Biotic structure and sediment stability facilitate benthic species and trophic diversity in an intertidal soft-bottom ecosystem

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In intertidal soft-bottom ecosystems, reef-building bivalves have strong effects on the associated community both by providing habitat structure and by stabilizing the sediment. However, these species have declined dramatically in the past centuries and consequences of their loss for the trophic structure of the intertidal benthic communities remain largely unclear. In this study, we empirically tested the hypothesis that recovery of above-ground structure and stable sediments are both important ecosystem functions provided by ecosystem engineers that facilitate distinctly different intertidal benthic communities. In a large-scale experiment at two different sites, one in the Eastern and one in the Western Dutch Wadden Sea, we applied anti-erosion mats and created adult mussel beds to test for separate effects of sediment stabilisation and biotic structure, respectively. The anti-erosion mats mainly enhanced species and trophic diversity of the infaunal community, while the addition of mussels mainly enhanced species and trophic diversity of the epifaunal community, irrespective of location. The effect size of mussel addition, however, was larger at the site in the Western part compared to the Eastern part of the Dutch Wadden Sea, probably due to higher abiotic stress alleviation in the latter area. We conclude that structure-providing and sediment-stabilizing species such as reef-building bivalves, and most likely also seagrasses and tube-worms, can play a crucial role in structuring the benthic community throughout the Wadden Sea by affecting species composition and trophic structure. These species are therefore of great value for intertidal soft-bottom ecosystems and restoration attempts can be beneficial for overall biodiversity.

In preparation for publication
Coastal ecosystems are of great importance to a multitude of marine species and provide crucial services to human society (Costanza et al. 1997; Beck et al. 2001; Hodgson and Liebeler 2002; Barbier et al. 2011). Ecosystem engineers, species that strongly modify their environment, such as reef-building bivalves, seagrasses and corals (Jones et al. 1994; 1997), play an important role in structuring coastal communities (e.g. Bruno and Bertness 2001; Bouma et al. 2009; van der Zee et al. 2012). They diversify the landscape by forming complex structures and relieve environmental stress for instance by attenuating currents and waves (Gutierrez et al. 2003; Koch et al. 2009; Donadi et al. 2013). Due to these habitat modifications, ecosystem engineers typically not only facilitate themselves (Rietkerk et al. 2004; van de Kopp 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. Nagelkerken et al. 2000; Gutierrez et al. 2003; van der Zee et al. 2012).

Over the last few decades, coastal ecosystems have become severely degraded worldwide (Lotze et al. 2006; van Gils et al. 2006; Barbier et al. 2008; Waycott et al. 2009). At the same time, many dominating ecosystem engineering species have been overexploited or destroyed, with potentially dramatic implications for associated species, community structure and overall biodiversity (Hodgson and Liebeler 2002; Lotze 2005; Waycott et al. 2009; Eriksson et al. 2010). Especially in soft-bottom ecosystems, large-scale losses of seagrass, tubeworm, mussel and oyster beds can have a significant impact on the associated community, since solid substrate and structure are almost exclusively provided by such species in these otherwise sandy and hostile environments. Moreover, natural recovery of engineering species and their associated communities is often slow, unpredictable or absent due to strong internal positive feedbacks, and even active restoration has proven difficult (Jackson et al. 2001; van der Heide et al. 2007; Schulte et al. 2009; Eriksson et al. 2010).

In the Dutch part of the Wadden Sea, one of the world’s largest intertidal ecosystems (Wolff 1983), intertidal mussels – ecosystem engineers that create hard substrate, reduce hydrodynamic stress, modify sediment conditions and increase the cohesiveness of the substrata (Kröncke 1996; Widdows and Brinsley 2002; Gutierrez et al. 2003; Donadi et al. 2013) – 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, largely due to a combination of dramatic overfishing and three years of recruitment failure (Dijkema 1991; Beukema and Cadée 1996). Furthermore, 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 (e.g. Riesen and Reise 1982; Van der veer et al. 1985; Piersma et al. 2001; Kraan et al. 2007), which decreased the availability of natural structure and stable
sediment even further. 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 in substantial densities and even though they have been slowly recovering, their reestablishment is currently still mainly restricted to the Eastern part of the Dutch Wadden Sea (Ens et al. 2009; Goudswaard et al. 2009).

