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RESEARCH ARTICLE

Restoring mussel beds in highly dynamic environments by lowering environmental stressors

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Restoration of coastal ecosystem engineers that trap sediment and dampen waves has proven to be difficult, especially in the wave-exposed and eroding areas where they are needed the most. Environmental stressors, such as hydrodynamic stress and predation, can only be overcome if transplanted organisms are able to establish self-facilitating feedbacks. We investigate if the artificial lowering of multiple environmental stressors can be used to give transplanted juveniles the opportunity to form a self-sustainable system and thereby increase their long-term survival on wave-exposed and eroding shores. We designed a large field experiment using juvenile mussels (*Mytilus edulis*) as model species on a wave-exposed tidal flat in the Oosterschelde estuary (the Netherlands). We tested if the environmental stress caused by a high predation pressure and wave-driven dislodgement could be reduced by a combination of artificial structures such as fences (to exclude predatory crabs), attachment substrates (such as coir-net or oyster shells), and breakwaters. Despite a low overall mussel survival (29%), we found that under strong hydrodynamic conditions, experimental fences and attachment substrates increased the retention of transplanted mussel seed. However, modification of local hydrodynamic conditions using breakwaters did not improve mussel coverage preservation. Overall, this study highlights the potential of using techniques that lower multiple environmental stressors to create a window of opportunity for establishment in highly dynamic ecosystems.

Key words: ecosystem engineers, environmental stressors, mussels, self-facilitation, transplantation, window of opportunity

Implications for Practice

- Engineering measures that diminish abiotic and/or biotic environmental stressors can potentially be used to create a window of opportunity, and constitute a valuable tool for restoration of ecosystem engineers in highly dynamic ecosystems, such as wave-exposed and eroding foreshores.
- It is important to customize engineering measures to the specific goals of the restoration, for example, coastal protection.
- Hydrodynamics have often been pointed out as the most important limiting factor for the establishment of intertidal mussel beds; however, managers restoring these kinds of systems should not overlook predation as a limiting factor.

Introduction

Climate change-related safety threats such as the intensification of storms (Donat et al. 2011) and accelerating sea level rise (Donnelly et al. 2004) are of growing global concern. Increasing coastal protection against flooding has become a key priority for many countries all over the world (Temmerman et al. 2013). It is increasingly recognized that classical methods that protect our coastlines such as dikes and dams have great impact on ecological functioning of our coastal ecosystems (Airoldi et al. 2005; Perkins et al. 2015). Continuous maintenance and strengthening also make these structures very expensive. The incorporation of ecology, especially ecosystem engineers, in coastal protection has therefore gained increasing interest over the last two decades (Borsje et al. 2011; Bouma et al. 2014). By attenuating wave energy and trapping sediment, coastal ecosystem engineers (Jones et al. 1994), such as mussels (Donker et al. 2013), oysters (Salvador de Paiva et al. 2018), seagrass (Christianen et al. 2013), mangroves (Zhang et al. 2012), and saltmarshes (Möller et al. 2014), may be able to keep up with sea-level rise (van Proosdij et al. 2006) and thereby form a sustainable and cost-efficient structure that can increase coastal flood protection (Borsje et al. 2011; Temmerman et al. 2013). Despite the growing body of literature showing the potential benefits of using ecosystem engineers as part of our coastal protection (Borsje et al. 2011; Temmerman et al. 2013; Bouma et al. 2014; Perkins et al. 2015), actual pilot studies that manage to successfully create such ecosystems on wave-exposed,

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erosion-vulnerable foreshores are still scarce (Nelson et al. 2004; Schulte et al. 2009).

Transplantation of ecosystem engineers is probably most challenging on wave-exposed and eroding shores, because environmental stressors, such as dislodgement by waves, impede the establishment of self-facilitating feedbacks (Suding et al. 2004; Halpern et al. 2007; Commito et al. 2014; Maxwell et al. 2017). Newly transplanted organisms are typically either too small and sparse (Bouma et al. 2009) or too unstable (Capelle et al. 2019) to modify their environment and establish such self-facilitating feedbacks. This makes establishing ecosystem engineers highly vulnerable to environmental stressors such as wave action, leading to dislodgement (Clark & Edwards 1995; de Paoli et al. 2015) and predation (van der Heide et al. 2014; Weerman et al. 2014). As a result, establishment might require a "window of opportunity," defined as a specific disturbance-free period (Balke et al. 2011; Balke et al. 2013). During such a period of reduced levels of environmental stress, the ecosystem engineers are given the opportunity to establish and reach the threshold beyond which they can withstand the normal environmental stress levels for that area. To successfully implement ecosystem engineers in coastal protection schemes, we need to understand which environmental stressors are most determinative in preventing a species from reaching their establishment thresholds. In this study, we investigated (1) whether the use of engineering measures to lower multiple environmental stressors can increase restoration success and (2) the relative effectiveness of several field engineering techniques compared to bare sediment.

There are multiple examples in which restoration projects made use of engineering measures to diminish establishment thresholds caused by physical or biological stressors. In the intertidal, important physical stressors include hydrodynamic forcing (Clark & Edwards 1995; Balke et al. 2011; de Paoli et al. 2015) and sediment dynamics (French 2006; Balke et al. 2013). In the Mekong Delta in Vietnam, mangrove restoration success increased significantly by reducing wave energy and increasing sediment accumulation using Melaleuca fences (*Melaleuca cajuputi*) as breakwaters (Van Cuong et al. 2015). Provision of stable substrates has been proposed as another measure to increase establishment success in bivalves by acting as an attachment substrate (e.g. mussels; Crooks 1998; Commito et al. 2014; de Paoli et al. 2015; Capelle et al. 2019, Oysters; Bartol & Mann 1997). Another possibility is to diminish potential negative biological stressors (van Wesenbeeck et al. 2007; Suykerbuyk et al. 2012) such as predation or bioturbation. Survival chances can be increased with the exclusion of predators with cages (van der Heide et al. 2014), or the addition of spatial heterogeneity in the form of a substrate (Almany 2004; Wilcox & Jeffs 2017). These examples show that there is some evidence indicating that artificially lowering thresholds using engineering measures can create a window of opportunity for the establishment of ecosystem engineers in highly dynamic ecosystems. However, the interplay between several limiting factors may hinder restoration efforts and has been generally overlooked in many studies (de Paoli et al. 2015).

