Putting self-organization to the test: labyrinthine patterns as optimal solutions for persistence

Abstract

Spatial patterns formed through the process of self-organization are found in nature across a variety of ecosystems. Pattern formation may reduce the costs of competition while maximizing the benefits of group living, and thus promote ecosystem persistence. This leads to the prediction that self-organizing to obtain locally intermediate densities will be the optimal solution to balance costs and benefits. However, despite much evidence documenting pattern formation in natural ecosystems, there is limited empirical evidence of how these patterns both influence and are influenced by trade-offs between costs and benefits. Using mussels as a model system, we coupled field observations in mussel-culture plots with manipulative laboratory experiments to address the following hypotheses: (1) Labyrinthine spatial patterns, characteristically found at intermediate to high patch densities, are the most persistent over time; this is because labyrinthine patterns (2) result in adequately heavy patches that can maximize resistance to dislodgement while (3) increasing water turbulence with spacing, which will maximize food delivery processes. In the field, we observed that labyrinthine 'stripes' patterns are indeed the most persistent over time, confirming our first hypothesis. Furthermore, with laboratory experiments, we found the 'stripes' pattern to be highly resistant to dislodgement, confirming the second hypothesis. Finally, with regards to the third hypothesis, we found positive effects of this pattern on local turbulence. These results suggest that the mechanisms of intraspecific facilitation not only depend on initial organism densities, but may also be influenced by spatial patterning. We hence recommend taking into account spatial patterns to maximize productivity and persistence in shellfish-cultivation practices and to increase the restoration success of ecosystems with self-organizing properties.

Keywords Benthic dynamics; Density-dependent**;** Facilitation; Habitat complexity; Mussel beds; Self-organization

Introduction

Ecological systems are governed by complex interactions between organisms and their surroundings. These interactions may result in the formation of spatial patterns (Levin and Segel 1985, Rohani et al. 1997, Solé and Bascompte 2006), which add layers of complexity to originally homogeneous environments and thus generate heterogeneity in landscapes (Guichard and Bourget 1998). Spatial patterns can result from ecological processes through a process called spatial self-organization, where organisms spontaneously arrange themselves in a non-random manner through interactions between organisms, or between organisms and their environment. Self-organized spatial patterns have been found in nature across a variety of ecosystems, ranging from arid environments through peatlands to intertidal flats and coral reefs (Levin and Segel 1985, Rietkerk and van de Koppel 2008). Self-organization is hypothesized to be driven by the interplay of short-range facilitative mechanisms that allow organisms to cope with limited resources or harsh environments (Rietkerk and van de Koppel 2008), and long-range mechanisms of inhibition and competition. While the ubiquity of pattern formation has been well-studied and predicted by theoretical models, empirical mechanistic studies have been limited on how these patterns affect ecosystem resistance (de Paoli et al. 2017), i.e. the ability of a system to remain ‘unchanged’ despite disturbance (Grimm and Wissel 1997).

Density is a key driver of spatial patterning (van de Koppel et al. 2008, Capelle et al. 2014, Liu et al. 2016). Density-dependent mechanisms, such as growth and mortality, are common features in resource-limited (by food, space) environments (Brook and Bradshaw 2006). In such environments, organisms’ ~~may have~~ strategies to minimise mortality risks may facilitate each the ~~other’s~~ growth and survival of conspecifics~~or help to minimize losses, thus gaining safety in numbers~~. These interactions may result in self-organized patterns, leading to locally optimal densities (Turing 1952) that result in both facilitation and protection. The existence of locally optimal densities has been suggested by models of organism movement and cooperation (e.g. de Jager et al. 2014). However, initial density depends upon external factors, for which the effects on pattern persistence are not yet fully understood.

Environmental contexts, such as amount of rainfall or number of consumers, can directly affect density and system resistance to acute stress (Weerman et al. 2011, Oliveira et al. 2013, Siteur et al. 2014), and thus drive the occurrence of spatial patterns. These patterns should then result in feed-backs to organisms, forming regulatory mechanisms that maintain the specific density required for system stability (Liu et al. 2014). Optimal density is therefore intrinsically linked with environmental context, and together the two processes can determine system stability (Rietkerk et al. 2004). Gaining a mechanistic understanding of the optimal patterning of patches, and how organisms exploit this process to optimize resistance to disturbance, can thus provide a useful basis for spatial planning in both conservation and commercial contexts, provided that the relation to specific environmental context is well understood.

The formation of self-organized spatial patterns in mussel beds provides a unique, easily accessible model system to study the relation between density-dependent pattern formation and environmental drivers, such as the minimization of individual mortality by decreasing wave-driven dislodgement via the formation of heavy clumps (Capelle et al. 2019) and other forms of population loss (e.g. predation). Density-dependent pattern formation has been well-described for mussel beds (van de Koppel et al. 2008) and can easily be investigated under changing environmental factors. This will not only improve the mechanistic understanding of ecosystem functioning, but can also serve as a guide to successful conservation and restoration of these complex temperate reef formers (Silliman et al. 2015) and help towards finding better culturing techniques to maximize yield (Capelle et al. 2016). Moreover, a deeper understanding of the mechanistic principles that underlie spatial self-organization would allow for insights into other ecosystems showing these patterns, such as arid bushlands and patterned peatlands.

