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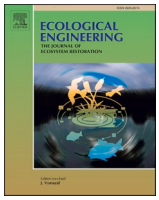

Increasing mussel transplantation success by initiating self-facilitating feedback mechanisms

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ABSTRACT

Transplantation success of ecosystem-engineering species can be low in dynamic environments, as such ecosystem-engineers often require density-dependent positive feedback mechanisms to overcome environmental stressors. These self-facilitating feedback mechanisms play an important role in self-organization, whereby complex systems tend to organize and create patterns in order to ameliorating physical and/or biological stressors. In this study we used biodegradable structures to ameliorate self-facilitating feedback mechanisms to overcome environmental stressors in the initial post-transplantation phase. The biodegradable structures tested are an innovation of the traditional Seed Mussel Collectors (SMCs) used in mussel cultivation. The so-called "BioShell-SMC" does not contain any plastic, but is made up of a coconut fiber rope surrounded by empty cockle shells and held together by a biodegradable net based on a compound of aliphatic polyesters. We tested if the survival of two size classes of blue mussel (*Mytilus edulis*) transplants, on a tidal flat in the Oosterschelde estuary in the Netherlands, increased when mussel seed was transplanted attached to the BioShell-SMCs instead of single mussels in combination with empty cockle shells. The results of this study revealed that the survival of larger mussel seed significantly improved when attached to the BioShell-SMC compared to those transplanted loosely. Factors contributing to the difference in mussel loss between BioShell-SMC mussels and loosely transplanted mussels include predation, competition and dislodgement due to hydrodynamic forces. For small mussel seed, mussel biomass decreased strongly in the first three days of the experiment, irrespective of transplantation method. This is due the small size of the mussels in combination with low mussel densities. Overall, this study highlights the potential of using biodegradable structures to initiate self-facilitating feedback mechanisms in establishment of ecosystem engineers in dynamic environments.

1. Introduction

Restoration of coastal ecosystems by transplantation of habitat-forming ecosystem-engineering species has become a key conservation tool to counteract coastal degradation (Byers et al., 2006). In recent years, incorporating ecological processes into restoration efforts such as harnessing of self-facilitation between transplants is increasingly recognized as a fundamental component of successful restoration (Ladd et al., 2018; Renzi et al., 2019; Silliman et al., 2015). Several studies have demonstrated that restoration success can be enhanced by using clumped individuals rather than spacing individuals out, or by stimulating the formation of natural aggregations (Fivash et al., 2022; Schotanus et al., 2020a; Shaver and Silliman, 2017; Silliman et al., 2015; Suykerbuyk et al., 2016). For example, salt-marsh grasses planted in clumps benefited each other by alleviating physical stressors such as anoxia and erosion that improved transplantation success (Silliman et al., 2015). Furthermore, by stimulating the formation of large-scale aggregation in transplanted mussels, the survival of a restored mussel bed increased (Schotanus et al., 2020a). All these restoration efforts were however still at an experimental scale. Integration of positive interactions on a large restoration scale as needed to have landscape-scale impact is still a challenge. Innovations are thus needed to improve the

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likelihood of truly large-scale restoration success, to decrease the numbers of transplants required for long-term restoration and to reduce the application costs (Temmink et al., 2020).

To learn about how to upscale restoration, we may look at how patterns form in natural landscapes. Self-organized spatial patterns as observed in a wide range of ecosystems (Rietkerk and Van de Koppel, 2008), including arid systems, peatlands, forests, mussel beds and diatom mats (Liu et al., 2020; van de Koppel et al., 2005; Weerman et al., 2010), typically result from positive intraspecific interactions at the local scale combined with negative intraspecific interactions at a larger scale. These local-scale self-facilitating interactions typically occur when a certain patch density and/or size threshold is surpassed (Bouma et al., 2009) following a window of opportunity, i.e. a sufficiently long period of calm conditions in which individual organisms can settle without being in a patch (Balke et al., 2011, 2014). Thus, establishment success of transplanted organisms in the absence of a natural window of opportunity may be increased, if a critical density threshold can immediately be surpassed in order to induce short-range facilitation. The latter may involve transplanting organisms in a way that mimics regular patterns, thereby induce local-scale self-facilitating while minimizing large-scale negative interactions (Rietkerk and Van de Koppel, 2008). Large-scale transplantations of individuals in regular patterns that mimic natural-patterned ecosystems can however be extremely time-consuming and costly. Hence, we propose to use innovative engineering measures that facilitate self-organization to increase transplantation success, using mussels as model system.

Mussel beds on soft sediment are an example of an ecosystem with a distinctive spatial patterning (van de Koppel et al., 2005). The patterning consists of high-density mussel clusters alternating with bare sediment patches and is thought to be the result of an interplay of facilitation and competition between mussels at different spatial scales (Liu et al., 2014; van de Koppel et al., 2005). Aggregation in clusters facilitates protection against predators and increases resistance to erosion by waves and currents. However, if clusters become too large, it also increases competition for food and space, impeding the growth and condition of the mussel (Commito et al., 2014; van de Koppel et al., 2005). For example, mussels in the middle of a mussel patch tend to be smaller than mussels on the outside of a mussel patch (Svane and Ompi, 1993). Transplantations of juvenile blue mussels (*Mytilus edulis*) on bare sediment have been carried out as an attempt to restore natural mussel beds (de Paoli et al., 2015; Schotanus et al., 2020a), but is much more common to cultivate mussels for consumption (Capelle et al., 2014). In both cases, the mussel bed restorer and the mussel farmer, face the same problem: juvenile mussels (mussel seed) are vulnerable from environmental stressors, such as hydrodynamic forces and/or predation, and losses in the first month after transplantation are high (Capelle et al., 2016a; Schotanus et al., 2020b). The newly transplanted mussels need sufficient time to establish self-facilitating interactions in order to increase the resilience of the mussel bed (Liu et al., 2014). Here we propose to use biodegradable structures, to initiate local-scale self-facilitating feedback mechanisms to overcome these environmental stressors in the initial post-transplantation phase, which will ultimately enhance the survival and growth of transplanted mussel seed. By spacing-out these biodegradable structures, we can avoid the long-distance negative effects resulting from competition.

The biodegradable structures tested are an innovation of the traditional Seed Mussel Collectors (SMCs) used in mussel cultivation (van den Bogaart et al., 2023). Normally, these SMCs consist of frayed nylon ropes suspended in the water column on which mussel larvae settle. When the mussel seed is large enough (2–3 cm), they are harvested from the ropes and transplanted to culture plots to grow to commercial size (Kamermans et al., 2002). The innovative SMCs, or so-called "BioShell-SMCs", do not contain any plastics, but comprise of a coconut fiber rope surrounded by empty cockle shells held together by a biodegradable net based on a compound of aliphatic polyesters (Fig. 2). Empty shells have shown to be an excellent attachment substrate for mussel larvae (wa Kangeri et al., 2014). Results of a first comparative field study showed that the mussel seed yield of the BioShell-SMCs was comparable to that of the traditional nylon SMCs at most locations (van den Bogaart et al., 2023). One potential advantage of using BioShell-SMCs is that the mussel seed does not have to be removed from the SMCs before transplantation to a cultivation or restoration site, as is the case for the traditional nylon SMCs. That is, mussels can be transplanted attached to the BioShell-SMC, in high-density clusters, which may provide protection from predators, such as crabs and sea stars, and may increase resistance to dislodgement by hydrodynamics. In addition, when the starch nets gradually dissolve (aimed to happen within a year), the cockle shells within will slowly disperse, which may provide an attachment substrate for mussels to spread further away from the BioShell-SMC, escaping competition for food and space and increase resilience to environmental disturbances (Capelle et al., 2019).

To test if innovative engineering measures that facilitate self-organization can increase transplantation success, we carried out three experiments using mussels as model system: i) a *field transplantation experiment* in the Dutch Oosterschelde estuary, ii) an *anti-predation cage field experiment* also in the Dutch Oosterschelde estuary, and iii) a *mesocosm experiment* in the lab. In the *field transplantation experiment*, we tested the hypothesis that the survival of mussel transplants increases when mussel seed is transplanted attached to the BioShell-SMCs, by providing a self-facilitating feedback mechanisms that help overcome environmental stress during the initial transplantation phase. In contrast, we expect that single mussels in combination with empty cockle shells do not have such self-facilitating feedback mechanisms, as we expect the empty shells do not provide a stable substrate for mussel-seed attachment but are prone to dislodgement. In addition to monitoring the biomass development of mussels attached to the BioShell-SMCs and mussels loose-seeded with shells, we also tested the intermediate treatment: the effect of cutting open the starch net on the development of the mussel biomass. We expect that the spilled-out cockle shells may provide a window of opportunity for mussels to escape competition after the initial transplantation phase, when a more stable environment is established. A complementary *anti-predation cage field experiment* was carried out within the field experiment to test the hypothesis that the growth of mussels in the cages will be lower when transplanted attached to a substrate in high-density clusters than loose transplanted mussels or mussels attached to cut-open nets due to greater competition for space and food, when the cages prevent thinning by predators and washing away by waves. Finally, a *mesocosm experiment* was carried out to test whether crabs or sea stars have a preference for foraging on loose mussels or mussels attached to substrate, in this case the biodegradable SMC. Since constrains such as the chance of predation or dislodgement are greater for smaller mussels while competition becomes more restrictive as the mussel grows larger, all experiments were carried out twice: once with small mussel seed in July and once with larger mussel seed in August.

