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Habitat modification drives benthic trophic diversity in an intertidal soft-bottom ecosystem

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ABSTRACT

In intertidal soft-bottom ecosystems, ecosystem engineers such as reef-building bivalves, can strongly affect the associated benthic community by providing structure and stabilizing the sediment. Although several engineering species have declined dramatically in the past centuries, the consequences of their loss for the trophic structure of intertidal benthic communities remain largely unclear. In this study, we experimentally test the hypothesis that above- and belowground habitat modifications by ecosystem engineers, facilitate distinctly different, but trophically more diverse benthic communities, using intertidal mussel and tube worm beds as model systems. We constructed a large-scale experiment at two intertidal mudflats in the Dutch Wadden Sea, with distinctly different environmental conditions. At both sites, we applied anti-erosion mats to simulate belowground structure and sediment stabilization by commonly found tube worm beds and crossed this with the addition of adult mussels to investigate effects of aboveground structure. The anti-erosion mats mainly enhanced species and trophic diversity (i.e., feeding guild richness and diversity) of the infaunal community, while the addition of mussels primarily enhanced species and trophic diversity of the epifaunal community, irrespective of location. The effect size of mussel addition was larger at the exposed site in the western Wadden Sea compared to the more sheltered eastern site, probably due to relatively stronger abiotic stress alleviation. We conclude that structure-providing and sediment-stabilizing species such as reef-building bivalves and tube worms, form the foundation for trophically diverse benthic communities. In intertidal soft-bottom ecosystems like the Wadden Sea, their conservation and restoration are therefore critical for overall ecosystem functioning.

1. Introduction

Coastal ecosystems are of great importance to a multitude of marine species and provide crucial services to human society (Barbier et al., 2011; Beck et al., 2001; Costanza et al., 1997; Hodgson and Liebeler, 2002). Ecosystem engineers, species that strongly modify their environment, such as reef-building bivalves, seagrasses and corals (Jones et al., 1994, 1997), typically play an important role within these ecosystems, because they diversify the landscape by forming complex structures and relieve environmental stress, for instance by attenuating currents and waves (Donadi et al., 2013a; Gutierrez et al., 2003; Koch et al., 2009). Due to these habitat modifications, ecosystem engineers typically not only facilitate themselves (Donadi et al., 2014; Rietkerk et al., 2004; van de Koppel et al., 2005; van der Heide et al., 2007), but also provide a key-habitat for a wide variety of species that depend on them for settlement, refuge or food supply (e.g., Donadi et al., 2013b; Gutierrez et al., 2003; Nagelkerken et al., 2000; van der Heide et al., 2012; van der Zee et al., 2012).

Over the last decades, ecosystem engineer-dominated coastal ecosystems have become severely degraded worldwide, often due to anthropogenic impacts (Barbier et al., 2008; Lotze et al., 2006; van Gils et al., 2006; Waycott et al., 2009). Moreover, natural recovery of ecosystem engineers is typically slow, unpredictable or absent due to strong internal positive feedbacks, and even active restoration has proven difficult (Eriksson et al., 2010; Jackson et al., 2001; Schulte et al., 2009; van der Heide et al., 2007). The loss of ecosystem engineers and their lack of recovery often have dramatic implications for many associated species, especially in soft-bottom ecosystems, where solid substrate and

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aboveground structure are almost exclusively provided by engineering species such as seagrass, tube worms, mussel and oyster beds (Eriksson et al., 2010; Hodgson and Liebeler, 2002; Lotze, 2005; Waycott et al., 2009). Although the importance of engineering species for overall biodiversity has been well established, there is little experimental evidence showing how ecosystem engineers affect the trophic structure (i.e., feeding guild richness and diversity) of the benthic community in intertidal soft-bottom ecosystems.

In this study, we empirically test the hypothesis that habitat modification by epi- and endobenthic habitat modifying species facilitates distinctly different, but trophically more diverse intertidal benthic communities, using intertidal mussel and tube worm beds as model systems. In the Dutch part of the Wadden Sea, one of the world's largest intertidal ecosystems (Compton et al., 2013; Wolff, 1983), intertidal mussels – ecosystem engineers that create hard substrate, reduce hydrodynamic stress, modify sediment conditions and increase the cohesiveness of the substrata (Donadi et al., 2013a; Gutierrez et al., 2003; Kröncke, 1996; Widdows and Brinsley, 2002) – covered an area of over 4000 ha at the end of the 1970s. In the beginning of the 1990s, however, intertidal mussel beds disappeared completely due to a combination of overfishing, storms and several years of recruitment failure (Beukema and Cadée, 1996; Dijkema, 1991). In addition to the direct physical removal of mussels, sand extraction and bottom trawling for shrimps (*Crangon crangon*) and edible cockles (*Cerastoderma edule*) also removed sediment-stabilizing species and resuspended the upper layer of the sediment (Kraan et al., 2007; Piersma et al., 2001; e.g., Riesen and Reise, 1982; van der veer et al., 1985). Despite a ban on mechanical dredging for intertidal mussels (1999) and cockles (2005), it took more than a decade for mussels to start to re-establish and even now their recovery is still mainly restricted to the eastern part of the Dutch Wadden Sea (Ens et al., 2009; Goudswaard et al., 2009).