In this study, we empirically test the hypothesis that recovery of aboveground structure and stable sediments are both important ecosystem functions provided by ecosystem engineers that facilitate distinctly different intertidal benthic communities by affecting species composition (i.e. species richness and diversity) and trophic structure (i.e. feeding guild richness and diversity). In a large-scale experiment, we applied anti-erosion mats and created adult mussel beds to test for separate effects of sediment stabilisation and habitat modification, respectively. The experiment was carried out at two different sites to investigate if the treatment effects were consistent across space. One site was located in the western part of the Dutch Wadden Sea, south of the island Terschelling, and one in the eastern part of the Dutch Wadden Sea, south of the island Schiermonnikoog. After three months, we investigated treatment effects on the invertebrate community.

**Methods**

**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. 5.1). 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 5.1). The site at Schiermonnikoog has a higher 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 5.1). 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).

**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, (2) addition of a
Figure 5.1 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). Light grey areas represent water, intermediate gray areas represent tidal flats exposed during low tide and land is represented by dark gray.

Table 5.1 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.

<table>
<thead>
<tr>
<th></th>
<th>West Terschelling</th>
<th>East Schiermonnikoog</th>
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<tbody>
<tr>
<td>Silt content (%&lt;63µm)</td>
<td>2.3</td>
<td>3.0</td>
</tr>
<tr>
<td>Sediment organic matter content (%)</td>
<td>0.58</td>
<td>0.64</td>
</tr>
<tr>
<td>Elevation (m NAP)</td>
<td>-0.8</td>
<td>-0.6</td>
</tr>
<tr>
<td>Tidal amplitude (m)</td>
<td>0.9</td>
<td>1.2</td>
</tr>
<tr>
<td>Diffuse light attenuation at 490nm (m⁻¹)</td>
<td>0.58</td>
<td>1.03</td>
</tr>
<tr>
<td>Particulate organic carbon (mg/m³)</td>
<td>552.33</td>
<td>893.90</td>
</tr>
<tr>
<td>Chlorophyll concentration (mg/m³)</td>
<td>8.76</td>
<td>14.85</td>
</tr>
<tr>
<td>Maximum current velocity (ms⁻¹)</td>
<td>0.55</td>
<td>0.60</td>
</tr>
<tr>
<td>Wave action - Orbital velocity (ms⁻¹) NW</td>
<td>0.21</td>
<td>0.14</td>
</tr>
<tr>
<td>Wave action - Orbital velocity (ms⁻¹) W</td>
<td>0.32</td>
<td>0.25</td>
</tr>
<tr>
<td>Average fetch length (km)</td>
<td>29.9</td>
<td>9.3</td>
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</table>
coco-coir mat on the sediment surface to stabilize the sediment, (3) addition of adult mussels, and (4) addition of a coco-coir mat and adult mussels. Coir mats consisted completely out of coconut fibre and are commonly used to prevent erosion of sediment and seeds on bare soil. 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. To increase sediment stability and deposition on the coir mat plots, we placed 128 knotted burlap balls (diameter ~10 cm) in each plot at regular distances underneath the mat that reduced water flow velocity between elevations of the balls.

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 by hand at regular distances from each other within each plot, yielding a total cover of around 30% (~2000 kg mussels/plot) – a cover commonly found in natural mussel beds in the Wadden Sea. Shells of the transplanted mussels were relatively clean with very low numbers of sessile epifauna such as barnacles, 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 was on Schiermonnikoog 1251 ± 70 mussels m⁻² and on Terschelling 999 ± 85 mussels m⁻². Furthermore, mussel patches on Schiermonnikoog had a 21% cover of the macroalgae *Fucus vesiculosus*, while patches on Terschelling had a 96% cover of the macroalgae *Ulva lactuca*.