2. Materials and method

2.1. Field experiments: Transplantation and anti-predation cages

2.1.1. Study site

The field experiment was conducted on an intertidal commercial mussel plot (51°33′26.6"N 3°53′55.0″E), located at the Oosterschelde, the Netherlands (Fig. 1). The sheltered study area is characterized by sandy sediments and the dominant water flow direction is from the southwest. The experimental plots only emerged from the water during extreme low tides, which occurred approximately 3 times throughout the experiment. For this experiment, 150 m of the BioShell-SMC was deployed at a widely used SMC location in the Nearshore North Sea, (51°46′22.0"N 3°48′10.4″E). The BioShell-SMCs were placed in the water column in April 2020 and the first mussel larvae settled at the end of May 2020.

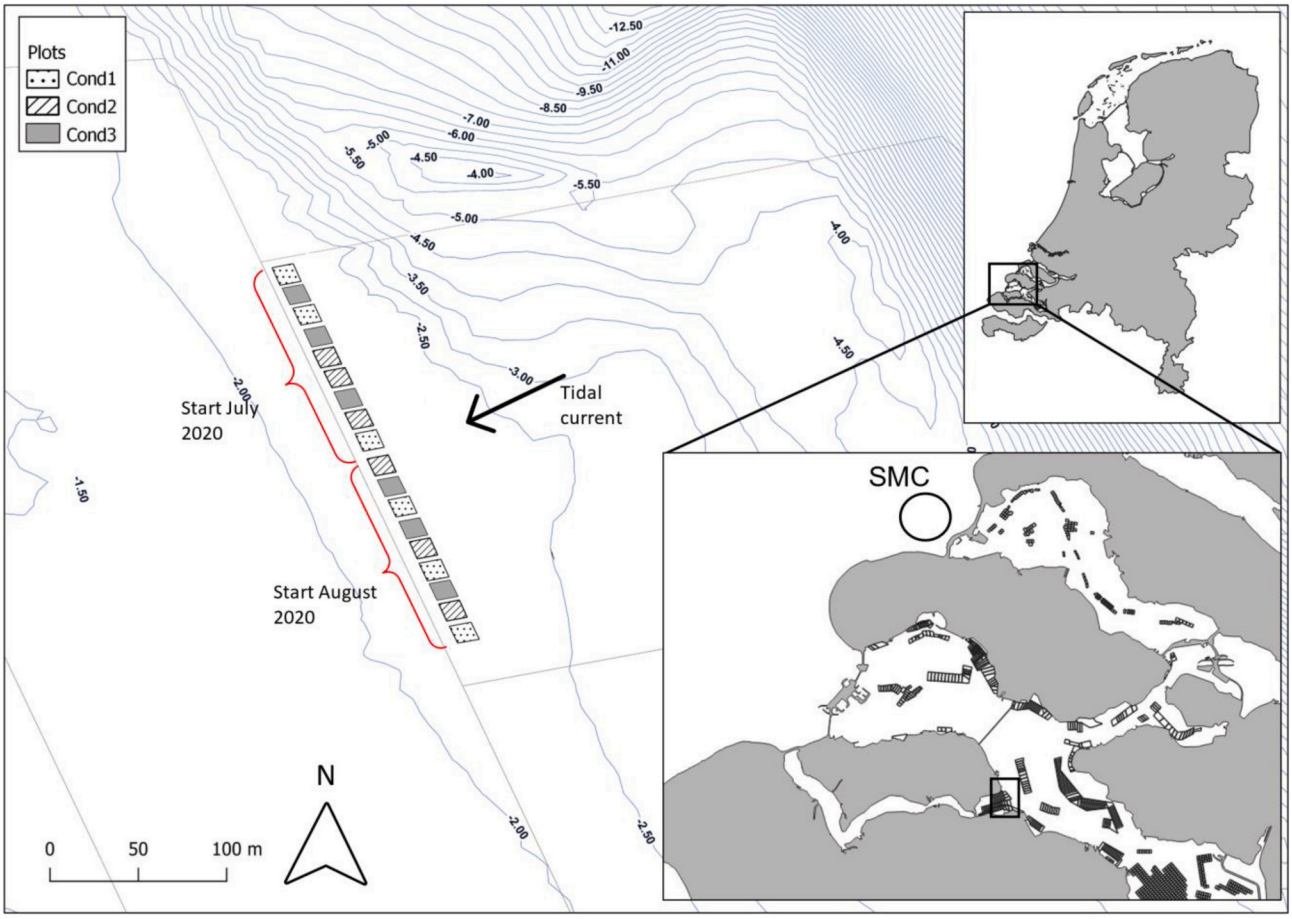

Fig. 1. Map of the study area. Land is shown in grey and water in white. Mussel culture plots are shown in grey on the overview maps and grey bordered in the close-up image. SMC: origin of the seed (Spat Mussel Collector, SMC). The three transplantation methods are each represented with a different patterned plot. Cond1 (dots): loose mussels and shells; Cond2 (dashed): cut-open net; Cond3 (grey): intact net. The plots measure each 6x6 m and are spaced 1 meter apart. There were three replicates of each treatment. The experiment was conducted twice. The first round trial started in July 2020 and the second round trial in August 2020.

2.1.2. Setup of the field transplantation experiment

Mussels were transplanted in three configurations; (1) *Loose mussels and shells;* the biodegradable net was cut open, the coconut fiber rope and biodegradable net were completely removed and only the mussels and cockle shells were placed on the plots, (2) *Cut-open net;* the biodegradable net was cut open to make sure that the shells and mussels were able to disperse, (3) *Intact net*; the BioShell-SMC was kept intact completely (Fig. 2). Each treatment comprised three replicates. Mussels were transplanted in plots (6 × 6 m), with randomly assigned treatments. Metal fences covered with chicken wire were placed around each plot to enclose them and prevent mussels from being washed out. The experimental plots were placed in a row to ensure that they were located at approximately the same depth and faced the prevailing current direction (southwest). To ensure an empty buffer zone between two plots, the mussels were placed in squares of 3 × 3 m within each plot. Each plot contained mussel seed from approx. 9 m of SMC. In treatment 1 the loose mussels and cockle shells were spread homogenously over the plot. In treatments 2 (cut-open net) and 3 (intact net) the SMC-rope was transplanted to the experimental plots in one long line (9 m) and placed down as homogeneously as possible over the plot.

Mussel farmers normally harvest the mussel seed from the SMCs and transport them to commercial mussel plots when they are around 2–3 cm (Capelle, 2017). To examine how mussel size influences mussel survival and growth, the experiment was conducted twice: the first trial (9 plots) started at the 14th of July 2020 and the second trial (9 plots) at the 31th of August 2020. Thus, after August 31, the experiment consisted of 18 experimental plots. The initial average mussel length and condition are summarized in Table 1. The condition index (CI) was calculated by dividing the ash-free dry weight (AFDW) by the cubed length of each mussel, resulting in units of mg cm^{-3} (Beukema and De Bruin, 1977). Additionally, the average biomass and density of transplanted mussels in July and August are also provided.

2.1.3. Setup of the anti-predation cages experiment

To gain a better understanding of the mussel losses caused by predation and hydrodynamic dislodgement and the interplay with intraspecific competition, a cage that excluded predators (anti-predation cage) was placed in each plot. The cages measured 40 × 20 × 25 cm and were covered with chicken mesh with a mesh size of 1 cm. Moreover, they were equipped with a removable lid that was also covered with chicken mesh, allowing for easy picture capture during the experiment. The lid was secured to the cage using tie wraps. The cages contained mussels of two pieces of SMC of approximately 12 cm. The mussels were placed in the cages in the same configuration as the plot in which they were placed, thus (1) only mussels and shells, (2) cut open SMC, or (3) intact BioShell-SMC.