To test our hypotheses, we constructed a large-scale experiment, in which we used the application of anti-erosion mats with the addition of adult mussels to test for the effects of above and belowground habitat modification by ecosystem engineers. We applied anti-erosion mats to simulate belowground structure and sediment stabilization by commonly found tube worm beds (Friedrichs et al., 2000; Volkenborn et al., 2009) and crossed this with the addition of adult mussels to investigate effects of aboveground structure. To investigate whether the treatment effects were consistent across our study system, the experiment was carried out at two different sites with distinctly different conditions and ambient benthic communities (Compton et al., 2013). The first site was located in the western part of the Dutch Wadden Sea, south of the island Terschelling, and the second was situated in the eastern part of the Dutch Wadden Sea, south of the island Schiermonnikoog (Fig. 1). After three months, we investigated treatment effects on the invertebrate community.

2. Methods

2.1. Study area

Large-scale experimental plots were established on the intertidal mudflats of two barrier islands in the Dutch Wadden Sea. The first site was located in the western part, south of the island of Terschelling (53°21′39.69″N, 5°18′29.18″E) and the second site was located in the eastern part, south of the island of Schiermonnikoog (53°28′3.43″N, 6°14″13.40″E) (Fig. 1). The site at Terschelling has a small tidal range (~0.9 m, based on mean high water levels), is exposed to waves from the southwest, and is typified by relatively clear water and sandy sediment (Table 1). The site at Schiermonnikoog has a somewhat larger tidal range (~1.2 m, based on mean high water levels), is situated in more sheltered conditions, and is characterized by very turbid water and more silty sediments (Table 1). Both sites were located at approximately the same tidal elevation (0.6 to 0.8 m below mean water level), which is similar to the elevation of natural intertidal mussel and oyster beds in the vicinity of the experimental plots (distance: ~1000–2000 m).

2.2. Experimental design

At each site, 12 plots of 20 × 20 m were established in a line parallel to the gully (distance from the gully ~100–150 m) and with a distance of ~20 m between plots. Plots were divided over three blocks. Within each block, we randomly assigned one replicate of each of the following treatments to the plots: (1) control, which represents the ambient bare sediment surface at each site, (2) addition of a coco-coir mat on the bare

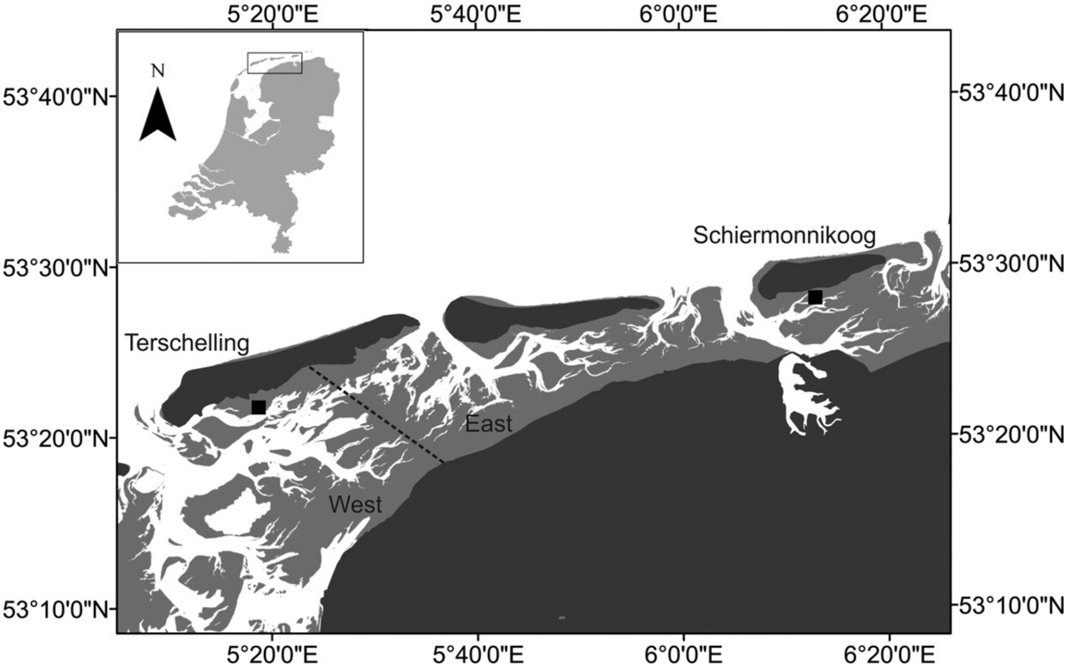

Fig. 1. Map with locations of the experimental plots in the western Dutch Wadden Sea at Terschelling and in the eastern Dutch Wadden Sea at Schiermonnikoog (black squares). White areas represent water, intermediate gray areas represent tidal flats exposed during low tide and land is represented by dark gray.

