 'clearing') on macrofauna diversity (H′), from the effect of four continuous predictors: 'seagrass biomass', 'lugworm density', 'sediment grain size' and 'sediment organic matter content'. We used the continuous variable 'seagrass biomass' (square-root transformed) instead of the categorical factor 'seagrass removal', because

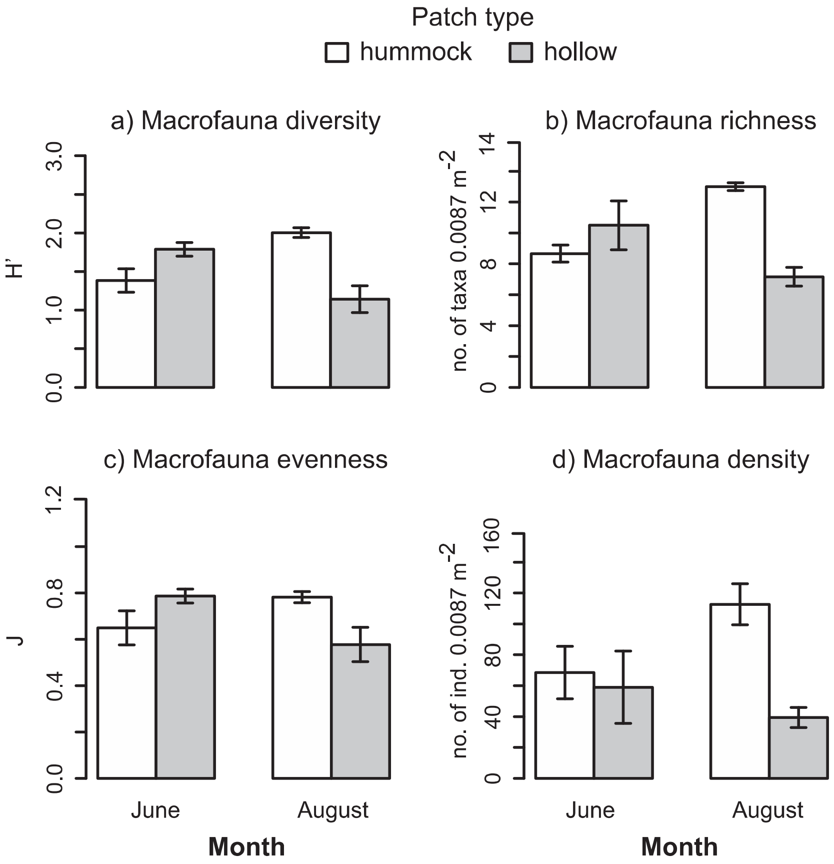

Fig. 2. Differences between patch types (hummock vs. hollow) and months (June vs. August) in macrofauna a) diversity, b) richness, c) evenness and d) abundance (mean ± 1 SE, n = 6).

i) considerable variation in seagrass biomass between replicates within both control and removal plots (see *Results*) could itself affect diversity, and ii) linear models are quite robust to the mild violation of linearity. The factors 'sediment grain size' and 'sediment organic matter content' were included even though they were unaffected by the treatments (see *Results*), because inclusion of the 12 natural hollow samples increased statistical power and could allow the identification of more subtle effects. Initial testing showed that there was no multicollinearity (all pairwise Spearman rank correlations between the five predictor variable < 0.7, and all Variance Inflation Factors [VIF] < 5) (Quinn and Keough, 2002). Following model selection based on AICc scores, the individual effects of the factors retained in the final model were visualized as conditional linear regressions using the *visreg* package (Breheny and Burchett, 2013).

We also assessed to what extent the five predictor variables influenced macrofauna community structure, using the *adonis* function in the *vegan* package (Oksanen et al., 2013). In short, *adonis* is a multivariate analysis of variance based on distance matrices, that in contrast to other types of tests could include the mix of categorical and continuous predictors, and account for the nestedness (by including the factor 'site' as a strata). The *adonis* analysis was based on Bray–Curtis dissimilarities and 9999 permutations. The results were visualized using a Constrained Analysis of Principal coordinates (CAP), using the *capscale* function in the *vegan* package. CAP is an ordination method similar to redundancy analysis, that allows non-Euclidean dissimilarities (here, Bray–Curtis). Note, however, that the resulting CAP plot does not account for differences between the two sites.

