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RESEARCH ARTICLE

Exploring the impact of spatial patterns on restoration efforts: promoting self-facilitating feedback mechanisms with an innovative biodegradable seed mussel collector

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Transplantations of organisms in aquatic ecosystems play an important role in ecological restoration and commercial practices. However, success rates of these transplantations, especially when ecosystem engineers are involved, are often low. To enhance transplantation success, the promotion of self-facilitation between transplants that mitigate environmental stressors is crucial. Besides, spatial patterns resulting from self-facilitation can enhance ecosystem resilience. Using blue mussels as a model organism, we explored the possibility of increasing transplantation success in a subtidal ecosystem. We used biodegradable structures ("BioShell-SMCs") to ameliorate self-facilitating feedback mechanisms to overcome environmental stressors in the initial post-transplantation phase, and to increase transplantation success by implementing large-scale spatial configurations, mimicking natural mussel bed patterns. The structures are an innovation of traditional seed mussel collectors (SMCs) used in mussel cultivation. They consist of a biodegradable net based on a compound of aliphatic polyesters, filled with empty cockle shells around a coconut fiber rope. We tested whether different spatial configurations could increase transplantation success of mussel seed: low versus high density labyrinth pattern and banded pattern. The results of this experiment showed high losses (approximately 75%), with no significant variation between configurations. The lack of migration due to unexpected retention of the biodegradable net hindered the initiation of natural aggregations, resulting in increased competition among mussels. Besides, factors such as hydrodynamic dislodgement, burial and interannual variation likely contributed to the observed losses. While the BioShell-SMC has not demonstrated large-scale success, this research contributes to understanding the mechanisms that underlie successful transplantation strategies in aquatic ecosystems.

Key words: configurations, ecosystem engineers, *Mytilus edulis*, positive feedback, transplantation, window of opportunity

Implications for Practice

- Transplantation practitioners should carefully consider the role of spatial configurations when restoring ecosystems. This study demonstrated that it is not easy to "print" a spatial configuration on a restoration site, as it did not enhance mussel survival.
- Enhancing small-scale organization within larger configurations may increase effectiveness of transplantations. Hence, using structures that enhance self-organization among transplanted organisms rather than competition is crucial.
- The lack of significant variation in transplantation success among different spatial configurations raises questions about the complexity of ecological interactions. This emphasizes the need for a nuanced understanding of ecosystem dynamics and spatial patterns, acknowledging that a one-size-fits-all approach may not be effective in achieving successful transplantations in diverse aquatic ecosystems.

Introduction

Transplantations of individuals or populations in aquatic ecosystems can be an important component in the success of

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ecological restoration (Horoszowski-Fridman & Rinkevich 2016), the provision of ecosystem services (e.g. mangroves providing coastal protection; Barbier 2016) and commercial practices (e.g. aquaculture; Kamermans et al. 2002). However, these transplantations tend to have low success rates, particularly when ecosystem engineers are involved (Griffith et al. 1989; Godefroid et al. 2011). Ecosystem engineers play a crucial role in modifying, maintaining, and creating habitats within their ecosystem (Jones et al. 1994; Bruno et al. 2003). This is due to their ability to directly or indirectly influence the availability of resources for conspecifics or other species by inducing physical changes in biotic or abiotic materials (Jones et al. 1994). In dynamic coastal environments, ecosystem engineers rely on self-facilitating feedback mechanisms that help to mitigate physical (e.g. wave exposure and salinity) and biological (e.g. nutrient availability and predation) stressors (van de Koppel et al. 2001; van der Heide et al. 2007; Liu et al. 2014). For example, macrophytes are ecosystem engineers that have the capability to decrease hydrodynamic energy and drag in their surroundings, resulting in local accretion or wave attenuation, which ultimately promotes the expansion of the species (Bouma et al. 2005; Maxwell et al. 2017). Likewise, reef-forming bivalves such as mussels minimize individual losses by attaching themselves to conspecifics and aggregating in dense clusters (Hunt & Scheibling 2001). The lack of a disturbance-free period immediately following transplantation (also referred to as a window of opportunity), along with the absence of a suitable settlement substratum for new recruits to establish positive feedback mechanisms, could contribute to the failure of transplantations (Balke et al. 2014; Capelle et al. 2019). The promotion of self-facilitation between transplants is, therefore, increasingly recognized as an important component of transplantation success (Silliman et al. 2015; Ladd et al. 2018).

The emergence of spatial patterns in ecosystems can significantly increase the overall resilience of an ecosystem (Liu et al. 2014). Patterns arise from the interplay between facilitation and competition, that drives pattern formation at a small scale, while the influence of negative interactions like physical forcing leads to the development of spatial patterns on a larger scale (Rietkerk & Van de Koppel 2008). Examples of ecological systems with large-scale patterns are arid ecosystems (HilleRisLambers et al. 2001), wetlands (Foster et al. 1983), coral reefs (Mistr & Bercovici 2003), and mussel beds (van de Koppel et al. 2005). Recent studies have shown that mimicking these natural spatial pattern formations in restoration efforts can increase transplantation success (de Paoli et al. 2017; Schotanus et al. 2020; Temmink et al. 2022). For example, when mussels were transplanted in high density bands (four bands of 16×5 m and spaced 5 m apart) positioned between fences, resulted in a loss that was over twice as small in comparison to the loss observed when mussels were homogenously transplanted at low density across a 16×40 m area (Schotanus et al. 2020). Using blue mussels (*Mytilus edulis*) as a model organism, we explored the possibility of increasing large-scale transplantation success in a subtidal ecosystem by (1) using biodegradable materials to promote self-organization into high-density clusters upon transplantation, thereby potentially offering protection against predators and increasing resistance to hydrodynamic dislodgement. We also tested (2) the efficiency of implementing different spatial configurations designed to mimic patterns found in natural mussel beds. To the best of our knowledge, no large-scale field study has previously attempted to create a subtidal ecosystem while incorporating spatial patterns.

Natural mussel beds on soft sediment often exhibit a distinctive spatial pattern, that is characterized by high-density mussel bands (5–10 m apart) perpendicular to the tidal direction, alternating with bare sediment patches (van de Koppel et al. 2005) (Fig. 1). These patterns are thought to result from a combination of small-scale positive feedback, and larger-scale negative feedback (van de Koppel et al. 2005, 2008). Small-scale aggregation leads to local high densities, which offers mussels safety from dislodgement and predation (Hunt & Scheibling 2001). However, high density also increases competition among the mussels. To mitigate this competition, large-scale formation of banded patterns reduces the overall density, thereby decreasing competition for food, while maintaining a local high density within the bands to ensure safety (van de Koppel et al. 2005). These large-scale patterns enhance the resilience of mussel beds and reduce the likelihood of collapses (de Paoli et al. 2017; Liu et al. 2020). Therefore, implementation of large-scale patterns (ranging from tens to hundreds of meters) in mussel transplantations may increase transplantation success.