Table 1
Description of environmental conditions for the site in the western part of the Dutch Wadden Sea (Terschelling) and for the site in the eastern part (Schiermonnikoog). For each site, we obtained sediment silt and organic matter content, tidal elevation and amplitude, diffuse light attenuation, particulate organic carbon and chlorophyll concentration of the water, maximum current velocity, orbital velocity (with NW and W wind direction) and average fetch length. Light attenuation, particulate organic carbon and chlorophyll concentrations were calculated over the monthly composites of May, June and July 2011 from the Modis Ocean satellite.

	West	East
	Terschelling	Schiermonnikoog
Silt content (% < 63 μm)	2.3	3.0
Sediment organic matter content (%)	0.58	0.64
Elevation (m NAP)	-0.8	-0.6
Tidal amplitude (m)	0.9	1.2
Diffuse light attenuation at 490 nm (m^{-1})	0.58	1.03
Particulate organic carbon (mg m^{-3})	552.33	893.90
Chlorophyll concentration (mg m^{-3})	8.76	14.85
Maximum current velocity (ms^{-1})	0.55	0.60
Wave action — orbital velocity (ms^{-1}) NW	0.21	0.14
Wave action - Orbital velocity (ms^{-1}) W	0.32	0.25
Average fetch length (km)	29.9	9.3

sediment surface to provide belowground structure and stabilize the sediment, (3) addition of adult mussels on the bare sediment surface to create biotic aboveground structure, and (4) addition of both coco-coir mat and adult mussels on the bare sediment surface to test for their interaction. These four different treatments were compared to test for the effects of above and belowground habitat modification on the benthic community. Coir mats consisted completely out of coconut fiber and are commonly used to prevent erosion of sediment on bare soil (e.g., Sutherland and Ziegler, 2007). The mats are woven and have a mesh size of 25 mm (HasTec, KGW 400, weight of 400 g m^{-2}). This mesh size still allows infaunal burrowing species to dig into the sediment. The mats were applied by hand, fixated along the edges by digging it in to a depth of ~20 cm and in the middle by inserting 15-cm long biodegradable pins into the sediment. Right after addition, mats were covered by a thin layer of sediment due to natural deposition and formed belowground structure. We placed 128 knotted burlap balls (diameter ~10 cm) at regular distances from each other (~2.5 m) underneath the coir mats to reduce water velocity and enhance sediment stability and deposition on the coir mat plots.

Two-year-old alive mussels (shell length: 51.0 ± 1.0 mm; $n = 60$) were obtained from a natural subtidal mussel bed by mechanical dredging and transported to the site in the beginning of May. Within two days after fishing, 25 circular mussel patches with a ~2.5-m diameter were created at regular distances from each other on either bare sediment (treatment 3) or on the coir mat (treatment 4), yielding a total cover of around 30% (~2000 kg mussels/plot) — a cover comparable to natural intertidal mussel beds in the Wadden Sea (pers. observ.). Based on visual inspection, shells of the transplanted mussels were relatively clean with only a very low cover of barnacles (<10%), most likely due to predation by starfish in the subtidal area (Saier, 2001). In addition, no macroalgae were present on the mussels. The few crabs and starfishes found after dredging were mostly dead. Therefore, the possibility of co-transplanting relevant numbers of species to the experimental mussel plots was minimal.

The experiment lasted from the beginning of May until the beginning of August 2011. After 3 months, the average density of adult mussels within the patches at Schiermonnikoog was 1251 ± 70 mussels m^{-2} and at Terschelling 999 ± 85 mussels m^{-2}. Schiermonnikoog mussel patches had a 21% cover of the macroalgae *Fucus vesiculosus*, while patches on Terschelling had a 96% cover of the macroalgae *Ulva lactuca*.

2.3. Sediment and benthos sampling

Sediment and benthos samples were collected in the beginning of August 2011. At each control plot, we randomly took sediment and benthos cores. In the coir mat plots, we avoided areas disturbed by the burlap balls and in the mussel plots we randomly sampled inside the mussel patches. We pooled three 5-cm deep sediment cores with a PVC corer with an area of 7.1 cm^2. Sediment organic matter content in dried sediment (24 h, 70 °C) was estimated as weight Loss On Ignition (LOI; 5 h, 550 °C). Sediment samples were freeze-dried for up to 96 h till dry. Prior to grain-size analysis, organic matter and carbonate were removed using HCl and H_2O_2. The samples were left overnight at 80 °C to speed up the reaction. Samples were measured in de-gassed Reversed Osmosis water. Percentage silt (fraction < 63 μm) was determined using a Coulter LS 13 320 particle size analyzer using laser diffraction (780 nm) and PIDS (450 nm, 600 nm and 900 nm) technology. The optical module 'Gray' was used for calculations. Increased sediment deposition on top of the anti-erosion mats was used as a proxy for sediment stability (Friend et al., 2003). Sediment deposition was determined with a ruler by 10 random measurements on each coir mat plot in areas without burlap balls. Depth values were averaged per plot afterwards. Two benthos samples were taken within each plot with a stainless steel core with an area of 179 cm^2 down to a depth of 20–25 cm. Benthos samples taken at the coir mat plots, included newly deposited sediment on top of the mat, the mat itself and the sediment layer below. Infaunal benthos species were not found attached to the mat. Samples were sieved over a 1 mm mesh and all fauna was fixed in 4% formalin solution in 2-L bottles for later analyses. In the laboratory, samples were stained with Rose Bengal (CAS 11121-48-5). All fauna were identified to species level and counted. Prior to data analyses, we pooled the two benthos samples and classified all species as either infaunal or epifaunal species in order to test for treatment effects on the infaunal and epifaunal community separately (Table S1 & S2).