The blue mussel (*Mytilus edulis*) is a typical model ecosystem engineering species on intertidal mud flats (de Paoli et al. 2015). Transplantation of young mussels (mussel seed) on soft-bottom intertidal mudflats has been done for centuries by mussel farmers. However, even in the usually sheltered aquaculture locations mussel losses can still reach up to 75% in the first month (Capelle et al. 2014). Mussels reduce losses caused by predation and hydrodynamic forces by attaching themselves to conspecifics and aggregating into large and dense groups (Cote & Jelnikar 1999; Hunt & Scheibling 2001; van de Koppel et al. 2008). However, on wave-exposed mudflats, transplanted mussels may not get the time to establish intra-specific interactions and self-organize before they are washed away or eaten.

In this study, we focused on decreasing two environmental stressors that impede mussels from establishing self-facilitating feedbacks and becoming a self-sustaining population: dislodgement by waves (de Paoli et al. 2015) and predation by crabs (van der Heide et al. 2014). In a large field experiment, we tested if environmental stress on blue mussels caused by both predation by crabs and wave-driven dislodgement could be lowered by a combination of engineering measures. These measures involved (1) constructing structures such as fences (to exclude predatory crabs) and breakwaters, and (2) adding attachment substrates.

Methods

Study Site

A field experiment was conducted on an eroding and wave-exposed intertidal mudflat at Viane, in the Oosterschelde estuary in the southwestern Netherlands (51.616211, 3.992755) from 18 August until 5 September, 2016. Natural intertidal mussel beds were present throughout the estuary in the past, including on the Viane mudflat (Fokker 1905). However, the estuary is now in a morphological disequilibrium due to the reduced water velocity entering the system since the construction of a storm surge barrier in 1986 that separates the estuary from the North Sea, and the two dams closing of the eastern part. As a result, sediment is slowly eroding from the tidal flats with an average net erosion rate of 10 mm yr^{-1}, and filling the adjacent channels (Santinelli & Ronde de 2012). At present, intertidal mussels can only be incidentally found on commercial mussel plots at sheltered sites, in oyster reefs or attached to other hard substrates such as wooden poles and stones. The Viane mudflat is characterized by sandy sediment and a few patchy oyster (*Crassostrea gigas*) reefs. The mudflat experiences high hydrodynamic forces, mainly coming from the southwest (www.knmi.nl), and an average net erosion rate of 15 mm yr^{-1} (Salvador de Paiva et al. 2018).

Experimental Design

We tested the effectiveness of three engineering measures to diminish environmental stressors on transplanted mussels, namely (1) fences to decrease predation pressure by crabs (Fig. 1A), (2) attachment substrates to decrease dislodgement by crabs or waves (Figs. 1B, 1C), and (3) breakwaters to decrease hydrodynamic forces on mussels (Fig. 1D).

Seven treatments were carried out in fourfold, resulting in a total of 28 experimental mussel plots (Fig. 1). Plots were laid out in a randomized pattern except for the oyster shell treatments which were clustered due to use of a natural oyster (*Crassostrea gigas*) bed. Twelve plots were placed behind a brush wooden breakwater and another 12 plots had no protection against hydrodynamic stress. All these plots (24 in total) were surrounded with a fence. In order to test the effect of the fence on the mussel coverage, four mussel plots placed on bare sediment were not surrounded by a fence. This partially unbalanced design was chosen because predation pressure on intertidal mussel seeds in the Oosterschelde is known to be extremely high (Capelle et al. 2016) and may cause a population to collapse in only a couple of days.

Fences. Anti-predator fences enclosed mussel plots of 5 × 5 m with a distance of 1 m from the edge, leaving a buffer zone of 1 m (Fig. 2A). Fences were made out of 50 cm high plastic mesh with a mesh size of 12 mm, attached between wooden poles 120 cm long that were drilled approximately 80 cm into the sediment. To prevent crabs from climbing over the fence, the top was curved into a U-shape with a diameter of 10 cm. In addition, the fences were dug 10 cm into the sediment to prevent crabs from digging underneath. Before transplantation of the mussels, all plots were searched thoroughly and any crabs present were removed.

Complex Attachment Substrates. Mussels were placed on three different substrates: bare sediment, coir-nets, and oyster shells. Using coir-nets as an attachment substrate for mussels to decrease the chance of getting dislodged has been used before in a large restoration project of intertidal mussel beds in the Dutch Wadden Sea (de Paoli et al. 2015). Unfortunately, in this experiment, the coir-nets quickly got buried underneath sediment. Nonetheless, this approach may still be of use in areas such as our study site, which is characterized by erosion instead of sedimentation. The sides of the coir-nets were dug 20 cm into the ground to keep them in place. As expected, almost no sedimentation on the nets was observed after leaving the nets for 5–7 days in the field.

In the Oosterschelde estuary, the only natural intertidal mussels are those that settled inside intertidal oyster beds (Fokker 1905). Oyster beds therefore provide a potentially suitable, stable, and available substrate for mussel settlement

