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Promoting self-facilitating feedback processes in coastal ecosystem engineers to increase restoration success: Testing engineering measures

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Abstract

1. Coastal ecosystem engineers often depend on self-facilitating feedbacks to ameliorate environmental stress. This makes the restoration of such coastal ecosystem engineers difficult. We question if we can increase transplantation success in highly dynamic coastal areas by engineering measures that promote the development of self-facilitating feedback processes.
2. Intertidal blue mussels *Mytilus edulis* are a typical example of ecosystem engineers that are difficult to restore. A lack of self-facilitating feedbacks at low densities limits establishment success when young mussels are transplanted on dynamic mudflats.
3. In a large field experiment, we investigated the possibility of increasing transplantation success by stimulating the formation of an aggregated spatial configuration in mussels, thereby reducing hydrologically induced dislodgment and the risks of predation. For this, we applied engineering measures in the form of fences that trapped wave dislodged mussels.
4. Mussel loss rates were significantly lower when mussels were placed between both artificial fences, and in high densities (4.2 kg/m^2) compared with mussels placed in areas without fences and in low densities (2.1 kg/m^2). The fences induced the formation of a banded pattern with high local mussel densities, which locally reduced predation.
5. *Synthesis and applications*. Our results underline the importance of actively promoting the development of self-facilitating processes, such as aggregation into patterns, in restoration projects of ecosystem engineers. In particular, the current study shows that engineering measures can help to initiate these kinds of self-facilitating interactions, especially in highly dynamic areas.

KEYWORDS
ecosystem engineers, engineering measures, large-scale, mussels, pattern formation, restoration, self-facilitating feedback

1 | INTRODUCTION

Transplantation of ecosystem engineers has been suggested as an useful tool to restore degraded ecosystems (Byers et al., 2006), and thereby provide ecosystem services such as enhanced biodiversity (Bouma, Olenin, Reise, & Ysebaert, 2009) and coastal protection (Borsje et al., 2011; Bouma et al., 2014). Unfortunately, transplantation success in highly dynamic environments, such as wave exposed shores, is generally low. This is especially true for ecosystem engineers, such as reef forming bivalves (Beck et al., 2011), seagrasses (Meehan & West, 2002), mangroves (Kamali & Hashim, 2011) and saltmarshes (Duggan-Edwards, Pagès, Jenkins, Bouma, & Skov, 2019), where a certain size or density threshold needs to be surpassed for self-facilitating feedback mechanisms to develop (Bouma, Friedrichs, et al., 2009; Suykerbuyk et al., 2016). These positive feedbacks ameliorate environmental stresses caused by physical (e.g. wave exposure, anoxia) or biological (e.g. predation) stress (Liu et al., 2014; Silliman et al., 2015). Seagrass and saltmarsh vegetation increasingly attenuate currents and trap sediment with higher shoot-density (Bouma, Friedrichs, et al., 2009; Maxwell et al., 2017; van de Koppel, Van der Wal, Bakker, & Herman, 2005). Reef-forming bivalves such as oysters and mussels reduce losses of individuals caused by predation and hydrodynamic forces, by attaching themselves to conspecifics and aggregating in large and dense groups (Bertness & Grosholz, 1985; Hunt & Scheibling, 2001). Recent studies emphasize the importance of integrating these kinds of positive intraspecific feedbacks to improve transplantation success (Renzi, He, & Silliman, 2019; Silliman et al., 2015; Valdez et al., 2020).

Several studies on coastal ecosystem restoration have already shown that clumping, rather than spacing individuals out, harnesses positive intraspecific interactions and can greatly enhance restoration success (Silliman et al., 2015; Sofawi, Rozainah, Normaniza, & Roslan, 2017). Salt marsh propagules planted in clumps benefit each other by alleviating physical stressors such as anoxia and erosion (Silliman et al., 2015). In addition, reef-forming bivalves transplanted in clumps appeared to have a higher resistance to wave stress (Capelle, Leuchter, de Wit, Hartog, & Bouma, 2019). This indicates that transplantation designs that more closely follow the natural patchiness observed in many emerging estuarine ecosystems may improve restoration success (Silliman et al., 2015). Nevertheless, experiments that specifically use the natural patchiness of the target species to enhance restoration success are still relatively scarce (but see: de Paoli et al., 2017). Most experiments on self-facilitating feedback processes are limited in scale and therefore do not provide a ready-to-go, cost-effective and practical design for large-scale restoration (Silliman et al., 2015). Large-scale effects such as wave attenuation, may be more evident with large experimental units (Renzi et al., 2019). We therefore explored the possibility of increasing large-scale restoration success using engineering measures that promote the development of self-facilitating feedback processes among newly transplanted organisms.