2.4. Data analyses

To get an overview of differences in the infaunal and epifaunal community compositions among sites and treatments, we first visualized the treatment effects with non-metric multidimensional scaling ordination models (nMDS) (Kruskall and Wish, 1978) based on the Bray–Curtis dissimilarity matrix (Clarke and Green, 1988). Multivariate analyses were performed on square root transformed data (i.e., for the epifauna data we used $\sqrt{(x + 0.1)}$). Differences in the infaunal and epifaunal community compositions among sites and treatments shown by these ordination models, were then tested for significant differences with a distance-based permutational multivariable analysis of variance (PERMANOVA) based on Bray–Curtis dissimilarity measures (Anderson, 2001; McArdle and Anderson, 2001).

Next, we tested for treatment effects on the benthic community structure by using four different community diversity indices. We determined species richness (number of species), species diversity (Shannon diversity index H′), feeding guild richness (number of feeding guilds), and feeding guild diversity (Shannon diversity index H′) for both the infaunal and epifaunal communities. Feeding guilds were based on data extracted from online databases for marine invertebrates (Appeltans et al., 2012; see Table S3 and S4 for guild list; MarLIN, 2006). To investigate if the addition of mussels and coir mats affected ambient sediment conditions, we tested for treatment effects on sediment organic matter content and silt content.

Prior to model selection for the community diversity indices and sediment conditions, all data were checked for normality using a Shapiro–Wilks test ($p = 0.05$). Based on this test, all community diversity indices and sediment conditions were then analyzed using three-way ANOVA models with a Gaussian error distribution and 'block' as random factor (organic matter and silt content were log-transformed to obtain normality). Next, to test for the significance of the random factor 'block', we repeated the analyses with three-way ANOVA models without the random factor 'block'(Van der Heide et al., 2014). Best models were selected based on AIC comparisons. This model selection procedure resulted in three-way ANOVA models without the random effect 'block' for all the community diversity indices and sediment conditions.

All statistical analyses were carried out in R (R Development Core Team, 2013). PERMANOVA models and nMDS plots were constructed with the functions *adonis* and *metaMDS,* respectively, in the *vegan* package (Oksanen et al., 2013). The significance of the random effect 'block' was tested with GLMMs and GLMs with the *glmmadmb* function in *glmmADMB* package (Fournier et al., 2012). Three-way ANOVA models were constructed using the *aov* functions from the *Stats* package.

3. Results

3.1. Sediment conditions

Sediment organic matter content did not differ between the sites ($F = 0.05$, $n = 12$, $p = 0.83$, Fig. 2A), but silt content was 1.2 times lower at Terschelling than at Schiermonnikoog ($F = 5.9$, $n = 12$, $p = 0.03$, Fig. 2B). The addition of mussels increased organic matter content by 1.6 times ($F = 47.8$, $n = 12$, $p < 0.001$, Fig. 2A) and doubled silt content ($F = 73.6$, $n = 12$, $p < 0.001$, Fig. 2B) compared to the control treatment. The coir mat did not significantly affect either organic matter ($F = 0.2$, $n = 12$, $p = 0.69$, Fig. 2A) or silt content ($F = 0.0$, $n = 12$, $p = 0.97$, Fig. 2B) compared to the control treatment. The coir mat increased sediment deposition, burying the mat under a thin layer of sand (Schiermonnikoog: 33 ± 2 mm; Terschelling: 44 ± 5 mm; mean ± SE; n = 6).

Table 2
F-values and significance levels of PERMANOVA based on Bray–Curtis dissimilarities for treatment effects on the infauna and epifauna communities compared to the control treatment. Significance levels: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Degrees of freedom: 24 in total; 16 residual.

Treatments	Infauna	Epifauna
Coir	3.4 (*)	1.4
Mussels	20.1 (***)	85.5 (***)
Site	9.7 (***)	2.3
Coir × mussels	1.8	1.4
Coir × site	1.4	2.1
Mussels × site	1.5	1.9
Coir × muss. × site	0.7	1.8

3.2. Infaunal community

PERMANOVA analyses revealed significant differences in the composition of the infaunal community depending on the site, coir mat and mussel additions, which are visualized by nMDS ordination models (Table 2, Fig. 3A). Overall, the most abundant infaunal species were *Capitella capitata*, *Urothoe poseidonis, Scoloplos armiger, Aphelochaeta marioni* and *Lanice conchilega* (Table S3). *C. capitata*, *U. poseidonis* and *A. marioni* (only present at Schiermonnikoog) were most abundant in the mussel plots. *S. armiger* was most abundant in the control plots and *L. conchilega* was most abundant in the coir mat plots (Table S3).