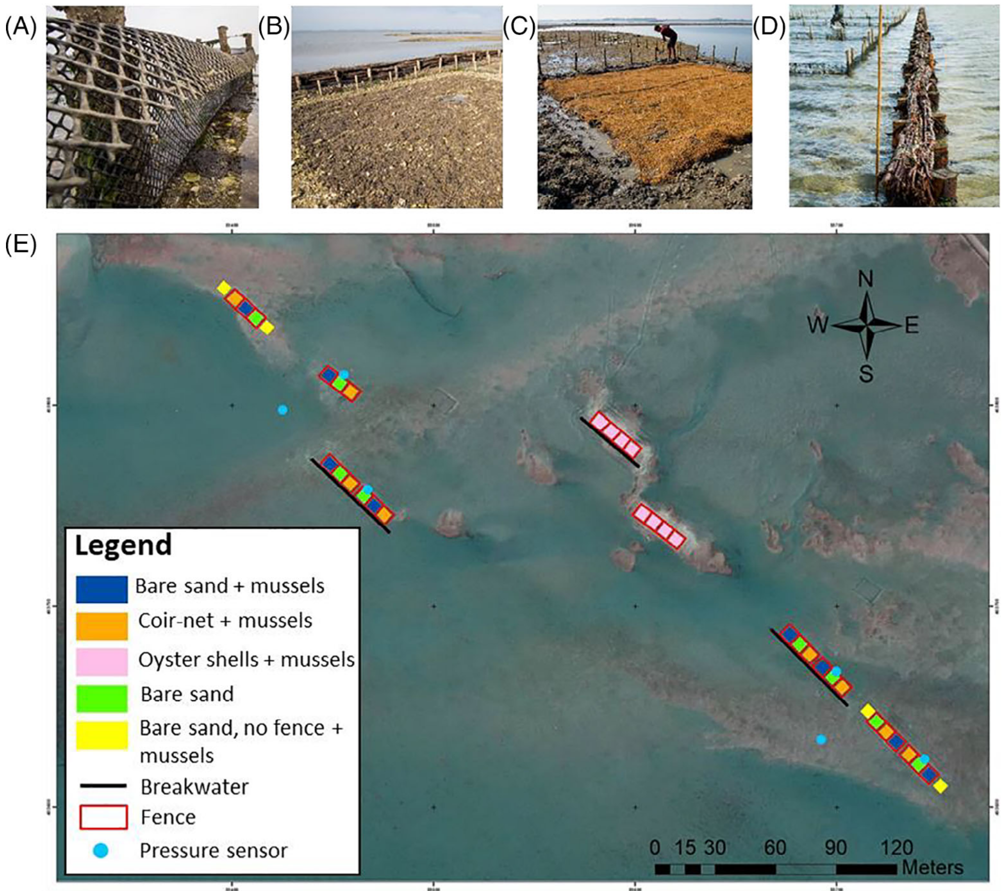

Figure 1 (A) Fence surrounding 24 plots (red lines on map). (B) Oyster shells on an old oyster bed as an attachment substrate. (C) Coir-net as an attachment substrate. (D) Brushwood breakwaters in front of half of the mussel plots. (E) Map of the experimental design.

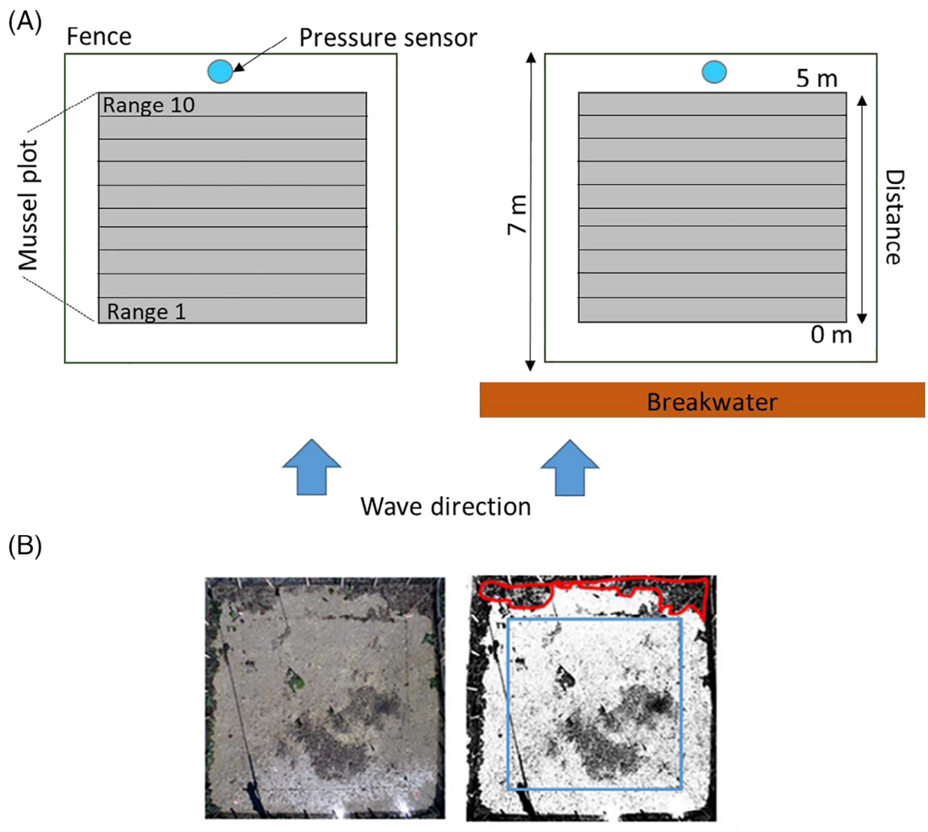

Figure 2 (A) Schematic drawing of the experimental mussel plots. (B) Example image of a mussel plot converted into a binary picture. Blue-marked area is the initial seeded plot (5 × 5 m), red-marked area is the area mussels washed against the fence in the buffer zone.

(Eschweiler & Christensen 2011; Reise et al. 2017). A naturally formed oyster (*Crassostrea gigas*) bed was located in close proximity to the other experimental mussel plots (Fig. 1E) and was therefore used to test the success of oyster shells as attachment substrate. The oyster bed was approximately 30 cm higher than the bare surroundings. However, the top layer of the oyster bed, on which the mussels were seeded, had approximately the same inundation time as the other plots. To make sure that there was no competition for food from nearby oysters, living oysters were removed or destroyed by breaking their shells 6 weeks before the actual start of the experiment. As a result, the top layer of the oyster beds mostly consisted of oyster shell fragments providing a rough, stable, and complex structure.

Breakwaters. Brush wooden dam breakwaters were constructed in front of 12 experimental plots (Fig. 1E). Breakwaters were 50 cm high, 30 cm wide, and placed 2 m in front of the mussel plots facing southwest. The breakwaters extended 5 m further from the sides of the outermost mussel bed to prevent edge effects.