In order to translate theories on density-dependent pattern formation into practice, we combined field observations with manipulative laboratory experiments. The aims of this study were to assess the development of patterns in real-life scenarios, quantify their resistance to disturbance (Donohue et al. 2013) and reveal the mechanisms behind these patterns. Specifically, we tested the hypotheses that (1) labyrinthine spatial patterns, characteristically found at intermediate to high patch densities, are the most persistent over time. We further hypothesized that this is because labyrinthine patterns (2) result in adequately heavy patches that can maximize resistance to dislodgement while (3) increasing water turbulence with spacing, which will maximize food delivery processes.

Methods

Pattern type and resistance (field observation)

In order to assess pattern development and persistence over time across an environmental gradient, a subtidal mussel culture plot was surveyed. Culture plots are ideal model systems to assess the interactions among spatial heterogeneity, pattern formation and stability. Bottom culture activities are prone to high losses, ~~(~~ca. 50%, especially during winter months; Capelle et al. 2016~~)~~. Currently, aquaculture of bivalves such as mussels using bottom culture techniques is carried out in such a way that mussels are relayed in a highly heterogeneous manner to the seabed by seeding in circular tracks with average densities adjusted according to farmers' experiences (Capelle 2017a). This results in different large-scale spatial patterns across the landscape. However, culture plots are also large enough to contain heterogeneous environmental conditions (Newell and Shumway 1993). This can lead to differential effects on shellfish behavior and growth (Newell and Richardson 2014); thus, density might be adjusted accordingly.

We used a subtidal plot (size: ca. 8 ha) located in the Oosterschelde, the Netherlands, (51 37' 14.99" N, 4 5' 16.89" E, Fig. 1), which spanned a depth gradient from 2 to 8 m (chart datum, Fig. 1). Hydrodynamic measurements taken in March 2015, as an index of environmental stress (Reusch and Chapman 1997), indicated that the predominant flow progressed from west to east with incoming tides and thus east to west with outgoing ebb tides). Flow velocities at the site averaged 0.45 m/s. This site is used for cultivation of 'year-1' seed and was seeded with mussels in July 2017 with the standard bottom-culturing techniques used in the Netherlands (for details on the bottom culture of mussels in the Oosterschelde, see Capelle 2017a).

Two photographic surveys were conducted. The first photo-survey was carried out in September 2017 just before the start of the storm season, which can cause major dislodgement of mussels, but two months after initial seeding to enable sufficient time for patterns to form. The second photo-survey was done in April 2018, one week before harvest, to maximize the period used for measuring persistence in relation to patterning. A frame (50 x 50 cm) was used to take top-down photos using a GoPro (Hero session 4, GoPro Inc.), which allowed us to take pictures of a constant area of seabed (Capelle 2017b). To ensure adequate representation of the whole plot area, the plot was divided into a grid of 8 (E-W) x 3 (N-S) squares to obtain a total of 24 squares. The frame was dropped three times in each square to obtain replicates, resulting in 72 images taken during each survey.

Images were then analyzed for 4 specific patterns: ‘no mussels’, ‘sparse clumps’, ‘stripes’, and ‘homogeneous’ (Fig. 2). These are the patterns that were identified in density-dependent self-organization by Liu et al. (2013), using a combination of models and field observation. In our images, we modified the categories found by Liu et al. (2013) by combining the ‘open labyrinth’ and ‘gapped patterned’ in the ‘stripes’ category. Approximate densities were calculated for each pattern from pictures taken in September 2017 (Table 1).

Dislodgement (flume and wave tank experiments)

To understand if patterns in stability over time are due to resistance from abiotic environmental stressors, we simulated flow and waves with two experiments to assess dislodgement thresholds. A racetrack flume (17.5 m long, 0.6 m wide, 0.25 m water deep) at the Royal Netherlands Institute for Sea Research (NIOZ) was used for this purpose. The flume experiment was run in April 2018. Four patterns of mussels organization (i.e. ‘sparse’, ‘clumps’, ‘stripes’ and ‘homogeneous’) were created on top of a layer of soft-sediment that was representative of field condition and deep enough to prevent attachment to the hard bottom of the tank. Pattern stability was tested sequentially in the flume, and each pattern was replicated twice in a random order. Mussels (30.1 ± 0.7 mm length) were left in the pattern in the flume overnight (minimum 12 hours) to acclimatize and form attachment before exposing them to water flow, and new mussels were used for each test. For the dislodgement measurements, flow was increased gradually from an engine setting of 100 rpm, which yields a flow velocity of circa 5 cm/s, in increments of 100 rpm (i.e. approximately 5 cm/s) every 2 minutes until full (100%) dislodgement was observed. At each step-wise increase, dislodgement was estimated as the proportion of the clump.