2.1.4. Monitoring of the transplantation experiment

Initial measurements - The mussels harvested for the first trial of experiments in July were by nature homogeneously distributed across the SMC-rope. Therefore, the initial mussel density and biomass were comparable for each plot. To estimate the initial mussel density and biomass in a plot, 4 subsamples of 10 cm SMC-rope were taken to the lab. The number of mussels were counted and weighed and the length of

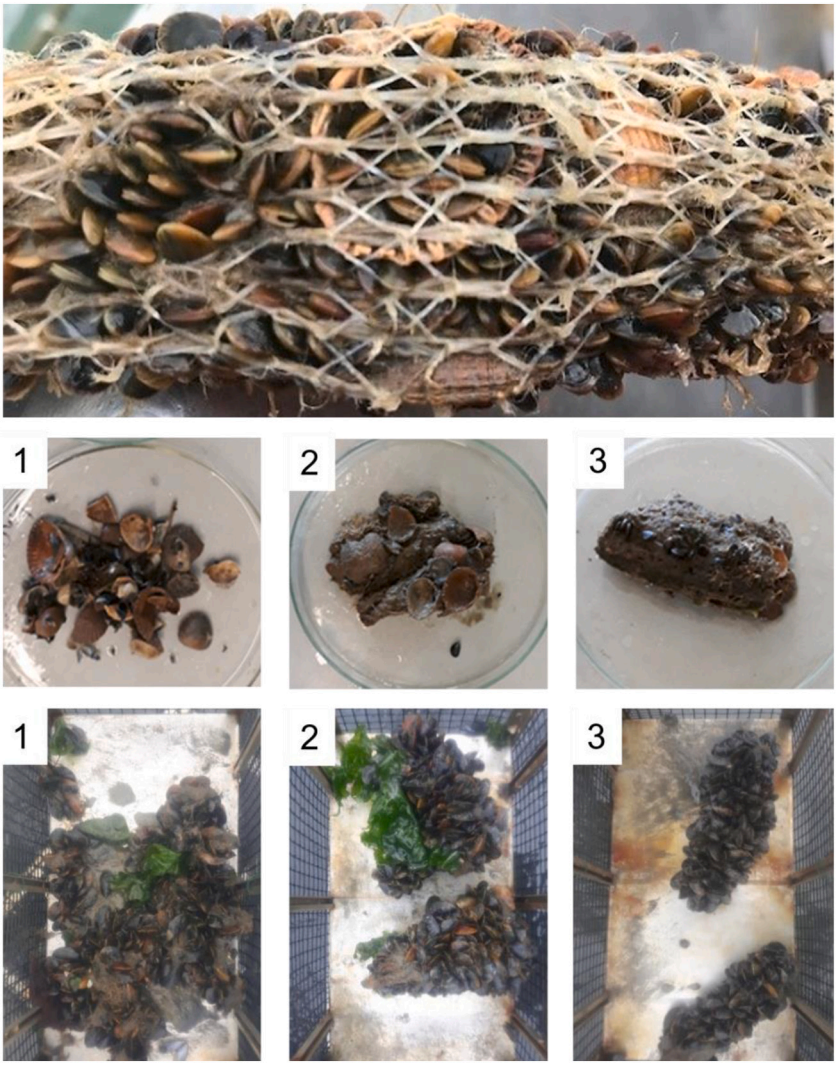

Fig. 2. A. Biodegradable SMC ("BioShell-SMC"), which consists of a coconut core surrounded by empty cockle shells that are held in place by a biodegradable sock. Mussel seed has settled on the cockle shells. **B/C.** Three configurations of mussel transplantation methods: (1) loose mussels and shells; the biodegradable net was cut open, the coconut fiber rope and biodegradable net were removed and only the mussels and cockle shells were transplanted, (2) Cut-open net; the biodegradable net was cut open to make sure that the shells and mussels were able to disperse, (3) Intact net; the SMC was kept intact completely. **C.** The three configurations in the anti-predation cages field experiment

Table 1
The initial average mussel length and condition and the average transplanted biomass and density of mussels harvested in July and August.

Start experiment	Shell length (cm ± SE)	Condition index (mg cm^{-3} ± SE)	Biomass (kg m^{-2} ± SE)	Density (nr m^{-2} ± SE)
July 14, 2020	1.24 ± 0.04 (n = 107)	6.4 ± 0.14 (n = 107)	2.3 ± 0.1 (n = 5)	12,481 ± 698 (n = 5)
August 31, 2020	2.46 ± 0.06 (n = 89)	9.5 ± 0.22 (n = 89)	2.6 ± 0.3 (n = 9)	2867 ± 379 (n = 9)

rope and amount of cockle shells were determined to estimate the average weight and number of mussels per 1 m SMC. The mussels harvested in August were already letting loose from the SMC as a result of the unexpected premature dissolution of the biodegradable net. The mussel seed was heterogeneously distributed along the rope, with alternately bare patches and very high-density mussel clumps. In order to estimate the initial mussel density and biomass for the plots started in August, top-view pictures were taken of all 9 m rope and the total rope was divided in 5 rope cross-section thickness classes, which included both the SMC and the mussels. The smallest rope thickness cross-section was 0 to 3 cm, which meant that the SMC was not baring any mussels. The thickest cross-section class contained all the ropes that were thicker than 12 cm, meaning that there was a very thick layer of mussels attached to the SMC. To determine the average mussel density per cross-section thickness class, three subsamples of 10 cm for every rope thickness cross-section class (0–3, 3–6, 6–9, 9–12, >12 cm) were taken to the lab and the mussels were counted and weighted. The mussel number and weight for every thickness class was summed and the total initial density per plot was calculated.

Long-term measurements - Mussel density and biomass development inside the plots were monitored for a period of almost 10 months for the larger mussels; from August 16, 2020 until May 5, 2021. The monitoring of the plots with the small mussels (starting in July) was carried out for 1 month because mussel survival was nearly 0 in all experimental plots by August 10th. For the larger mussels (starting August), the experimental plots were monitored weekly during 4 weeks after transplantation, whereafter the monitoring frequency decreased to monthly. To estimate the biomass of mussels for every monitoring time, top-view pictures and samples (approx. 10 cm in length) were taken while snorkeling over the 18 mussel plots and the 1-m buffer-zone around the plots. Monitoring could only take place when visibility was good enough to distinguish the mussels.

The analysis of the pictures and samples followed the same methodology as the initial measurements. However, in addition to that, the samples were categorized into three groups, namely: mussels attached to the rope, mussels aggregated into patches and mussels washed against the fences. Of every category, three random samples per plot were taken. In case of the mussels attached to the rope, the mussel density and biomass were estimated using the same method as with the

determination of the initial mussel density per m rope in August. Thus, the average mussel biomass per rope thickness cross-section class (0–3, 3–6, 6–9, 9–12, >12 cm) was determined by analyzing three samples of approx. 10 cm in length. For the mussels aggregated into patches or washed against the fences, similar top-view pictures were taken while holding a ruler next to the patch. The patch area was then determined using the software program ImageJ. After taking pictures, three samples of whole mussel patches and patches washed against the fence were taken to the lab and the mussels were counted and weighed. These values were then correlated to the total mussel patch area to estimate the overall mussel biomass detached from the ropes. By adding up the estimated mussel biomass of the detached and the attached mussels, the overall mussel biomass inside a plot was determined.

2.1.5. Monitoring of the anti-predation cages experiment

Mussel growth and biomass development inside anti-predation cages were monitored from July 17, 2020 until May 5, 2021. At the end of the experiment, on May 5, 2021, all mussels were taken out of the anti-predation cages. Per cage the mussels were counted and weighted. One of the cages placed in July was excluded from the experiment because a hole in the chicken mesh made it possible for crabs to enter. From every cage a subsample of 30 mussels was taken and the shell length was determined. Some of the mussels that were initially attached to the SMC had dispersed from the rope to another location inside the cage. To ensure that there were no differences in growth between the mussels that had dispersed from the rope and the mussels that stayed inside the mussel clump, we subsampled 15 mussels of each condition, resulting in 30 mussels per cage total.