Reef-forming bivalves such as blue mussels *Mytilus edulis* are an example of ecosystem engineers that provide many ecosystem services including shoreline protection from erosion (Borsje et al., 2011), and habitat provision for other species (Palomo, People, Chapman, & Underwood, 2007). However, mussel beds are notoriously hard to restore in dynamic environments like wave-exposed intertidal mudflats (de Paoli et al., 2015; Geraldi, Simpson, Fegley, Holmlund, & Peterson, 2013; Mann & Powell, 2007). Newly transplanted mussels are highly vulnerable to dislodgement by hydrodynamics and to predation (Capelle et al., 2014). On soft bottom mudflats, where hard substrate is scarce, mussels attach themselves to conspecifics and aggregate into distinctive patterns (Commito et al., 2014; van de Koppel, Rietkerk, Dankers, & Herman, 2005). Active aggregation into patterns increases their resistance to dislodgement by hydrodynamic forces (Liu et al., 2014) and creates a safety in numbers effect, diluting the chance of falling prey to predators (Cote & Jelnikar, 1999; Hunt & Scheibling, 2001). These patterns result from an interplay of between-mussel facilitation and competition, and translate into small-scale (<1 m) net-shaped patterns embedded in large-scale (5–10 m) banded patterns (Liu et al., 2014; van de Koppel, Rietkerk, et al., 2005). Aggregation into small-scale patterns only takes a couple of days while the formation of bands can take months (Liu et al., 2014). However, on wave-exposed mudflats the question is whether transplanted mussels have enough time to establish sufficient intraspecific interactions and self-organize into bands, before they are washed out. In other words, the mussels may never get the necessary window of opportunity to establish in a disturbance-free period (Balke, Herman, & Bouma, 2014).

In a large field experiment using blue mussels *M. edulis* as a model system, we investigated whether a restoration design that stimulates the natural development of self-facilitating feedback processes, can increase transplantation success in highly dynamic environments. Previous studies artificially aggregated individuals prior to transplantation in the restoration efforts of for example, mussels (de Paoli et al., 2017), mangroves (Toledo, Rojas, & Bashan, 2001), seagrasses (Suykerbuyk et al., 2016) and saltmarshes (Silliman et al., 2015). In our study, however, we specifically investigated the effectiveness of engineering measures to both prevent mussels washing out and stimulate the natural development of their spatial configurations (i.e. banding patterns). We hypothesized that stimulation of the natural spatial configurations (i.e. high-density bands with bare areas in between) found in intertidal mussel beds (a) reduces the likelihood of dislodgement by hydrodynamic forces due to mutual attachment and (b) dilutes the chance of falling prey to predators by creating a safety in numbers effect, which ultimately increases the restoration success. Our engineering measures consisted of fences between which loose mussels were placed. We expected the fences to trap wave-dislodged mussels over time, resulting in banded mussel patterns with local high mussel densities which enable mussels to attach to each other to minimize permanent hydrodynamic dislodgement from the restoration site and to create a safety in numbers effect reducing predation losses, hence leading to higher and longer overall survival. To gain a better insight in the role that safety in numbers may play on local mussel survival, the experiments were done with two mussel densities and three fence patterns (no-fence control, spaced out fences, placed-together fences). To further enhance our understanding of the underlying mechanisms causing mussel loss (i.e. dislodgement vs. predation), a cage experiment was carried out within the larger experiment. We expected that local mussel losses caused by predation would be lower with higher surrounding mussel densities.

2 | MATERIALS AND METHODS

2.1 | Study site

A large field experiment was conducted from the 18 August 2017 until 16 April 2018 on a wave-exposed intertidal mudflat (Viane) in the Oosterschelde estuary in the Southwest of the Netherlands (51.616211, 3.992755). The Oosterschelde estuary is a 351 km^2 tidal basin with 118 km^2 of tidal flats (Smaal & Nienhuis, 1992). Due to the construction of a storm surge barrier in 1986, that separates the estuary from the North sea, and the construction of two dams closing off the eastern part of the estuary, the size of the basin area, the tidal prism, the tidal range and the tidal currents have decreased (de Vet, van Prooijen, & Wang, 2017). Since the changes in hydrodynamic conditions, the estuary has been in disequilibrium resulting in a net sediment transport from tidal flats into the adjacent gullies. As a result, tidal flats are slowly eroding with an average net erosion rate of 10 mm/year (Santinelli & Ronde de, 2012). The mudflat at the study site experiences high hydrodynamic forces and is eroding with an average net erosion rate of 15 mm/year (Salvador de Paiva, Walles, Ysebaert, & Bouma, 2018). In the past, natural intertidal mussel beds were present throughout the estuary, including on the Viane mudflat (Fokker, 1905). At present, intertidal mussels can only be found incidentally on commercial mussel plots at sheltered sites, in oyster reefs or attached to other hard substrates such as wooden poles. Viane is characterized by sandy sediment and few patches of old oyster reefs. The experiment was positioned on an elevation suitable for mussels with an average inundation time of approximately 60% (Brinkman, Dankers, & Van Stralen, 2002). The experiment received wind driven waves mainly from the southwest, as this is the dominant wind direction in Netherlands. Local wind conditions at the study site were obtained from the Royal Netherlands Meteorological Institute (www.knmi.nl, Appendix A).

2.2 | Experimental design

2.2.1 | Large-scale experiment: Effectiveness of engineering methods

To test the potential for inducing natural mussel aggregation, fences intended to trap wave-dislodged mussels were constructed. The fences consisted of concrete mesh cut into 0.3 × 2.5 m pieces and covered with chicken wire with a mesh size of 13 mm (Figure 1A).