Infaunal species richness was significantly affected by coir mat, mussels and site (Fig. 4A, Table 3). Species richness was around 1.6 times higher in the coir mat plots, the mussel plots and in the plots with both coir mat and mussels compared to the control plots. At Terschelling, the increase in species richness due to the addition of mussels was 1.9 times stronger than at Schiermonnikoog. Infaunal species diversity was significantly affected by coir mat and site (Fig. 4B; Table 3). Diversity was 1.3 times higher in the coir mat plots compared to the plots without coir mats. Furthermore, species diversity was approximately 1.5 times higher at Schiermonnikoog compared to Terschelling, but only in plots without mussel additions. Mussel addition atn Terschelling increased species diversity by 1.3 times compared to plots without mussels, while Schiermonnikoog infaunal diversity was unaffected by mussel addition. Feeding guild richness was 1.5 times higher in the coir mat plots and in the mussel plots compared to the control plots (Fig. 4C; Table 3). Feeding guild diversity was significantly affected by coir mat and mussel addition and by the interaction of mussel addition and site (Fig. 4D; Table 3). Feeding guild diversity was around 1.5 times higher in the coir mat plots and in the mussel-addition plots compared to control plots. Guild diversity was 2 times higher in plots where both coir mat and mussels were added compared to control plots. At Terschelling, the increase in feeding guild diversity due to the addition of mussels was 1.7 times stronger than at Schiermonnikoog.

3.3. Epifaunal community

PERMANOVA analyses revealed clear differences in the composition of the epifaunal community depending on mussel addition and site, which are visualized by nMDS ordination models (Table 2, Fig. 3B). Overall, the most abundant epifaunal species were *Balanus crenatus*, *Carcinus maenus*, *Gammarus locusta* and *Mytilus edulis* spat (Table S4). These species were most abundant in both mussel treatments (mussel and coir ∗ mussel) (Table S4).

Further analyses showed that epifaunal species richness was significantly affected by mussels and site (Fig. 5A; Table 3). Species richness was 14 times higher in the plots with mussel addition compared with plots without mussel additions. At Terschelling, the increase in species richness due to the addition of mussels was 1.4 times stronger than at Schiermonnikoog. Epifaunal species diversity was also significantly

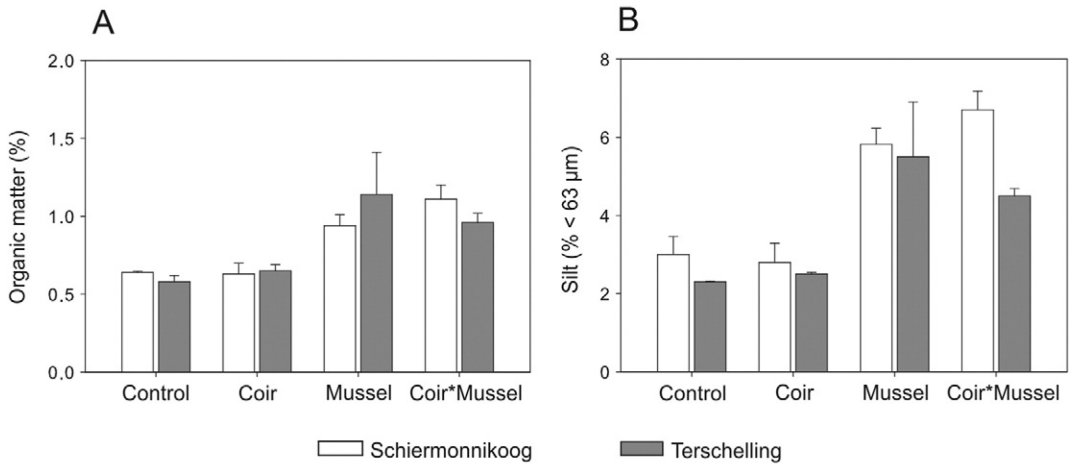

Fig. 2. Organic matter (A) and silt content (B) for each treatment (Mean ± SE, n = 3).

