Biogenic gradients in algal density affect the emergent properties of spatially self-organized mussel beds

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Theoretical models highlight that spatially self-organized patterns can have important emergent effects on the functioning of ecosystems, for instance by increasing productivity and affecting the vulnerability to catastrophic shifts. However, most theoretical studies presume idealized homogeneous conditions, which are rarely met in real ecosystems. Using self-organized mussel beds as a case study, we reveal that spatial heterogeneity, resulting from the large-scale effects of mussel beds on their environment, significantly alters the emergent properties predicted by idealized self-organization models that assume homogeneous conditions. The proposed model explicitly considers that the suspended algae, the prime food for the mussels, are supplied by water flow from the seaward boundary of the bed, which causes in combination with consumption a gradual depletion of algae over the simulated domain. Predictions of the model are consistent with properties of natural mussel patterns observed in the field, featuring a decline in mussel biomass and a change in patterning. Model analyses reveal a fundamental change in ecosystem functioning when this self-induced algal depletion gradient is included in the model. First, no enhancement of secondary productivity of the mussels comparing with non-patterns states is predicted, irrespective of parameter setting; the equilibrium amount of mussels is entirely set by the input of algae. Second, alternate stable states, potentially present in the original (no algal gradient) model, are absent when gradual depletion of algae in the overflowing water layer is allowed. Our findings stress the importance of including sufficiently realistic environmental conditions when assessing the emergent properties of self-organized ecosystems.

1. Introduction

Self-organized spatial patterns, resulting from the interaction among organisms and their physical environment, have been found in a wide range of ecosystems, ranging from arid bush lands to marine corals (for a review, see [1]). Theoretical studies emphasize that self-organized patterns are critically important for the functioning of ecosystem. Spatially self-organized ecosystems are more diverse, [2,3], have higher primary or secondary productivity [4–6] and are better able to withstand disturbance [4,7–11] compared with non-patterned ecosystems. Hence, self-organized patterns may generate important emergent properties that affect ecosystem functioning. Yet, they can also induce alternate stable states, making ecosystems vulnerable to sudden state shifts once a tipping point in externally imposed conditions is crossed [12–14]. Understanding of the mechanism behind the development of patterned landscape structures and their emergent effects on ecosystem functioning is therefore critical for the conservation of these unique and highly valued ecosystems.
It is common for self-organization models to assume homogeneity of background environmental conditions, for instance by assuming a uniform soil type and a homogeneous distribution of limiting resources [15–17]. Under these homogeneous conditions, self-organized systems can exhibit multiple stable states, as was predicted for arid environments [16,18]. Gradients are caused by externally imposed spatial variation, such as elevational variation in mountain areas affecting vegetation zonation [19]. But strikingly, strong gradients can also result from the interactions of the organisms with the physical templates or biological environment, where biotic and abiotic processes are altered by the system at large spatial scales. Potential examples include the modification of rainfall patterns by forest in situ-captions of unidirectional winds, or interception by vegetation of downhill run-off of water and nutrients. Field observations reveal that conspicuous large-scale gradients generally occur [19–22], as found for instance in mussel beds (figure 1a). To the best of our knowledge, no theory exists of how such landscape-scale feedbacks affect the emergent properties of spatial self-organization for the functioning of ecosystems.

Here, we present a study on the importance of self-induced resource gradients for system-level properties in regular spatial patterns observed in mussel beds in the Wadden Sea, The Netherlands. In prior studies, we argued that the formation of banded patterns in mussel beds at large spatial scale results from a scale-dependent feedback arising from the long-range competition for algae in the lower water layer [4] and small-scale facilitation between mussels resulting from the effects of accumulation of sediment on mussel growth [23]. These emerging patterns have an important role in promoting overall mussel survival and minimizing the effects of competition [24]. Mathematical models predict, based on homogeneous environmental settings, that mussel beds are more productive when they are organized in spatial patterns, but are also more vulnerable to regime shifts at low algal availability or high wave disturbance rates. However, how these predictions are affected by large-scale, self-induced gradients in environmental conditions, for instance caused by depletion of algae in the higher water layers, is currently unknown.