3. Results

3.1. Field survey

In the field survey we collected a total of 1677 organisms belonging to 38 taxa (for a list of all species, see Table S1). Polychaetes were the most diverse group (16 taxa), followed by crustaceans (9 taxa), bivalves (six taxa) and gastropods (four taxa). Numerically, polychaetes, gastropods and bivalves were equally abundant, constituting 29, 27 and 25% of all individuals, respectively.

Macrofauna diversity (H′) depended on an interaction between patch type and month (Fig. 2a; Table 1). In June there was no difference in diversity, but in August, diversity was nearly two times higher on hummocks than in hollows. This difference was caused by similar patterns in macrofauna richness, evenness (J) and density (Table 1, Fig. 2b, c and d, respectively).

Also, macrofauna community structure differed between patch types ($p = 0.01$, Table S2. For MDS-plot, see Fig. S1). This difference was largely caused by higher densities of *Mytilus edulis* and *Pygospio elegans* on hummocks than in hollows, and higher densities of *Hydrobia ulvae* and *Crangon crangon* in hollows than on hummocks (together explaining ~30% of the total difference). Moreover, the difference was stronger in August than in June (patch type × month interaction; $p = 0.006$, Table S3), due to seasonally increasing densities of *M. edulis*, *Littorina littorea*, *Carcinus maenas* and juvenile *A. marina* on hummocks (together explaining 40% of the difference). Finally, there was a weak difference between the two sites in June (month × site interaction; $p = 0.044$, Table S3), caused by high densities of the barnacle *Balanus* *improvisus* in the western site; a typical hard-bottom species here growing attached to drift macroalgae.

3.2. Experiment

3.2.1. Treatment effects on ecosystem engineers and sediment conditions

Seagrass biomass was 90% lower in seagrass clearings than in control plots, but was unaffected by lugworm addition, regardless of seagrass removal (Fig. 3a; Table 2). The seagrass encountered in the clearings had colonized over summer via elongation of rhizomes from surrounding hummocks (Eklöf et al., 2011).

Lugworm density nearly doubled following lugworm addition, increased by 2.5 times following seagrass removal, and there was also a strong synergistic effect whereby seagrass removal quadrupled the addition effect (Fig. 3b; Table 2). Importantly, sediment median grain size and sediment organic matter content were unaffected by seagrass removal, lugworm addition, and their potential interaction (Fig. 3c and d, respectively; Table 2). This lack of engineering effects on sediment conditions was most likely caused by the strong spatial effects of seagrass plants surrounding the plots, which reduced hydrodynamic disturbance (Eklöf et al., 2011).

3.2.2. Treatment effects on macrofauna

In the experiment we collected a total of 2702 organisms belonging to 31 taxa (Table S1). Polychaetes were the most diverse group (14 taxa), followed by crustaceans (eight taxa), bivalves (five) and gastropods (three taxa). Numerically, gastropods dominated (61% of all individuals) and were followed by bivalves (23%), polychaetes (10%), and crustaceans (4.5%).

Macrofauna diversity was negatively affected by seagrass removal, but was unaffected by lugworm addition (Fig. 3e; Table 2). Macrofauna richness, on the other hand, was explained equally well by three competing statistical models (ΔAICc < 2); the factor ‘seagrass removal’ alone or combined with ‘lugworm addition’, or both factors plus their interaction term (Fig. 3f; Table 2). Model averaging based on AICc showed that seagrass removal had the by far strongest effect, reducing richness by on average 3.1 taxa. Meanwhile ‘lugworm addition’ had a much weaker effect, reducing density by 0.84 taxa in uncleared seagrass plots, and by 1.33 taxa in the cleared plots (suggesting that seagrass removal strengthened the lugworm effect by ca. 60%). Meanwhile, hypothesis testing showed that the lugworm effects were statistically non-significant in all three models ($p > 0.11$). Finally, macrofauna evenness and density were negatively affected by seagrass removal alone (Fig. 3g and h, Table 2).