Mussel Placement and Monitoring

All mussel plots, including the mussels transplanted to the oyster reefs, were situated in an elevation range between −0.90 and −1.00 m below mean sea level with an inundation duration of 60%. The mussel seed used in this experiment was harvested from subtidal seed mussel collectors (SMCs) situated in the Oosterschelde and was transplanted on to the plots 12 hours after harvest. All mussel plots, independent of the treatment, were seeded homogeneously with 300 kg of mussel seeding material (i.e. mixture of live mussels, empty mussel shells, and other materials such as algae and debris), resulting in an initial coverage of 100%. After seeding, a subsample of 400 g of mussel seeding material was taken to the lab to determine the percentage of living mussels, the average ash free dry weight (AFDW), and the average shell length (L). Based on these data, the condition index (CI) was calculated as $AFDW/L^3$ (Capelle et al. 2016).

Wave Height. During the entire experiment, six pressure sensors (Ocean Sensor Systems, Inc. Wave Gauge, OSSI-010-003B/C) were placed to monitor the wave exposure at the plots, and the effectiveness of the breakwaters on dampening waves. Sensors were placed at the northwest and southeast of the experiment. At each side of the experiment, a sensor was placed (1) inside breakwater plots, (2) inside plots without breakwaters, and (3) in a location outside the experiment (Fig. 1E & 2A). For every sensor, the average significant wave height (Hs), which is the mean wave height at the highest third of the wave, was analyzed. The Hs was analyzed only during the period of the tidal cycle where the breakwaters were most likely to have an effect on the wave dynamics. As large waves are expected to have the greatest influence on the mussels during low water levels, and because the breakwaters were only 50 cm high, we focused on analyzing the Hs in the window between 0 and 50 cm of water on top of the tidal flat. If no measurable effects were measured during this time frame, no effects could be expected at higher water levels.

Mussel Coverage. In this study, mussel coverage is defined as the area occupied by live mussels and the substrate on which they are attached. This is because during transplantation, a mixture of live mussels, shell hash (i.e. both whole and fragmented empty shells) and other material (i.e. algae, debris) was placed in the empty plots. After transplantation, mussels attach to, in decreasing order of importance, other live mussels, empty shells, and other hard substrates (Commito et al. 2014). Due to the high wave energy at our study site, empty shells and other substrates that were not anchored by the mussels, are expected to be rapidly washed away, so that the coverage is expected to predominantly represent live mussels with some attachment substrate. Mussel coverage was monitored by taking top-view pictures of the experimental plots every week, starting the day after transplantation and ending 3 weeks later when mussel coverage became too low. Pictures were taken with a camera on timer mode, mounted on two 5 m long bamboo sticks and held above a plot. The percentage mussel coverage in the initial seeding square (5×5 m, see blue area Fig. 2B) was estimated using the package *Imager* (Barthelme et al. 2020) in R (version 3.5.1). To determine the effect of wave energy on mussel distribution, mussel coverage was determined in 10 ranges (0.5 m wide and 5 m long) from just behind the breakwater to the other end of the plot (Fig. 2A). Dislodged mussels could end up washed against the fence along all four sides of the plot. Because it was difficult to make a distinction between mussel or fence on the binary pictures, the mussel area against the fences was separately calculated in image-J (version 1.52a) by drawing a polygon around the mussel covered area by hand (Fig. 2B, red-marked area).

Mussel Density. Mussels transplanted on coarse shell material rather than bare sediment are less likely to aggregate into patches, resulting in a lower within-patch density (n/m^2) (Bertolini et al. 2019; Capelle et al. 2019). To determine if mussels aggregated closer together when transplanted on bare sediment in comparison with mussels transplanted on oyster shells or coir-nets, the within-patch density (n/m^2) was estimated after 21 days. This was done by taking mussel cores (diameter of 10 cm) in every plot in the middle of three different mussel patches. The plots were divided in nine equally sized squares and a patch in the middle of three randomly chosen squares was sampled. In the lab, mussels were sorted, counted, and weighted. The factor of aggregation was calculated as: final within-patch density (n/m^2)/ starting density (n/m^2) (Capelle et al. 2019).

Statistical Analysis

All statistical analyses were carried out in R, 3.5.1 (R Core Team 2018). Prior to model fitting, all data were visually checked for normality (Q–Q plot) and homogeneity of residuals. If necessary, data were transformed to meet assumptions. For all models, backward stepwise regression was used to find the minimal adequate model, and non-significant ($p > 0.05$) interactions and explanatory factors were removed. Post hoc comparisons were used to test for significant differences between treatments (R-package *emmeans*, Lenth 2019).

To determine if the significant wave height (Hs) differed significantly between sensors, a linear mixed-effects model (LME) was carried out using the R package *nlme* (Pinheiro et al. 2019). In this model, the significant wave height was set as the response variable, the treatment at which a sensor was placed was set as fixed effect (inside breakwater plots, inside plots without breakwaters, outside of the experiment), and the location (northwest or southeast of the experiment) as a random factor.

The effect of the fence on the mussel coverage in the initial mussel plots (blue-marked area, Fig. 2B) was tested using a LME (Pinheiro et al. 2019) with plot as random variable and a temporal autocorrelation structure containing the factors time and plot. In this model, only the mussel plots placed on bare sediment were included as these plots contained the treatments: (1) no protection, (2) protection by a fence, or (3) protection by a fence and a breakwater. The protection and time and their interaction were set as fixed effects.

A LME (Pinheiro et al. 2019) with plot as random variable and a temporal autocorrelation structure containing the factors time and plot was carried out to analyze the difference in mussel coverage washed against the fence in the buffer zone (red-marked area, Fig. 2B) between different treatments. Substrate type, presence of a breakwater, and time were set as fixed effects.

Another LME (Pinheiro et al. 2019) was used to analyze the effect of the breakwaters, different substrates (bare sediment, coir-net, or oyster shells), time, and their interaction on the total mussel coverage of a plot. For this model, plot was set as random variable and a temporal autocorrelation structure containing the factors time and plot was incorporated. Because we were dealing with an unbalanced design, in which only four mussel plots on bare sediment were not surrounded by a fence, these plots were excluded from this model. In order to analyze the effect of the breakwaters on the distribution of the mussels inside the plots, an LME was carried out with substrate type, presence of a breakwater, time, and the distance to the breakwater as fixed effects. Distance to the breakwater was nested within plot as a random variable and a temporal autocorrelation was incorporated.