In this paper, we unravel the implications of such self-induced gradients in food availability, generated by depletion of algae in higher water layers, for the functioning of self-organized mussel beds. The mussels bind to each other using byssus threads to reduce the effects of wave disturbance and predation, improving mussel survival. However, aggregation also negatively affects their growth owing to local depletion of

Figure 1. A mussel bed in the Wadden Sea and the effect of position on the properties of the mussels. (a) Aerial photographs clearly show gradients in mussel cover over a mussel bed at The Netherlands (53.46798° N, 6.22494° E), suggesting depletion of algae at large spatial scale. The arrow indicates the direction of flow of the tidal current, whereas the characters (E and C) on the mussel bed denote the edge and the centre position, respectively. Within the patches, edge-to-centre gradients in mussel density per unit area (b), dry biomass for individual mussel (c) and dry soft tissue biomass per unit area (d) between the edge and centre position, respectively; error bars denote ± s.e.
algal food. Here, we analyse an extended version of the mussel pattern formation model of Liu et al. [23], in which we introduce a more realistic description of horizontal algal transport through the system. Specifically, we assume that algae enter the system with the tidal water flow from the seaward mussel bed edge, using a fixed upstream concentration instead of a periodic boundary condition that creates pre-depleted lower water layers. Moreover, we allow for gradual depletion of algae from the entire water column by consumption, generating a gradual horizontal decrease in availability of algae to the mussels along the main direction of tidal water flow, which is reflected in the spatial pattern. This again deviates from previous approaches in which the algal concentration in the upper water column was kept fixed. We then analyse how this self-induced depletion gradient affects the emergent properties of pattern formation in the mussel bed, in terms of amount of mussels that is supported, the range of algae concentrations in the incoming water under which beds can persist, and the resilience of the bed to disturbances. Using our model results, we discuss whether current theoretical models can provide a reliable and realistic description of the large-scale dynamics and properties of real-world ecosystems.

2. Field observations

2.1. Material and methods

We investigated the presence of large-scale spatial gradients in the properties of the mussel bed and of individual mussels across mussel beds in a field study. We selected a mussel bed at the south edge of the island Schiermonnikoog, The Netherlands (53.46798°N, 6.22494°E), which displays clear spatial patterns that are oriented perpendicular to the advective direction of incoming tidal flow with the highest densities visually observed the closest to the seaward edge (figure 1a). The bed has a size of 300 m × 400 m and has an age of about 8 years since the mussels established through a single spatfall. We sampled the biomass of mussels at the edge and in the centre of the mussel bed using a corer (diameter 20 cm: 0.0314 m²). Samples were taken with fully covered mussel patches. From each sample, the number of mussels, the volume (approximated as width by height by length) and dry weight of each individual mussel were analysed. Shell-free dry mass per square metre was obtained from the samples after drying the soft tissue at 80 °C for 48 h. We used a one-way ANOVA to analyse the difference in mussel density and shell-free dry mass between the mussel bed edge and centre positions, respectively. All statistics were computed using the R package (http://www.r-project.org).

We further used aerial photographs to analyse changes in the properties of the spatial patterns in terms of the cover percentage of mussels. Here, the cover percentage indirectly reflects the mussel density. The original remote sensing photographs are RGB images reflecting mussel aggregated banding and bare sediment (figure 1a). These colour images were converted into binary images for subsequent analysis of the cover of the mussel patches. Black pixels then corresponded to areas occupied by mussels, whereas white areas corresponded to bare sediment. We measure the change of cover percentage using a moving window method, which we moved over the bed in the overall direction perpendicular to the patterns in the bed. To analyse the influence of the distance along the transects on the cover of mussel patches, we applied a general linear model.