To assess how patterns responded to wave action in subtidal environments, a second dislodgement experiment was conducted in wave tanks (NIOZ wave tanks, 350 cm x 100 cm x 80 cm, experimental area 200 cm x 89 cm) between March and May, 2018. For this experiment, 500 mussels (corresponding to 300 individuals/m^2 or 0.9 kg/m^2) from the same source as those used in the flume experiment were added to the experimental arenas. Mussels were organized according to the four treatments (‘sparse’, ‘clumps’, ‘stripes’, ‘homogeneous’) on top of a layer of soft-sediment representative of field conditions, deep enough to prevent attachment to the hard bottom of the tanks. For this experiment, four wave tanks were used. For every new experimental day, two of the tanks were used as controls (no waves, to disentangle dislodgement from behavioral movement) and two were used with wave action (wave strength ca 1.7 N). A total of 32 trials (N = 8) was conducted over 8 days, with treatments assigned to tanks in a randomized order. To be able to monitor dislodgement of individual mussels, each tank was divided into 5 zones of equal size, from the front to the back of the tank, perpendicular to wave direction. In each zone 10 out of the 100 mussels were painted with nail varnish (i.e. a different color in each zone). Dislodgement was quantified as the proportion of colored mussels missing from their original location at the end of 24 h trials, when the number of colored mussels in each zone was counted and the color noted. This gave a total of 160 observation ‘zones’. New mussels were used for each trial.

Flow modification (flume experiment)

From the same flume experiment described above, we took velocity profiles to assess the role of patterns in modifying flow, which could potentially affect resource availability (Frechette et al. 1989, Widdows et al. 2009). Vertical flow velocity profiles were measured with a 3D Acoustic Doppler Velocimeter (ADV, Nortek). The beams of the ADV measure velocity in a sample volume of 0.6 cm in diameter and 3.4 cm in vertical range. The sampling frequency was set at 100Hz and the recording time at 4 minutes for each measuring point. The sample volume can be divided into a finite number of cells: for all the experiments, the size of the cells was set at 0.2cm for a total number of 18 cells. Profiles were measured in a 3 x 3 grid, spanning the width of the flume (5 cm from the edges and middle), and included measurements of flow 5 cm before the patches started, over the mussel patches and 5 cm after the patches ended. Measurements were initiated at the beginning of exposure to flow and conducted at two flow velocities: a slow flow setting (100 rpm, circa 5 cm/s) and a faster flow (400 rpm, circa 20 cm/s). From these measurements, we could obtain both velocity changes and turbulence measurements (Turbulent Kinetic Energy, TKE).

Data analyses

Pattern type and resistance (field observations)

Statistical analyses were conducted in R (R Development Core 2018). We ran a multinomial model (*multinom* in package *nnet*, Ripley and Venables 2016) with pattern set as the response variable and position on the grid (east to west), time of sampling event (September or April) and their interactions as predictor variables. The Wald z-test was used to obtain overall factor significance using the package *afex*, followed by Tukey adjusted post-hoc comparisons of estimated marginal means of the probabilities (*lsmeans*, Lenth 2016). A pseudo-R^2 to assess model fit was calculated as the 1-log likelihood of the model/log likelihood of the null model.

Dislodgement (flume and wave tank experiments)

For the two laboratory experiments, linear models were used to address dislodgement. The first linear model was used to assess how the proportion of the clump dislodged was affected by the interaction between patterns of organization and flow speed settings in the flume experiment. A second linear model was used to assess how the proportion of colored mussels dislodged from their original zone was affected by the interaction between patterns of organization and wave presence in the wave tank experiment.

Flow characteristics (flume experiment)

The data collected were first filtered to remove unreliable data, i.e. beam correlation and signal-to-noise ratios lower than 95% and 30 dB, respectively. Second, the time-averaged velocity of every cell was calculated in order to obtain the velocity profile of the components u, v, w. TKE was then calculated as $\frac{1}{2}$ (u^2+v^2 + w^2). Extraction of velocities and TKE were carried out using custom-made functions in MATLAB (MATLAB 2016) while R was used for statistical analyses. Linear models were used to assess how flow velocity and TKE were affected by patterns of organization (‘sparse’, ‘clumps’, ‘stripes’ and ‘homogeneous’), position along the x axis and their interaction for each flow velocity.

Models were visually validated for normality (qqplot) and homogeneity of residuals (Zuur et al. 2013). For the dislodgement experiments in the flume, residuals were also tested for autocorrelation using an ACF plot. To assess model fit, adjusted R^2 values were considered and reported. ANOVA tables, with type III sums of square when interactions were significant and type II when there were no significant interactions to allow for appropriate detection of single-term effects (Langsrud 2003), were then produced to assess overall factor significance. Then pairwise comparisons were carried out using Tukey-adjusted post-hoc comparisons of estimated marginal means (*lsmeans)*.