Table 1
Summary of minimal adequate mixed-effects linear models (fitted by REML) testing the single and joint effects of ‘patch type’ (hummock vs. hollow) and ‘month’ (June vs. August) on a) diversity, b) richness, c) evenness and d) total density, of macrofauna. Factor ‘site’ (two levels) was treated as random offset (parameter estimates not reported). P-values in **bold** mark significant effects (at $\alpha = 0.05$).

	df	F	P
a) Diversity			
Patch type (P)	1	3.48	0.075
Month (M)	1	0.012	0.914
P × M	1	26.55	<**0.001**
Error	19		
b) Richness			
Patch type (P)	1	6.38	0.021
Month (M)	1	0.22	0.64
P × M	1	16.61	<**0.001**
Error	19		
d) Evenness			
Patch type (P)	1	0.372	0.55
Month (M)	1	0.492	0.49
P × M	1	9.54	**0.006**
Error	19		
e) Density			
Patch type	1	8.72	**0.008**
Error	21		

Macrofauna community structure was affected by seagrass removal, but not by lugworm addition (Fig. S2; Table S3). The seagrass removal effect was caused by (in decreasing order of importance) a 500% increase in *H. ulvae*, a 98% reduction in *M. edulis*, a 50% reduction of *L. littorea*, a 75% reduction of *P. elegans* (6.7% of dissimilarity), and a 70% reduction of *Macoma balthica* (together explaining 83% of the removal effect). There was also a difference in community structure between the two sites (Table S3), caused by minor differences in densities of >15 taxa, each explaining $<10\%$ of the overall difference (most importantly, slightly more *M. edulis* and slightly less *P. elegans* in the western site, explaining 10 and 7% of the difference, respectively).

3.2.3. Relative effects of ecosystem engineers, abiotic conditions and physical disturbance

The univariate mixed model showed that macrofauna diversity was positively affected by seagrass biomass ($t_{1,32} = 4.66$, $p = 0.011$; Fig. 4a), and negatively affected by experimental disturbance ($t_{1,32} = -2.68$, $p = 0.001$; Fig. 4b). Lugworm density, sediment grain size and sediment organic matter (SOM) content had no effects ($p \gg 0.05$) and were not retained in the final model.

The multivariate *adonis* analysis showed that three of the five variables affected macrofauna community structure; seagrass biomass (pseudo-$F_{1,32} = 12.13$, $p = 0.0001$, $R^2 = 0.24$), experimental disturbance (pseudo-$F_{1,32} = 4.11$, $p = 0.0008$, $R^2 = 0.08$) and lugworm density (pseudo-$F_{1,32} = 2.25$, $p = 0.033$, $R^2 = 0.06$). The plotting of the effects onto the macrofauna ordination (Fig. 5) suggested that seagrass facilitated organisms such as *M. edulis*, juvenile *A. marina*, oligochaetes and cockles (*Cerastoderma edule*), whereas high lugworm density facilitated various infaunal worms (e.g., *Nephtys caeca*, *Polydora cornuta*) but also the highly abundant epifauna snail *H. ulvae*. Meanwhile, the physical disturbance (which structured the macrofauna community along another axis) negatively affected some other species of infauna, e.g., *Lanice conchilega*, *Hediste diversicolor*, and *Aphelochaeta marioni*. Finally, there were no effects of sediment grain size or organic matter content ($p \gg 0.05$).

4. Discussion

Ecosystem engineers with contrasting effects on sediment conditions are often suggested to facilitate different communities in otherwise similar environments (Bouma et al., 2009a). Meanwhile, most studies testing this hypothesis have either not manipulated the engineers (which could confound their effects with effects of abiotic gradients), or have not excluded antagonistic engineers (which could reduce the actual engineering effects). Here, we used a field survey and a field experiment to demonstrate that two contrasting ecosystem engineers – sediment-stabilizing seagrasses and bioturbating lugworms – indeed facilitate different macrofauna communities on a local scale.