2.2. Results

We observed a clear decrease of both individual and total shell-free mussel biomass per area from the edge to the centre of the mussel bed. While the density of the mussels did not change significantly from the edge to the centre of the mussel bed (figure 1b; F₁,₉ = 1.512, p = 0.25), mussels near the edge contained relatively more flesh (figure 1c; one-way ANOVA, F₁,₉ = 9.78, p < 0.01) and showed a higher net shell-free dry biomass per square metre (figure 1d; one-way ANOVA, F₁,₉ = 8.03, p < 0.01) compared with mussels near the centre. These findings suggest that a large-scale spatial gradient in algal availability occurs over the mussel bed, which is reflected in heavier individual mussels and higher net dry biomass per square metre near the edge of the mussel bed. Hence, under the assumption that mussels are the main consumers of algae over the bed, our results support the hypothesis that mussels further way from the seaward edge of the bed have less food to consume than the mussels close to the edge owing to an overall depletion gradient of algae across the mussel bed.

Analysis of aerial photographs of a larger set of mussel beds in the Wadden Sea revealed a clear change in the spatial properties of the mussel bed from the seaward edge inward. Regression analysis of the relationship between mussel cover and distance across the bed revealed a near linear decline (figure 2; linear regression, p < 0.001, R² = 0.905), pointing at a decrease in local carrying capacity, possibly because of decrease in the input of food from the higher water layers to the benthic boundary layer in which the mussels feed. This relation is closely matched by model predictions.

3. Modelling

3.1. Model description

In previous papers [4,23], we identified that the formation of self-organized spatial patterns depends crucially on two important aspects of the way that mussels interact with
their environment. In the first process, mussels promote their own growth rate by accumulating sediment, which leads to the formation of hummocks. On top of these hummocks, mussels have better access to pelagic algae, their primary food source. At the same time, consumption of algae by the mussels depletes algal concentrations from the lower water layer. This process acts over a larger distance than hummock formation, which is a critical element for pattern formation.

Below, we present an extended version of the model of Liu et al. [23], in which we analyse the effects of large-scale depletion of algae from the overall water column from the mussel bed edge at which the tidal water enters to the other side where the water exits. We examine the effect of algal depletion on the functioning of mussel beds in terms of productivity and ecological resilience as well as the effect of environment conditions on mussel bed size. Here, we consider the simplest model that includes the concentration of algae in the water, mussel density on the bottom and the thickness of the mud layer on top of the sediment. Our model differs from that of Liu et al. [23] in that it describes the algal concentration in the entire water column, and we assume that algae enter the water column from the side, i.e. we use a fixed upstream edge concentration of algae. As a consequence, this model induces a heterogeneous environment for pattern formation where the overall availability of algae declines owing to consumption as the water moves over the mussel bed.

Our model considers a column of seawater of thickness \( H \), where the mussels have direct access only to the algae at the bottom. Algal concentration near the bottom is supplemented by vertical diffusion in the water column and by advection from the tidal current in a horizontal direction (figure 3a).

First, we consider the dynamics of the suspended algal food. The supply of algae is determined by horizontal advection...
of seawater by the tidal current. Algal concentration is subject to horizontal and vertical diffusion, with different diffusion coefficients for horizontal and vertical directions. The depletion of the algae occurs at the bottom owing to the predation of mussels; concentration change of algae in middle layers only occurs by diffusion and advection processes. The relations between horizontal advection and diffusion, vertical diffusion and consumption can be expressed as

$$\frac{\partial A}{\partial t} = -V(z)\frac{\partial A}{\partial x} + D_h (\frac{\partial^2 A}{\partial x^2} + \frac{\partial^2 A}{\partial y^2}) + D_v \frac{\partial^2 A}{\partial z^2},$$

(3.1)

with the following boundary conditions (i) a fixed upstream concentration: \(A_{\mid x=0} = A_i\); (ii) a no-gradient downstream concentration: \(\partial A/\partial x = 0, x = x_{\text{max}}\); (ii) periodic boundary conditions in y-direction; (iv) no-flux upper boundary condition: \(\partial A/\partial z = 0, z = H\) and (v) a grazing flux at lower boundary condition: \(-D(V\partial A/\partial z) = -cAM((S + k_s)/ (S + K_s))\) \((1 - M/K)\). There the term \((S + k_s)/ (S + K_s)\) captures the enhanced filter rate on mussels induced by the hummocks of spatial patterns in mussel beds. Using this set of partial differential equations, we study the implications of spatial heterogeneity for the functioning of self-organized mussel beds, in terms of productivity and vulnerability to catastrophic shifts. All parameters are based on empirical data, either measured at our study sites, or obtained from previous studies. In electronic supplementary material, table S1, we provide the units and explanations of the parameters that were used in the model.