The biodegradable structures ("BioShell-SMCs") used in our experiment were used to mimic the large-scale spatial patterns in mussel beds and simultaneously provide substrate and protection for the establishment of self-facilitating interactions. BioShell-SMC is an innovation of traditionally used nylon seed mussel collectors (SMCs) (van den Bogaart et al. 2023*a*). The BioShell-SMC consists of a biodegradable sock based on a compound of aliphatic polyesters, filled with empty cockle shells and placed around a coconut-fiber carrying rope. SMCs are used to collect mussel seed (juvenile mussels) from the water column (Kamermans et al. 2002), which can be used for aquaculture practices or for restoration efforts. Collection of mussel seed using BioShell-SMCs was comparable with the biomass obtained with traditionally used SMCs (van den Bogaart et al. 2023*a*). Normally, in benthic mussel culture, mussel seed is removed from the SMCs and individual seeds are subsequently dispersed over the bottom. However, the small size of the mussels and the lack of hard substrate on soft-sediment (culture) plots makes the newly transplanted mussels highly vulnerable to loss factors, such as hydrodynamic dislodgement, predation, and sedimentation (Murray et al. 2007; Kamermans et al. 2010; Temmink et al. 2022). The use of the BioShell-SMC makes it possible to directly transplant the mussels onto the bottom in high-density clusters, while still attached to the biodegradable structure. The presence of pre-clustered mussels on the BioShell-SMCs has shown to increase the survival of the mussels by offering protection against crab predation, as well as enhancing resistance to hydrodynamic dislodgement (van den Bogaart et al. 2023*b*). Consequently, the BioShell-SMCs hold the potential to enhance restoration or cultivation success by reducing the number of transplants needed. To improve long-term transplantation success, establishment of spatial patterns is crucial (van de Koppel et al. 2008; Schotanus et al. 2020; Temmink et al. 2022). Although mussels typically

Figure 1. Aerial photograph of a mussel bed displaying a large-scale banded pattern in the Wadden Sea, situated right below the island Ameland in the Netherlands. The mussel bed covers an area of about 1.2 ha. *Source*: Photograph taken by Karin Troost on 19 February, 2019.

self-aggregate into patterns, this process leads to substantial losses (Capelle et al. 2016), and in dynamic environments, it can even hinder restoration success (de Paoli et al. 2015). Since mussels attached to the BioShell-SMC are more stable than loose mussels (van den Bogaart et al. 2023*b*), we provide the mussels with an attachment substrate, and by mimicking spatial patterns of mature mussel beds, we offer them a kickstart that potentially increases transplant success.

In a large field experiment, mussels attached to the biodegradable substrate were relayed into three different patterns: (1) *Low density labyrinth pattern*: low local density mussels attached to short pieces of BioShell-SMC homogeneously distributed, hypothesized to result in low competition among mussels but in an increased risk of hydrodynamic loss, (2) *high density labyrinth pattern*: high local density mussels attached to short pieces of BioShell-SMC homogeneously distributed, hypothesized to result in high competition but in a reduced risk of hydrodynamic loss, and (3) *banding pattern*: high local density mussels attached to the BioShell-SMC placed in regularly spaced banded patterns, hypothesized to result in low competition (due to optimal utilization of algal concentrations) and a reduced risk of hydrodynamic loss. Overall, the results of our experiment will help to understand the importance of combining (1) self-organization by using biodegradable substrates; and (2) optimal spatial configurations to increase (mussel) transplantation success.

Methods

Study Site

We conducted a field experiment on a subtidal mussel culture plot from 7 September, 2021 until 28 June, 2022. The study site was situated in a sheltered area of the Oosterschelde in the Netherlands, the Zandkreek (51°33′26.6″N 3°53′55.0″ E) (Fig. 2A). The location is characterized by sandy sediments and the dominant water flow direction is from the southwest (Fig. 2B). The experimental plots were all situated at the same depth, ranging from a water depth of approximately 1–4 m from low to high tide. The mussels used in this experiment were collected on 5 km of biodegradable BioShell-SMC (van den Bogaart et al. 2023*a*), which was deployed at a location in the nearshore North Sea (SMC in Fig. 2A: 51°46′22.0″N 3°48′10.4″ E) in May 2021. The BioShell-SMCs were harvested on 6 September, 2021 and relayed on the study site the next day.

Setup of the Field Experiment

The BioShell-SCMs (Fig. 3A) were relayed in three configurations: (1) short (4 m) fragments of single BioShell-SMC (low density) homogeneously distributed over the experimental plot (*low density labyrinth pattern*); (2) short fragments (4 m) of three BioShell-SMCs tied together (high density) homogeneously distributed over the experimental plot (*high density labyrinth pattern*); and (3) eight long (8 m) structures of three BioShell-SMCs tied together (high density) placed plot-wide in perpendicular lines (*banding pattern*) (Fig. 3). Each configuration was replicated four times, resulting in 12 plots. The SMCs were manually dropped from a boat and placed in randomly assigned experimental plots measuring 20 × 24 m each. A buffer zone of approximately 5 m was maintained between adjacent plots. The plots were arranged in a row to minimize variation in depth and current between the plots. In total, each plot contained approximately 850 kg of BioShell-SMC (structures and mussels). The initial mussel biomass (*Mytilus edulis*)