2.2. Mesocosm experiment

2.2.1. Setup of the food preference experiment

To investigate whether there is a difference in predation rates by crabs and starfish on different mussel seed sizes and various transplantation configurations, two food preference experiments were carried out in mesocosms; one for the mussel seed harvested in July (~1.24 cm, Table 1) and one for the mussel seed harvested in August (~2.46 cm, Table 1). These mussels seeds originated from the same location as the ones used in the field experiment. The experiment in July took place between July 27, 2020 and August 19, 2020 and the experiment with mussels harvested from August took place between August 23, 2020 and October 5, 2020. In the middle of a 1 × 1 × 1 m tank, filled with 900 L unfiltered Oosterschelde seawater, four configurations of mussels were placed on a 10 cm thick layer of sand collected in the Oosterschelde. For each mussels configuration a 10 cm piece of SMC, that was 100% covered with mussels, was cut-off. Configurations corresponded largely with the mussel transplantation methods used in the field experiment, namely: (1a) the biodegradable net the coconut fiber rope and cockle shells were removed, only the mussels were placed in the tank, (1b) like 1a, but now the mussels plus cockle shells were placed in the tank, (2) the biodegradable net was cut open to make sure that the shells and mussels were able to spill out, (3) the BioShell-SMC was kept intact completely. The configurations of mussels were then placed in a square 30 cm apart in the middle of the tank. In each tank two crabs with an average carapax width of 4.8 cm ± 0.37 sd ($n = 8$) or four sea stars with an average wet weight of 65 g ± 14.1 sd ($n = 9$) were kept. When a crab or sea star died during the experiment, it was replaced with a new one. Each of these treatments was carried out in triplicate, resulting in 6 experimental units. Each tank was aerated. In addition, the water in all tanks circulated with an inflow and outflow port connected to an additional water tank, providing a steady circulation flow rate of 6 L h^{-1} $tank^{-1}$. Mussels were fed weekly with instant algae with a concentration of 2 billion cells per ml (shellfish diet 1800/Reed Mariculture Inc.). The tanks were cleaned and refilled with unfiltered Oosterschelde seawater between the experiment taking place in July with small mussels and the experiment in August, with larger mussels.

2.2.2. Monitoring of the food preference experiment

To measure the effect of the predators on the survival of the mussels, the number of mussels in each food source (loose mussels, loose mussels and shells, open net, intact net) was determined at the beginning and at the end of the experiment and the percentage difference was recorded as the mortality rate. A trendline was used to determine the correlation between the total weight of a 10 cm piece of SMC and the number of mussels on this piece of SMC. This correlation was used to estimate the initial number of mussels on the cut open and intact net food sources.

Mortality rates have been corrected for the duration of the experiments, as the trial for the smaller mussels, harvested in July, lasted only 3 weeks, while the duration in August was 6 weeks.

2.3. Statistical analysis

All statistical analyses were carried out in R, 3.5.1 (R Core Team 2022). Prior to model fitting, all data were visually checked for normality (Q–Q plot) and homogeneity of residuals, following the procedure described in Zuur et al. (2010). If necessary, data were transformed to meet assumptions. Models were simplified according to Akaike's information criterion (AIC) scores and non-significant factors were removed.

2.3.1. Field experiment: Transplantation experiment

In order to compare the biomass loss rates between the three mussel transplantation methods (loose mussels and shells, cut open net, intact net) a survival analysis was carried out based on maximum likelihood (Miller, 1981) and comparable to the survival analysis carried out in Schotanus et al. (2020a). In short, the mean loss rate (ε) per transplantation method was estimated as the inverse of the mean life time of a mussel bed (τ) for the mussels transplanted in July and the mussels transplanted in August:

$\varepsilon = 1/\tau$.

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

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

Finally, a one-way ANOVA was carried out with loss rates (ε) as the response variable and the transplantation method as the explanatory variable (Loss rate ~ Transplantation method).

For both the mussels seeded in July and in August the difference between transplantation methods in average final mussel biomass inside the experimental plots (3 x 3 m) and outside the experimental plots, in the 1-m buffer zone, were analyzed with a one-way ANOVA, which resulted in the following models: Mussel biomass inside plot ~ Transplantation method and Mussel biomass outside plot ~ Transplantation method. The biomass data was square-root transformed to meet the assumptions for homogeneity of variance. Post-hoc Tukey tests were used to test for significant differences between treatments at specific timepoints (R-package emmeans, Lenth, 2016).

2.3.2. Field experiment: Anti-predation cages experiment

The effect of the starting month (July vs. August) and the transplantation method (loose mussels and shells vs. cut open net vs. intact net) on the average mussel biomass increase rate inside the anti-predation cages was analyzed with a two-way ANOVA (Mussel biomass increase rate ~ Transplantation method × starting month). In order to meet the assumptions, the biomass data was log-transformed prior to analysis. The effect of the transplantation method, starting month and location of the mussel (i.e. whether the mussels were located inside or outside the original mussel patch) on the average mussel length was analyzed with a linear mixed effect model, with the cage from which the mussels were sampled entered as random effect (Length ~

Transplantation method × starting month × Location + (1 | Cage). Pairwise comparisons were obtained by Tukey posthoc tests with the *contrast* and *lsmeans* functions from the lsmeans package (Lenth, 2016).

2.3.3. Mesocosm experiment: Food preference experiment

The mussel mortality per week (proportion of dead mussels per week over start number) in the mesocosm experiment was analyzed with a quasi-binomial generalized linear model (GLM), implemented with the glm function (family set to quasi-binomial). The size of the mussels (small mussels harvested in July vs. larger mussels harvested August), transplantation method (loose mussels and shells vs. cut open net vs. intact net), predator type (crabs vs. sea stars) and the interactions between these three factors were entered as explanatory variables. The best model based on AIC resulted in: Mussel mortality ~ Predator × Mussel size. The analysis evaluated 12 samples total (three replicates × two predator types × two mussel sizes = 12 samples). We used a post hoc comparison on the least-squares mean (lsmeans) with no adjustment.

3. Results

3.1. Biomass loss rate field transplantation experiment

3.1.1. Small mussels transplanted in July

For the small mussels seeded in July, there was no significant difference in mussel loss rate between treatments ($F_{2,6} = 2.47$, $p = .17$, Fig. 3A). Regardless of the transplantation method, mussel biomass decreased strongly (98% ± 0.8 SE) in all plots in the first three days after transplantation on the 14th of July 2020 (Fig. 3B). In addition, no mussels were found outside of the 3x3m plots, in the 1 m buffer zone, or against the fences surrounding the plots, indicating there was no hydrodynamic dislodgement. After 4 weeks, on August 10th, mussel survival was 0% in plots with the configuration *loose seeded mussels and shells (treatment #1)* and nearly 0% for mussels transplanted attached to *cut open biodegradable nets (treatment #2)* or to *BioShell-intact nets (treatment #3)*. Monitoring of these plots was therefore concluded.

3.1.2. Larger mussels transplanted in August

The overall loss rate of the larger mussels that were transplanted on the experimental plots in August was much lower in comparison with the mussels seeded in July. Besides, there were significant differences between transplantation methods ($F_{2,6} = 31.52$, $p < .001$, Fig. 3C). The biomass loss rate was significantly higher for the *loose seeded mussels and shells (treatment #1)* than for the mussels attached to *cut open nets (treatment #2)* ($p = .001$) or *BioShell-intact nets (treatment #3)* ($p < .001$).

After the first 4 weeks, in which the biomass decreased in all treatments, the mussel biomass stayed relatively stable over the remaining course of the experiment in the plots with mussels attached to *cut open* or *intact net* (Fig. 3D). At the end of the experiment, mussel biomass was significantly higher in plots with mussels attached to *cut-open net* ($p < .001$) and *intact net* ($p < .001$) compared to plots seeded with *loose mussels and shells (treatment #1)*. The final biomass between plots with mussels attached to *cut-open net (treatment #2)* and *BioShell-intact net (treatment #3)* did not significantly differ ($p = .092$).

Larger mussels seeded in August washed against the fences, which indicates hydrodynamic losses (Fig. 3E). This was especially true for the *loose seeded mussels with shells (treatment #1)*. On December 6th, 3 months after the start of the experiment, 100% of the initially seeded mussels from the *loose mussels and shells* treatment were washed out of