Note also that, although the current is described as a ‘tidal current’, we do not consider the effect of varying height of the water column, and have not incorporated it into the geometrical layout of the model. Thus, the height of the water column is assumed homogeneous throughout. Here, \(D_v\) is very small compared with the other diffusion constants in the model. This diffusion process is caused by water flow and hydrodynamic processes.

As we consider the variation of sediment height as a result of pseudo-faecal accumulation small in comparison with the height of the water column, and have not incorporated it into the geometrical layout of the model. Thus, the height of the water column is assumed homogeneous throughout. Here, \(D_v\) is very small compared with the other diffusion constants in the model. This diffusion process is caused by water flow and hydrodynamic processes.

Here, \(A\) is defined as the sediment elevation on the top of the pre-existing tidal flat surface, \(k_t\) describes the deposition of sediment in the form of pseudo-faeces per mussel biomass, whereas \(d_p\) describes the erosion rate of the sediment. Sedimentation is assumed to disperse in a diffusive manner, where the diffusion is proportional to the diffusion coefficient \(D_v\). Here, \(D_v\) is very small compared with the other diffusion constants in the model. This diffusion process is caused by water flow and hydrodynamic processes.

Equations (3.1)–(3.4) govern the formation of regular spatial patterns in mussel beds. Using this set of partial differential equations, we study the implications of spatial heterogeneity for the functioning of self-organized mussel beds, in terms of productivity and vulnerability to catastrophic shifts. All parameters are based on empirical data, either measured at our study sites, or obtained from previous studies. In electronic supplementary material, table S1, we provide the units and explanations of the parameters that were used in the model.

3.2. Model analyses

The development of mussel beds is simulated numerically with forward Euler integration of the differential equations (3.1)–(3.4) using the compute unified device architecture C programming environment of NVidia (www.nvidia.com/ cuda) on a HP z800 workstation with an NVIDIA Tesla C1060 computing processor. We simulated the grid space of 1024 × 1024 by eight points representing a natural length of 400 × 400 by 1 m in the real world. The used algorithm was based on an existing two-dimensional model for mussel pattern formation [25] and further extended to allow three-dimensional computations. Starting conditions are homogeneous with a slight spatially variable, random perturbation of mussel biomass, in order to mimic the initial settlement of young mussels on the sediment surface. It should be noted that this slight spatial
perturbation is an essential prerequisite for the symmetry breaking and patterns formation.

4. Results

We first present the qualitative predictions resulting from the theoretical model, and then compare the predicted patterns with field observations, in terms of the changes of the patterns and size of mussel beds under different environmental conditions. Then, using this model, we further infer how self-induced resource depletion gradients affect the emergent properties of spatial patterns in mussel beds, in terms of mussel productivity and alternative stable states (ASS).

4.1. Development of self-organized patterns

Using the parameters presented in electronic supplementary material, table S1, model simulations predict that a large-scale, spatially heterogeneous pattern can indeed develop owing to the gradual depletion of algae entering from the seaward edge. The concentration of algae in the overlaying water mirrors this pattern, and reveals the gradual depletion of the algae in the higher water layers (figure 3d). Comparison of the predictions of the model with field observations reveals similar spatial features in terms of the decrease of cover (cf. figures 1a and 3d), although the increase in wavelength is not closely matched by the observations. Yet, the model captures essential features of natural mussel beds, in terms of the broad band of mussels when the algal-rich water enters the bed, and a gradual decrease of the width of bands as one moves into the bed from the seaward edge (figure 1a). This gradient depletion of algae is predicted with our model (figure 3e). The term ‘gradient’ here refers to the gradient in algae over the entire mussel bed rather than the interband gradients at small scales. It should be noted that the patterns observed in the field display a reversed trend in wavelength distribution relative to model predictions (cf. figures 1a and 3d). This probably results from the additional effects that mussels have on wave dissipation and the flow rate of the water. Addressing these was beyond the scope of this paper, which focuses on the principle point of the effects of large-scale algal depletion over the mussel beds.