The field survey showed that the seagrass-dominated hummocks and lugworm-dominated hollows housed quite different macrofauna communities, particularly in August (Fig. 2). The field experiment, in which seagrass were removed and lugworms were added, showed that variation in seagrass biomass drove most of the differences in macrofauna diversity and community structure between seagrass-dominated hummocks and lugworm-dominated hollows, whereas lugworms had a much weaker effect. The multivariate analysis showed that while seagrass removal negatively impacted various species, the ones most affected were epifauna growing attached to hard substrates, for example juvenile blue mussels *M. edulis*. Mussel larvae settle on hard substrates (including seagrass leaves) and are sheltered by the seagrass canopy from predators and hydrodynamic disturbance (Peterson and Heck, 2001). Therefore, it is not uncommon to in seagrass beds encounter juvenile *M. edulis* in densities of

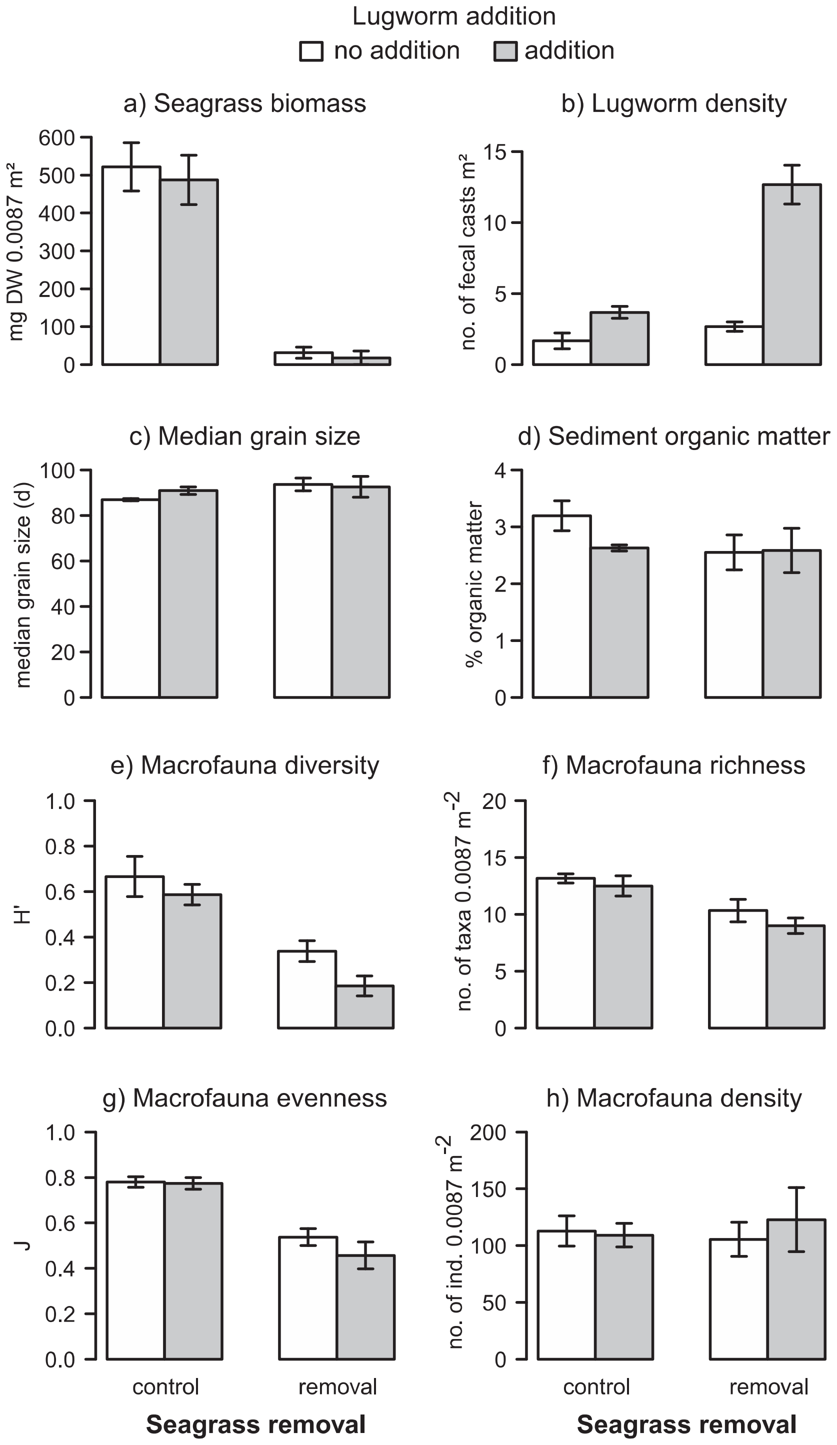

Fig. 3. Effects of experimental seagrass removal ('control' vs. 'removal' of seagrass *Zostera noltei* Hornemann.) and lugworm addition ('no addition' vs. 'addition' of 32 adult lugworms *Arenicola marina* L.) on a) seagrass biomass, b) lugworm fecal cast density, c) sediment median grain size, d) sediment organic matter (SOM) content, e) macrofauna diversity, f) macrofauna richness, g) macrofauna evenness, and h) macrofauna density (mean ± 1 SE, n = 6).

>100.000 m^{-2} (Bologna et al., 2005; Reusch et al., 1994). The community analysis also showed that seagrass biomass hampered some other types of organisms, most notably the mud snail *H. ulvae* (which increased by 500% due to seagrass removal, Table S1). This inhibitory seagrass effect was unexpected, since *H. ulvae* is often closely associated to aquatic plants like *Z. noltei* (e.g., Bouma et al., 2009b; Cottet et al., 2007; Herkul and Kotta, 2009). Potential explanations for our result could be that i) seagrass removal strongly reduced densities of the gastropod *Retusa truncata* (see Table S1); a predatory gastropod specialized on *H. ulvae* (Berry, 1988), and/or that