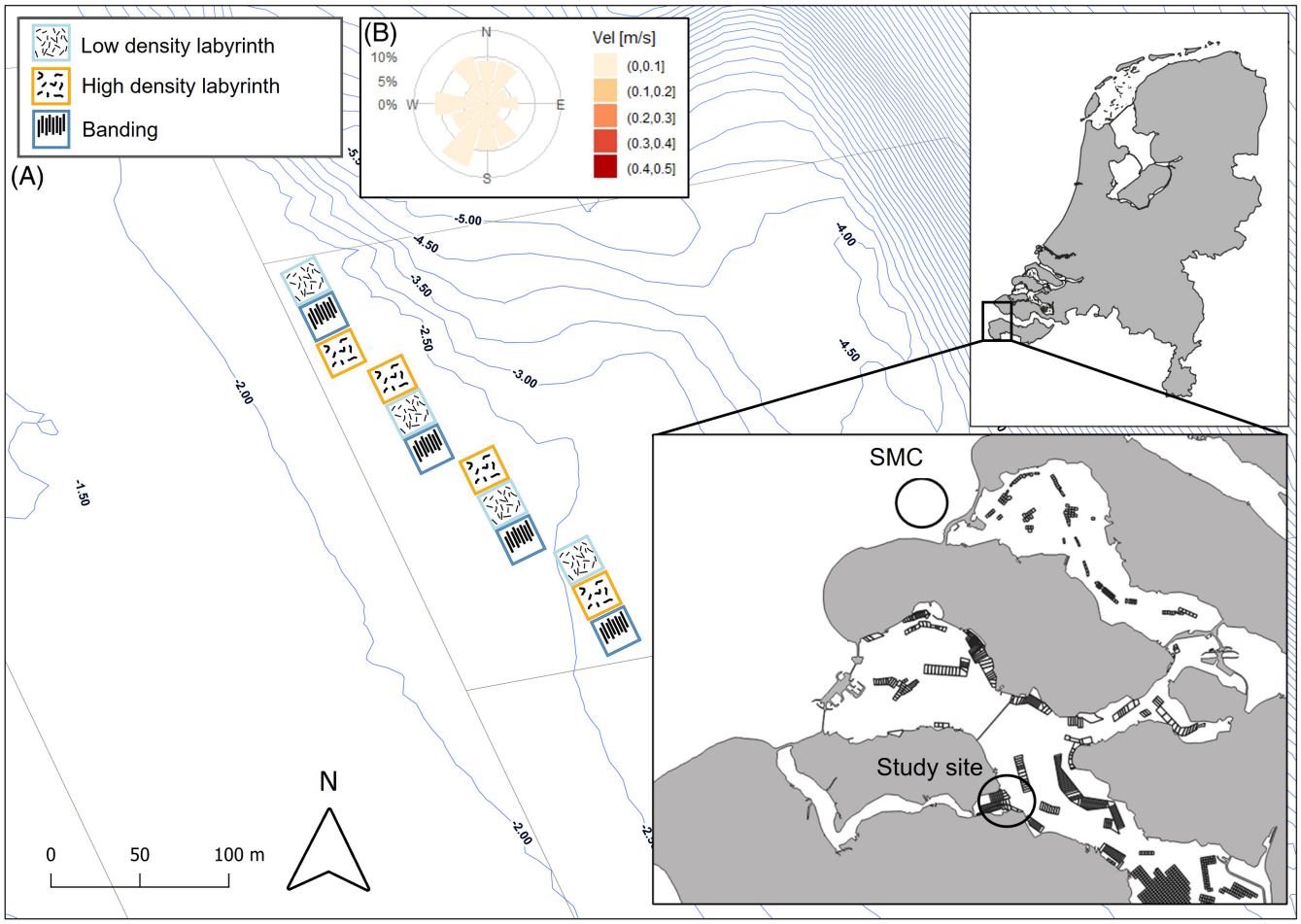

Figure 2. (A) Map of the study area. Land is shown in gray and water in white. Mussel culture plots are shown in dark gray on the overview maps. SMC: origin of the seed (seed mussel collector). The three transplant configurations are: low density BioShell-SMC homogeneously distributed (*low density labyrinth pattern*, light blue); high density SMCs homogeneously distributed (*high density labyrinth pattern*, orange); and high density perpendicular lines (*banding pattern*, dark blue). The plots measure 20 × 24 m each and are 5 m apart, with four replicates per configuration. (B) Near-bed orbital velocity (m/s) and direction.

attached to the BioShell-SMC was 6.0 kg/m. In comparison, the typical average obtained biomass with traditional seed collectors in the Dutch Voordelta is 2.6 kg/m, with fluctuations ranging from 0.3 to 5.0 kg/m (Capelle 2023). The average length of the mussels was 22.34 ± 0.57 mm, based on measurements from 210 mussels.

Mussel Cover Based on Sonar Data

We used side scan sonar (Kongsberg GeoAcoustics PulSAR Sidescan) to map change in hard substrate cover. Notably, the sonar lacks the capability to discriminate between mussel and BioShell-SMC structure due to their shared classification as hard substrates. Through continuous monitoring of changes in hard substrate cover over time, insights can be gained regarding potential horizontal migration of mussels onto the substrate, or the dislodgment of entire structures or clusters of mussels. We further refer to this hard substrate cover as "mussel cover," anticipating its increase as a result of the mussels' horizontal migration. Approximately every month (on days with little wind and current) from September 2021 until June 2022, we collected sonar data during high tide (water depth of 4–5 m) with a 7 m long vessel. The side scan towfish was connected with a tow cable to a reel and launched from starboard. A deck cable ensured data transmission from the towfish to the interface deck unit, which was connected to a laptop with PulSAR software (version 0100 B6-r7235) for real-time visualization. The vessel was equipped with a global positioning system (GPS) (Trimble R8s with real-time kinematic positioning) for accurate positioning. For consistent sonar imagery, the vessel moved in a constant speed of approximately 8 km/h to avoid distortion and stretching of the scans. The transects were sailed as straight as possible and areas were scanned multiple times to ensure a good coverage. We used high-frequency scans (600 kHz) with a range of 20 m. Captured side-scan images were saved as xtf files and the corresponding GPS coordinates were recorded.

The xtf files were imported into SonarWiz 7 software (V7.09.05) and processed into a complete geo-referenced image mosaic with a 2 cm resolution. Errors in the heading of the