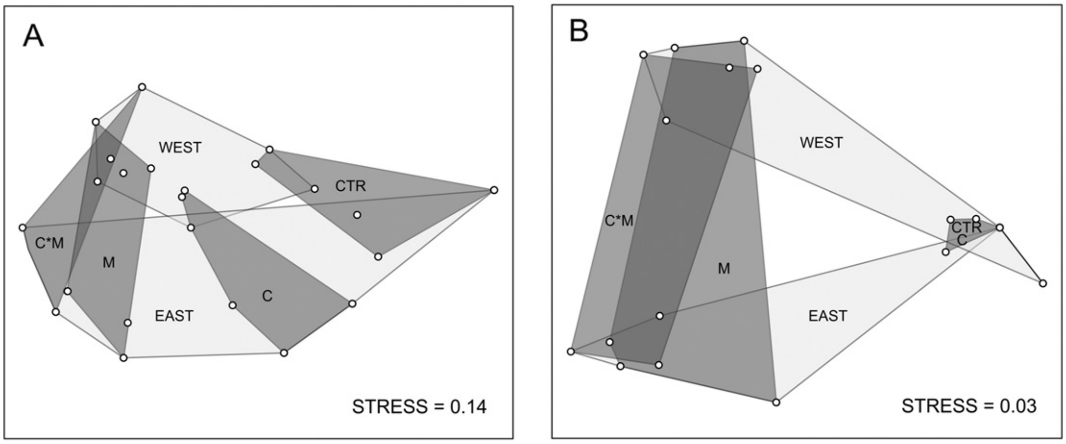

Fig. 3. Non-metric multi-dimensional scaling (nMDS) for differences among treatments for the infauna (A) and epifauna (B) communities. Coir mat and mussel treatments are represented by the dark gray polygons, sites by the light gray polygons and samples by the white circles (CTR = control, C = coir, M = mussel, C ∗ M = coir ∗ mussel, WEST = Terschelling, EAST = Schiermonnikoog). A stress value below 0.2 indicates a reliable ordination.

affected by mussels (Fig. 5B; Table 3). Species diversity was 1.1 times higher in the plots with mussel additions compared with the plots without mussel additions and the increase in species diversity due to the addition of mussels was 1.3 times stronger on Terschelling than on Schiermonnikoog. Furthermore, addition of mussels on top of the coir mats yielded a 1.2 times higher diversity compared to mussel plots at Terschelling, while at Schiermonnikoog, diversity in these plots was 1.1 times lower compared to mussel plots. Feeding guild richness was significantly affected by mussel addition (Fig. 5C; Table 3), with 8 times higher values in the plots with mussels compared to the plots without mussels. Feeding guild diversity was 9.5 times higher in the plots with mussel addition compared to the plots without mussel addition (Fig. 5D; Table 3). At Terschelling, the increase in guild diversity due to the addition of mussels was 2 times stronger than at Schiermonnikoog (Fig. 5D; Table 3).

4. Discussion

In coastal soft-bottom systems, the direct physical removal of ecosystem engineers in combination with mechanical dredging activity itself can result in a reduced availability of hard substrate and stable sediment with potentially dramatic implications for the associated community (Ferns et al., 2000; Piersma et al., 2001; Thrush and Dayton, 2002; Thrush et al., 1996). Here, we experimentally demonstrate that