ii) vegetation-free hollows can contain highly productive mats of benthic diatoms, which are a major food source for *H. ulvae* (Weerman et al., 2011). Regardless of the exact mechanism(s), the simultaneous facilitation of *M. edulis* and inhibition of *H. ulvae* by seagrass – two epifaunal mollusks – indicate that the division of macrofauna into coarse functional or taxonomic groups (Bouma et al., 2009a) may be of limited use when trying to understand what factors determine the strength of engineering effects.

Table 2
Summary of minimal adequate mixed-effects linear models (fitted by REML, selected based on AICc) on single and joint effects of 'seagrass removal' (control vs. removal) and 'lugworm addition' (control vs. addition) on a) seagrass biomass (g DW sample^{-1}), b) lugworm density (# fecal casts m^{-2}), c) sediment grain size, d) % sediment organic matter (SOM) content, e) macrofauna diversity (H′), f) macrofauna richness, g) macrofauna evenness (J), and h) macrofauna density, in the experimental 1 m^2 plots. The factor 'site' (two levels) was included as a random offset in all models (parameter estimates not shown). P-values in **bold** mark significant effects (at $\alpha = 0.05$).

	df	F	P		df	F	p
a) Seagrass biomass				e) Macrofauna diversity			
Seagrass removal	1	152.62	<**0.001**	Seagrass removal	1	58.9	<**0.001**
Error	21			Error	21		
b) Lugworm density				f) Macrofauna richness*			
Seagrass removal (S)	1	33.3	<**0.001**	Seagrass removal (S)	1	20.89	<**0.001**
Lugworm addition (L)	1	53.2	<**0.001**	Lugworm addition (L)	1	2.55	0.127
S × L	1	9.94	**0.0052**	S × L	1	0.83	0.37
Error	19			Error	19		
c) Sediment grain size				g) Macrofauna evenness			
Seagrass removal (S)	1	0.54	0.57	Seagrass removal	1	42.95	<**0.001**
Lugworm addition (L)	1	0.32	0.47	Error	21		
S × L	1	0.12	0.73				
Error	19						
d) % SOM content				f) Macrofauna density			
Seagrass removal (S)	1	1.58	0.22	Seagrass removal (S)	1	0.09	0.76
Lugworm addition (L)	1	0.92	0.35	Lugworm addition (L)	1	1.27	0.81
S × L	1	1.16	0.29	S × L	1	0.92	0.66
Error	19			Error	19		

* Average best model, based on three competing models with equally good fit (based on AICc scores).