Results

Pattern type and resistance

We observed a clear relation between the presence of self-organized spatial patterns and the spatial locations across the sampled grid, although this proved quite variable over time. The probability of finding specific patterns (Fig. 3) was found to depend on the position in the spatial grid from east to west (X^2= 78.7, $p < 0.001$) and time of sampling (X^2= 16.35, $p < 0.01$), and no interaction was found between space and time ($p > 0.05$, pseudo $R^2 = 0.3$). The probability of finding areas without mussels (Fig. 3), in particular, increased during the winter from September to April (Tukey adjusted comparisons: $p < 0.01$). In April the probability of finding area without mussels (Fig.3) decreased from the eastern-most edge towards the west (Tukey adjusted post-hoc: $p <0.0001$), and then increased again at the western-most edge (Tukey adjusted post-hoc: $p < 0.05$). In April we found a decrease in the probability of finding ‘homogeneous’ patterns compared with before winter in September (Tukey adjusted comparisons: $p < 0.05$, Fig 3). This result was consistent across the grid. The other patterns were consistent across both time (sampling points) and space (grid); however, there was a greater overall probability of finding ‘stripes’ and ‘clumps’ compared with ‘sparse’ patterns in mussels (Tukey adjusted comparisons: $p < 0.05$). The probability of finding ‘stripes’ was the same for both sampling points (Tukey adjusted comparisons: $p > 0.05$).

Dislodgement

The flume experiments revealed that self-organized patterns determined the ability of mussels to avoid dislodgement by water flow. Critical dislodgement depended on the organization pattern (organization*speed: $F_{3,73}= 3.5$, $p < 0.05$, Fig 4a, adjusted $R^2 = 0.53$), with ‘sparse’ showing higher dislodgement rates than the other treatments, with dislodgement starting at a current velocity of 25 cm/s (Tukey adjusted comparisons of ‘sparse’ vs ‘stripes’ and ‘homogeneous’ $p < 0.001$, vs ‘clumps’ $p < 0.05$). While there was no interaction between wave presence and organization (organization*wave presence $p > 0.05$, adj $R^2= 0.27$), the percentage of mussels missing from their original position in the tanks was affected by organization ($F_{3,152} = 19.4$, $p < 0.0001$, Fig. 4b, adjusted $R^2 = 0.27$). As expected, dislodgement was always greater in the presence of wave action ($F_{1,152} = 3.9$, $p < 0.05$). Initial ‘pattern’ effects were due to ‘sparse’ and ‘clumps’ showing the greatest percentages of movement from the initial zone compared with ‘stripes’ and ‘homogeneous’ (Tukey adjusted comparisons $p < 0.05$). The ‘homogeneous’ and ‘stripes’ were the most resistant, showing nearly no movement and no dislodgement.

Flow modification

Spatial self-organization was found to modify benthic water flow patterns in ways that may potentially benefit mussels by both slowing velocity and increasing turbulence. Spatial patterns were able to modify bottom flow profiles in different ways across the patches under both slow and fast velocity settings (organization*position, slow velocity: $F_{6,320}$=4.8, $p <$ 0.001, adjusted $R^2 = 0.29$; TKE: $F_{6,320}$=5.7, $p < 0.001$, adjusted $R^2 = 0.14$; fast velocity: $F_{6,409}$=4.5, $p < 0.001$, adjusted $R^2 = 0.14$, TKE: $F_{6,409}$=10.8, $p < 0.001$, adjusted $R^2 = 0.25$; Fig. 4a-d). Flow was slower in the middle of the patches, particularly when the mussels were organized in 'stripes' or 'homogeneous' (for both, Tukey adjusted post-hoc: middle vs. front p <0.001). The observed slowing down of velocity was associated with an increase in TKE when mussel patches were organized into 'stripes' (Tukey adjusted post-hoc: $p < 0.001$). Moreover, in all treatments, there was accelerating flow at the back of patches compared with both the front and middle under both flow conditions (Tukey adjusted post-hoc back-front and back-middle: $p < 0.0001$), but only when mussels were organized in 'stripes' or 'homogenous' distribution patterns. TKE increased at the back of the patches under both flow conditions (Tukey adjusted hoc: $p < 0.001$).

Discussion

We tested experimentally whether the formation of self-organized patterns affects the resistance of mussel bed ecosystems in stressful environments. Our results highlight the higher resistance conferred by the local densities of mussels when aggregated into patterns. The labyrinthine spatial patterns formed in beds with densities of ca. 1500 mussels/m^2 (Table 1) were found to be the most resistant to hydrodynamic disturbance in our experiments. Our results suggest that two main mechanisms may be responsible for these observed responses to labyrinthine patterns: reduction in critical dislodgement velocities and local decreases in water flow accompanied by increases in turbulence, which is expected to increase resource acquisition by increasing the mixing of water layers.

Observation: Labyrinths are the most persistent

Our field observations in September 2017 and April 2018 revealed that the stability of mussel beds was clearly related to spatial patterning. In particular, we observed the patterns in mussel loss between these two sampling points in the year, which occurred before and after the harsher season during the culturing period, i.e. winter. In winter, environmental conditions are more stressful due to food limitation and more extreme weather patterns, driven by increased storm intensity and frequency (Smaal and Haas 1997). The losses were particularly high when no self-organization was present (particularly for the sparse mussel pattern), and increased along the environmental stress gradient (east compared with west, consistent with flow direction). The probability of finding mussels that had not self-organized at low densities was already low in September. However, it should be noted that the site had been seeded in July, so the time of our first sampling was already two months after seeding had taken place. Self-organization and dislodgement have been found to operate over short time scales (van de Koppel et al. 2008, Capelle et al. 2014). Thus, initial dislodgement of sparsely distributed individuals could have led to the formation of clumps and stripes, by increasing encounters with conspecifics with which to form aggregations (de Jager et al. 2014).