We analysed how changes in the properties of the incoming tidal water, in terms of its algal content and its flow velocity, affect properties of the beds that are relevant to ecosystem functioning. Increase of the algal concentration clearly increased the size of the bed and the total biomass of mussels that it sustains (figure 4). Increased flow velocity similarly increased mussel bed size, primarily by spacing out the mussels more extensively, as a longer distance is required to replenish the lowest water layer before it can support another band of mussels.

4.2. The effects of spatial heterogeneity on ecosystem functioning

Theoretical models of self-organized systems generally predict that patterned ecosystem states can exhibit a discontinuous
transition when environmental stress reaches a critical threshold or ‘tipping point’ [14,26,27]. Under homogeneous conditions, this property also holds for the model in the absence of gradients in algal availability [23] (figure 5b). Under such uniform resource conditions, the model exhibits alternate stable states at low values of $A_s$, one lacking mussels, and one characterized by a patterned mussel bed. However, when we include depletion of algae in the upper water layers, no alternate stable states are observed; a continuous transition is found as mussel biomass decreases gradually with decreasing algal input (figure 5a). Moreover, results reveal that there is no enhancement of productivity, an important emergent effect of patterning in many self-organized models, when internal gradients in algal availability are present, independent of parameter settings. This prediction appears quite robust: similar results are obtained when we use mortality rate $d_m$ as a bifurcation parameter (figure 5c,d). Both results (figure 5a,c) reveal consistently that there is no tipping point in the model that allows for large-scale gradients in algal density. Hence, heterogeneity in the biotic conditions along the direction of water flow fundamentally changes the emergent properties of mussels beds, the most important of which is that mussel beds are as vulnerable to large-scale collapse as is presumed on the basis of standard self-organization models operating under homogeneous conditions.

5. Discussion

The formation of regular, self-organized spatial patterns has been widely described in ecosystems ranging from arid bush lands to marine coral reefs [1,15,17,28]. These patterns have typically been modelled assuming a uniform initial distribution of limiting resources. This assumption, however, is violated in many ecosystems, as gradients in resource conditions are more the rule than an exception [19–21]. Our study reveals that large-scale heterogeneous conditions can fundamentally change the emergent properties that self-organized spatial patterns have on ecosystem functioning. Using patterned mussel beds as a case study, we show that large-scale gradients in algal availability, caused by depletion of algae from higher water layers, affects both the productivity of the mussel bed and the response of the bed to...
changing conditions. More specifically, we found that the gradients in algal availability eliminate the potential for ASS, and hence mussel beds are predicted to respond in a much more continuous way to degrading conditions than previously anticipated. Moreover, no increased productivity is predicted, irrespective of parameters settings. Said more generally, self-induced resource gradients in self-organizing systems seem to stabilize their dynamics.

Real-world self-organized ecosystems develop under complex physical or biological conditions that can lead to spatial heterogeneity [19,29]. The results of our field experiments clearly point out that in mussel beds, the tidal setting imposes a gradient in algal availability, as the mussels progressively deplete the algae in the overlying water. We found that the biomass, the cover and the size of mussel patches decrease from the side of the incoming tidal water to the opposite side. We hypothesize that this is most probably explained by the gradual decrease in algae availability, caused by consumption by the mussels. Alternative mechanisms can contribute to this, such as a decline of wave disturbance, because mussel beds can also generate gradients in wave action [30–32]. However, this possible explanation can be excluded based on field measurement of wave energy, detected from the edges to the rear of the mussel bed. Here, no significant dissipation of wave energy between the edges of mussel beds and the rear of mussel beds was detected, in part, owing to increased elevation across the bed [32]. Hence, our model captures an important, though not necessarily the only possible mechanism that can cause intrinsic heterogeneity.