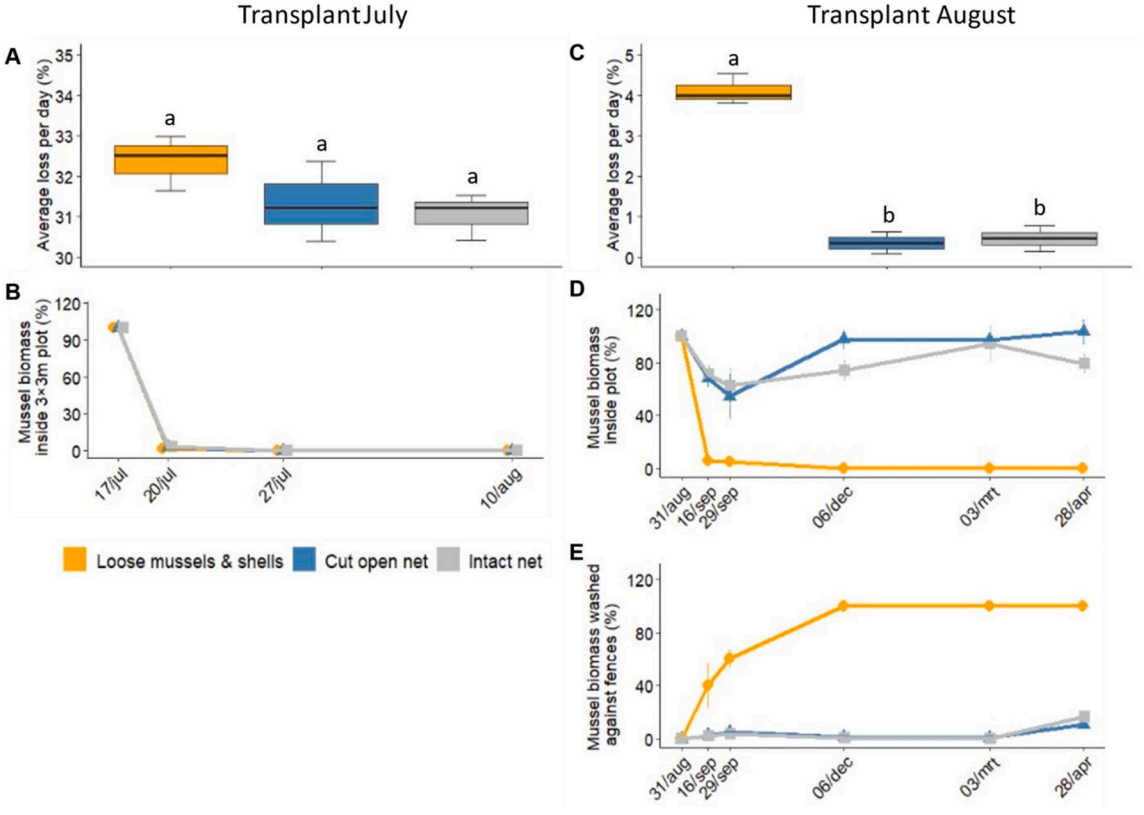

Fig. 3. A. Average loss rate of mussels per day (%), between start and final measurement (23 days), for mussels transplanted in July. B. Mussel biomass development over time (%) inside experimental plot (3x3m) for mussels transplanted in July in the configurations: loose mussels & cockle shells, cut open BioShell-SMCs net, or intact BioShell-SMCs net. C. Average loss rate of mussels per day (%) between start and final measurement (240 days) for mussels transplanted in August. D. Mussel biomass development over time (%) inside experimental plot (3x3m) for mussels transplanted in August. E. Mussel biomass development over time (%) outside experimental plot, within 1 m buffer zone, relative to initial mussel biomass inside experimental plot (3x3m) in August in the configurations: loose mussels & cockle shells, cut-open BioShell-SMCs net, or intact BioShell-SMCs net. Data are means ± SE ($n = 3$).

the experimental squares against the fences surrounding the plots, while almost none of the mussels washed out of the *cut-open net (treatment #2)* and *intact net (treatment #3)* plots. At the final sampling date, we found that there was a significant difference in mussels washed against the fences between the treatments *loose mussels and shells*, and *cut-open net* ($p < .001$) or *intact net* ($p < .001$) but no significant difference between *cut-open* and *BioShell-intact net*.

3.2. Mussel survival and growth inside anti-predation cages field experiment

Mussel survival was high in all cages, both for the small mussels transplanted in July and the larger mussels transplanted in August. There was a significant interaction between initial mussel size and treatment ($F_{2,11} = 6.01$, $p = .017$). Besides, overall biomass increase inside the cages was significantly affected by treatment ($F_{2,11} = 5.59$, $p = .021$). The difference in biomass increase was explained by the lower mussel biomass increase of small mussels transplanted in July on *BioShell-intact nets (treatment #3)* (Fig. 4), which was significantly lower in comparison with the biomass increase in July for *loose mussels & shells (treatment #1)* ($p = .028$), *cut open net (treatment #2)* ($p = .034$).

At the end of the experiment, the average mussel length was significantly lower in the cages with small mussels harvested in July than in the cages with larger mussels harvested in August ($F_{1,2} = 25.79$, $p < .001$). Mussel length did not significantly differ between mussels located inside a mussel clump or mussels that moved outside the mussel clump. Therefore, these data have been merged. There was no significant interaction between initial mussel size and transplantation method and the transplantation method had no significant effect on the final length of the mussels.

3.3. Mussel predation in mesocosm experiment

In the mesocosm experiment, transplantation method (loose mussels – treatment #1a; mussels with shells – treatment #1b; cut-open SMC – treatment #2; and intact SMC – treatment #3) had no significant effect on the survival rate of the mussels when exposed to crabs or sea stars ($F_{3,41} = 1.57$, $p > .05$). We found a significant interaction between predator type and initial mussel size ($F_{1,44} = 7.57$, $p = .006$). Survival of smaller mussels was significantly lower when exposed to crabs than to sea stars (Fig. 5).

4. Discussion

Transplantations of juvenile blue mussels (*Mytilus edulis*) are carried out as an attempt to restore natural mussel beds (de Paoli et al., 2017; Schotanus et al., 2020b) and to cultivate mussels for consumption (Capelle et al., 2014). However, the small size of the mussels and the lack of attachment substratum after transplant makes them highly vulnerable to predation and hydrodynamic dislodgement, leading to huge initial losses (Capelle et al., 2016b). Hence, there is need to improve transplantation success, to decrease the number of individuals needed and to decrease costs of large-scale transplantations. Therefore, we tested transplantation of mussels attached to the innovative biodegradable BioShell-SMC and evaluated the transplant success compared to loose seeded mussels. Our findings demonstrated that mussel seed survival in the field experiment was significantly higher when mussels were attached to the biodegradable BioShell-SMC than when they were transplanted without attachment. The cage experiment showed high mussel seed survival when predation and hydrodynamic dislodgement were excluded, and the mesocosm experiment revealed higher loss of small mussels compared to larger mussels due to predation by crabs. The higher loss of loosely transplanted mussels compared to BioShell-SMC-mussels are caused by a mix of factors such as dislodgement due to

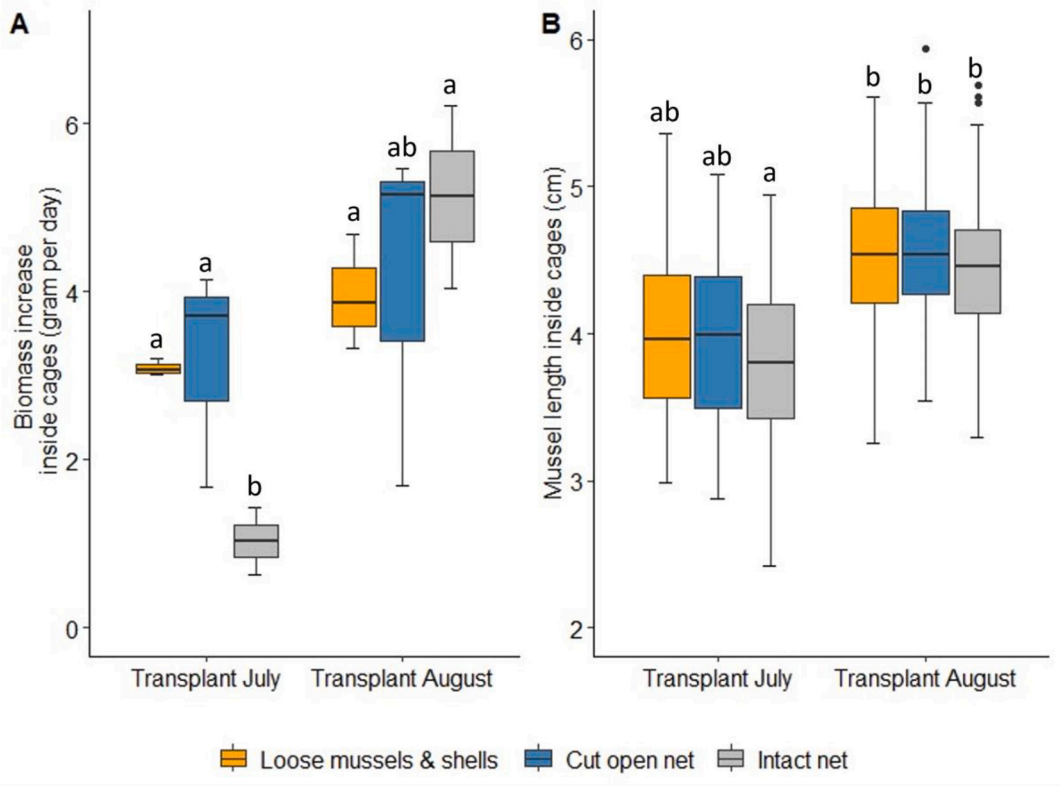

Fig. 4. A. Mussel biomass development (gram per day) B. Mussel length inside the anti-predation cages at the end of the experiment for mussels transplanted in July and August in the configurations: loose mussels & cockle shells, cut-open BioShell-SMCs net, or intact BioShell-SMCs net.