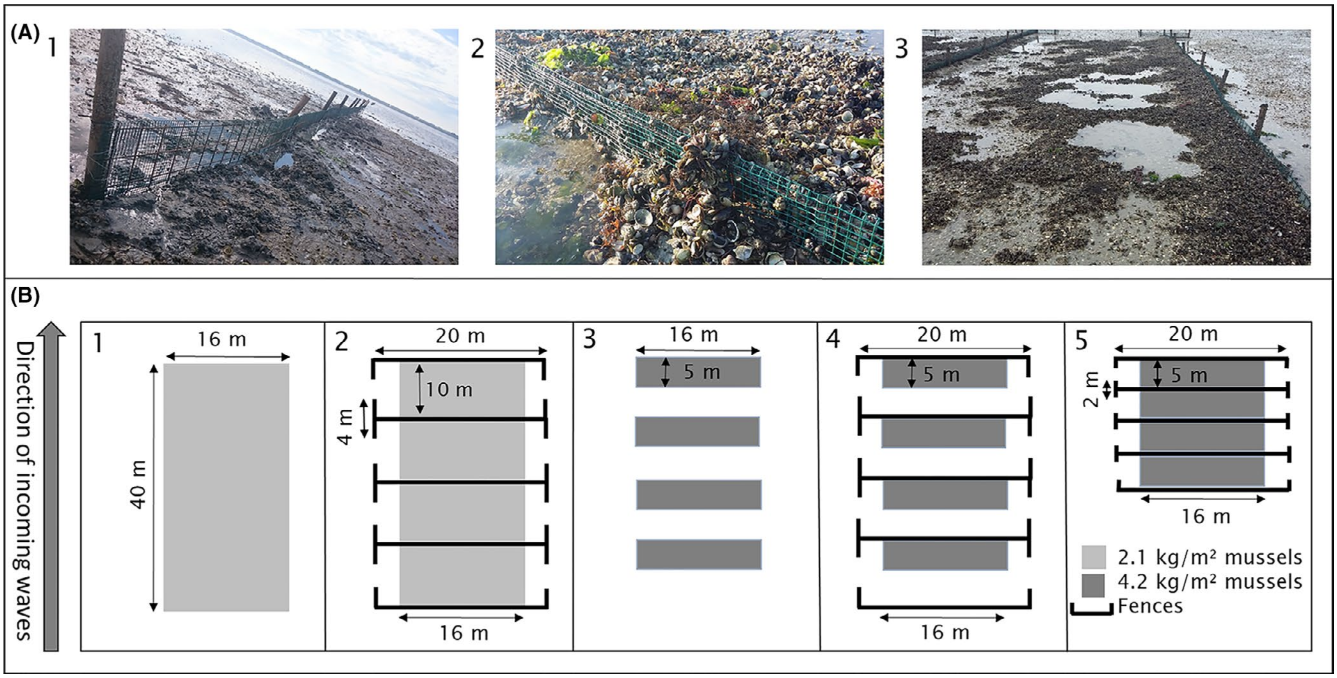

FIGURE 1 (A) 1. Fences to trap dislodged mussels and promote formation of bands in transplanted mussel beds consisting of fences made of concrete mesh covered with chicken wire. Fences were dug into the sediment approximately 10 cm deep, and anchored with wooden poles in rows of 20 m. 2. Close-up of mussels against fences on 19 September 2017, 4 weeks after placement of the mussels. 3. Example of how the mussels are spread over time. Picture is taken on 11 March 2018 of a band in treatment 5. (B) Schematic representation of the five treatments in which mussel seed was transplanted. The light grey corresponds with a low mussel density of 2.1 kg/m^2 and the dark grey with a high mussel density of 4.2 kg/m^2. The black lines represent the placement of fences. There were three replicates of each treatment

Fences were placed perpendicular to the incoming waves in rows 20 m in length, 5 or 10 m apart, depending on the treatment (Figure 1B). These distances were chosen to mimic the banding patterns found in natural intertidal young mussel beds (van de Koppel, Rietkerk, et al., 2005). The fences were dug 10 cm into the sediment and anchored with wooden poles. An extension of 3 m was added, right-angled on the sides of the 20 m long fences as an extra measure to prevent mussels from washing out.

To test the effect of fences on local mussel densities, configurations and mussel bed persistence on a highly dynamic mudflat, mussels were placed in five different patterns (Figure 1B), each with three replicates. Because self-organization is a density-dependent process (van Bertolini, Geraldi, Montgomery, & O'Connor, 2017; van de Koppel, Rietkerk, et al., 2005), mussels were transplanted in two different densities; a low density of 2.1 kg/m^2 and a high density of 4.2 kg/m^2 (Figure 2B). The low density of 2.1 kg/m corresponded with the average densities used in Dutch mussel aquaculture on culture plots (Capelle et al., 2014). The two mussel densities were determined by placing the same amount of mussels (±1,344 kg) homogeneously on surface areas differing in size; in a compartment of 16 × 40 m or in 4 bands of 16 × 5 m. In this way, there were no differences in mussel biomass between treatments, only a difference in local densities and in configuration of mussels placed in bands or homogeneously spread.

The first treatment (Figure 1B 1) involved mussels transplanted homogenously in a 16 × 40 m area, resulting in a low density. In the second treatment (Figure 1B 2) mussels were transplanted homogenously in a 16 × 40 m area, and the area was divided into four compartments by five, 20 m long fences placed 10 m apart and perpendicular to the incoming waves. In the third treatment (Figure 1B 3), mussels were transplanted in four bands of 16 × 5 m, resulting in high mussel densities, separated by a 16 × 5 m bands of bare sediment. For treatment four (Figure 1B 4), the same banded mussel configuration as that in treatment 3 was used, but with fences behind each band. In these four treatments, we could test the effect of banding patterns and of the fences on the mussel bed persistence. A fifth treatment (Figure 1B 5) was carried out as an extra control to investigate the effect of very high mussel densities placed between fences. To enable this control, the same amount of mussels (±1,344 kg) was transplanted homogenously on an area of 16 × 20 m separated by fences placed 5 m apart.