The initial accumulation of high-density patches on the western edge of the beds in September 2017 could have been driven by seeding patterns initiated by the farmer, greater food available on the 'flow' side of the tide, or simply by the physical effects of the water current. The probability of finding homogeneous patches, however, also unexpectedly decreased between September 2017 and April 2018, suggesting that pattern formation emerges from more than simply the principle of 'safety in numbers'. Winter months have the lowest primary production; thus, depletion could occur at short distances from edges (Smaal and Haas 1997). Our observations suggest two potential mechanisms for pattern persistence over time: a reduction of risk and maximization of resource availability (Guichard 2017).

Mechanism 1: Minimizing risk of dislodgement

With laboratory experiments simulating realistic flow and wave conditions, we confirmed that labyrinthine spatial patterns can maximize resistance to dislodgement (e.g. van de Koppel et al. 2008, Liu et al. 2013). Previous studies in a similar flume set-up found that clump dislodgement thresholds were directly related to clump mass (Capelle et al. 2019). For our experimental design, we did not weigh clumps. The focus in this study was to understand the specific role of patterns resulting from mussel self-organization, which is an intrinsically density-dependent process, so different biomasses would be expected. Thus, we specifically only manipulated shape and did not standardize mass across treatments. We observed in the flume that clumps and stripes did not separate into single mussel individuals before dislodgement, but rather dislodged as a whole clump or a whole stripe. Observations suggest that this was due to the erosion of sediments around the mussels, similarly to what has been observed in aquatic vegetation systems (Vandenbruwaene et al. 2011), but this should be investigated further with measurements of bed level changes. The first stripes to dislodge were at the edges, and the last to go was the stripe in the middle, suggesting spatial heterogeneity in the velocity profiles, which might be created by this specific way of self-organization with neighboring stripes, creates protection for the stripes formed in the middle, which again warrants further examination.

Overall, our results indicate that hydrodynamic forces can interact with direct animal movement to aid the formation of mussel bed patterns. In the wave experiments, we observed that wave action initially leads to dislodgement of mussels in the middle of tank and the formation of larger, stronger bands. Moreover, initial dislodgement of sparsely distributed mussels can lead to the formation of small clusters, increasing the resistance of mussel beds. The interplay of hydrodynamic forcing and animal movement should be investigated more thoroughly as it can provide important insights into the mechanisms of mussel bed formation, as well as improvements in restoration and cultivation practices.

Mechanism 2: Maximizing facilitation by altering flow (improving food access)

Results from the present study suggest that self-organization leading to labyrinthine patterns can maximize facilitation. In our system, mussel aggregation into stripes may be the optimal solution to maximize food delivery processes. The physical presence of the bed increased water turbulence, which can maintain a high level of food by sustaining concentrations of plankton due to improved mixing (Fréchette and Bourget 1985, Fréchette et al. 1989, Lassen et al. 2006) and resuspension of benthic food sources (Prins et al. 1992, Widdows et al. 2009, Lauringson et al. 2014). Clustered mussels formed obstacles that slowed down the water directly flowing over the mussels, deflecting moving water to the sides of the patches. This phenomenon has already been observed for other mussel beds (e.g. Carrington et al. 2008) and plant tussocks (e.g. van Wesenbeeck et al. 2008), and can be attributed to the presence of raised beds or to the biological activity of mussels (Van Duren et al. 2006, Widdows et al. 2009). In plant systems, this reduction of flow rate was found to be a facilitative mechanism leading to increased growth (Van Hulzen et al. 2006). In mussel bed systems, on the contrary, reduced flow may be considered detrimental, particularly for homogeneous, high-density patches. Slow flow could cause food depletion, leading to slower growth rates in the middle of beds compared with edges (Newell 1990, Svane and Ompi 1993).

Large clumps in our trials slowed down the flow to a larger degree than stripes, but did not modify turbulence compared with the situation before patch formation. This effect may lead to increased competition in homogeneous patches, even at the small-scales investigated in our experiments (Commito et al. 2006). Striped patterns still slowed flow, but they also increased turbulence both in the middle and back of patches. This differs from previous experiments where changes in turbulence were only observed at the back or downstream of patches

(Folkard and Gascoigne 2009). The direct relationship between bed roughness and turbulent flow in mussel beds has already been observed by Butman et al. (1994), and topographic heterogeneity was also found to be directly linked with changes in turbulent flow in boulders and artificial reef systems (Guichard and Bourget 1998, Guichard et al. 2001). Thus, if the structural presence itself causes a reduction in flow rates, a pattern which is able to maximize turbulent flow should be beneficial. This has already been demonstrated at larger scales where alternation of mussels patches with bare sediment patches increased overall productivity of the system via changes to the boundary layer and resuspension-inducing mechanisms (Folkard and Gascoigne 2009, Saurel et al. 2013). Here, we showed it to be a potential driver of the pattern formation at smaller scales that is common in behavioral self-organization (van de Koppel et al. 2005, Gascoigne et al. 2005, Commito et al. 2006).