**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. At the coir mat and mussel plots, however, we sampled randomly in between the burlap balls and in the mussel patches, respectively. We pooled three 5-cm deep sediment cores with a PVC corer with an area of 7.1 cm². 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 hours till dry. Prior to grain-size analysis, organic matter and carbonate were removed using HCl and H₂O₂. The samples were left overnight at 80°C to speed up the reaction. Samples were measured in de-gassed Reversed Orsmosis 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. Burial depth of the anti-erosion mats 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 cm² down to a depth of 20–25 cm. 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 infauna or epifauna species in order to test for treatment effects on the infauna and epifauna community separately (Table S1 & S2).

Data analyses
To get an overview of the differences in the infaunal and epifaunal assemblages among sites and treatments, we first visualized the treatment effects with non-metric multidimensional scaling (nMDS) (Kruskall and Wish 1978) ordination models 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 assemblages among sites and treatments were than analyzed with a distance-based permutational multivariable analysis of variance (PERMANOVA) based on Bray-Curtis dissimilarity measures (Anderson 2001; McArdle and Anderson 2001).

To further test for treatment effects on community structure, we determined species richness (number of species), species diversity (Shannon diversity index \( H' \)), feeding guild richness (number of feeding guilds), feeding guild diversity (Shannon diversity index \( H' \)) for both the infaunal and epifaunal community. Feeding guilds were based on data extracted from online databases for marine invertebrates (MarLIN, 2006; Appeltans et al. 2012; see Table S3 and S4 for guild list).

During model selection for the sediment conditions and community diversity, we first selected the best residual error distribution for each model (Gaussian, Poison and negative binomial distributions were tested) and subsequently tested for significance of the random effect ‘Block’ by analyzing all models with generalized linear mixed-effects models (GLMM) and repeating them with generalized linear models (GLM). The final models were selected based on AIC comparisons. After model fitting, normality of the residual distribution was checked for normality by using a Shapiro-Wilks test \(( P = 0.05)\). Both sediment organic matter and silt content were log-transformed to obtain normality of the residual distribution and three-way ANOVA models were used based on AIC comparisons. The model selection procedure also selected three-way ANOVA models for species richness, species diversity, feeding guild richness and feeding guild diversity for the infauna community and epifauna community. 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). GLMMs and GLMs were constructed 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.

**Results**

**Sediment conditions**
Sediment organic matter content did not differ between the sites (*F* = 0.05, *n* = 12, *P* = 0.83, Fig. 5.2A), but silt content was 1.2 times lower at Terschelling than at Schiermonnikoog (*F* = 5.9, *n* = 12, *P* = 0.03, Fig. 5.2B). The addition of mussels increased organic matter content by 1.6 times (*F* = 47.8, *n* = 12, *P* < 0.001, Fig. 5.2A) and doubled silt content (*F* = 73.6, *n* = 12, *P* < 0.001, Fig. 5.2B). The coir mat did not significantly affect either organic matter (*F* = 0.2, *n* = 12, *P* = 0.69, Fig. 5.2A) or silt content (*F* = 0.0, *n* = 12, *P* = 0.97, Fig. 5.2B). The anti-erosion mat increased suspended sediment deposition, burying the mat under a thin layer of sand (Schiermonnikoog: 33 ± 2 mm; Terschelling: 44 ± 5 mm; mean±SE; *n* = 6).

**Infaunal community**
PERMANOVA analyses revealed significant differences in the composition of the infaunal community depending on site, coir mat and mussel additions, which are visualized by nMDS ordination models (Table 5.2, Fig. 5.3A). The infauna species *Capitella capitata*, *Hediste diversicolor* and *Alitta succinea* were abundant in the mussel plots with and without the coir mat (Table S3). *Scoloplos armiger* was abundant in the control plots and in the coir mat plots and *Lanice conchilega* was abundant in the coir mat plots, mussel plots and in the plots with coir mat and

![Figure 5.2](image-url)  
**Figure 5.2** Organic matter (A) and silt content (B) for each treatment (Mean ± SE, *n* = 3).
mussels (Table S3). Eleven infaunal species were only found on Terschelling, while six species were exclusive to Schiermonnikoog (Table S3).