2.2.2 | Small-scale cage-experiment: Predation versus wave dislodgement

An additional experiment was carried out within the large-scale experiment (Figure 2) to quantify the relative importance of losses caused by hydrodynamic dislodgement or predation, and to quantify the effect of small-scale (i.e. patch scale) and large-scale (i.e. mussel bed scale) mussel densities may have on local mussel survival. Mussels were transplanted (a) in completely closed cages (40 × 20 × 25 cm) to provide protection against both predation and washing out due to waves, (b) in half-open cages that allowed predatory crabs to enter, but prevented mussels being washed out and (c) completely open on bare sediment, covering the same surface area as in the cages (40 × 20 cm; Figure 2A). Within these cages, mussels were placed in three different densities (2.5, 5 and 10 kg/m^2) to determine small-scale density effects on mussel persistence. In order to test for safety in numbers effect on a larger scale, cages were

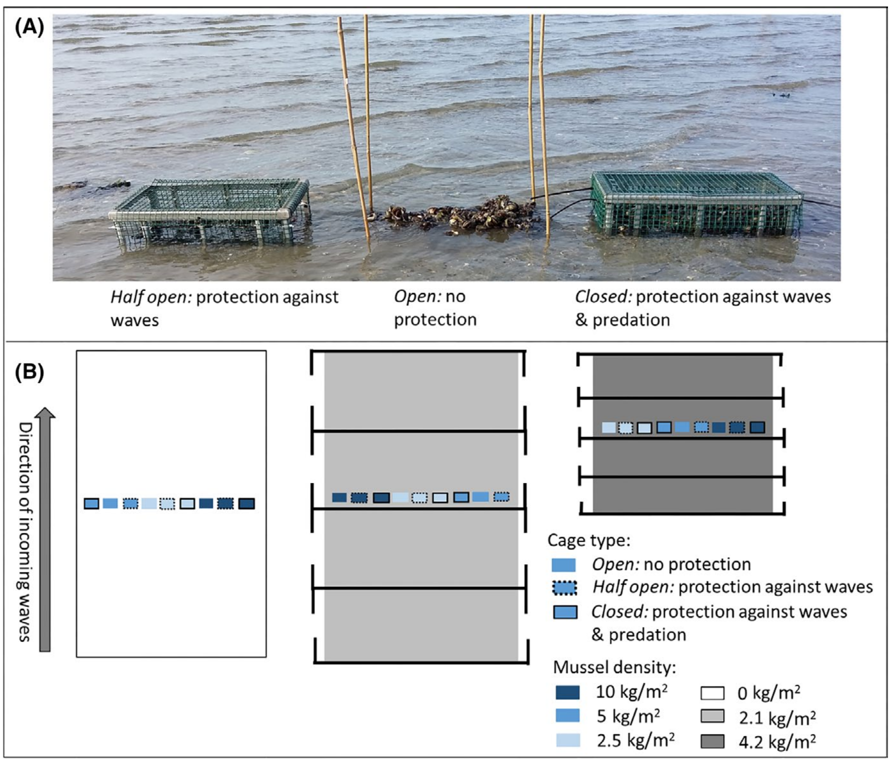

FIGURE 2 (A) The three types of cages in which mussels were placed in three different densities (2.5, 5, 10 kg/m^2). (B) Locations where cages were placed inside of mussel plots: no surrounding mussels, low-density surrounding mussels (treatment 3, large-scale experiment) or high-density surrounding mussels (treatment 5, large-scale experiment)

placed in two different plots (nine for every plot) of the large-scale transplantation experiment. Cages were placed in all three replicates of the plot in which mussels were seeded homogenously between fences (treatment 2) and in the high-density plot with fences placed 5 meters apart (treatment 5; Figure 2B). In addition, nine cages were placed in three bare sediment plots. This full factorial design resulted in a total of 81 experimental units.

2.3 | Mussel placement and monitoring

Mussel seed of approximately 4 months old with an average length of 17.9 ± 0.41 mm *SE* (subsample, $n = 78$) was transplanted on 18 August 2016. The distribution and coverage were monitored monthly for 8 months. Young mussels were used because of their high plasticity and better capability of adjusting to the harsh intertidal conditions (Schotanus, Capelle, Leuchter, van de Koppel, & Bouma, 2019) than subtidal adult mussels (de Paoli et al., 2015), and due to the paucity of intertidal mussels in the Oosterschelde. The mussel seed was harvested from subtidal seed mussel collectors situated in the Oosterschelde. Within 12 hr of harvest, the mussel seed was deposited onto the mudflat near the experimental site during high tide. During the following low tide, the mussels were manually transplanted to the treatments.