With the R package *lme4* (Bates et al. 2015), a Generalized Linear Mixed Model (GLMM) with a poisson family was used to analyze the difference in number of mussels found in cores taken in mussel patches. Substrate type and presence of a breakwater were set as fixed effects and plot as a random factor. The aggregation factors were analyzed using the same explanatory factors but with a linear mixed-effects model instead of a GLMM.

Results

Mussel Condition During Seeding

The mussel material seeded on the plots contained 4.9 kg/m^2 living mussel seeds and 7.1 kg/m^2 of shell hash (empty whole and fragmented shells) and other material such as algae and debris. The mussels had an average length of 18.8 ± 0.49 SE mm (n = 132) and wet weight of 613 ± 47.33 SE (n = 130) mg. The condition index (CI, mg cm^{-3}) was 3.58 ± 0.09 SE (n = 132) mg cm^{-3}.

Effect of Breakwaters on Wave Height

Two days after mussel transplantation, the experiment endured a summer storm with peak wind speeds reaching 19 m/s coming from the southwest (www.knmi.nl). The average significant wave height (Hs) during this period increased to a maximum of 0.2 m. Overall, there was no significant difference in average Hs between sensors placed at the northwest or southeast of the mudflat, indicating that there was no spatial difference in wave exposure between plots placed at different locations on the mudflat. The pressure sensors did not measure a significant difference in Hs between plots behind a breakwater, plots without a breakwater, or outside plots (Fig. 3).

Effect of Fences on Mussel Coverage

After six days in the field, mussel coverage in bare sediment plots remained 33% higher when protected by a fence (Fig. 4, Tukey, $p < 0.001$). The protection ($F_{2,9}$ = 89.51, $p < 0.001$), the time ($F_{4,35}$ = 1,009.08, $p < 0.001$), and the interaction between protection and time ($F_{8,35}$ = 24.62, $p < 0.001$) all had a significant effect on the mussel coverage. The protective effect of the fences stayed visible till the end of the experiment. In addition, the fence acted as a safety net for mussels that were dislodged out of the initial mussel plot (Fig. 2B, blue-marked area), into the 1-m-wide buffer zone. As the experimental mussel beds received waves mainly coming from the southwest, most mussels were found along the fences placed at the northeast side of the mussel plot (Fig. 2B, red-marked area). The surface area of the dislodged mussels washed against the fences was larger in the bare sediment plots than in the oyster shell plots (Fig. 5, Tukey, $p < 0.001$). The area calculation of the mussels washed against the fences was only done for the second and third photo series. At the first monitoring moment, one day after transplantation, no mussels were visible against the fences, suggesting that no mussels had washed into the buffer zone at that time. During the fourth monitoring, algae coverage of the mussels made accurate measurements impossible. However, there was no significant difference between the surface area of mussels washed against the fence in the second or third measurement so the data were combined.

Effect of Substrate and Breakwaters on Mussel Coverage

Over time, the mussel coverage decreased in all mussel plots surrounded by a fence ($F_{4,892}$ = 687.13, $p < 0.001$). However, mussel coverage in the initial mussel covered plots was positively influenced by the presence of oyster shells or coir-net as an attachment substrate ($F_{2,102}$ = 39.15, $p < 0.001$). The presence of a breakwater did not influence the total mussel coverage ($F_{1,102}$ = 1.75, p = 0.39). There was a significant interaction only between substrate type and time ($F_{8,102}$ = 4.49, $p < 0.001$). The

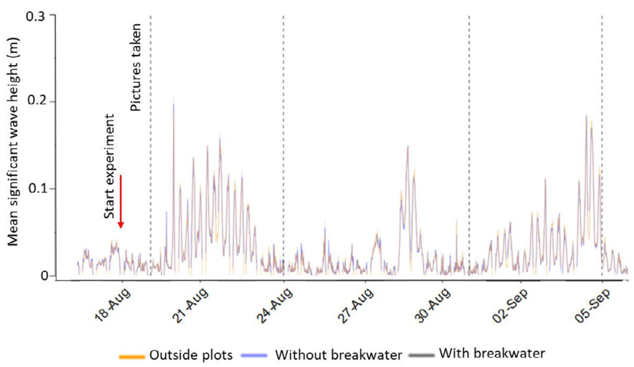

Figure 3 The mean significant wave height (Hs) in meters over time. Two pressure sensors were placed outside the experimental plots (yellow), two inside experimental plots with a fence but without a breakwater (blue), and two inside experimental plots with a fence and behind a breakwater (grey). The red arrow indicates the day the mussels were placed in the field. The dashed lines indicate when pictures of the plots were taken.

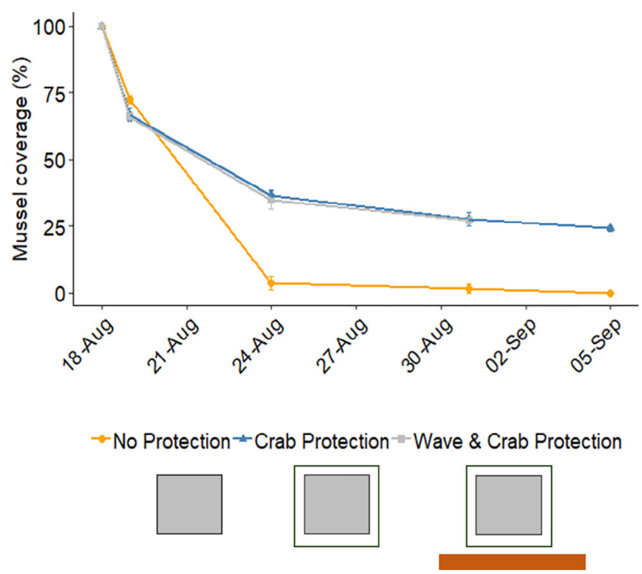

Figure 4 Effect of fences and breakwaters on mussel coverage (i.e. mixture of live mussels, shell hash, and other material) in the initial seeded mussel plot (grey-marked area in schematic drawings, 25 m^2) of only the bare sediment plots. Mussel plots were either completely unprotected (yellow), protected against crabs with a fence (blue), or protected against crabs and waves with a fence and a breakwater (grey). Data are means ± SE (n = 4).