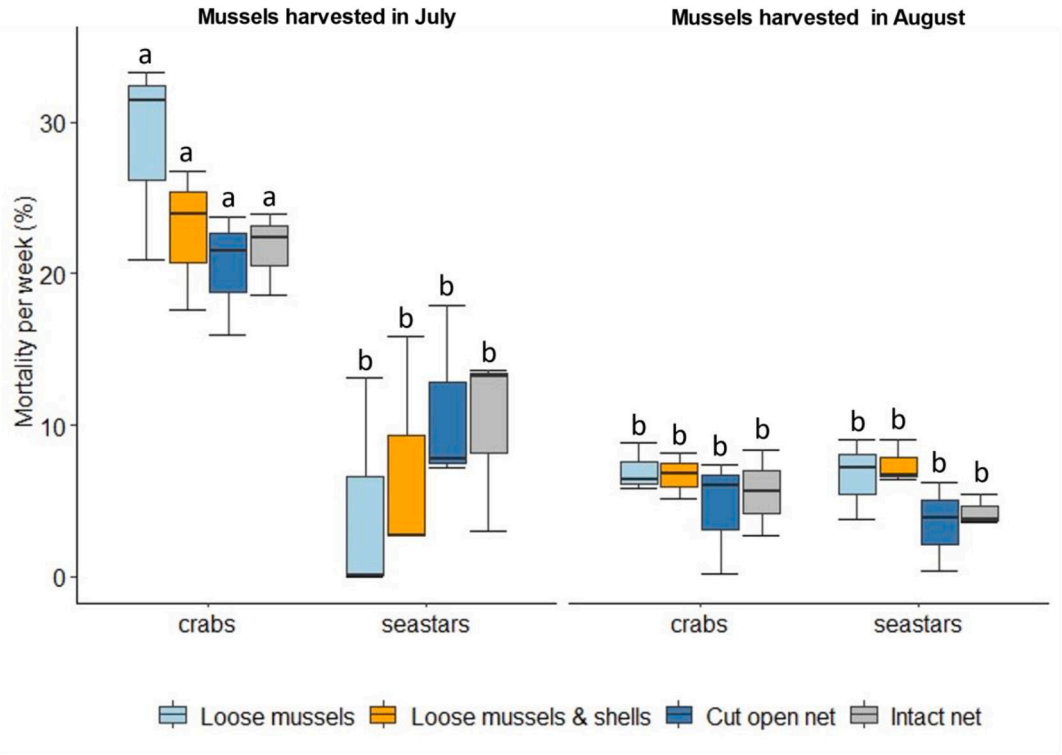

Fig. 5. Average mussel survival (%) for mussels harvested in July and August for four configurations: Only loose mussels, loose mussels and cockle shells, mussels attached to cut open BioShell-SMC and mussels attached to an intact BioShell-SMC.

predation, hydrodynamic forces or competition.

4.1. Role of predation on losses

During the initial three days of the July trial, we observed a substantial decrease in mussel biomass across all transplantation methods, with no mussels found against the surrounding fences. However, high mussel survival rates were observed in the anti-predation cages, indicating that predation was the primary cause of losses in the plots. This is in line with a study by Alder et al. (2021), who showed that biodegradable substrates (coir matting and rope) were ineffective at preventing loss of cultured juvenile (10–30 mm) and subadult (30–70 mm) mussels against predation by snappers and rays within the first 24 h following experimental set-up. In contrast, in our August experiment with larger mussels, the survival of mussels attached to the (cut-open) SMC was much higher compared to the loose mussels and compared to all treatments in July. The higher predation pressure observed in July may be due to the smaller size of the mussels in combination with low mussel densities. During the first week of the July-experiment, we observed many crushed mussel shells. According to Davidson (1986), crabs prey on mussels by either crushing the shell or chipping it, leaving behind only shell fragments. In contrast, sea stars utilize their tubefeet to force open the mussels' valves, resulting in two intact shells, rather than fragments (Ruppert and Barnes, 1994). Based on this observation, it appears that crabs were the primary predators in our July field experiment.

In the mesocosm experiment, a similar outcome was observed where crabs showed a higher predation rate on smaller mussels harvested in July, compared to larger mussels harvested in August. This suggests that crabs preferred smaller mussels, over larger mussels, irrespective of whether the mussels were attached to a substrate or not. Earlier work showed that crabs have a preference for certain size classes of mussels, and that the preferred prey size increases with crab size (Enderlein et al., 2003; Murray et al., 2007). Kamermans et al. (2009) demonstrated that small mussel seed (<11 mm) was consumed faster by crabs (carapace width of 44–63 mm) than larger mussels with a size of 22 mm. In our mesocosm experiment, the crabs had an average carapace width of 48 mm, indicating that the small mussels in July (12 mm) were easier prey for the crabs than the larger mussels in August (25 mm), resulting in lower survival rates. Predation mortality could be expected to decrease with increasing mussel densities (Frandsen and Dolmer, 2002). Because of the small scale, our field-transplantation experiment used relatively low mussel densities, suggesting that the small mussels harvested in July may have been transplanted below the density threshold necessary to provide protection against predators, even with attachment substratum. Due to their larger size, the mussels harvested in August were not as vulnerable to predators. The mussels attached to the (cut-open) SMC showed an improved survival compared to loose mussels, which is in line with previous research, indicating that increased substrate complexity (Frandsen and Dolmer, 2002; Reimer and Tedengren, 1997) and aggregation into dense clumps (Côté and Jelnikar, 1999) reduced predation risk.

4.2. Role of hydrodynamics on losses

The field experiment revealed that mussels attached to the cut-open and intact BioShell-SMC (i.e., treatment #2 & #3) experienced lower losses due to hydrodynamic force compared to those that were transplanted loosely, without attachment substrate (treatment #1). That is, during the experimental trial in August, a significant reduction in the number of mussels washed up against the fences surrounding the plots was observed when the mussels were attached to the BioShell-SMCs. These findings align with the results of a previous study by Bertolini et al. (2019), in which the hydrodynamically induced dislodgement thresholds of four different spatial patterns of mussels were tested. Here, mussel stripes created sufficiently dense patches that maximized resistance to dislodgement. The mussels attached to the biodegradable BioShell-SMCs in our study formed a comparable striped spatial pattern. Furthermore, the cockle shells in the biodegradable socks likely added extra weight to the mussel patches, which may have further increased

the dislodgement threshold. This induced dislodgement for mussels attached to the BioShell-SMCs was not observed in July, which can be attributed to the fact that most mussels did not survive high crab predation during the initial three days of the experiment.

The addition of empty cockle shells during the transplantation of loose mussel seed did not appear to enhance the dislodgement threshold of the mussels, as evidenced by the majority of the loosely transplanted mussels washing up against the fences in the second trial, despite the use of empty shells (treatment #1). Previous studies have shown that the presence of a complex substratum can increase the chances of mussel establishment by enhancing the critical hydrodynamic dislodgement threshold (Capelle et al., 2019; Christensen et al., 2015). However, in these papers, the complex substratum was already naturally present in the form of coarse shell material or artificially added in the form of shells embedded in cement, which created more stable substrates than the loose shells used in our experiment. The loose mussels in our study may not have had sufficient time without experiencing hydrodynamic forces (i.e., window of opportunity) to establish positive feedback mechanisms before being washed away or preyed upon.

For the mussels in the cut-open net condition, we found no higher survival rates compared to those attached to the intact BioShell-SMCs. We originally expected that by cutting open the BioShell-SMCs, cockle shells could fall out of the SMC and thereby provide additional attachment substrate away from the SMC. This might increase mussel survival, as mussels could utilize these shells to escape high densities and subsequently reduce competition. However, this was apparently not the case, possibly because harsh environmental conditions did not offer benefits for mussels dispersing away from the SMC.