2.3.1 | Effect of fences and transplantation density on mussel coverage, distribution and density

Mussel coverage was monitored by taking monthly top-view pictures with a drone (Appendix A). The pictures were transformed to black (mostly mussels) and white (bare sediment). The black represented mostly mussels but sometimes also shadows, seaweed or shells because differentiation could be difficult and complete exclusion of these anomalies out of the analysis was not always possible. The percentage mussel coverage was estimated by classifying the proportion of black pixels using the program ImageJ. Total mussel coverage (100%) at t_0 was estimated to be 480 m^2 for treatments 1 and 2 which were transplanted with 2.1 kg/m^2 mussels, and 240 m^2 for treatments 3, 4 and 5 which were transplanted with 4.2 kg/m^2 mussels. Besides determining the development of the total mussel coverage per treatment, we also analysed the distribution of mussels within plots. To do this, all plots were divided into four 16 × 10 m compartments for treatments 1, 2, 3 and 4, and 16 × 5 m compartments for treatment 5 (Figure 4A). By determining the mussel coverage per compartment, we investigated how the fences influenced mussel coverage and distribution.

We determined the effect of fences on local mussel densities by taking 10 cm deep core samples (10 cm ⌀) at the end of the experiment. Three core samples were taken in front of each fence (treatments 2, 4 and 5). If no fences were present (treatments 1 and 3), three core samples were taken in each compartment (Figure 4A). No samples were taken if mussels were no longer present within the compartment. In the laboratory the mussels in each sample were counted, cleaned and weighed.

2.3.2 | Effect of safety in numbers on mussel losses: Predation versus wave dislodgement

After 5 months, some small cages with mussels were lost during the winter storms in January (Appendix A). We therefore decided to conclude the experiment with the cages. A top view picture of every cage was taken after which all the mussels were bagged and brought to the laboratory. In the laboratory, the number and weight of mussels were determined for each cage.

2.4 | 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. Models were simplified according to Akaike's information criterion (AIC) scores and non-significant factors were removed. Post-hoc comparisons were used to test for significant differences between transplantation treatments and cage treatments (R-package EMMEANS, Lenth, 2019).

2.4.1 | Effect of fences and transplantation density on mussel coverage

In order to compare the loss rates between the five different treatments, a survival analysis was carried out based on the maximum likelihood (Miller Jr., 1981), which we modified to apply to aerial coverage loss (see Appendix B). In short, the mean loss rate (ε) per treatment was estimated as the inverse of the mean lifetime of a mussel bed (τ).

$$\varepsilon = 1/\tau.$$

The mean lifetime of a mussel bed was estimated by determining the difference in proportion of mussel coverage (ρ_i) for every monitoring time (t_i). As most mussel beds did not disappear completely during the course of the experiment, a correction for these right-censored observations was included to prevent underestimation of the mean lifetime:

$$\tau = 1/(1-\rho_{t\_end})\,\Sigma((1-\rho_{i+1})-(1-\rho_i))t_{i+1}.$$

Finally, a one-way ANOVA was carried out with loss rates (ε) as the response variable and the presence of fences and the transplantation density as the explanatory variables. Differences between treatments at a certain timepoint were analysed with a linear mixed effects model (LME, R-package NLME, Pinheiro, Bates, DebRoy, & Sarkar, 2019) with coverage as the response variable, treatment as the explanatory variable and plot as a random factor.

2.4.2 | Effect of fences and transplantation density on mussel distribution and density

As previously described, the plots were divided into four equally sized compartments and the coverage was determined for every compartment to determine the effect of the incoming waves on the distribution of the mussels (Figure 4A). The effect of the fences on the distribution was analysed by estimating the slope (*b*) of the log transformed mussel coverage (log(*y*)) over the four compartments (*x*), with compartment one being the furthest away from incoming waves, and compartment four the closest to incoming waves, for every plot and timepoint.

$$\log(y) = a + bx.$$

A LME model was carried out with the slope (*b*) as the response variable, the treatment as the explanatory variable and time as the random factor. The number of mussels per m^2 was analysed with a general linear model with a quasipoisson family to correct for overdispersion. Treatment and the plot compartment in which samples were taken were set as explanatory variables.

2.4.3 | Effect of safety in numbers on mussel losses: Predation versus wave dislodgement

An LME was carried out to analyse the effect of cage type (open, half open, closed), transplantation density and surrounding mussel density on mussel losses. The proportion of mussel biomass left in the cages at the end of this experiment was set as the response variable. Cage type (open, half open, closed), mussel density (2.5, 5, 10 kg/m^2) and plot treatment (no mussels, low-density mussels, high-density mussels) were set as explanatory variables and plot number was set as a random factor. However, comparing the AIC values of the model with and without plot number as a random factor revealed that the simplified model fitted the data best. We therefore continued with the simplified model containing only fixed factors. Due to a storm (Appendix A; Figure 1, red arrow), three closed and one half-open cages disappeared.

3 | RESULTS

3.1 | Effect of fences and transplantation density on mussel coverage

The fences ($F_{1,11}$ = 6.33, p = 0.029) and the density in which the mussels were transplanted ($F_{2,11}$ = 4.27, p = 0.043) both had a significant effect on the average mussel loss rate (Figure 3). Mussels placed between fences and in a higher density (treatment 4) had a significant lower mean loss rate per week (Tukey, p = 0.03) than mussels placed in low densities and without fences (treatment 1, Figure 3A). For all treatments, the greatest loss was found in the first 2 weeks after transplantation (64 ± 3% *SE*, Figure 3B). During these 2 weeks, the low mussel density treatments (treatments 1 and 2) decreased in mussel coverage (77 ± 3% *SE*) more than the high mussel density treatments ($F_{2,11}$ = 12.26, p = 0.002, treatments 3, 4 and 5), regardless of whether or not they were placed between fences ($F_{1,11}$ = 1.72, p = 0.216). On the 13 September, 3 weeks after the start of the experiment, there was a storm with average hourly wind speeds of up to 17 m/s (Appendix A). Following this storm only the treatment with a high mussel density between fences 10 m apart (treatment 4) had a significantly higher mussel coverage than the low mussel density treatment without fences (Tukey: treatment 1–4 p = 0.039). This difference was visible until the ninth week, after that no significant differences between treatments were observed.