Lugworms also affected macrofauna communities, facilitating other taxa that than seagrass (primarily other burrowing worms and the epifaunal mollusk *H. ulvae*; Fig. 6) and thereby 'pulling' the community in the opposite direction to seagrass. These contrasting effects of seagrass and lugworms support the hypothesis that opposing ecosystem engineers may locally facilitate different associated communities in otherwise similar abiotic environments, as suggested by studies conducted in other areas including South Africa (Siebert and Branch, 2007), New Zealand, and the USA (Berkenbusch et al., 2007). However, the lugworm effects were in our study much weaker than the seagrass effects, or were completely absent. This surprised us, since lugworms are known to strongly affect macrofauna communities elsewhere, including other parts of the Wadden Sea (Flach and Debruin, 1993; Reise, 1983; Suykerbuyk et al., 2012; van Wesenbeeck et al., 2007; Volkenborn and Reise, 2006). The absent effects in our experiment may have been caused by the relatively low sample size and substantial within-group variation, but the statistically significant lugworm effects we did find were much weaker than the effects of seagrass. We suggest that there are at least three not mutually exclusive explanations for these differences in results. The first is *scale-dependence*; we estimated effects of lugworms in relatively small (0.5–2 m wide) natural and experimental hollows surrounded by typically larger seagrass-dominated hummocks (see e.g., the photo in Fig. 1b). Importantly, the effect of ecosystem engineers typically depends not only on the local abundance of engineers, but also on the *size* of engineered patches (e.g., van Wesenbeeck et al., 2007). Consequently, it is likely that the hollows were too small for the lugworms to affect communities in the way they can do in lugworm-dominated sand flats (Reise, 1983; Volkenborn et al., 2007). The second explanation is *conditionality*; we have in a previous study demonstrated that the seagrass canopies on the elevated hummocks can weaken hydrodynamic activity also in nearby unvegetated hollows, which reduces local sediment erosion (Eklöf et al., 2011). Consequently, seagrass ecosystem engineering is likely to weaken the local effect of lugworms on sediment conditions and, indirectly, macrofauna within hollows. Engineering effects that spatially extend way beyond engineering species are common in ecosystems (Hastings et al., 2007). We have previously shown that engineering effects of strong sediment-stabilizing engineers like

Fig. 4. Conditional effects of a) seagrass biomass (g DW) and b) physical disturbance (control vs. removal) on macrofauna diversity (Shannon index, H′) in experimental and natural plots in intertidal areas (n = 36).