Conclusion and research directions

We showed that the survival of an ecosystem-engineering species in a physically stressful environment not only depends on their density (Bouma et al. 2009), but also on the spatial pattern in which they are distributed. In mussels, organising as a labyrinth was found to confer the advantages of group living while minimizing competition between conspecifics. We demonstrated that not organizing in spatial patterns, whether at low or high densities, was not sustainable. Trade-offs between being the right shape and size to maximize facilitation in terms of decreasing dislodgment risk (e.g. de Paoli et al. 2017) and minimizing competition have been shown for other ecosystem engineers, such as the saltmarsh plant *Spartina anglica.* In *S. anglica* systems, dislodgement is decreased by greater shoot densities, but densely packed tussocks limit light penetration. Moreover, this investment in density limits investment in lateral expansion (Van Hulzen et al. 2006). However, as behavioral organization in shapes is known to be both environment- and density-dependent (Gascoigne et al. 2005, Bouma et al. 2009, Capelle et al. 2014), we can say that these processes are inherently interlinked, and density could be used as a good proxy to maximize cultivation methods.

The theoretical emergent properties of spatial self-organization proposed for patterned ecosystems as diverse as arid bushlands, patterned peatlands, and mussel beds have been subject to very limited experimental verification (e.g. de Paoli et al. 2017). Here, using patterns observed in real-world mussel beds, we provide a solid and process-oriented experimental test on the benefits of (presumably self-organized) patterning for mussels, and highlight its importance for both restoration practices and the optimization of culturing techniques (Guichard 2017). Results from this study can also be used to plan restoration of degraded habitats, including drivers to develop optimal ‘facilitative’ patterns. This should lead towards low-maintenance restoration for ecosystems with self-organizing properties that can persist over time with limited human intervention (Silliman et al. 2015).

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Table 1. Mean (± SE) density and biomass estimates from patterns (estimation from September 2017)

Patterns	Estimated density (number/m^2)	Estimated biomass (kg/m^2)
Clumps	305 ± 79	0.6 ± 0.16
Stripes	1513 ± 210	3 ± 0.4
Homogeneous	4229 ± 360	8.5 ± 0.7

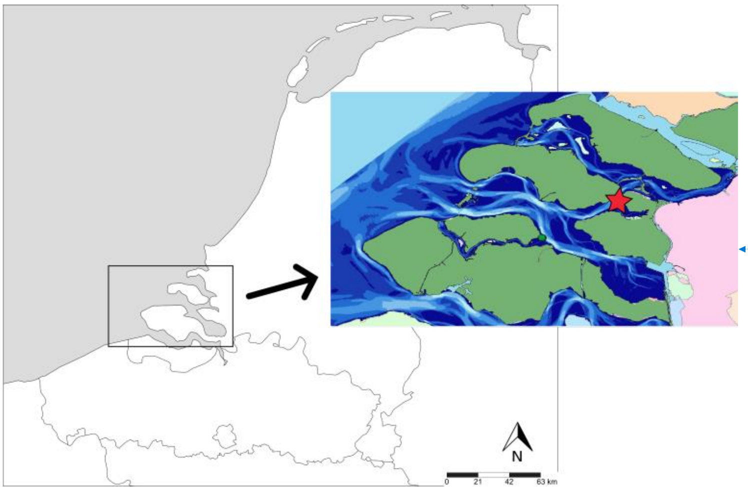

Figure 1 site location (red star in insert)