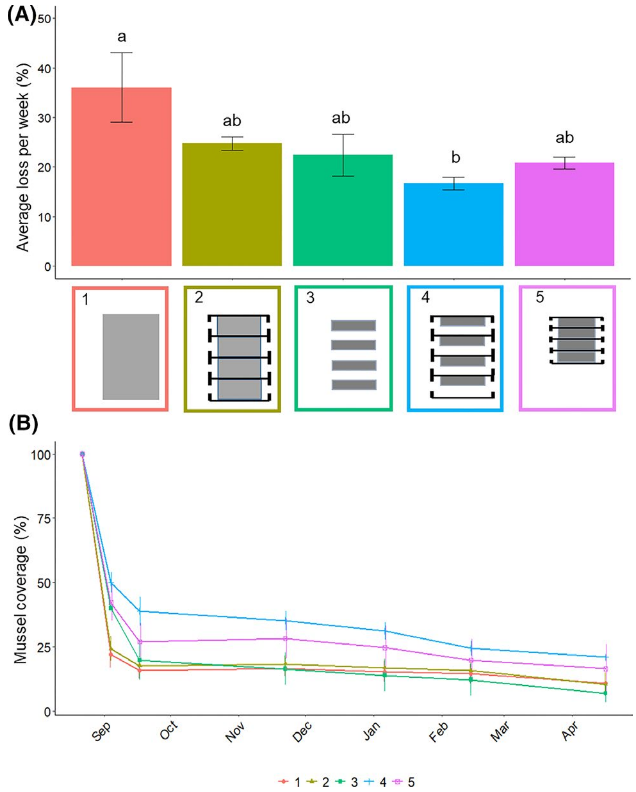

FIGURE 3 (A) Average loss of mussels per week for each mussel treatment, schematically drawn underneath the *x*-axis, letters above denote significance. (B) Mussel coverage over time. Data are means ± *SE* (*n* = 3)

3.2 | Effect of fences and transplantation density on mussel distribution and density

The fences successfully acted as barriers, trapping wave-dislodged mussels, resulting in banding patterns of mussels (Figure 4A). Mussel

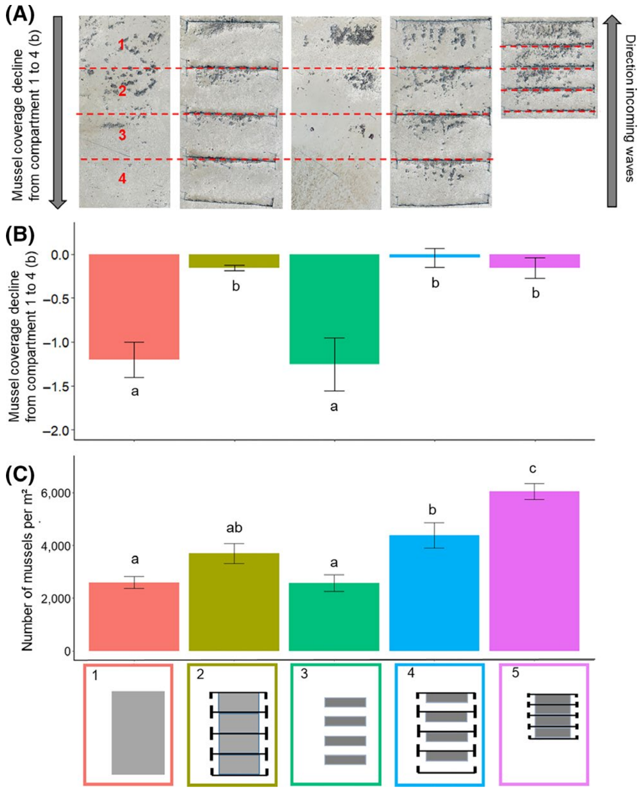

FIGURE 4 (A) Top view photos of the mussel plots in February (2017). Red dotted lines separate the compartments (1, 2, 3, 4) for which the mussel coverage was calculated, and in which three core samples (10 cm) were taken at the end of the experiment to determine mussel densities. (B) The slope (*b*), which is the decline in mussel coverage (log(*y*)) from compartment 1 to compartment 4 (*x*) for every plot ($\log(y) = a + bx$). Data are means ± SE ($n = 18$). (C) Number of mussels per m^2 within mussel patches. Data are means ± *SE* ($n = 3$), letter on top denote significance