Infannual species richness was significantly affected by coir mat, mussels and site (Fig. 5.4A, table 5.3). Species richness was around 1.6 times higher in the coir mat plots, in the mussel plots and in the plots with both coir mat and mussels compared to the control plots. On Terschelling, the increase in species richness due to the addition of mussels was 1.9 times stronger than on Schiermonnikoog. Infannual species diversity was significantly affected by coir mat and site (Fig. 5.4B; table 5.3). Diversity was 1.3 times higher in the coir mat plots compared to the plots without coir

Figure 5.3 Non-metric multi-dimensional scaling (nMDS) for differences among treatments for the infauna (A) and epifauna (B) community. Coir mat and mussel treatments are represented by the darkgrey polygons, sites by the lightgrey 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.

Table 5.2 F-values and significance levels of PERMANOVA based on Bray-Curtis dissimilarities for treatment effects on the infauna and epifauna community. Significance levels: * P < 0.05, ** P < 0.01, *** P < 0.001. Degrees of freedom: 24 in total; 16 residual.

<table>
<thead>
<tr>
<th>Treatments</th>
<th>Infauna</th>
<th>Epifauna</th>
</tr>
</thead>
<tbody>
<tr>
<td>Coir</td>
<td>3.4 (*)</td>
<td>1.4</td>
</tr>
<tr>
<td>Mussels</td>
<td>20.1 (***)</td>
<td>85.5 (***)</td>
</tr>
<tr>
<td>Site</td>
<td>9.7 (***)</td>
<td>2.3</td>
</tr>
<tr>
<td>Coir × Mussels</td>
<td>1.8</td>
<td>1.4</td>
</tr>
<tr>
<td>Coir × Site</td>
<td>1.4</td>
<td>2.1</td>
</tr>
<tr>
<td>Mussels × Site</td>
<td>1.5</td>
<td>1.9</td>
</tr>
<tr>
<td>Coir × Muss. × Site</td>
<td>0.7</td>
<td>1.8</td>
</tr>
</tbody>
</table>
mats. Furthermore, species diversity was approximately 1.5 times higher on Schiermonnikoog compared to the Terschelling, but only in plots without adult mussels added. Mussel addition on Terschelling, increased species diversity by 1.3 times compared to plots without adult mussels, while on 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. 5.4C; table 5.3). Feeding guild diversity was significantly affected by coir mat and mussel addition and by the interaction of mussel addition × site (Fig. 5.4D; table 5.3). 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. On Terschelling, the increase in feeding guild diversity due to the addition of mussels was 1.7 times stronger than on Schiermonnikoog.

**Epifaunal community**

PERMANOVA analyses revealed clear differences in the composition of the epifauna community depending on mussel addition, which are visualized by nMDS ordination models (Table 5.2, Fig. 5.3B). The most abundant epifauna species (i.e. *Balanus*...
crenatus, Carcinus maenus, Gammarus locusta and Mytilus edulis spat) were strongly structured by mussel addition and site (Table S4). Four epifauna species were exclusive to Terschelling, while three species were only found on Schiermon-
nikoog (Table S4). Further analyses showed that epifauna species richness was significantly affected by mussels and site (Fig. 5.5A; table 5.3). Species richness was 14 times higher in the plots with mussel addition compared with plots without mussel additions. On Terschelling, the increase in species richness due to the addition of mussels was 1.4 times stronger than on Schiermonnikoog. Epifauna species diversity was also significantly affected by mussels (Fig. 5.5B; table 5.3). Species diversity was 11 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 on Terschelling, while on Schiermonnikoog, diversity in these plots was 1.1 times lower compared to mussel plots. Feeding guild richness was significantly affected by mussel addition (Fig. 5.5C; table 5.3), 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. 5.5D; table 5.3). On Terschelling, the increase in guild diversity due to the addition of mussels was 2 times stronger then on Schiermonnikoog (Fig. 5.5D; table 5.3).

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 (Thrush et al. 1996; Ferns et al. 2000; Piersma et al. 2001; Thrush and Dayton 2002). In this study, we empirically demonstrate that stable sediments and aboveground structure are two important properties of structure-providing organisms that can facilitate distinctly different intertidal benthic communities.