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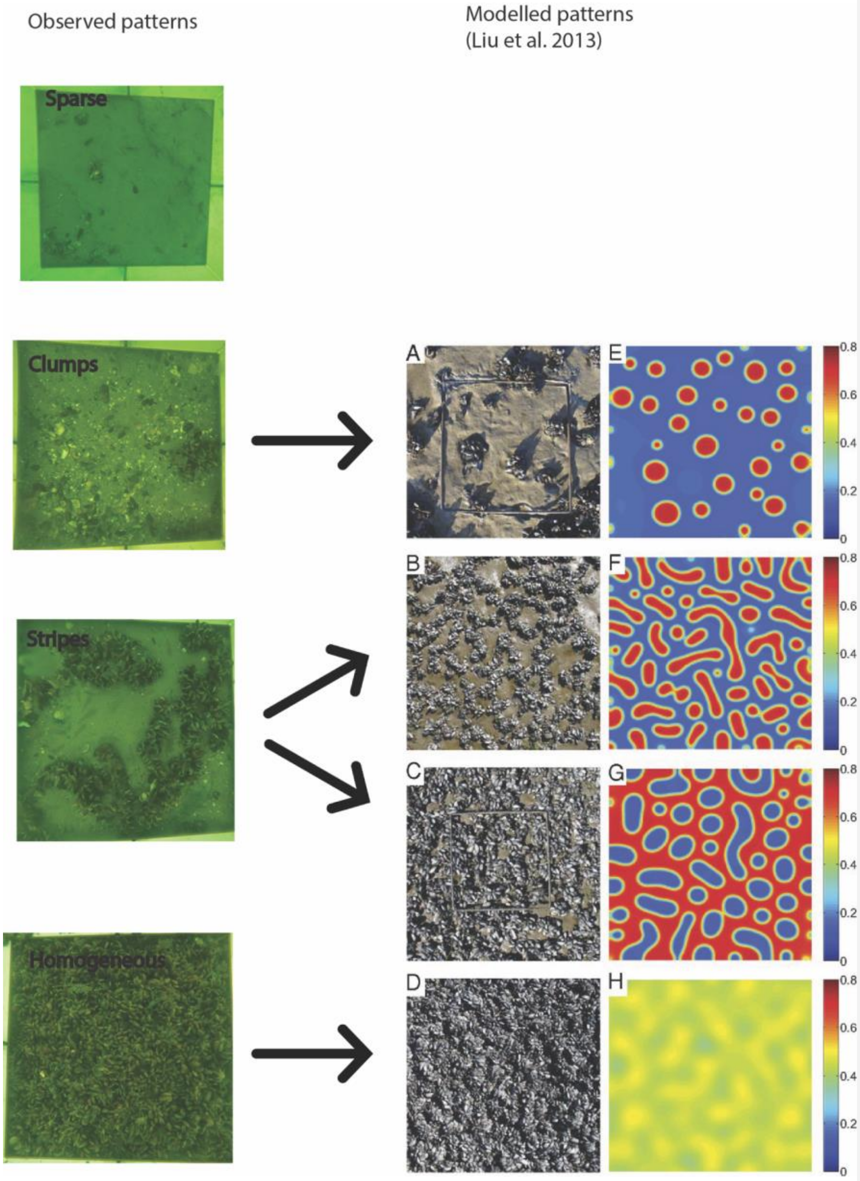

Figure 2 pictures of frames from the field (50 x 50 cm) and their classification (left) from top to bottom, sparse, clump, stripes and homogeneous, corresponding respectively to field observation (quadrat for scale 50 x 50 cm) and model outcomes (right) by Liu et al. (2013): “isolated clumps” (A,E), “open labyrinth" & "gappedpatterned" (B,C,F,G) and “uniform” (D,H). Colours in E-H represent density of mussels.

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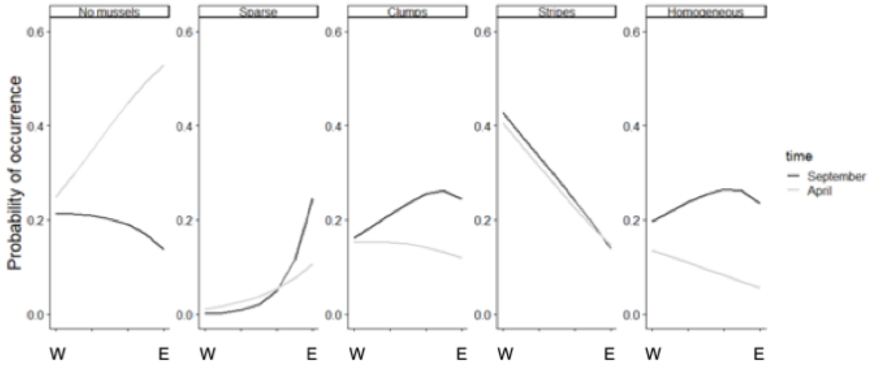

Figure 3. Probability of occurrence of areas of no mussel cover and patterns from sparse to homogeneous in September 2017 (black line) and April 2018 (grey line) from West to East (left to right).

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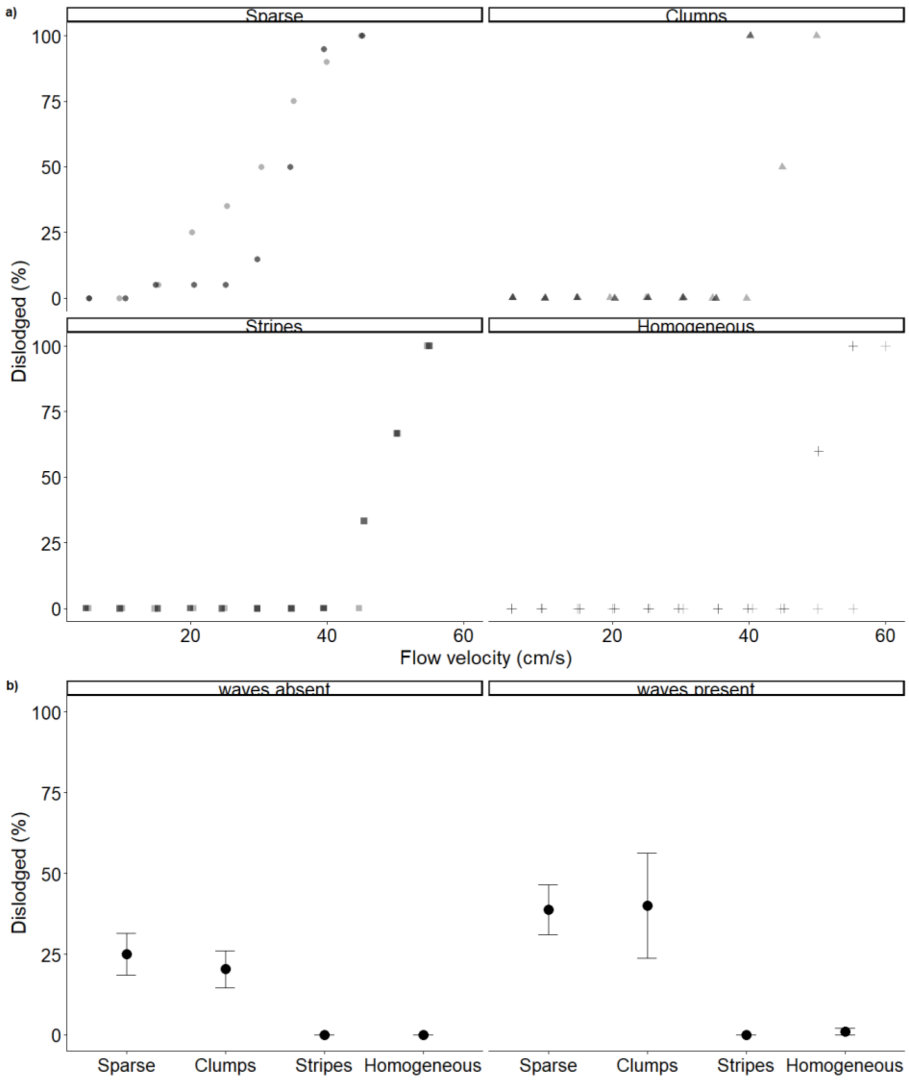