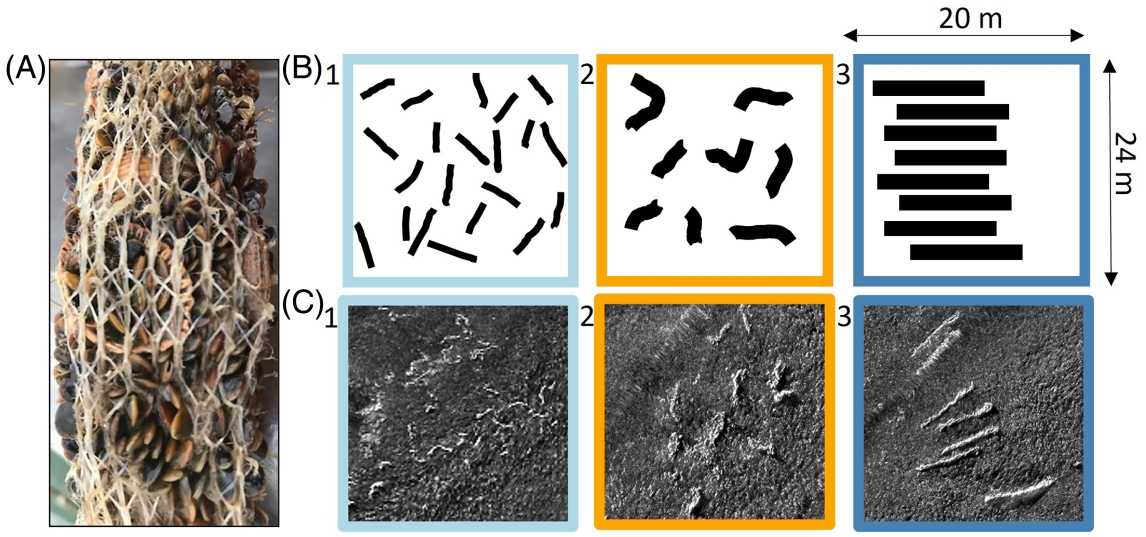

Figure 3. (A) Biodegradable BioShell-SMC, consisting of a biodegradable sock based on a compound of aliphatic polyesters, filled with empty cockle shells and placed around a coconut-fiber carrying rope. Mussel seed can settle on the cockle shells. (B) Schematic representation of the transplant configurations of the BioShell-SMC: (1) Low density SMCs homogeneously distributed (low density labyrinth pattern); (2) High density SMCs homogeneously distributed (high density labyrinth pattern); (3) High density perpendicular lines (banding pattern). The data were collected with four replicates per configuration. The SMCs were relayed on plots measuring 20 × 24 m, with an empty buffer zone of approximately 5 m between two plots. (C) Images obtained with sonar scanning, corresponding with configurations in (B).

towfish were removed by visually selecting a threshold to remove outlying pings. The water column was removed with bottom tracking, as we were only interested in the sea floor. Then, empirical gain normalization was used to sum up and average out all amplitudes for every ping, resulting in a smoother surface where artifacts were easier to spot. Removal of noise in the sonar images, such as ripple marks or stones, was done by time-varying-gain to equalize the backscatter. De-stripe filter was applied to slightly repair errors caused by waves, turns of the vessel and speed differences that occurred as stripes in the scan. Finally, map corrections were applied to sheave sonar offsets and the files were exported in greyscale.

The geo-referenced files were imported in Python (Version 3.9.7), where smaller tiffs were separately created for each experimental plot. To remove noise, median convolution was applied with a kernel of 8 by 8 pixels. This recalculates every pixel by taking the median from an 8 by 8 square around the pixel. The threshold value for mussels was defined on band 140. Band 0 resulted in a black pixel, while 255 resulted in a white pixel. To determine the percentage coverage, the number of white pixels (representing mussels) was divided by the total number of pixels within each plot. These numbers were then converted to square meters (m^2) coverage. We used 6 out of the 10 measurements, as they obtained good quality data.

Mussel Biomass Based on Sample Data

We conducted five moments where biomass of mussels attached to the BioShell-SMC was monitored, spanning from September 2021 to June 2022, including initial sampling. The third sampling campaign (January/February 2022) was interrupted due to unfavorable weather and tide conditions that intercepted the fieldwork. The fieldwork campaign could only be resumed 28 days after the start on19 January. As there was no significant difference in mussel biomass between these sampling moments in January and February ($t_{33.8} = 0.87$, $p = 0.389$), we used the average sampling date between those two dates to account for this division. During each sampling moment, three samples were taken per plot from different BioShell-SMCs, resulting in 12 samples per configuration and a total of 36 samples per sampling moment. Due to very limited visibility and because the experiment was always submerged, we relied on locating the SMCs by touch. The samples were obtained by snorkeling and selecting a piece of BioShell-SMC where we would come across. Using a knife, samples of approximately 10 cm in length were taken and transported to the laboratory. In the case of the high density configurations, only one of the three structures tied together was sampled. For each sample, total weight and weight of the mussels were noted. To determine the mussel biomass, we calculated the proportion of mussel biomass attached to the BioShell-SMC. This was achieved by dividing the weight of the mussels by the total weight of the sample. We applied this approach as some samples did not include the inner carrying-rope from the BioShell-SMC, making it impossible to calculate mussel biomass per meter of collector material.

Mussel Length and Condition

We collected three random samples from the BioShell-SMCs at the start, analyzing a total of 210 mussels for shell length. Over a period of nearly 10 months, we measured shell length using the same three samples from each plot that were used for density determination. In total, we measured 3707 mussels by randomly

subsampling 70 mussels (or fewer if there were less than 70 present) from each sample.

The condition index (mg/cm^3) was obtained at the beginning (8 September) and at the end (14 June, 2022) of the experiment. All 70 mussels from each initial sample ($n = 3$) were pooled together, as they originated from the same location and had no initial differences in seeding configuration. At the end of the experiment, mussels were processed individually to obtain more precise data. Ash-free dry-weight (AFDW) was obtained by drying the flesh at 65°C for 2–4 days and subsequently ashing it at 510°C for 4 hours. The condition index was calculated by dividing the AFDW (mg) by the cubed length (cm^3) for all mussels collectively in September, or for each individual mussel in June (Beukema & De Bruin 1977).

Effect of Hydrodynamics on SMCs

From 12 November, 2021 until 19 April, 2022, a wave gauge sensor (OSSI-10-003) was placed on a metal frame to measure hydrodynamic forces within the experimental area. In order to measure the impact of storms on the BioShell-SMCs, we deployed the sensor in November rather than September, as storms typically occur during the winter season in the Netherlands. This decision was also influenced by the battery capacity, as it would not have lasted with the same measuring interval from September until June. The gauge was placed approximately 50 cm above the sediment. Pressure samples were recorded at a rate of 10 Hz (datapoints per second) with a burst length of 7 minutes and a burst interval of 15 (resulting in four recordings of 7 minutes with 10 Hz per hour). Spectral analysis was performed on the pressure measurements to obtain significant wave height, while accounting for depth-dependent pressure. Subsequently, near-bed orbital velocity (m/s) was calculated based on the linear wave theory.

Statistical Analysis

All statistical testing was conducted in R studio (2023.03.1). 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 the assumptions. Post hoc comparisons were used to test for significant differences between configurations (r-package emmeans; Lenth 2016).

Mussel Cover Based on Sonar Data. In order to compare the rate of cover loss between the three configurations, a survival analysis was carried out based on maximum likelihood (Miller 1981). In summary, the average daily mussel cover loss rate (ε) per configuration was estimated as the inverse of the mean lifetime of the mussel structures (τ). To estimate the mean lifetime of the mussel structures, the difference in proportion of mussel cover (ρ_i) was determined for each monitoring time (t_i). As the BioShell-SMCs did not completely disappear throughout the duration of the experiment, a correction for these right-censored observations was incorporated to avoid underestimation of the mean lifetime (Equation 1):

$$\tau = \frac{1}{1 - \rho t\_\text{end}} \sum ((1 - \rho_i + 1) - (1 - \rho_i)) t_i + 1 \qquad (1)$$

Differences in cover loss rate (ε) were analyzed with a linear mixed-effects model from the R package *lme4* (Bates et al. 2015), with the log transformed cover loss rate as the response variable, the configuration as the explanatory variable and plot as random factor (mussel cover loss rate ~ configuration + [1|plot]).