Sediment stabilization through the addition of anti-erosion mats stimulated the development of the infaunal community by increasing species and trophic diversity (i.e. richness and Shannon diversity index). The mats prevented erosion, while we detected no changes in sediment organic matter and silt content. This indicated that sediment stabilization alone can enhance this diversity. Depending on location, the addition of mussels slightly increased or had no effect on infaunal diversity. However, it did cause a shift in infaunal species composition, probably due to deposition of faeces and pseudofaeces (Pearson and Rosenberg 1978; Kautsky and Evans 1987; Ragnarsson and Raffaelli 1999). Furthermore, the addition of adult mussels strongly stimulated the development of the epifaunal community by increasing species and trophic diversity, most likely due to the availability of substrate (Thiel
and Dernedde 1994; Gutierrez et al. 2003; Norling and Kautsky 2007). The effects of mussel addition on species richness are consistent with previous experimental studies in intertidal soft-bottom systems (Ragnarsson and Raffaelli 1999; Beadman et al. 2004; Norling and Kautsky 2007; Kochmann et al. 2008). However, by including more functionally-informative metrics of community structure, we show that mussel addition not only influences the benthic community structure by species enrichment, but also by trophic enrichment and diversity. This suggests that by attracting 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 corresponds to the idea that facilitation by ecosystem engineers becomes more important when environmental stress increases (Bertness and Callaway 1994; Bruno et al. 2003; Crain and Bertness 2006). With regard to the effects of mussels on the infaunal community, mussels can increase the cohesiveness of the substrata and reduce hydrodynamic stress (reviewed by Widdows and Brinsley 2002), which can result in suitable substrate for larval settlement (Commito et al. 2005) and this seems relatively more important at the more exposed conditions of Terschelling than at the sheltered conditions of Schiermonnikoog. With regard to the effects of mussels on the epifaunal community, mussel addition provides attachment substrate, and shelter from water movement and desiccation (e.g. Stephens and Bertness 1991; Thiel and Dernedde 1994), which also seems to be more important under the more exposed conditions of Terschelling. This differential site effect to the epifaunal community is probably further enhanced by the much higher coverage of epibenthic macroalgae (*Ulva lactuca*) at Terschelling that profit from the relatively high water clarity at this site. These algae on top of the mussels further increase habitat complexity, but may also serve as an additional food source (e.g. Goecker and Kall 2003).

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 (Reise et al. 1989; Lotze 2005; Reise 2005), 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 most likely also seagrasses and tube-worms (Orth 1977; Widdows et al. 1998; Friedrichs et al. 2000; Gutierrez et al. 2003; Volkenborn et al. 2009) 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 can form the foundation for a trophic-divers ecosystem. Moreover, the loss of ecosystem engineers often coincides with the loss of species at higher trophic levels (Jackson et al. 2001; Lotze et al. 2006), suggesting that the overexploitation of ecosystem engineers might have had a significant share in the overall reduction of trophic diversity in coastal ecosystems.

The loss of top-down processes, however, can also strongly determine the trophic structure of coastal systems (e.g. Pinnegar et al. 2000; Steneck and Sala 2005; Eriksson et al. 2011). Predation pressure by crustaceans, for instance, is increasing in many marine areas due to overfishing of top-predators, which can result in mesopredator-release (Worm and Myers 2003; Eriksson et al. 2011). In the Dutch Wadden Sea, shrimp numbers are over twice as high compared to other European coastal waters and increased strongly in the western part of the Dutch Wadden Sea since 1995 (Campos et al. 2010; Tulp et al. 2012). In addition, shore crab densities strongly increased since 1995, with numbers still rising (Tulp et al. 2012). Although underlying causes for this increase of crustaceans in the Wadden Sea are presently unknown, crustacean do play a very important role in determining bivalve recruitment (van der Veer et al. 1998; Strasser 2002; van der Heide et al. submitted), and may even explain the low recovery rate of mussels in the western part of the Dutch Wadden Sea. Hence, we propose that, in addition to altered abiotic conditions, the Wadden Sea community is disrupted from two biotic directions: loss of ecosystem engineers affects its foundation by decreasing (trophic) diversity, while loss of top-predators affects its top-down regulation.