Figure 4 Cumulative dislodgement of mussels in a) flume during dislodgement trials, b) wave tanks experiments at the end of each trial, according to organization treatments and hydrodynamic conditions (continuous flowvelocity (a) and absence or presence of wave action (b)). The two levels of grey in (a) represent two replicates.

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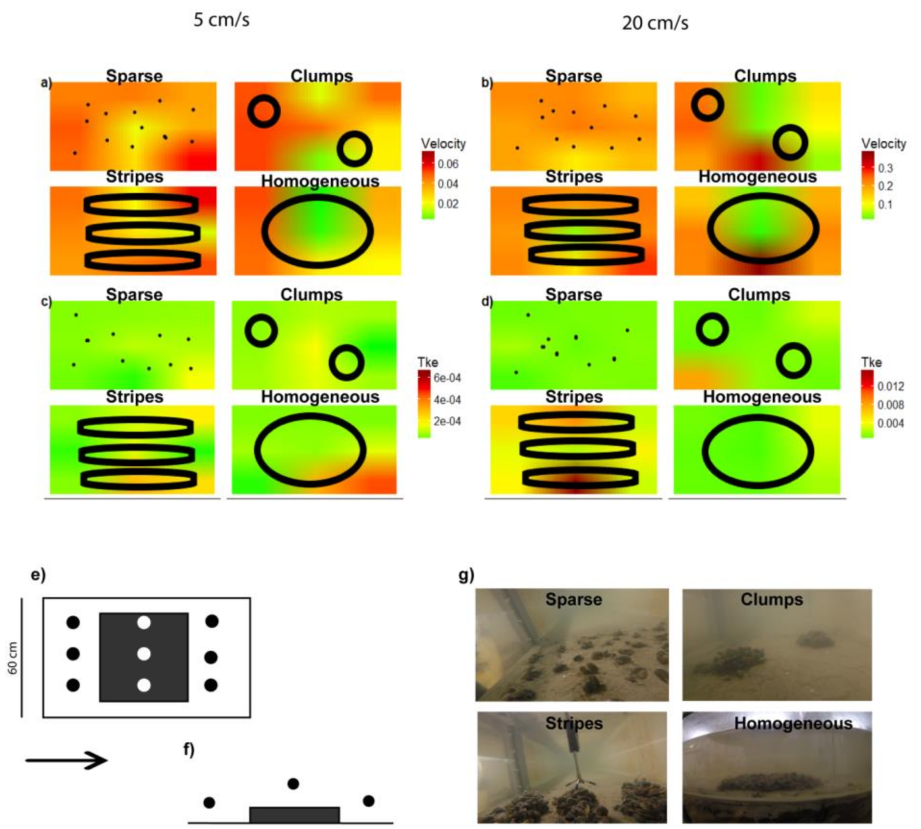

Figure 5 Panels a-d represent results of velocity profiles (a-b) and turbulence (c-d) averaged over the tworeplicates for the four designs with patches drawn in black outlines. Y axis represents flume width (60 cm); X axis represent legth of experimental arena (80 cm). Flow direction as show by the arrow was from left to right and measurementswere taken at three points along the x axis: 10 cm before patches, in the middle and 10 cm behind the patches,and at 3 points on the y axis (panel e) and 2 cm above substratum (panel f). Colours represent measurements of flow speeds (expressed as m/s) close to seabed (c.ca 2cm) in experimental patches when flow was set at a) 5 cm/s and at, b) 20 cm/s & TKE (expressed as (m/s)2) at c) 5 cm/s and at, d) 20 cm/s. Panel g) shows pictures of the mussels in the four patterns in the flume

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