Our new model differs from the original models in two crucial ways. In the first place, we presume a fixed algal concentration in the entire water column, although depth-dependent, rather than a periodic boundary condition that creates pre-depleted water in the lower layer. As a consequence, the mussel beds starts with a thick initial band, very similar to what is found in real-world mussel beds. As this band always gets increasingly depleted for algae from the lowest layer upwards, the potential for alternate stable states is much reduced in this model. Furthermore, the survival threshold with regard to the algal concentration in the incoming water is much lower. Second, depletion occurs in the entire water column rather than only in the benthic boundary layer. As a consequence, the patterns slowly change in character as one moves over the mussel bed, again similar to what is found in natural mussel beds. Yet, a sound numerical comparison between the models is very difficult, as the way the two models approach algal influx into the system is completely different, which explains, for instance, the huge difference in equilibrium biomass, as can be observed in figure 5.

In the past decades, a number of studies have highlighted that self-organized spatial patterns can have important emergent implications for the functioning of ecosystems [4–6,14,23]. However, how large-scale spatial heterogeneity affects the predicted emergent properties is still unknown. Mussel beds are not a unique ecosystem in revealing gradients in the properties of the observed patterns, similar changes from a banded pattern to a labyrinth pattern can be observed in arid ecosystems as the slope of the landscape decreases [21]. Our study highlights that these changes in the nature of the patterns can have a large impact on the functioning of these systems at large spatial scales, as was predicted by our model analysis. Hence, our study underlines the importance of including realistic environmental settings when assessing the emergent properties of self-organized ecosystems.

It is an important and interesting exercise to infer what determines the robustness of ecosystems to disturbance. A recent study suggests that the size of mussel beds has a strongly nonlinear effect on the chances of persistence of the bed as a whole (data collected from Wadden Sea in the Netherlands by Tjisse van der Heide and Ellen Weerman 2012, unpublished). Our results highlight that the size of mussel beds is under the control of a number of abiotic and abiotic factors. Logically, the most important effect is the amount of food available to the mussels. This is, in the first place, determined by the concentration of algal food in the incoming water. However, the flow rate of the water, a second factor determining the net influx of food, was also found to determine the realized size of the mussel bed in the model. In other words, conditions with high flow rates support larger mussel beds that (i) harbour more mussels and (ii) occupy more space. Our study thereby highlights that the algal flux rate determines the size of the mussel bed.

The phenomenon of ASS is increasingly seen as a key concept in conservation ecology [33,34]. If true, then it implies that the way backward (ecosystem restoration) is often different from the way forward (ecosystem impairment). And, that increasing pressures on a system may not lead to much change for a long time, until a sudden collapse occurs. Generally, positive feedback (self-reinforcing behaviour or species interactions) gives a runaway effect that moves the entire ecosystem into a new state, replacing the existing ecosystem state. Yet, this topic is currently still mostly based on theoretical models that presume conditions that are violated in nearly real ecosystem [35–38]. In many ecosystems, mechanisms may exist that can buffer against alternate stable states, as shown here, and hence the presence of alternate stable states is by no means certain when positive feedbacks are at play. In our study, we highlighted that a simple mechanism causing spatial heterogeneous conditions for growth at large spatial scales (i.e. beyond the scale of the single band of mussels) could entirely inhibit the potential of alternate stable states in mussel beds. Our results now highlight an important general question: are runaway responses in ecosystems overwhelming enough to generate a system-wide shift to an ASS, or do spatial heterogeneity within ecosystems provide sufficient buffer against such runaway responses to preclude the possibility of state switches.

In this paper, we argue that it is crucial to infer both the underlying ecological mechanisms generating observed spatial patterns in ecosystems [39] as well as the large-scale physical context in which these patterns are formed. A number of recent studies suggest that morphologically similar patterns can be produced by distinctly different ecological processes and mechanisms [23,40]. Moreover, the complex physical templates that characterize the real world, for instance in microtopography, can alter both the patterns generated by self-organization processes as well as their emergent effects on ecosystems functioning [19,29]. Hence, beyond making studying self-organized pattern formation using simple models in idealized setting, it is important to understand how these patterns influence ecosystem functioning when set in large-scale, realistic physical environments [25]. For this
reason, we expect that the case put forward in the current paper to be applicable also to other ecosystems.

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