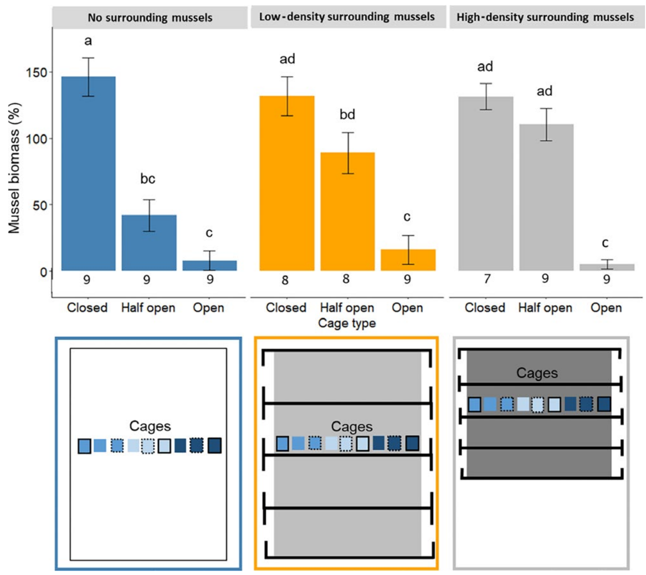

FIGURE 5 The percentage of mussel biomass remaining in: *closed* cages (protected against predatory crabs and washing out by waves); *half-open* cages (protected against washing out but not against predatory crabs); *open* (not protected against predation or against washing out). Cages were placed in plots with no surrounding mussels (blue), in low-density mussel plots (yellow) or in high-density mussel plots (grey). Cages with different densities were grouped together as density had no significant effect on the number of surviving mussels. Data are means ± *SE*. Letter on top of bar denote significance and numbers underneath the sample size

coverage was highest at the most wave-exposed areas in front of the plots when seeded between fences. Mussels transplanted into plots without any fences were either washed away or to the back of the plots. Mussel coverage therefore declined more strongly from the back of the mussel plot (less wave-exposed area, Figure 4A, compartment 1) to the front of the plot (most wave-exposed area, Figure 4A, compartment 4) when no fences were placed ($F_{4,10} = 4.30$, $p = 0.028$) than when mussels were placed between fences (Figure 4B). In treatment 2, 4 and 5 mussel densities were significantly higher in front of a fence than in the middle of mussel patches in plots without any fences (Figure 4C, GLM, $p < 0.001$, corrected for an overdispersion of: 1,090). Mussel density was highest in front of fences in treatment 5, than in all other treatments (Tukey 1, 2, 3–5 $p < 0.001$, 4 – 5 $p = 0.025$).

3.3 | Effect of safety in numbers on mussel losses: Predation versus wave dislodgement

The presence of a cage, offering protection against either hydrodynamic stress, predation, or both (cage type: half open or closed) had a significant effect on the survival of the mussels ($F_{2,66} = 94{,}18$, $p < 0.001$, Figure 5). Mussel survival was lowest in the completely open cages (7 ± 2% *SE*, Tukey $p < 0.001$), followed by mussels in half-open cages (36 ± 4% *SE*, Tukey $p < 0.001$) and highest is the completely closed cages (68 ± 4% *SE*, Tukey $p < 0.001$). The density in which the mussels were transplanted inside the cages had no significant effect on mussel survival ($F_{2,66} = 2.51$, $p = 0.09$), neither did the mussel density surrounding the cages ($F_{2,66} = 2$, $p = 0.14$). However, there was a significant interaction between cage type and the mussel density surrounding the cages ($F_{4,85} = 4.47$, $p < 0.001$). Mussel survival in half-open cages, (protection from hydrodynamic stress but not predatory crabs), was significantly higher when placed in plots with mussels transplanted in high density (4.2 kg/m^2) than in half-open cages placed in plots with no surrounding mussels (Tukey $p = 0.001$), indicating that there was a safety in numbers effect.

4 | DISCUSSION

The success of transplantation of organisms that depend on self-facilitating feedbacks in order to overcome environmental stress, is often limited by low survival when transplanted in low densities (e.g. seagrass: Meehan & West, 2002; Orth et al., 2006, mangroves: Kamali & Hashim, 2011; mussels: de Paoli et al., 2015). Restoration techniques therefore require improvement to increase transplantation success. The results of the large-scale mussel transplantation experiment presented here showed that artificially lowering mussel loss rates by using fences as engineered mussel traps, helps to increase transplantation success. The fences successfully trapped wave-dislodged mussels, resulting in higher local mussel densities in a banding pattern. The small-scale cage experiment also showed that higher surrounding mussel densities create a safety in numbers effect against predation, where increased mussel densities improved survival/persistence. Mussels protected in cages against wave forces, but not against predatory crabs had a higher chance of survival when surrounded by a larger group of conspecifics. Our approach of using engineering measures to give transplanted organisms a window of opportunity to establish could inspire methods to enable restoration of other ecosystem engineers, and their corresponding ecosystem services on a large scale at highly dynamic wave-exposed locations.

4.1 | Importance of self-facilitating interactions in restoration efforts

The restoration of coastal ecosystems is increasingly advocated as an important strategy to halt and counteract the increasing erosion along coastlines world-wide (Gedan, Kirwan, Wolanski, Barbier, & Silliman, 2011; Lai, Loke, Hilton, Bouma, & Todd, 2015). This means that the restoration of ecosystem engineers that trap sediment and attenuate wave energy, such as wetland vegetation and reef-building organisms, is most important on highly dynamic wave-exposed and eroding foreshores (Möller et al., 2014; Salvador de Paiva et al., 2018). Coastal wetland restoration generally focusses on reducing physical stressors such as wave energy, and avoiding competition between organisms, while the importance of self-facilitating interactions is often overlooked (Renzi et al., 2019). Engineering measures that ameliorate environmental stress, and at the same time promote self-facilitation, can be especially helpful in highly dynamic areas. However, engineering measures should be adapted to overcome the specific bottlenecks that hamper establishment of the target species. For example, breakwaters that attenuate wave energy and stimulate sedimentation have shown to improve mangrove restoration (Van Cuong, Brown, To, & Hockings, 2015), while the provision of an attachment substrate can be beneficial for the establishment of mussels (Capelle et al., 2019). To determine how engineering can be used in restoration efforts, it is of utmost importance to understand the mechanisms behind pattern formation, and the role of positive interactions in determining the resilience of different natural systems.