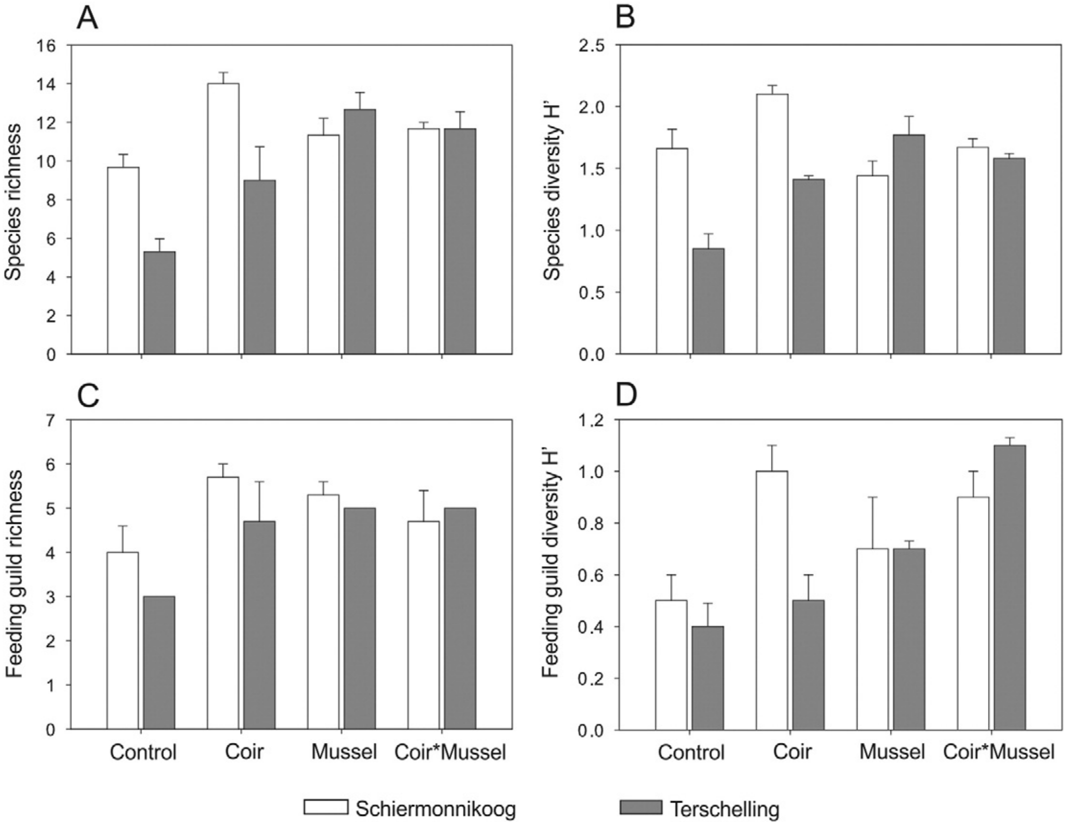

Fig. 4. Treatment effects on species richness (A), species diversity (B), feeding guild richness (C) and feeding guild diversity (D) of the infauna community (Mean ± SE, n = 3).

Table 3
F-values and significance levels of three-way ANOVA of all treatments and their interactions for species richness (S), species diversity (H′), feeding guild richness (F_S) and feeding guild diversity (F_H′) of the infauna and epifauna communities. Significance levels: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Degrees of freedom: 24 in total; 16 residual.

Treatments	Infauna				Epifauna			
	S	H′	F_S	F_H′	S	H′	F_S	F_H′
Coir	8.1 (*)	23.4 (***)	4.0	18.2 (***)	2.6	1.8	2.3	1.7
Mussels	13.1 (**)	2.3	4.0	6.0 (*)	243.4 (***)	43.0 (***)	168.1 (***)	73.7 (***)
Site	9.6 (**)	18.8 (***)	2.3	2.5	16.0 (**)	1.5	2.3	1.9
Coir × mussels	11.3 (**)	4.2	9.0 (**)	0.0	0	1.0	0.8	0.9
Coir × site	0.6	0.1	0.3	0.4	0.2	0.9	0.1	0.4
Mussels × site	17.1 (***)	34.9 (***)	2.3	7.3 (*)	10.2 (**)	9.0 (**)	0.1	4.5 (*)
Coir × muss. × site	0.1	0.3	0.3	3.1	0.2	3.9 (*)	0.1	1.9

above- and belowground structure and stable sediments are important properties of structure-providing organisms that facilitate distinctly different, and trophically more diverse, intertidal benthic communities.

Sediment stabilization through the application of anti-erosion coir mats stimulated the development of the infaunal community by increasing species and trophic diversity. The mats prevented erosion and increased sediment deposition, burying the mats under a 33-mm layer of sand (van der Heide et al., 2014). Moreover, as we did not detect any changes in sediment organic matter and silt content, these results suggest that sediment stabilization, rather than sediment composition, enhanced diversity. Depending on location, the addition of mussels slightly increased infaunal diversity or had no effect at all. However, this treatment did cause a shift in infaunal species composition, probably due to deposition of feces and pseudofeces (Kautsky and Evans, 1987; Pearson and Rosenberg, 1978; Ragnarsson and Raffaelli, 1999). Furthermore, the addition of adult mussels strongly stimulated the development of the epifaunal community by increasing epifaunal species and trophic diversity, most likely due to the availability of substrate (Gutierrez et al., 2003; Norling and Kautsky, 2007; Thiel and Dernedde, 1994). The effects of mussel addition on species richness are consistent with previous experimental studies in intertidal soft-bottom systems (Beadman et al., 2004; Kochmann et al., 2008; Norling and Kautsky, 2007; Ragnarsson and Raffaelli, 1999). However, by including more functionally-informative metrics of community structure, we show that mussel addition influences the benthic community structure not only by species enrichment, but also by enhancing the number and diversity of feeding guilds. This suggests that by sustaining more or different species and feeding guilds, stable sediments and mussel beds have the potential to alter the number and strength of biotic interactions among species such as predation and competition, thereby affecting overall ecosystem functioning.

Despite the environmental background differences between the communities of the western (Terschelling) and eastern (Schiermonnikoog) Dutch Wadden Sea, the overall effects of our treatments were similar. Nevertheless, the positive effect size of the mussel treatments on the infaunal and epifaunal community was significantly larger at Terschelling. These more pronounced positive effects on the more exposed and sandy site of Terschelling support the idea that facilitation by ecosystem engineers becomes more important when environmental stress increases due to for instance hydrodynamics (Bertness and Callaway, 1994; Bruno et al., 2003; Crain and Bertness, 2006). Mussels affect the infaunal community mainly by increasing substrate cohesiveness and reducing