Our findings can have implications for ecosystem-based management and large-scale restoration strategies of intertidal soft-bottom ecosystems as they indicate that the loss of stable sediments and substrate, caused by removal of ecosystem engineers or mechanical dredging, can negatively affect the structure of the benthic community throughout the Wadden Sea. In addition, 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 restoration and conservation (Boogert et al. 2006; Byers et al. 2006; Crain and Bertness 2006).

Acknowledgements
We thank Natuurmonumenten, Staatsbosbeheer and many volunteers for their help with setting up the experiment. This study was carried out within project ‘Waddensleutels’, funded by the ‘Waddenfonds’. In addition, EZ, SD and BKE were financially supported by grant 839.08.310 of the NWO-ZKO programme.
### Supplementary tables

**Table S1** Infauna species feeding guilds, based on literature data on macrofauna feeding modes from reference literature and websites for European macrofauna (Fauchald and Jumars 1979; MarLIN. 2006; Appeltans *et al.* 2012).

<table>
<thead>
<tr>
<th>Infauna species</th>
<th>Feeding guilds</th>
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<tbody>
<tr>
<td>Aphelochaeta marioni</td>
<td>Deposit feeder</td>
</tr>
<tr>
<td>Arenicola marina</td>
<td>Deposit feeder</td>
</tr>
<tr>
<td>Autolytus prolifer</td>
<td>Predator</td>
</tr>
<tr>
<td>Capitella capitata</td>
<td>Deposit feeder</td>
</tr>
<tr>
<td>Ensis directus</td>
<td>Filter feeder</td>
</tr>
<tr>
<td>Cerastoderma edule</td>
<td>Filter feeder</td>
</tr>
<tr>
<td>Eteone longa</td>
<td>Predator - Deposit feeder</td>
</tr>
<tr>
<td>Eulalia viridis</td>
<td>Predator</td>
</tr>
<tr>
<td>Eumida sanguinea</td>
<td>Predator</td>
</tr>
<tr>
<td>Harmotheo imbricata</td>
<td>Predator</td>
</tr>
<tr>
<td>Harmothoe sarsi sarsi</td>
<td>Predator</td>
</tr>
<tr>
<td>Hediste diversicolor</td>
<td>Predator - Opportunist</td>
</tr>
<tr>
<td>Heteromastus filiformis</td>
<td>Deposit feeder</td>
</tr>
<tr>
<td>Lanice conchilega</td>
<td>Deposit - Filter feeder</td>
</tr>
<tr>
<td>Macoma baltica</td>
<td>Deposit - Filter feeder</td>
</tr>
<tr>
<td>Malacoceros fuliginosus</td>
<td>Deposit - Filter feeder - Grazer</td>
</tr>
<tr>
<td>Malmgreniella lunulata</td>
<td>Predator - Opportunistic</td>
</tr>
<tr>
<td>Marenzelleria wireni</td>
<td>Deposit - Filter feeder - Grazer</td>
</tr>
<tr>
<td>Mya arenaria</td>
<td>Filter feeder</td>
</tr>
<tr>
<td>Nephtys hombergii</td>
<td>Predator - Opportunistic</td>
</tr>
<tr>
<td>Nereis longissima</td>
<td>Predator - Opportunistic</td>
</tr>
<tr>
<td>Alitta succinea</td>
<td>Predator - Opportunistic</td>
</tr>
<tr>
<td>Nereis virens</td>
<td>Predator - Opportunistic</td>
</tr>
<tr>
<td>Oligochaeta sp</td>
<td>Deposit feeder - Grazer</td>
</tr>
<tr>
<td>Phyllodoce maculate</td>
<td>Predator - Opportunistic</td>
</tr>
<tr>
<td>Phyllodoce mucosa</td>
<td>Predator - Opportunistic</td>
</tr>
<tr>
<td>Polydora cornuta</td>
<td>Deposit - Filter feeder - Grazer</td>
</tr>
<tr>
<td>Pygospio elegans</td>
<td>Deposit - Filter feeder</td>
</tr>
<tr>
<td>Scoloplos amiger</td>
<td>Deposit feeder</td>
</tr>
<tr>
<td>Spio martinesis</td>
<td>Deposit - Filter feeder</td>
</tr>
<tr>
<td>Streblospio benedictii</td>
<td>Deposit - Filter feeder - Grazer</td>
</tr>
<tr>
<td>Urothoe poseidonis</td>
<td>Deposit feeder</td>
</tr>
</tbody>
</table>
**Table S2**  Epifauna species feeding guilds, based on literature data on macrofauna feeding modes from reference literature and websites for European macrofauna (Fauchald and Jumars 1979; MarLIN. 2006; Appeltans et al. 2012).