Differences in mussel cover over time were analyzed with a repeated measures analysis of variance (ANOVA), with time as the within-subject factor (repeated), nested within the "Plot" factor, and configuration as the between-subjects factor (mussel cover ~ configuration + [1|plot/time]).

Differences in mussel cover at the final date were also analyzed with a linear mixed-effects model (mussel cover on final day ~ configuration + [1|plot]).

Mussel Biomass Based on Sample Data. A similar survival analysis (Equation 1) as for cover loss was used to assess changes in mussel biomass. Here, instead of calculating the difference in the proportion of mussel cover at each monitoring time, the difference in the proportion of mussel biomass was determined. Mussel density loss rate (ε) could not be transformed to meet the assumptions; we therefore used Friedman's tests (based on ranks). Plot was included as blocking factor, similarly to the random factor in a linear mixed-effects models (mussel density loss rate ~ configuration|plot).

Differences in mussel density over time were analyzed with a repeated measures ANOVA, with time as the within-subject factor (repeated), nested within the "plot" factor, and configuration as the between-subjects factor (mussel density ~ configuration + [1|plot/time]).

Differences in mussel density at the final date were analyzed with a linear mixed-effects model, with mussel density as the response variable, the configuration as the explanatory variable, and plot as random factor (mussel density on final day ~ configuration + [1|plot]).

Mussel Length and Condition. Differences in mussel length between configurations was analyzed with a linear mixed-effects model, with mussel length as the response variable, the configuration as the explanatory variable and plot as random factor (mussel length ~ configuration + [1|plot]). The condition index was analyzed in a similar way, with condition index as the response variable.

Results

Mussel Cover Based on Sonar Data

Based on the sonar data, we found a significant difference in cover loss between configurations ($F_{[2,6]} = 12.64$, $p = 0.007$; Figs. 4A & S1–S3). Contrary to what was expected, rate of cover loss was higher for the high density *banding pattern* than for the *low density labyrinth pattern* (Tukey, $p = 0.006$) but not

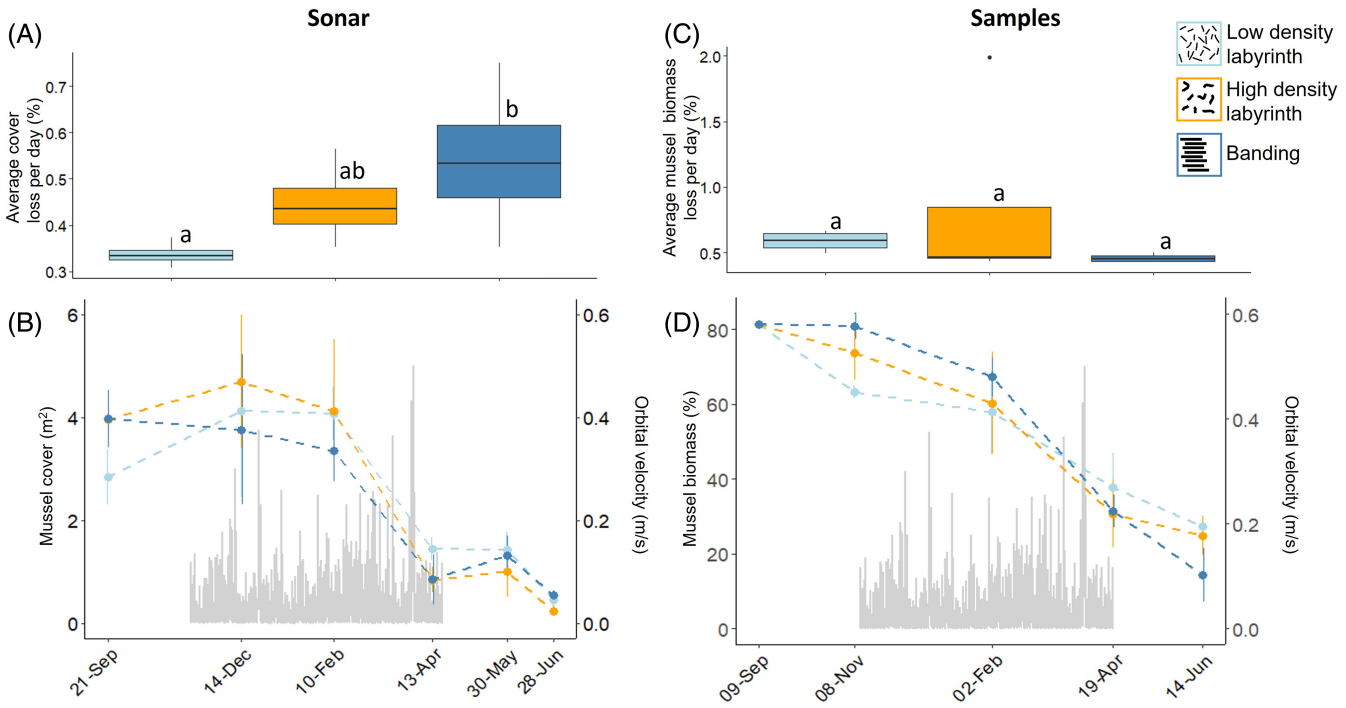

Figure 4. (A). Average loss rate of mussel coverage per day (%), between start and final measurement (293 days) based on sonar data. (B). Mussel coverage development over time (m^2) inside experimental plot (20 × 24m) for mussels transplanted in three configurations: low density homogenously spread SMC's (low density labyrinth pattern), high density homogenously spread SMC's (*high density labyrinth pattern*), and high density perpendicular SMC's (*banding pattern*). Gray graph on background is the orbital velocity (m/s). (C) Average mussel biomass loss per day (%) between start and final measurement (278 days). (D) Mussel biomass (%) over time inside experimental plot (20 × 24 m) for mussels transplanted in the same three configurations. Data are means ± SE ($n = 4$).

significantly higher for *high density labyrinth pattern* than for the *low density labyrinth pattern* (Tukey, $p = 0.050$). Cover loss rate was similar between both high density configurations (*banding pattern* and *high density labyrinth pattern*).

From September to mid-February, mussel cover was more or less constant across all experimental configurations (Fig. 4B). A nearly 80% strong decline in mussel cover occurred from mid-February to mid-April. Coinciding with this timeframe, there were instances of elevated near-bed orbital velocities (reaching up to 50 cm/s), which might signify losses attributed to hydrodynamic impact. Following this decline, the cover remained relatively stable again until the end of May, after which a subsequent decrease was observed. The pattern in mussel cover was consistent and not different ($F_{[2,9]} = 0.04$, $p = 0.959$) between configurations, which suggests the factors influencing mussel survival and distribution were not significantly influenced by the different spatial configurations.