4.3. Role of competition on losses

Mussel losses on culture plots after seeding typically dependent on seeding density (Bertolini et al., 2020; Capelle et al., 2014; Capelle et al., 2016b; Gascoigne et al., 2005). When seeding in bottom culture, the distribution of mussels is highly heterogeneous, with high densities in the spaces occupied by mussels (Capelle et al., 2014), leading to competition for food and space (Commito et al., 2014; Fréchette and Bourget, 1985; van de Koppel et al., 2005). Capelle et al. (2016a) found that seeding in high density resulted in increased mortality due to intraspecific competition. In our experiment, we found that mussels attached to the BioShell-SMCs had significantly lower biomass increase compared to (surviving) loose mussels and mussels attached to a cut-open net in July. We did not find a similar difference in transplantation methods in August. The reason for this discrepancy might be that initial mussel density was more than four times higher in July compared to August. The difference in biomass increase in July suggests that mussel densities on the SMC may have been too high, leading to competition for food and space, hindering growth and condition. These mussels may not have had the opportunity to disperse, whereas loose seeded mussels and those attached to the cut-open net may have been able to escape competition by dispersal onto the empty cockle shells. Our findings are supported by (Christensen et al., 2015), who found lower growth rates on a complex substrate, and Eschweiler and Christensen (2011), who documented reduced growth rates for mussels in protective interspaces of a Pacific oyster reef. Frandsen and Dolmer (2002) demonstrated that complexity can negatively impact growth rate due to limited food supply caused by decreased water flow in cavities of complex substrates. Further research is needed to determine the optimal transplantation density for mussel seeds using our BioShell-SMCs.

4.4. Management implications and outlook

Creating density-dependent positive feedback mechanisms to mitigate environmental stressors during large-scale transplantation of ecosystem-engineers is a key challenge to overcome both for ecosystem restoration and aquaculture applications. Using mussels as a model system, we demonstrated that using biodegradable structures (i.e., BioShell-SMC) can initiate self-facilitating feedback mechanisms by keeping the mussels grouped together and enable outplacement in distinct patterns. More specifically, our results demonstrated that attaching larger mussel seed to the BioShell-SMC significantly improved their survival rate compared to those transplanted without any attachment substrate and compared to small mussel seed. This transplantation method holds great promise for restoring sub- and intertidal mussel beds for nature conservation, as well for efficiency gains in aquaculture. Since the yield of the BioShell-SMC was comparable to traditionally used SMCs (van den Bogaart et al., 2023), but with significantly increased survival rates, it could reduce the costs of long-term restoration by requiring fewer transplants and by larger control on the spatial deployment. Additionally, our BioShell-SMC approach could provide a promising solution to the significant losses in mussel bottom cultivation (Capelle et al., 2016b). Follow-up research should focus on optimizing degradation times for different applications and environmental settings. The biodegradable substrate should maintain long enough for mussels to settle, stabilize and grow. Nevertheless, our study's results provide a promising step towards developing a more successful approach to restore mussel beds. In line with studies on other species (Temmink et al., 2020), present approach of using biodegradable structures to restoring ecosystem engineering species is expected to have broad applicability beyond our case study on mussels. Since our BioShell-SMC facilitates self-organization between individuals and provides greater control on transplanting in regular patterns that mimic patterns in natural ecosystems, restoration success can be enhanced by using our BioShell-SMC.

CRediT authorship contribution statement

Lisanne A. van den Bogaart: Formal analysis, Investigation, Writing – original draft, Writing – review & editing, Visualization, Supervision. **Jildou Schotanus:** Conceptualization, Methodology, Formal analysis, Investigation, Writing – original draft, Writing – review & editing, Visualization, Supervision. **Jacob J. Capelle:** Conceptualization, Methodology, Writing – review & editing, Supervision. **Tjeerd J. Bouma:** Conceptualization, Methodology, Writing – review & editing, Supervision, Project administration.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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References

Alder, A., Jeffs, A., Hillman, J.R., 2021. Considering the use of subadult and juvenile mussels for mussel reef restoration. Restor. Ecol. 29 (3), e13322 https://doi.org/10.1111/rec.13322.

Balke, T., Bouma, T.J., Horstman, E.M., Webb, E.L., Erftemeijer, P.L., Herman, P.M., 2011. Windows of Opportunity: thresholds to mangrove seedling establishment on tidal flats. Mar. Ecol. Prog. Ser. 440, 1–9. https://doi.org/10.3354/meps09364.

Balke, T., Herman, P.M., Bouma, T.J., 2014. Critical transitions in disturbance-driven ecosystems: identifying Windows of Opportunity for recovery. J. Ecol. 102 (3), 700–708. https://doi.org/10.1111/1365-2745.12241.

Bertolini, C., Cornelissen, B., Capelle, J., Van De Koppel, J., Bouma, T.J., 2019. Putting self-organization to the test: labyrinthine patterns as optimal solution for persistence. Oikos 128 (12), 1805–1815. https://doi.org/10.1111/oik.06373.

Bertolini, C., Capelle, J., ter Veld, J., van de Koppel, J., Bouma, T., 2020. Understanding scales of density-dependence to improve the use of resources in benthic mussel aquaculture. Aquaculture 528, 735477. https://doi.org/10.1016/j.aquaculture.2020.735477.

Beukema, J., De Bruin, W., 1977. Seasonal changes in dry weight and chemical composition of the soft parts of the tellinid bivalve *Macoma balthica* in the Dutch Wadden Sea. Neth. J. Sea Res. 11 (1), 42–55. https://doi.org/10.1016/0077-7579(77)90020-5.

Bouma, T.J., Friedrichs, M., Van Wesenbeeck, B., Temmerman, S., Graf, G., Herman, P., 2009. Density-dependent linkage of scale-dependent feedbacks: a flume study on the intertidal macrophyte *Spartina anglica*. Oikos 118 (2), 260–268. https://doi.org/10.1111/j.1600-0706.2008.16892.x.

Byers, J.E., Cuddington, K., Jones, C.G., Talley, T.S., Hastings, A., Lambrinos, J.G., Crooks, J.A., Wilson, W.G., 2006. Using ecosystem engineers to restore ecological systems. Trends Ecol. Evol. 21 (9), 493–500. https://doi.org/10.1016/j.tree.2006.06.002.

Capelle, J.J., 2017. Production Efficiency of Mussel Bottom Culture. Wageningen University and Research.

Capelle, J.J., Wijsman, J.W., Schellekens, T., van Stralen, M.R., Herman, P.M., Smaal, A. C., 2014. Spatial organisation and biomass development after relaying of mussel seed. J. Sea Res. 85, 395–403. https://doi.org/10.1016/j.seares.2013.07.011.

Capelle, J.J., Scheiberlich, G., Wijsman, J.W., Smaal, A.C., 2016a. The role of shore crabs and mussel density in mussel losses at a commercial intertidal mussel plot after seeding. Aquac. Int. 24, 1459–1472. https://doi.org/10.1007/s10499-016-0005-1.

Capelle, J.J., Wijsman, J.W., Van Stralen, M.R., Herman, P.M., Smaal, A.C., 2016b. Effect of seeding density on biomass production in mussel bottom culture. J. Sea Res. 110, 8–15. https://doi.org/10.1016/j.seares.2016.02.001.

Capelle, J.J., Leuchter, L., de Wit, M., Hartog, E., Bouma, T.J., 2019. Creating a window of opportunity for establishing ecosystem engineers by adding substratum: a case study on mussels. Ecosphere 10 (4), e02688. https://doi.org/10.1002/ecs2.2688.

Christensen, H.T., Dolmer, P., Hansen, B.W., Holmer, M., Kristensen, L.D., Poulsen, L.K., Stenberg, C., Albertsen, C.M., Støttrup, J.G., 2015. Aggregation and attachment responses of blue mussels, *Mytilus edulis*—impact of substrate composition, time scale and source of mussel seed. Aquaculture 435, 245–251.

Commito, J.A., Commito, A.E., Platt, R.V., Grupe, B.M., Piniak, W.E.D., Gownaris, N.J., Reeves, K.A., Vissichelli, A.M., 2014. Recruitment facilitation and spatial pattern formation in soft-bottom mussel beds. Ecosphere 5 (12), 1–26. https://doi.org/10.1890/ES14-00200.1.

Côté, I.M., Jelnikar, E., 1999. Predator-induced clumping behaviour in mussels (*Mytilus edulis* Linnaeus). J. Exp. Mar. Biol. Ecol. 235 (2), 201–211. https://doi.org/10.1016/S0022-0981(98)00155-5.

Davidson, R.J., 1986. Mussel selection by the paddle crab *Ovalipes catharus* (White): evidence of flexible foraging behaviour. J. Exp. Mar. Biol. Ecol. 102 (2–3), 281–299. https://doi.org/10.1016/0022-0981(86)90182-6.

de Paoli, H., van de Koppel, J., van der Zee, E., Kangeri, A., van Belzen, J., Holthuijsen, S., van den Berg, A., Herman, P., Olff, H., van der Heide, T., 2015. Processes limiting mussel bed restoration in the Wadden-Sea. J. Sea Res. 103, 42–49. https://doi.org/10.1016/j.seares.2015.05.008.

de Paoli, H., van der Heide, T., van den Berg, A., Silliman, B.R., Herman, P.M., van de Koppel, J., 2017. Behavioral self-organization underlies the resilience of a coastal ecosystem. Proc. Natl. Acad. Sci. 114 (30), 8035–8040. https://doi.org/10.1073/pnas.1619203114.