<table>
<thead>
<tr>
<th>Epifauna species</th>
<th>Feeding guilds</th>
</tr>
</thead>
<tbody>
<tr>
<td>Asterias rubens</td>
<td>Predator - Opportunist</td>
</tr>
<tr>
<td>Balanus crenatus</td>
<td>Filter feeder</td>
</tr>
<tr>
<td>Carcinus maenus</td>
<td>Predator - Opportunist</td>
</tr>
<tr>
<td>Corophium sp</td>
<td>Deposit - Filter feeder - Grazer</td>
</tr>
<tr>
<td>Crangon crangon</td>
<td>Predator</td>
</tr>
<tr>
<td>Crassostrea gigas spat</td>
<td>Filter feeder</td>
</tr>
<tr>
<td>Crepidula fornicata</td>
<td>Filter feeder</td>
</tr>
<tr>
<td>Gammarus locusta</td>
<td>Deposit feeder</td>
</tr>
<tr>
<td>Idotea sp</td>
<td>Predator - Opportunist</td>
</tr>
<tr>
<td>Jaera sp</td>
<td>Deposit feeder - Grazer</td>
</tr>
<tr>
<td>Melita palmata</td>
<td>Deposit - Filter feeder - Grazer</td>
</tr>
<tr>
<td>Metridium senile</td>
<td>Filter feeder</td>
</tr>
<tr>
<td>Mytilus edulis spat</td>
<td>Filter feeder</td>
</tr>
</tbody>
</table>
Table S3  Infauna species abundance (mean ± SE) per treatment (Ctr=Control, C=Coir, M=Mussel, C*M=Coir*Mussel).

<table>
<thead>
<tr>
<th>Infauna species</th>
<th>Schiermonnikoog</th>
<th>Terschelling</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Ctr</td>
<td>C</td>
</tr>
<tr>
<td>Aphelochaeta marioni</td>
<td>21.3±13.0</td>
<td>19.0±16.0</td>
</tr>
<tr>
<td>Arenicola marina</td>
<td>2.0±0.6</td>
<td>2.0±0.6</td>
</tr>
<tr>
<td>Autolytus prolifer</td>
<td>10.7±4.1</td>
<td>38.0±9.0</td>
</tr>
<tr>
<td>Capitella capitata</td>
<td>0.3±0.3</td>
<td>0.3±0.3</td>
</tr>
<tr>
<td>Cerastoderma edule spat</td>
<td>1.3±0.3</td>
<td>6.0±3.5</td>
</tr>
<tr>
<td>Eulalia viridis</td>
<td>0.3±0.3</td>
<td>0.7±0.3</td>
</tr>
<tr>
<td>Holarca sarsi sarsi</td>
<td>1.0±0.6</td>
<td>1.3±0.7</td>
</tr>
<tr>
<td>Hediste diversicolor</td>
<td>0.3±0.3</td>
<td>6.0±0.0</td>
</tr>
<tr>
<td>Heteromastus filiformis</td>
<td>0.3±0.3</td>
<td>1.0±0.6</td>
</tr>
<tr>
<td>Lanice conchilega</td>
<td>15.0±5.3</td>
<td>1.3±0.9</td>
</tr>
<tr>
<td>Macoma baltica</td>
<td>3.7±0.9</td>
<td>3.3±0.7</td>
</tr>
<tr>
<td>Macoma baltica spat</td>
<td>0.7±0.7</td>
<td>0.3±0.3</td>
</tr>
<tr>
<td>Malacoceros fuliginosus</td>
<td>0.3±0.3</td>
<td>1.3±0.3</td>
</tr>
<tr>
<td>Marenzellia lunulata</td>
<td>0.7±0.7</td>
<td>0.3±0.3</td>
</tr>
<tr>
<td>Mya arenaria</td>
<td>0.3±0.3</td>
<td>0.3±0.3</td>
</tr>
<tr>
<td>Nematis hombergii</td>
<td>0.3±0.3</td>
<td>0.3±0.3</td>
</tr>
<tr>
<td>Nereis longissima</td>
<td>0.3±0.3</td>
<td>3.0±0.6</td>
</tr>
<tr>
<td>Alitta succinea</td>
<td>0.3±0.3</td>
<td>0.7±0.7</td>
</tr>
<tr>
<td>Oligochara sp</td>
<td>0.3±0.3</td>
<td>0.7±0.7</td>
</tr>
<tr>
<td>Phyllodoce maculate</td>
<td>6.0±5.0</td>
<td>0.3±0.3</td>
</tr>
<tr>
<td>Phyllodoce mucosa</td>
<td>9.0±2.0</td>
<td>7.0±2.9</td>
</tr>
</tbody>
</table>
Table S3  Continued.