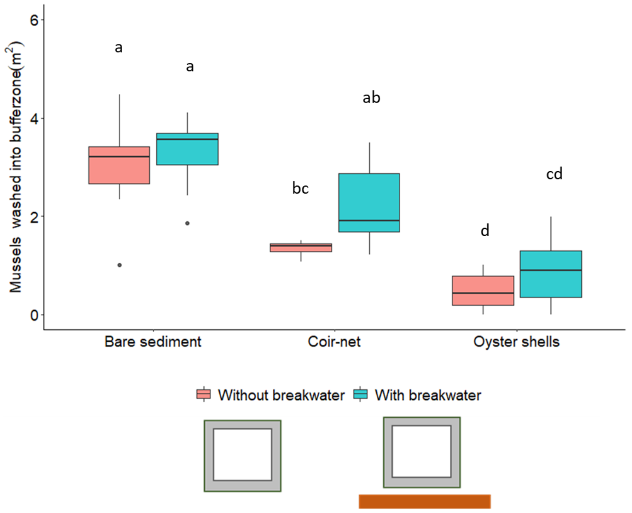

Figure 5 Area (m^2) of mussels found washed against the fence behind plots into the buffer zone (grey-marked area in the schematic drawings), with bare sediment, coir-net, or oyster shells and without (red) or with a breakwater (blue). Data are averaged over the second and third time pictures of the plots were taken. n = 8.

first day after seeding, mussel coverage had decreased by an average of 26% (Fig. 6A–C). The mussel coverage decreased most on the bare sediment plots with 33%, in comparison with coir-net (27%, Tukey: $p = 0.002$) or oyster shell plots (21%, Tukey: $p < 0.001$). The second measurement took place two days after the mussel beds had endured a storm (Fig. 3). Again, mussel coverage had dropped relative to the start of the experiment most severely in bare sediment plots with an average decrease of 64% compared to coir-net (45%, Tukey: $p = 0.03$) and oyster shell plots (50%, Tukey, $p = 0.001$). Between the second and third measurements, the mussel plots again endured a short increase in average significant wave height (Fig. 3). After 13 days, mussel coverage decreased to 27% in the bare sediment plots, 41% in the coir-net plots (Tukey: $p < 0.001$), and 36% in the oyster shell plots (Tukey: $p = 0.021$). After 18 days, only 23% of the bare plots, 33% of the coir-net (Tukey: $p = 0.029$), and 29% of the oyster shell plots (Tukey: $p = 0.22$) were on average still covered with mussels.

Effect of Breakwaters on Mussel Distribution Within Plots

Although the presence of a breakwater did not seem to influence the total mussel coverage in the initial mussel covered plots ($F_{1,18} = 0.78$, $p = 0.389$), there was a negative correlation between mussel coverage and distance to a breakwater ($F_{1,210} = 34.57$, $p < 0.001$, Fig. 6). Mussel coverage in the initial mussel plot (Fig. 2B, blue-marked area) was significantly higher just behind the breakwater and decreased further away from the breakwater. This pattern emerged at the beginning of the experiment for bare sediment plots ($F_{1,35} = 4.59$, $p = 0.039$, Fig. 6A) and for coir-net after the first measuring date ($F_{1,35} = 26.17$, $p < 0.001$, Fig. 6B) and oyster shell plots ($F_{1,35} = 51.92$, $p < 0.001$, Fig. 6C). We also found a similar negative

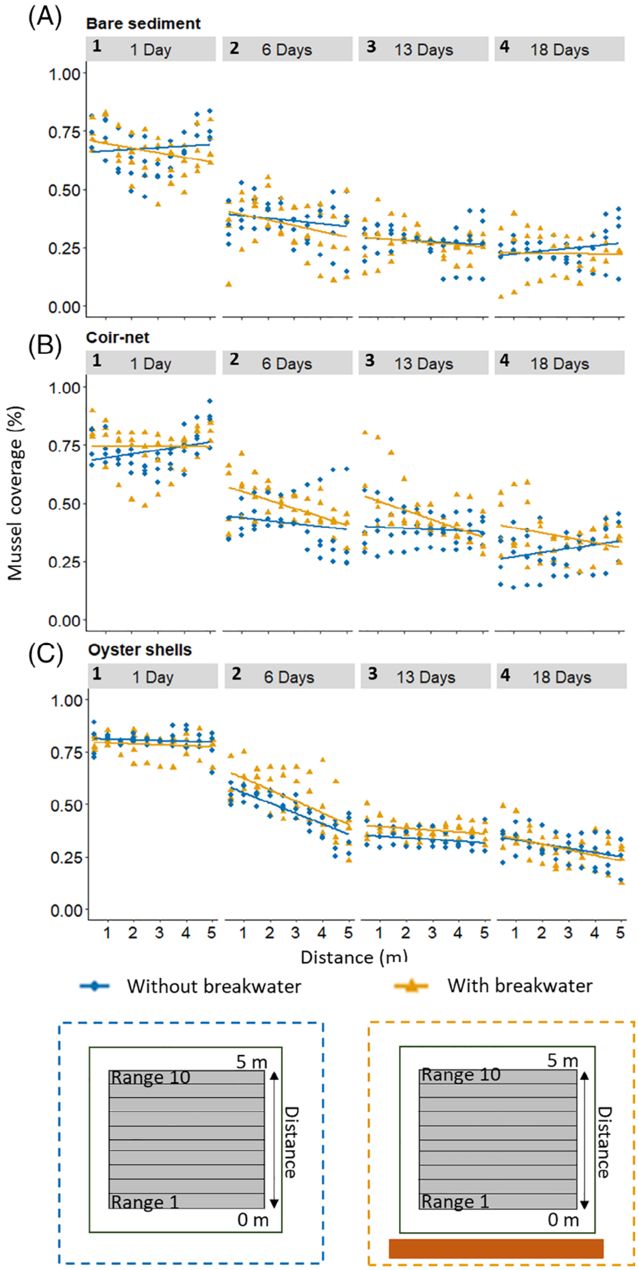

Figure 6 Percentage mussel coverage (i.e. mixture of live mussels, shell hash, and other material) of the initial mussel plot (grey-marked area in schematic drawings below the graph legend, 25 m^2) on three different substrates; bare sediment (A), coir-net (B), oyster shells (C), over time. Percentage mussel coverage is measured in 10 ranges of 0.5 × 5 m (distance between plot edges [m] in schematic drawing).