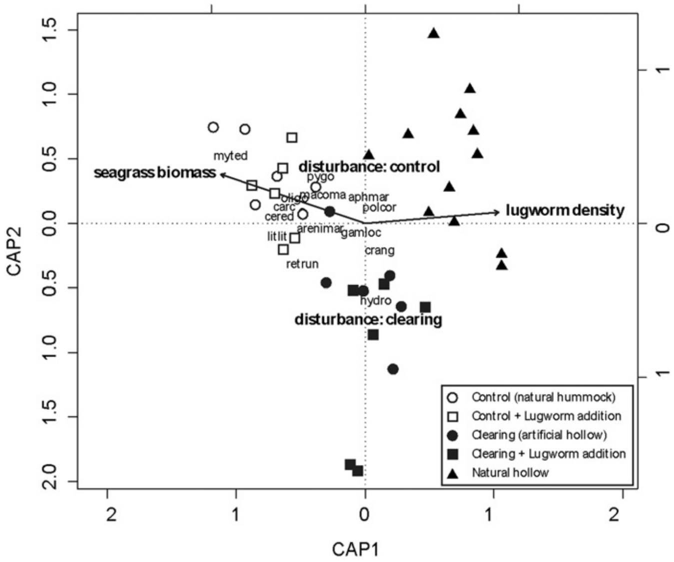

Fig. 5. Constrained Analysis of Principal coordinates (CAP) plot illustrating effects of three predictor variables – 'seagrass biomass' (continuous), 'lugworm density' (continuous), and 'disturbance' (categorical: control vs. clearing) – on 4th root transformed density of 40 macrofauna taxa in experimental plots and natural hollows (N = 36, illustrated by the symbols). The species acronyms note the position of the 14 discriminating taxa in ordination space (for species acronym key, see Table S1).

intertidal blue mussel beds can stretch >100 m away from actual beds (Donadi et al., 2013; van der Zee et al., 2012), and there weaken the local effect of another engineer, cockles (*C. edule*), on diatoms (Donadi et al., 2013). The third and final explanation is *context-dependence*; lugworms prefer sandy sediments that are easy to burrow and feed in (Montserrat et al., 2011; Volkenborn et al., 2009). Meanwhile, our study area was a relatively sheltered mudflat with fine-grained sediments and a relatively high silt content (Philippart and Dijkema, 1995): conditions known to impede lugworm bioturbation (Volkenborn et al., 2007). Therefore, we suggest unfavorable sediment conditions combined with the spatially extended engineering effect of seagrasses (Eklöf et al., 2011) explained the relatively low lugworm densities (max. 18 ind. m^{-2}) and weak lugworm effects found in our area.

A third factor that also structured the macrofauna community was the physical disturbance caused by the seagrass removal. This disturbance was an unavoidable part of the experimental treatment, but unintentionally resembled the naturally recurring sediment disturbance in hollows that migrating geese caused when feeding on seagrasses that had expanded from hummocks into hollows (Eklöf et al., 2011; Nacken and Reise, 2000; van der Heide et al., 2012). Consequently, we suggest the differences in macrofauna communities between seagrass-dominated hummocks and lugworm-dominated hollows were in fact caused and maintained by three factors; higher seagrass biomass in hummocks, higher lugworm density in hollows, and physical disturbance from geese grazing in hollows during autumn (van der Heide et al., 2012). Moreover, these factors are likely to interact; waterfowl herbivory will affect macrofauna both directly (mechanical disturbance) and indirectly (by removing seagrass, and by facilitating the competitively inferior lugworms), and high lugworm density increases the likelihood that waterfowl disturbance occurs in medium-sized hollows (Eklöf et al., 2011). Similar direct and indirect effects of bioturbation by large consumers on smaller organisms are well-known to occur in both terrestrial and aquatic ecosystems (e.g., Meysman et al., 2006).

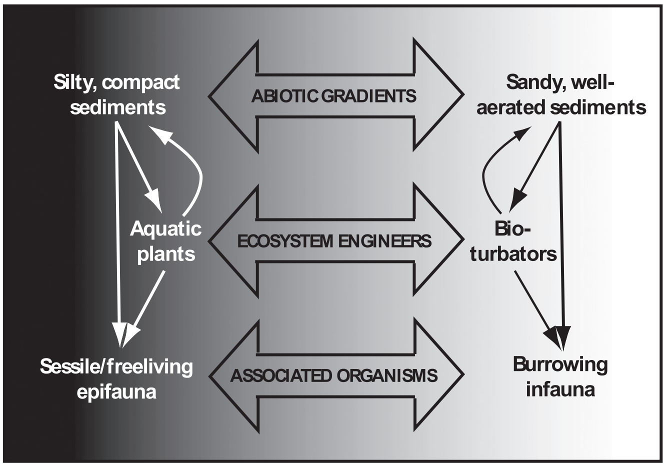

Fig. 6. Conceptual model of how regional variation in abiotic conditions affects intertidal organisms including ecosystem engineers, and how ecosystem engineers locally increase biotic spatial variation by influencing abiotic conditions.