At the start of the experiment, mussel cover was comparable for all configurations ($F_{[2,9]} = 1.43$, $p = 0.288$). In June, at the end of the experiment, mussel cover was affected by treatment ($F_{[2,6]} = 6.08$, $p = 0.036$). The high density *banding pattern* configuration exhibited significantly higher mussel cover compared to *high density labyrinth pattern* (Tukey, $p = 0.033$). Contrary to what we expected, mussel cover in the *low density labyrinth pattern* was not distinct from the high density configurations.

Mussel Biomass Based on Sample Data

We did not find a difference in average biomass loss per day between configurations ($\chi^2(2) = 2$, $p = 0.368$; Fig. 4D). This indicates that over the experimental period each configuration lost a comparable biomass of mussels from the BioShell-SMC.

We found a strong decline in mussel biomass (%) on the structures from the start until the end of the experiment (more than 70%; Fig. 4D). It started with more than 80% of the total weight being mussels and it ended with slightly more than 20%. We found no difference in proportion loss rates between configurations ($F_{[2,9]} = 0.08$, $p = 0.923$).

At the end of the experiment, mussel biomass within the structures was affected by configuration ($F_{[2,6]} = 7.69$, $p = 0.021$). However, we found no significant difference between the three configurations with post hoc analyses.

Mussel Length and Condition

Mean (± SE) mussel length at the start of the experiment was 22.34 ± 0.57 mm. At the end of the experiment after 278 days, mussels increased almost 75% to an average length of 38.95 ± 0.20 mm. The configuration in which the mussels were seeded, had no effect on mussel length at the final sampling date in June ($F_{[2,9.6]} = 0.3164$, $p = 0.736$; Fig. 5A). A lower growth rate was observed from November until April.

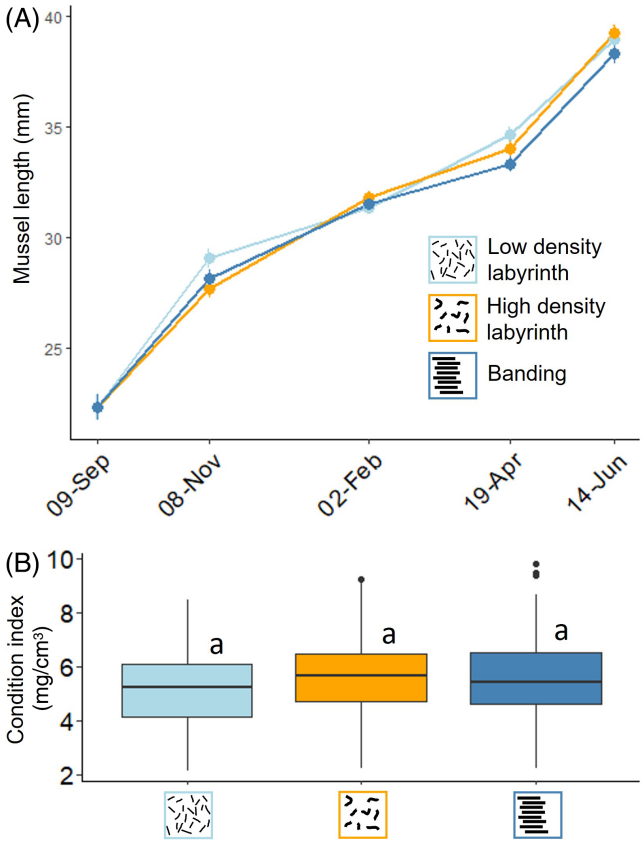

Figure 5. (A). Length (mm) over time of mussels transplanted in three configurations: low density homogenously spread SMCs (low density labyrinth pattern), high density homogenously spread SMCs (*high density labyrinth pattern*), and high density perpendicular SMCs (*banding pattern*). (B) Condition index (mg/cm^3) of the mussels at the end of the experiment (June 2022) for each configuration.

The initial condition index of the mussels was 10.12 ± 0.40 mg/cm^3. This CI decreased over the experimental period for mussels in all configurations by 54% to 5.51 ± 0.06 mg/cm^3 (Fig. 5B). The condition of the mussels was not affected by the seeding configuration ($F_{[2,9.7]} = 1.50$, $p = 0.271$).

Discussion

In a previous field experiment at the same location, mussels that were transplanted while attached to the BioShell-SMC demonstrated significantly higher survival rates compared to loose mussels (van den Bogaart et al. 2023*b*). Encouraged by these results, we aimed to conduct further research to improve and scale up restoration and aquaculture efforts, incorporating knowledge about the functioning of natural mussel beds. Specifically, during transplantation we (1) included a suitable attachment substrate for the mussels, to provide protection against predation and hydrodynamic dislodgement. And, we (2) tested the efficiency of implementing large-scale spatial patterns resembling the spatial organization of natural mussel beds to increase their resilience. As far as we are aware of, no large-scale field study has ever attempted to restore a subtidal ecosystem by actively incorporating large-scale spatial patterns (tens to hundreds of meters), that mimic the established patterns that are found on naturel ecosystems.

In contrast to our expectations, we observed overall high losses (approximately 75%) with no meaningful differences between spatial configurations, indicating that the BioShell-SMC is not effective on a large scale. When comparing these findings with those from the earlier study (van den Bogaart et al. 2023*b*), it became evident that the losses observed in the current study were more pronounced. Several factors may account for this difference in loss up to April, with one crucial consideration being the substantial impact of year-to-year variations on mussel survival. While the precise causes of this variability remain unclear, it is a well-recognized phenomenon that some years are more favorable for mussel survival than others. Due to resource and space limitations, we chose not to include loose mussels again in this experiment, as we anticipated significant losses of loose mussels due to hydrodynamics once again. This renders a direct comparison between the survival rates of loose mussels and BioShell-SMC mussels impractical. However, considering the findings from the earlier study, we anticipate even greater losses among loose mussels compared to BioShell-SMC mussels.