correlation for mussels seeded on oyster shells that were not protected by a breakwater ($F_{1,35} = 89.11$, $p < 0.001$). Coverage of mussels seeded on oyster shells was highest closest to the plot edge facing the waterline, and decreased with increasing distance from this edge. Mussel coverage on coir-net plots without a breakwater increased significantly with increasing distance from the plot edge facing the prevailing wave direction

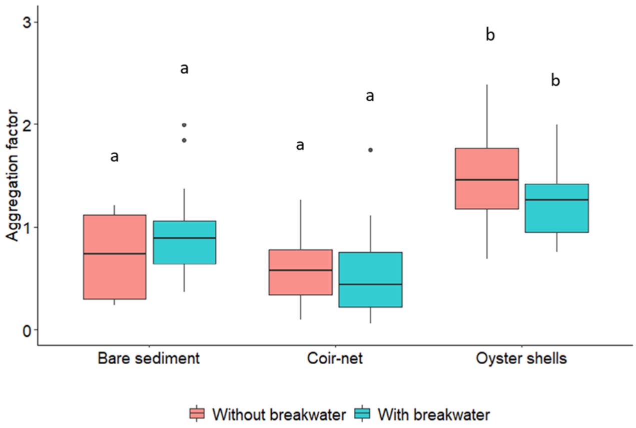

Figure 7 The factor of aggregation after 21 days calculated as: final within-patch density $t = 4$/starting density $t = 0$. $n = 4$.

($F_{1,35} = 2.07$, $p < 0.001$). No distance correlation was found in bare sediment plots that were not protected by a breakwater.

Effect of Protection Measures on Mussel Density

After 21 days, the within-patch density was significantly higher in the oyster plots in comparison with bare sediment (Tukey: $p < 0.001$) or coir-net plots (Tukey: $p < 0.001$) (Fig. 7). Aggregation increased by a factor of 1.6 when mussels were seeded on oyster shells in comparison with mussels on bare sediment and a factor of 2.4 in comparison with mussels seeded on coir-net. There was no significant difference in aggregation of mussels on bare sediment or coir-net (Tukey: $p = 0.076$).

Discussion

Ecosystem engineers typically need to overcome establishment thresholds caused by the effects of multiple and combined biotic and abiotic environmental stressors (van Wesenbeeck et al. 2007; Suykerbuyk et al. 2012; Balke et al. 2013). In the current study, we tested the effect of three engineering measures, with each of them targeted at reducing a specific environmental stressor: protection from hydrodynamic dislodgement (breakwaters, substrates, and fences) and protection from predation (fences and complex substrates). Fences increased the preservation of transplanted mussels most efficiently, and created a window of opportunity for establishment by acting as traps for dislodged mussels. The provisioning of a complex attachment substrate, such as coir-net or oyster shells, also increased the retention of transplanted mussel seed substantially. Interestingly, results suggest that protection against predation and offering an attachment substrate is more effective than changing local hydrodynamic conditions in order to increase survival of transplanted mussels. However, this requires more study as to cause and effect. A combination of these engineering measures that lower multiple environmental stressors simultaneously could be used to increase transplantation success by increasing the window of opportunity for successful establishment under highly dynamic conditions.

Spatial and Temporal Conditions

Restoration guidelines often recommend spreading of risks among transplantation sites, transplantation in habitats where organisms historically occurred, and the use of donor material from comparable habitats (van Katwijk et al. 2009). However, in our case, it was not desirable, or not possible to meet all these conditions. First, we wanted to study if transplantation of ecosystem engineers on a highly dynamic and eroding mudflat could be made possible. Second, intertidal mussels are in limited supply in the Netherlands (van den Ende et al. 2015) and moreover not always available for restoration purposes. For this reason, we specifically tested whether mussels that originate from SMCs are able to adjust to intertidal conditions (Schotanus et al. 2019). Our results highlighted that SMC mussels are a suitable alternative donor source. Third, unpredictable circumstances determining site-to-site and year-to-year environmental variability can be exceptionally severe in a given year, determining the long-term restoration success. In 2016, the year the present experiment was carried out, mussel seed yields from the subtidal mussel seed collectors were unexpectedly and inexplicably low and the quality of the mussel seed was poor (Capelle & van Stralen 2017). The approach we endorse for creating coastal protection schemes is (1) obtain large quantities of easily available donor material in an environmentally non-damaging way, and (2) make multiple and regular transplantations over time, so that a rare summer storm does not determine the ultimate restoration success.

Diminishing Establishment Thresholds Using Fences

Mussel coverage on bare sediment plots remained higher when mussel plots were surrounded by a fence. The fences were designed to decrease the predation pressure by crabs and thereby increase mussel survival. However, it is possible that the fences also influenced additional biotic or abiotic environmental factors, affecting the preservation of the transplanted mussels. First, while the fences could have been expected to deter predatory birds such as oystercatchers and seagulls (Hilgerloh 1997), this did not seem to be the case. Both seagulls and oystercatchers were observed foraging on the experimental plots. Second, the fences may have reduced physical stress on the mussels by influencing the hydrodynamics, but the effect may be scale-dependent. There was no difference in measurements by pressure sensors placed in the back of plots surrounded by fences and those placed outside plots. However, the higher retention of mussels just behind breakwaters, and in front of coir-net and oyster shell plots, suggest that the structures did influence the hydrodynamics on a small scale. Therefore, it is likely that the fences had similar effects to that of breakwaters and reduced the physical force on the mussels which may have led to a higher retention of mussels. Third, like the fences used by Reusch and Chapman (1997) to estimate the abundance of mussel clumps transported along shore to deeper water, our fences acted as traps for dislodged mussels. The mussel covered area against the fences was highest for the bare sediment treatment and lowest for the oyster shell treatment. However, since mussels were probably stacked on top of each other against the fences these results must be treated with caution. Dislodged mussels may have crawled, or passively drifted by water currents, back to the initial plot. Mussels have shown to attach preferentially to other live mussels or mussel shells rather than to other hard substrates (Commito et al. 2014), they may therefore have re-attached themselves to mussels within the plots.