<table>
<thead>
<tr>
<th>Infauna species</th>
<th>Schiermonnikoog</th>
<th>Terschelling</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Ctr</td>
<td>C</td>
</tr>
<tr>
<td>Pygospio elegans</td>
<td>9.0±5.1</td>
<td>14.3±4.9</td>
</tr>
<tr>
<td>Scoloplos amiger</td>
<td>22.0±5.5</td>
<td>22.0±5.7</td>
</tr>
<tr>
<td>Spio martinesis</td>
<td>1.7±0.9</td>
<td>0.7±0.7</td>
</tr>
<tr>
<td>Streblospio benedictii</td>
<td>0.7±0.7</td>
<td>0.3±0.3</td>
</tr>
<tr>
<td>Urothoe poseidonis</td>
<td>19.7±8.2</td>
<td>31.3±8.8</td>
</tr>
</tbody>
</table>

Table S4  Epifauna species abundance (mean ± SE) per treatment (Ctr=Control, C=Coir, M=Mussel, C*M=Coir*Mussel).

<table>
<thead>
<tr>
<th>Epifauna species</th>
<th>Schiermonnikoog</th>
<th>Terschelling</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Ctr</td>
<td>C</td>
</tr>
<tr>
<td>Asterias rubens</td>
<td>3.3±1.5</td>
<td>5.7±0.3</td>
</tr>
<tr>
<td>Balanus crenatus</td>
<td>129.3±28.8</td>
<td>237.7±59.4</td>
</tr>
<tr>
<td>Carcinus maenus</td>
<td>0.3±0.3</td>
<td>7.3±2.4</td>
</tr>
<tr>
<td>Corophium sp</td>
<td>0.3±0.3</td>
<td>1.0±0.6</td>
</tr>
<tr>
<td>Crangon crangon</td>
<td>0.3±0.3</td>
<td>1.0±0.6</td>
</tr>
<tr>
<td>Crassostrea gigas spat</td>
<td>0.3±0.3</td>
<td>0.3±0.3</td>
</tr>
<tr>
<td>Crepidula fornicata</td>
<td>0.3±0.3</td>
<td>1.0±0.6</td>
</tr>
<tr>
<td>Gammarus locusta</td>
<td>6.0±3.0</td>
<td>7.0±2.5</td>
</tr>
<tr>
<td>Idotea sp</td>
<td>0.3±0.3</td>
<td>0.3±0.3</td>
</tr>
<tr>
<td>Jaera sp</td>
<td>2.3±1.9</td>
<td>1.3±0.7</td>
</tr>
<tr>
<td>Melita palmata</td>
<td>5.7±3.2</td>
<td>4.3±1.2</td>
</tr>
<tr>
<td>Metridium senile</td>
<td>6.3±2.0</td>
<td>6.3±2.3</td>
</tr>
<tr>
<td>Mytilus edulis spat</td>
<td>0.3±0.3</td>
<td>19.3±12.8</td>
</tr>
<tr>
<td>Treatment addition</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mytilus edulis adults</td>
<td>43.2±2.9</td>
<td>46.5±4.5</td>
</tr>
</tbody>
</table>