The losses found in our study were not excessive when compared to other experimental restoration efforts with mussels. For instance, Schotanus et al. (2020) reported an average decline of 65% in mussel coverage within the first month in their best-performing treatment. Similarly, Temmink et al. (2022) used biodegradable settlement substrates and observed a decline of intact structures during the first year, with a 42% decline due to burial, and an additional 28% of the structures being lost. However, when compared to mussel cultivation in subtidal areas, which is more similar in terms of environmental conditions with our experiment than the above intertidal restoration efforts, we observed a lower final mussel biomass. In mussel aquaculture, initial seeding losses are also substantial, reaching up to 69% (Capelle et al. 2016), often influenced by seeding density. Nevertheless, this trend is counterbalanced by a subsequent rise in relative biomass production, resulting in an average harvest of 1.5–2.5 kg per kg mussel seed after approximately 1–1.5 years (Capelle 2017). The low final cover and biomass observed in our study and previous restoration efforts highlight the difficulty of restoring mussel beds in dynamic environments. They also raise questions what factors might have contributed to the high losses observed in our study, even though our experiment was conducted within a designated mussel cultivation area. We delve into this problem from diverse viewpoints, including the way we implemented the spatial patterns, hydrodynamic dislodgement, burial, algal coverage, and predation.

Implementation of Spatial Patterns

Several studies have shown the importance of small-scale positive feedback-mechanisms in transplantation efforts by using clumped individuals rather than spacing individuals out, or by stimulating the formation of natural aggregations

(Silliman et al. 2015; Ladd et al. 2018; Temmink et al. 2020). However, there has been comparatively less research on implementing large-scale pattern formations in restoration efforts, even though there are numerous studies underlying the importance of natural patterns in ecosystems (Lejeune et al. 2002; Rietkerk et al. 2004; Pringle et al. 2010). Promoting small-scale facilitation in transplantation efforts involves transplanting organisms in a density that meets specific threshold levels. Additionally, arranging these organisms on a large-scale aims to optimize the utilization of limited resources (Rietkerk & Van de Koppel 2008).

Our experiment involved the attachment of mussels to biodegradable structures as a means to create stable small-scale aggregations. These structures provide shelter and attachment points during transplantation. They also enable mussels the potential to form patches by migrating away from these structures, while retaining the option to use them as stable structures for shelter or anchor points for forming clusters. Based on previous research (van den Bogaart et al. 2023*b*, 2023*c*), where migration behavior was observed, we had anticipated a greater degree of mussel dispersion from the structures in this study, due to the substantially higher initial densities. However, we did not observe this horizontal migration, either because it did not occur or because limited visibility at the study site prevented us from capturing it. Moreover, the side scan sonar recorded no increase in hard substrate cover, indicating a lack of migration of mussels onto the surrounding substrate. It is possible that the high initial densities (6 kg/m) triggered intense competition for space, resulting in smothering of mussels, leading to elevated mortality rates (Newell 1990; Capelle et al. 2014). The concept of competition for space has been demonstrated in other studies involving mussels (Fréchette & Despland 1999; Lauzon-Guay et al. 2005), as well as in other invertebrates such as barnacles (Lohse 2002) and Baltic macoma (Olafsson 1986). Capelle et al. (2014) found that as mussel density increased, redistribution decreased. A similar pattern could have occurred in the present study. Our findings indicate no differences in condition and growth between the various configurations, implying that the mussels exhibited similar performance across all situations. However, the limited variation in local densities between configurations makes it challenging to demonstrate clear competition effects based on the results from the current study. The condition index of the mussels decreased from September until April with approximately 50%, which could be due to competition. However, the condition index of mussels exhibits a clear seasonal cycle, with improved conditions in summer and autumn, followed by a gradual decline during winter, reaching their lowest point in spring, before rapidly rising again as summer approaches (Okumuş & Stirling 1998).Throughout the entire study period, the BioShell-SMC's mesh remained intact, preventing the dispersion of cockle shells onto the seafloor. Ideally, the net should have degraded within 6 months after its deployment in spring. This degradation would have allowed the cockle shells to naturally disperse, starting from mid-winter onward as the net gradually began to break down. Consequently, the limited availability of attachment points on the adjacent seafloor potentially impeded mussels from migrating away from the BioShell-SMC structures. Mussels favor hard substrate above soft substrate (van den Bogaart et al. 2023*c*), a preference that may be facilitated by the earlier dissolution of the biodegradable net used in the BioShell-SMC. The initial high densities and the minimal dispersal away from the structures onto the surrounding substrate (as evidenced by the decreasing hard substrate cover) raises questions about the effectiveness of this method in initiating natural aggregations. The fact that we observed high biomass losses but limited migration from the SMCs onto the surrounding substrate, implies that either the mussels that undertook migration were subsequently lost, or migration itself was a rare occurrence. The suboptimal use of the available substrate area may have resulted in increased competition rather than facilitation in all configurations.

In addition to potential constraints at a small scale, there are also potential challenges arising from the large-scale spatial arrangement of the BioShell-SMCs. For instance, in terms of the optimal configuration, structures positioned too far apart from one another could potentially give rise to fragmented patterns rather than cohesive ones. This, in turn, could potentially limit mussel bed resilience to wave disturbance (de Paoli et al. 2017). Conversely, too closely spaced structures could lead to resource depletion, as indicated by Saurel et al. (2013). That is, the water flow over a mussel bed leads to seston depletion in the boundary layer. When bare patches without mussels are encountered, vertical mixing replenishes nutrients upon reaching the subsequent mussel patch. *Re*-suspension, as identified by Saurel et al. (2013), happens during high current velocities. Therefore, optimal configuration and mussel band size depends on prevailing environmental conditions. At our experimental location, we measured relatively low near-bed orbital velocities (mostly 0–10 cm/s). It is plausible that the patch dimensions in which the mussels were placed were unsuited for an environment where strong currents, causing re-suspension, are minimal. Another possible explanation for low survival rates might be the low initial cover. We placed the mussels in concentrated stripes and anticipated redistribution into wider striped patterns that are consistent with natural beds. With an initial cover of 0.75% in our plots, and a comparable amount of attachment substrate (i.e. BioShell-SMC) in every configuration, the significance of the initial spatial arrangement of the BioShell-SMCs might have been attenuated, resulting in comparable loss rates across all configurations. As demonstrated by Sleeman et al. (2005), slow-growing corals at low initial transplant densities (0.45% cover) had less dependency on specific spatial arrangements than evenly spaced gridded transplanting arrangements. To address this, reducing plot size and a better dispersion of initial cover, rather than highly clustered aggregations, could enhance small-scale positive feedback and long-range negative feedback, ensuring regular patterns in the structures.