When considering the use of fences for future restoration efforts, the practicalities should be considered. The placement and maintenance of the fences were very labor intensive and thereby relatively costly. Fences broke and poles were pulled out of the sediment due to the high drag-force of the hydrodynamics in the area. These kinds of engineering measures in highly dynamic areas are likely to be more suitable for small-scale experiments and less so for the large-scale efforts required for successful coastal protection interventions.

Diminishing Establishment Thresholds Using Stable Substrates

Soft sediment environments are challenging for mussel establishment because there is little suitable substrate available to which byssal threads can attach (Büttger et al. 2008; Commito et al. 2014). However, under very high spatfall densities, mussels are able to aggregate into extensive beds on sandy or muddy substrates by attaching their byssus threads to each other rather than to primary substratum (Reusch & Chapman 1997; Bertolini et al. 2017, 2019). This form of self-organisation enhances the persistence of the mussel bed and increases its resistance to wave disturbance (Liu et al. 2014; de Paoli et al. 2017). Self-organization may have also played a role in the decline of mussel coverage measured after just one day in the present experiment. The decline in coverage may have been the result of mussels aggregating into patches rather than mussel loss caused by dislodgement, as no dislodged mussels had yet been found washed against the fences. In the present study, both coir-net and oyster shells increased the retention of the transplanted mussels. In addition, and to our surprise, we observed that mussels on oyster shells formed patches with a higher density than mussels seeded on bare sediment or coir-nets. This result contrasts with a study done by Capelle et al. (2019) in which aggregation decreased when coarse shell material was added. It is possible that the relatively deep and small crevices between the oyster shells formed traps in which hydrodynamically dislodged mussels accumulated (Reise et al. 2017). This would also explain why we found significantly fewer mussels washed against the fences in the oyster plots compared with the bare sediment and coir-net plots. In addition, an increase in habitat complexity has shown to disturb prey–predator interactions by decreasing foraging efficiency (Grabowski et al. 2008). The complex structure of the oyster bed may have provided refuges, making it more difficult for predators such as crabs or birds to reach them. Thus, the addition of a complex substrate may lower dislodgement caused by both hydrodynamic stress and predators (Bartol & Mann 1997; Schulte et al. 2009; Capelle et al. 2019). Rough substratum, such as coir-nets or oyster shells, may also have affected the mussels by reducing local bedload transport of sediment (Commito et al. 2018; Commito et al. 2019), or by increasing the retention of water and thereby reducing the thermal stress experienced by the mussels during daytime low tides (Helmuth & Hofmann 2001).

Diminishing Establishment Thresholds Using Breakwaters

Hydrodynamics have often been suggested as the most important limiting factor for the establishment of self-sustainable ecosystems (mussels: Capelle et al. 2014; de Paoli et al. 2015, seagrass: Infantes et al. 2011, saltmarsh: Möller et al. 2014, mangroves: Van Cuong et al. 2015). In our experiment, the transplanted mussel beds had to endure a summer storm right after transplantation, shortly followed by two subsequent storms in the following weeks. These kinds of summer storms are uncommon in the Netherlands, but were a good test for the effectiveness of the artificial structures on the retention of the transplanted mussel seed. The breakwaters affected the configuration of the mussels behind them. Higher mussel coverages were found directly behind the breakwaters for all substrates and surprisingly also at the leading edge of oyster plots without a breakwater. The elevation of the oyster shell plots may have attenuated wave action, contributing to mussel retention at the leading edge of plots. However, the breakwaters did not significantly increase the overall higher mussel coverage compared with plots without breakwater protection. This was unexpected, as the implementation of breakwaters has proven to be efficacious in previous coastal ecosystem restoration projects (Mangrove restoration: Tamin et al. 2011; Van Cuong et al. 2015). Breakwaters may, however, be more effective in stimulating sediment accretion than in attenuating storm waves. These discrepancies could not be explained by misplacement as breakwaters were placed facing the incoming direction of the storms (www.knmi.nl). The only possible explanation is that the design of the breakwater simply did not meet the requirements to sufficiently lower hydrodynamic stress. The breakwaters may have been too low and/or narrow to lower the hydrodynamic stress further than directly behind the breakwater.

Implementation

To incorporate ecosystem engineers into coastal protection, transplantation would be most valuable on wave-exposed and eroding mudflats (Borsje et al. 2011). Establishment thresholds in these types of environments are likely to be very high, and may often be impossible to overcome under normal conditions. A window of opportunity in which an ecosystem engineer can successfully establish in a new environment may never naturally occur in the time and space desired. The present study shows that engineering measures that diminish or counteract limiting abiotic and/or biotic factors for successful establishment of ecosystem engineers may constitute a valuable tool in ecosystem restoration and coastal protection. However, it is important to customize the engineering tools to the specific goals and locations of the restoration. Some measures are more applicable for specific species or locations and some are may only be suitable for small-scale restoration. In our study, we found that the fences were very effective in lowering establishment thresholds, but they were also labor intensive and costly and therefore inadvisable for large-scale restorations. Furthermore, unpredictable circumstances such as severe weather conditions and low quality of the donor source can still determine long-term survival chances. Overall, our study emphasizes that managers restoring ecosystem engineers in dynamic systems should try to account for these kinds of uncertainties by spreading risks over time or space. This requires identifying easily accessible transplantation material, and making use of smart, affordable engineering solutions.

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