Ecosystem engineers with contrasting effects on abiotic conditions have frequently been suggested to facilitate different communities in otherwise similar environments, partly by altering local abiotic conditions (Fig. 1a). Here, we demonstrate that even though sediment-stabilizing seagrass and bioturbating lugworms indeed facilitate different macrofauna taxa, the seagrass effect was much stronger, and seagrasses locally outcompeted lugworms. Moreover, even though seagrass removal increased lugworm density, the lugworm effects were much weaker than those found in more hydrodynamically exposed areas (Flach, 1992; e.g., Reise, 1983; Volkenborn and Reise, 2007), where lugworms instead dominate and exclude seagrass (Philippart, 1994; Suykerbuyk et al., 2012). We suggest these contrasting results can be explained by a revised conceptual model (Fig. 6), where ecosystem engineering (acting primarily on a local scale) and variation in abiotic conditions (acting on larger scales, e.g., hydrodynamic gradients along the Dutch coastline) interact to dictate local abiotic conditions and benthic communities. In the relatively sheltered mudflat area where our study was conducted, seagrass thrived, recovered quickly from experimental disturbance (this study; Eklöf et al., 2011; van der Heide et al., 2012) and appeared to overrule the local effect of the weaker competitor, lugworms (this study; Eklöf et al., 2011). Meanwhile, in more exposed and sandy areas of the Wadden Sea, lugworms naturally thrive (Montserrat et al., 2011; Volkenborn et al., 2009) and often exclude the locally weaker competitor, seagrass (Philippart, 1994; Suykerbuyk et al., 2012). In line with predictions, lugworm exclusion here benefits seagrass by increasing sediment stability (Philippart, 1994; Suykerbuyk et al., 2012), but seagrasses do not thrive (potentially because of the generally unfavorable abiotic conditions). This conceptual model concurs with knowledge about context-dependent effects of single (e.g., Needham et al., 2011) and multiple engineering species on abiotic conditions and associated communities (Berkenbusch et al., 2007; Siebert and Branch, 2007), and with suggestions that also more complex emergent properties like spatial self-organization are highly context-dependent (van de Koppel et al., 2012). However, most studies showing context-dependent effects of ecosystem engineers have transplanted engineers into relatively small plots (typically < 100 m^2). But since engineering effects typically increase with patch size (e.g., Eklöf et al., 2011), and the importance of patch size should increase with level of stress (Bertness and Callaway, 1994), much larger transplantations may be required to trigger self-facilitation and override context-dependent effects (see e.g., Schulte et al., 2009 for experimental demonstration). Clearly, we need more studies assessing not only how the effects of ecosystem engineers vary along abiotic gradients, but the extent to which context-dependence varies with patch size.

Our results are also important from a management point-of-view. Multiple lines of evidence suggests that the Wadden Sea ecosystem has undergone a shift in community composition, from a historical dominance of sediment-stabilizing ecosystem engineers such as seagrasses and blue mussels, to a current dominance by bioturbators such as lugworms (Eriksson et al., 2010; Lotze et al., 2005). On the one hand, our study shows that even small-scale (1 m^2) seagrass loss from seagrass-dominated areas impacts certain macrofauna (e.g., attached filter-feeders), and reduces macrofauna diversity (and possibly, ecosystem functions) at the local scale. On the other hand, the same seagrass loss benefits lugworms, who in turn facilitate (albeit weakly) other burrowing organisms in hollows. Consequently, the checkerboard-like mosaic with seagrass-dominated hummocks next to lugworm-dominated hollows (Fig. 1) is likely to maintain a considerable spatial macrofauna community heterogeneity and diversity at the landscape level. Moreover, because of the seasonally fluctuating density and distribution of the engineers (this study; Eklöf et al., 2011; van der Heide et al., 2012) these effects on associated macrofauna are likely to vary over the year. The effects of this spatial and temporal heterogeneity on ecosystem functions and services in the landscape are beyond the scope of this study, but should be assessed and potentially accounted for in future management plans.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.seares.2014.12.003.

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