Hydrodynamic Dislodgement and Burial

A second factor to consider in relation to the overall high losses is hydrodynamic dislodgement. Despite relatively low average near-bed orbital velocities measured in our study, we found a decline in cover across all configurations, indicating a loss of structures or mussel clumps, notably between February and

April. In this period, a series of storms with wind originating from the northeast, had a notable impact on the near-bed orbital velocity. This was attributed to the bay's sheltered location by the surrounding landmass, resulting in diminished effects from winds originating from alternative directions. When comparing the outcomes of this field experiment to those of a previous study conducted at the same location, we observed lower survival rates of mussels attached to the BioShell-SMC in the current study compared to the earlier one (41 vs. 79% by the end of April). When comparing the highest wind velocities originating from the northeast during the first experiment with those in our study, the earlier study documented higher maximum wind speeds from the northeast direction (79.2 vs. 72 km/h). Other studies have shown that mussel in clumps or stripes persisted at higher orbital velocities than measured in our experiment, between 40 and 60 cm/s (Bertolini et al. 2019) and patches with shells even persisted at 70 cm/s (Capelle et al. 2019). Moreover, on soft substratum, similar to the conditions found at the Zandkreek, it was found that erosion around a mussel patch and sedimentation behind it contributed to enhancing patch stabilization by reducing the height above the sediment (Capelle et al. 2019). This scouring was linked to patch weight, indicating that heavier patches were less prone to hydrodynamic dislodgement. Therefore, we expected the BioShell-SMCs to be stable structures in the field due to reduced mussel dislodgement with increasing biomass. Hence, we anticipate that hydrodynamic dislodgement is unlikely to be the primary cause of the substantial losses.

Another factor worth considering as contributor to high losses is burial. It is possible that our structures were partly buried under the sediment and thus became invisible to the sonar, leading to a decrease in cover. This phenomenon was observed in a large-scale (20 × 10 m plots) mussel restoration experiment by Temmink et al. (2022), where biodegradable structures were placed in bands mimicking natural patterns. Suspended sediment deposition on top and around their structures caused significant burial (25–70%). Notably, bands closest to the gully were buried the least (25%), while bands behind the first row were buried most deeply (60–70%). Also on mussel plots, mussels are known to trap sediment and accumulate pseudofaeces up to 10 cm during the summer (ten Brinke et al. 1995). In our sheltered experiment away from a gully, the structures might have experienced significant burial, potentially leading to a decrease in cover visibility observed with sonar. These findings raise concerns about the suitability of placing structures for future mussel bed restoration efforts. Nonetheless, a more rapid degradation of the BioShell-SMCs would require mussels to reorganize autonomously, which could potentially lead to increased survival.

Macroalgal Coverage

In our field observations, we noted that mussels served as attachment substrates for various organisms, especially macroalgae. The side scan sonar's ability to distinguish between vegetation and sediment has been shown to be largely unaffected by high algal cover (Greene et al. 2018). Several studies have examined the impact of algal epibionts on mussel populations, for example by reducing mussel growth by affecting mussel energetics (Dittman & Robles 1991). Furthermore, macroalgae have been suggested to potentially impede mussel feeding (Paine & Suchanek 1983), although this effect was not confirmed in another study by O'Connor et al. (2006). Macroalgae coverage may also affect mussel survival by increasing flow-induced forces leading to dislodgement and increasing mussel loss rate by an increase in drag-induced lift (Witman & Suchanek 1984; Denny 1987; Dittman & Robles 1991; O'Connor et al. 2006; O'Connor 2010). As previously mentioned, wind and currents were not expected to be the primary factors causing mussel loss, given the relatively low orbital velocities we measured. However, when we consider that the dislodgement threshold significantly decreases when algae are attached to the mussels, it raises the possibility that the structures may have been set in motion due to drag-induced lift, particularly between February and April. In contrast, we observed almost no algae during the previous small-scale experiment (van den Bogaart et al. 2023*b*), which could potentially account for the greater resilience of the structures during that period. Nonetheless, it is essential to emphasize that without a direct comparison with uncovered mussels during the same time period, the overall mussel loss attributable to macroalgae remains speculative.

Predation

To minimize predation risk, we used larger mussels in our experiment based on findings from our previous study (van den Bogaart et al. 2023*b*). Moreover, we anticipated reduced predation pressure attributed to a safety-in-numbers effect, given the considerably larger scale of the current experiment compared to the previous one. This scaling-up was anticipated to lead to a reduction in predation pressure. However, despite these precautionary measures, we observed numerous crabs and crushed mussel shells on the experimental plots. According to Davidson (1986), crabs prey on mussels by either crushing the shell or chipping it, leaving behind only shell fragments. This observation suggests that crabs were a significant cause of mussel loss in our field experiment, even when larger mussels were used.

Challenges and Opportunities for Restoration

Our findings revealed significant cover and biomass loss rates across all configurations, indicating the challenges faced by mussel transplantations. One important explanation might be the lack of migration from the BioShell-SMCs, resulting in suboptimal space utilization and fostering high competition rather than facilitation. Nevertheless, when compared to other studies involving mussel transplantations in intertidal zones, our losses were not considered excessive. But in comparison to mussel cultivation, which aligns more closely with our study in terms of environmental conditions, an increase of at least 1.5–2.5 times the original seeding amount would be expected within a year. The typical average seeding density in Dutch mussel cultivation is 1.0–2.5 kg/m^2 on plot scale, although there are locally higher densities up to 10 kg/m^2 (Capelle et al. 2014). In our study, with

an initial mussel biomass of 6 kg/m on the BioShell-SMCs, the local densities on the plots became excessively high due to the intensely clustered configuration. Enhancing the dispersion of BioShell-SMCs and encouraging mussels to migrate from the structure—perhaps achieved through the earlier dissolution of the biodegradable mesh—holds the potential to reduce transplantation losses. It is important to note that mussel survival is significantly influenced by year-to-year variability, a phenomenon widely acknowledged among Dutch mussel farmers. The underlying causes of this interannual variation remain uncertain. To address and minimize this inherent variability, a promising approach would be to conduct the current experiment consistently over several consecutive years, with loose mussels and BioShell-SMC mussels. Furthermore, we used sonar analyses to monitor mussel cover, a technique that demonstrated its reliability, evident from the consistent decrease in mussel presence compared to samples. In summary, our study highlights the complex interplay of factors influencing facilitation and competition of ecosystem engineers in dynamic environments. It also demonstrates that the lack of small-scale facilitation can hamper large-scale facilitation. Future research in this direction should aim to comprehend the potential benefits of implementing self-facilitation and spatial patterns simultaneously and to expand their applicability to a wider range of species and restoration contexts. In the context of mussels, it may be interesting to uncover the effectiveness of one of the applied configurations when transplanting loose mussels and cockle shells in a pattern, as opposed to using the BioShell-SMC.

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Supporting Information

The following information may be found in the online version of this article:

Figure S1. Evolution of transplant configurations acquired through sonar scanning.
Figure S2. Evolution of transplant configurations acquired through sonar scanning.
Figure S3. Evolution of transplant configurations acquired through sonar scanning.

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