4.2 | Using engineering measures to harness self-facilitation

Recent studies demonstrate that harnessing beneficial intraspecific interactions by applying transplantation designs that more closely follow the natural patchiness of the target organisms can increase restoration efforts (Renzi et al., 2019; Silliman et al., 2015; Valdez et al., 2020). However, the manual placement of individuals in these kinds of patterns by hand can be very labour intensive and is therefore not a practical or cost-efficient method for large-scale restoration. Fences similar to those applied in current experiment have been used previously in mussel projects to estimate the abundance of mussel clump dispersal (Reusch & Chapman, 1997) or to protect transplanted mussels against predatory crabs (Schotanus, Capelle, et al., 2020). Just as in our experiment, the fences successfully trapped dislodged mussels. Nevertheless, to our knowledge, these kinds of engineering measures have never been explicitly deployed with the intention of stimulating the formation of natural patterning in order to increase restoration success. Our results demonstrate that engineering measures that harness self-facilitation are a useful restoration tool in areas where environmental stressors are extremely high. Organisms can resist mechanical forces by grouping together and organizing themselves into distinct patterns. These patterns protect against wave action and stimulate sedimentation (Rietkerk & van de Koppel, 2008). Newly transplanted organisms still need to establish these kinds of patterns and self-facilitating feedbacks, and are therefore especially vulnerable. This is evident even in Dutch commercial mussel farming where in the first month, average mussel losses on intertidal, on-bottom sites are around 69% (Capelle, Wijsman, Van Stralen, Herman, & Smaal, 2016). In our experiment, mussel coverage declined by an average of 65% in the first month in the best performing treatment (treatment 4, with fences seeded in a high density), even though these plots were situated at a much more wave-exposed and eroding mudflat (Capelle, 2017). After the first month, the average mussel loss declined and the mussels seemed to have established successfully. However, overall losses were still high, and significant differences were small and only found between two treatments. This highlights a potential need for optimizing the restoration design with respect to spacing of fences and density of initial sowing.

The cage experiment showed that a safety in numbers effect can arise in plots with a high mussel density. Mussel survival in cages accessible to predatory crabs was significantly higher when cages were placed in plots with a high mussel density compared with that inside similar cages placed in plots without any surrounding mussels. In other words, a high mussel density diluted the predation pressure (Bednekoff & Lima, 1998; Mauck & Harkless, 2001; Ray & Stoner, 1994). These results emphasize once again the importance of scale in restoration efforts (Bertness & Leonard, 1997). Mussel bed restoration efforts executed at too small a scale in systems where there is high predation pressure on mussels are likely to fail due to predation. This is also recognized by commercial mussel growers, who aim to seed as many mussels as possible in a single plot. However, increasing local densities are only advantageous until a certain threshold is reached; beyond that threshold competition between individuals becomes too high (Capelle et al., 2016). Density is a key driver of self-organization leading to locally optimal densities and facilitation of the growth and survival of conspecifics (de Jager, Weissing, & van de Koppel, 2017). Thus, an in-depth understanding of both what an optimal density is and how engineering measurements affect local densities, is necessary to provide a useful basis for designing future mussel restoration efforts.

4.3 | Implementation

Many intertidal coastal ecosystems that provide valuable services such as coastal protection, enhanced biodiversity and water quality have become greatly degraded (Barbier & Hacker, 2011). In terms of using ecosystems for coastal protection, restoration can be particularly challenging as these foreshores are often subjected to high hydrodynamic stress and erosion, resulting in higher establishment thresholds (Bouma et al., 2014; Temmerman et al., 2013). In temperate areas, biogenic reefs, as formed by mussels and oysters, stabilize sediment, attenuate wave energy (Donker, van der Vegt, & Hoekstra, 2013; Salvador de Paiva et al., 2018; Walles et al., 2015), and can grow at the pace of sea level rise (van Leeuwen et al., 2010; Walles et al., 2015). This may make them a sustainable and cost-effective addition in coastal defense schemes (Borsje et al., 2011; Bouma et al., 2014; Temmerman et al., 2013). To our knowledge, the current restoration project is the first large-scale effort in which engineering measures were used not only to lower environmental stressors, but also simultaneously stimulate self-facilitating feedback processes, with the goal to increase restoration success in extremely stressful environments. The restoration method we have tested to restore intertidal mussel beds on wave-exposed and eroding foreshores appears promising. This may inspire the development of similar approaches for cost-effective and practical design for large-scale restorations of ecosystem engineering species.

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AUTHORS' CONTRIBUTIONS

J.S., B.W., J.J.C., T.J.B. and J.v.d.K. conceived and designed the research; J.S. and B.W. performed the experiments; J.S. and J.v.B. analysed the data. All authors wrote and edited the manuscript.

DATA AVAILABILITY STATEMENT

Data available from the 4TU database: https://doi.org/10.4121/uuid:04b25e70-ca3e-489f-9510-36385c1a4104 (Schotanus, Walles, et al., 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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