Enderlein, P., Moorthi, S., Röhrscheidt, H., Wahl, M., 2003. Optimal foraging versus shared doom effects: interactive influence of mussel size and epibiosis on predator preference. J. Exp. Mar. Biol. Ecol. 292 (2), 231–242. https://doi.org/10.1016/S0022-0981(03)00199-0.

Eschweiler, N., Christensen, H.T., 2011. Trade-off between increased survival and reduced growth for blue mussels living on Pacific oyster reefs. J. Exp. Mar. Biol. Ecol. 403 (1–2), 90–95. https://doi.org/10.1016/j.jembe.2011.04.010.

Fivash, G.S., van Belzen, J., Temmink, R.J., Didderen, K., Lengkeek, W., van der Heide, T., Bouma, T.J., 2022. Increasing spatial dispersion in ecosystem restoration mitigates risk in disturbance-driven environments. J. Appl. Ecol. 59 (4), 1050–1059. https://doi.org/10.1111/1365-2664.14116.

Frandsen, R., Dolmer, P., 2002. Effects of substrate type on growth and mortality of blue mussels (*Mytilus edulis*) exposed to the predator *Carcinus maenas*. Mar. Biol. 141, 253–262. https://doi.org/10.1007/s00227-002-0831-8.

Fréchette, M., Bourget, E., 1985. Energy flow between the pelagic and benthic zones: factors controlling particulate organic matter available to an intertidal mussel bed. Can. J. Fish. Aquat. Sci. 42 (6), 1158–1165.

Gascoigne, J.C., Beadman, H.A., Saurel, C., Kaiser, M.J., 2005. Density dependence, spatial scale and patterning in sessile biota. Oecologia 145, 371–381. https://doi.org/10.1007/s00442-005-0137-x.

Kamermans, P., Brummelhuis, E., Smaal, A., 2002. Use of spat collectors to enchange supply of seed for bottom culture of blue mussels (*Mytilus edulis*) in the Netherlands. World Aquacult. 33 (3), 12–15.

Kamermans, P., Blankendaal, M., Perdon, J., 2009. Predation of shore crabs (*Carcinus maenas* (L.)) and starfish (*Asterias rubens* L.) on blue mussel (*Mytilus edulis* L.) seed from wild sources and spat collectors. Aquaculture 290 (3–4), 256–262. https://doi.org/10.1016/j.aquaculture.2009.02.031.

Ladd, M.C., Miller, M.W., Hunt, J.H., Sharp, W.C., Burkepile, D.E., 2018. Harnessing ecological processes to facilitate coral restoration. Front. Ecol. Environ. 16 (4), 239–247. https://doi.org/10.1002/fee.1792.

Lenth, R.V., 2016. Least-Squares Means: the R Package lsmeans. J. Stat. Softw. 69 (1), 1–33. https://doi.org/10.18637/jss.v069.i01.

Liu, Q.-X., Herman, P.M., Mooij, W.M., Huisman, J., Scheffer, M., Olff, H., Van De Koppel, J., 2014. Pattern formation at multiple spatial scales drives the resilience of mussel bed ecosystems. Nat. Commun. 5 (1), 1–7. https://doi.org/10.1038/ncomms6234.

Liu, P., Wang, W., Bai, Z., Guo, Z., Ren, W., Huang, J., Xu, Y., Yao, J., Ding, Y., Zang, R., 2020. Competition and facilitation co-regulate the spatial patterns of boreal tree species in Kanas of Xinjiang, northwest China. For. Ecol. Manage. 467, 118167 https://doi.org/10.1016/j.foreco.2020.118167.

Miller, R.G., 1981. Survival analysis. In: Wiley Series in Probability and Mathematical Statistics. NY.

Murray, L., Seed, R., Jones, T., 2007. Predicting the impacts of *Carcinus maenas* predation on cultivated *Mytilus edulis* beds. J. Shellfish. Res. 26 (4), 1089–1098. https://doi.org/10.2983/0730-8000(2007)26[1089:PTIOCM]2.0.CO;2.

Reimer, O., Tedengren, M., 1997. Predator-induced changes in byssal attachment, aggregation and migration in the blue mussel, *Mytilus edulis*. Mar. Freshw. Behav. Physiol. 30 (4), 251–266. https://doi.org/10.1080/10236249709379029.

Renzi, J.J., He, Q., Silliman, B.R., 2019. Harnessing positive species interactions to enhance coastal wetland restoration. Front. Ecol. Evol. 131 https://doi.org/10.3389/fevo.2019.00131.

Rietkerk, M., Van de Koppel, J., 2008. Regular pattern formation in real ecosystems. Trends Ecol. Evol. 23 (3), 169–175. https://doi.org/10.1016/j.tree.2007.10.013.

Ruppert, E., Barnes, R., 1994. Invertebrate Zoology. Saunders College Publishing, New York, pp. 68–94.

Schotanus, J., Walles, B., Capelle, J.J., Van Belzen, J., Van De Koppel, J., Bouma, T.J., 2020a. Promoting self-facilitating feedback processes in coastal ecosystem engineers to increase restoration success: Testing engineering measures. J. Appl. Ecol. 57 (10), 1958–1968. https://doi.org/10.1111/1365-2664.13709.

Schotanus, J., Capelle, J.J., Paree, E., Fivash, G.S., Van De Koppel, J., Bouma, T.J., 2020b. Restoring mussel beds in highly dynamic environments by lowering environmental stressors. Restor. Ecol. 28 (5), 1124–1134. https://doi.org/10.1111/rec.13168.

Shaver, E.C., Silliman, B.R., 2017. Time to cash in on positive interactions for coral restoration. PeerJ 5, e3499. https://doi.org/10.7717/peerj.3499.

Silliman, B.R., Schrack, E., He, Q., Cope, R., Santoni, A., van der Heide, T., Jacobi, R., Jacobi, M., van de Koppel, J., 2015. Facilitation shifts paradigms and can amplify coastal restoration efforts. Proc. Natl. Acad. Sci. 112 (46), 14295–14300. https://doi.org/10.1073/pnas.1515297112.

Suykerbuyk, W., Govers, L.L., Bouma, T.J., Giesen, W.B., de Jong, D.J., van de Voort, R., Giesen, K., Giesen, P.T., van Katwijk, M.M., 2016. Unpredictability in seagrass restoration: analysing the role of positive feedback and environmental stress on *Zostera noltii* transplants. J. Appl. Ecol. 53 (3), 774–784. https://doi.org/10.1111/1365-2664.12614.

Svane, I., Ompi, M., 1993. Patch dynamics in beds of the blue mussel *Mytilus edulis* L.: effects of site, patch size, and position within a patch. Ophelia 37 (3), 187–202. https://doi.org/10.1080/00785326.1993.10429917.

Temmink, R.J., Christianen, M.J., Fivash, G.S., Angelini, C., Boström, C., Didderen, K., Engel, S.M., Esteban, N., Gaeckle, J.L., Gagnon, K., 2020. Mimicry of emergent traits amplifies coastal restoration success. Nat. Commun. 11 (1), 3668. https://doi.org/10.1038/s41467-020-17438-4.

van de Koppel, J., Rietkerk, M., Dankers, N., Herman, P.M., 2005. Scale-dependent feedback and regular spatial patterns in young mussel beds. Am. Nat. 165 (3), E66–E77. https://doi.org/10.1086/428362.

Van den Bogaart, L.A., Schotanus, J., Capelle, J.J., Bouma, T.J., 2023. Comparing traditional vs. biodegradable seed mussel collectors (SMCs) for seed settlement, seed density, and seed growth: effect of deployment depth and location. Aquacult. Eng. 102344 https://doi.org/10.1016/j.aquaeng.2023.102344.

wa Kangeri, A.K., Jansen, J.M., Barkman, B.R., Donker, J.J., Joppe, D.J., Dankers, N.M., 2014. Perturbation induced changes in substrate use by the blue mussel, *Mytilus edulis*, in sedimentary systems. J. Sea Res. 85, 233–240. https://doi.org/10.1016/j.seares.2013.06.001.

Weerman, E.J., Van de Koppel, J., Eppinga, M.B., Montserrat, F., Liu, Q.-X., Herman, P. M., 2010. Spatial self-organization on intertidal mudflats through biophysical stress divergence. Am. Nat. 176 (1), E15–E32. https://doi.org/10.1086/652991.

Zuur, A.F., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid common statistical problems. Methods Ecol. Evol. 1 (1), 3–14. https://doi.org/10.1111/j.2041-210X.2009.00001.x.