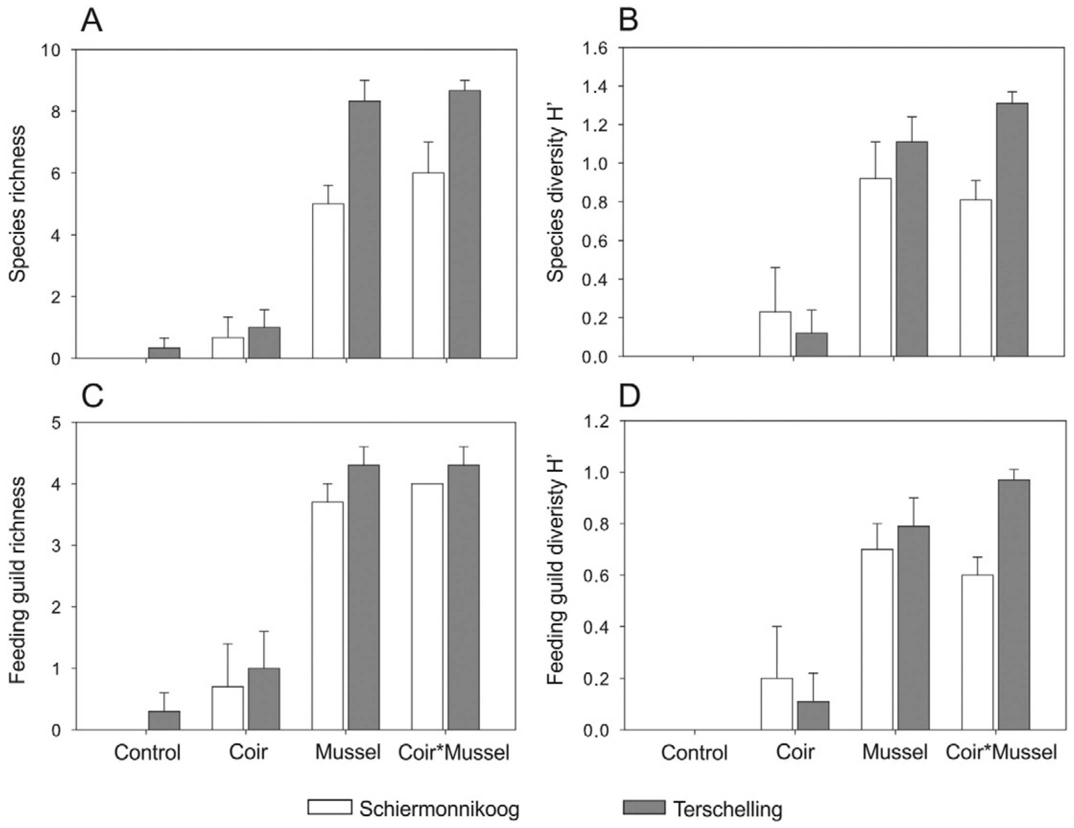

Fig. 5. Treatment effects on species richness (A), species diversity (B), feeding guild richness (C) and feeding guild diversity (D) of the epifauna community (mean ± SE, n = 3).

hydrodynamic stress (reviewed by Widdows and Brinsley, 2002), resulting in more suitable substrate for larval settlement (Commito et al., 2005), which seems particularly important at the exposed site of Terschelling. The epifaunal community, on the other hand, is most strongly affected by mussels through provision of aboveground attachment substrate, and shelter from water movement and desiccation (e.g., Stephens and Bertness, 1991; Thiel and Dernedde, 1994). Also these effects are likely more important at Terschelling than at Schiermonnikoog. The differential site effect on the epifaunal community is probably further enhanced by the much higher coverage of epibenthic macroalgae (*U. lactuca*) at Terschelling that profit from the relatively high water clarity at this site. *U. lactuca*, that was attached to the mussels, further increased habitat complexity. Moreover, the very high cover of this palatable algae species likely also served as an important additional food source to the surrounding epifauna and adjacent infauna (e.g., Goecker and Kall, 2003), further facilitating the benthic community.

Although it has been widely acknowledged that the loss of ecosystem engineers caused a loss of associated species and a homogenization of the Wadden Sea landscape (Lotze, 2005; Reise, 2005; Reise et al., 1989), the actual consequences for the trophic structure of the intertidal soft-bottom community remained largely unclear. Our results show that structure-providing and sediment-stabilizing ecosystem engineers such as mussels and tube worms, but likely also engineering effects generated by seagrasses and oysters (Friedrichs et al., 2000; Gutierrez et al., 2003; Orth, 1977; Volkenborn et al., 2009; Widdows et al., 1998) may strongly affect the trophic structure of the intertidal benthic community by increasing the number and diversity of feeding guilds. This suggests that ecosystem engineers may form the foundation for a trophically diverse ecosystem and illustrates the importance of protecting and restoring them.

Our findings can have important implications for ecosystem-based management and large-scale restoration strategies of intertidal soft-bottom ecosystems. We suggest that the loss of above- and belowground structure combined with sediment destabilization, caused by removal of ecosystem engineers or mechanical dredging, will negatively affect the trophic structure of the benthic community of the Wadden Sea. This study contributes to the growing awareness that the use of facilitative interactions is important in conservation efforts and that ecosystem engineers should be considered as one of the first target species for conservation (Boogert et al., 2006; Byers et al., 2006; Crain and Bertness, 2006).

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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.jembe.2015.01.001.

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