The emergent properties of spatial self-organization

Liu, Quan-Xing

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Chapter 5

Spatial heterogeneity affects the emergent properties of spatially self-organized mussel beds

Abstract

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 mussels on their environment, significantly alters the emergent properties predicted by idealized self-organization models that use 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, generating a gradual depletion of algae over the simulated domain. Predictions of the model are consistent with properties of natural mussel patterns, featuring a decline in mussel' biomass and a change in patterning. Model analysis reveals a fundamental change in ecosystem functioning when this intrinsic algal depletion gradient is included in the model. Firstly, no enhancement of productivity is predicted irrespective of parameter setting; the equilibrium amount of mussels is entirely set by the input of algae. Secondly, alternate stable states, potentially present in the original model, are absent when gradual depletion of algae in the upper water layer is allowed. Our findings stress the importance of including realistic environmental settings when assessing the emergent properties of self-organized ecosystems.

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 (see Rietkerk and Van de Koppel, 2008, for a review). Theoretical studies emphasize that self-organized patterns are critically important for the functioning of ecosystem. Spatially self-organized ecosystems are more diverse, (Kapral and Showalter, 1995; Sole and Bascompte, 2006), have higher productivity (van de Koppel et al., 2005; Pringle et al., 2010; Weerman et al., 2010) and are better able to withstand disturbance (Pascual and Guichard, 2005; van de Koppel et al., 2005; Kefi et al., 2007; Bailey, 2011; Dakos et al., 2011) compared to non-patterned ecosystems. Hence, self-organized patterns may generate important emergent properties for ecosystem functioning. Yet, they can also induce alternate stable states, making ecosystems vulnerable to sudden state shifts once a tipping point is crossed (Scheffer et al., 2001; Scheffer and Carpenter, 2003; Rietkerk et al., 2004). Understanding of the mechanism behind the development of patterned landscape structures and their emergent effects on ecosystem functioning is critical for the conservation of these unique and highly valued ecosystems.

It is common for self-organization models to assume homogeneity in environmental conditions, for instance by assuming a flat underlying landscape and a homogeneous distribution of limiting resources. However, field observations reveal that conspicuous large-scale gradients occur, most likely resulting from changed environmental conditions, as found for instance in mussel beds (Figure 5.1a). Strikingly, these gradients can result from the interactions of the organisms with the physical or biological environment, where biotic and abiotic processes are altered by the system at large spatial scales. Currently, little theory exists of how heterogeneity in conditions affects 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 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 (van de Koppel et al., 2005) and small-scale facilitation between mussels resulting from the effects of accumulation of sediment on mussel growth (Liu et al., 2012). These spatially heterogeneous patterns have an important role in promoting mussel survival and minimizing the effects of competition (van de Koppel et al., 2008). Mathematical models predict, based on homogeneous environmental settings, that mussel beds are more productive when they have spatial patterns, but they are more vulnerable to regime shifts at low algal availability or high wave disturbance rates. However, how these predictions are affected by 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 internal gradients in food availability, generated by depletion of algae in higher water layers, for the functioning of self-organized mussel beds. We analyze an extended version of the mussel pattern formation model of Liu et al. (2012), in which we introduce a more realistic description of algal transport through the system. Specifically, we assume that algae enter the system with the tidal water flow from the seaward boundary, 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, generating a gradual decrease in availability of algae to the mussels, 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 analyze 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.

Experiment
(a) Material and methods

We investigated the presence of large-scale spatial gradients in the properties of the mussel bed and of individual mussels across mussels 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 (see Figure 5.1a). This mussel bed has a size of 300 m by 400 m and has an age of about 8 years. We sampled the biomass of mussels at the edge and in the center of the mussel bed using a corer (diameter 20 centimeter: 0.0314 m^2). Samples were taken with fully-covered mussel patches. From each sample the number of mussels, and the volume (approximated as width by height by length) and dry weight of each individual mussel were analyzed. Dry weight per square meter was obtained from the samples after drying the soft tissue at 80 °C for 48 hours. We used a one-way ANOVA to analyze the difference in density and biomass between the mussel bed edge and center positions, respectively. All statistics were computed using the R package (http://www.r-project.org).

We further used aerial photographs to analyze 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 5.1a). These color images are converted to binary images of subsequent analysis of the cover of the mussel patches. Black pixels correspond to areas occupied by mussels, whereas white areas correspond to bare sediment. We measure the change of cover percentage using a moving window method, which we move over the bed in the overall direction perpendicular to the patterns in the bed. To analyze the influence of the distance along the transects on the cover of mussel patches, we applied a general linear model (GLM).

(b) Results

We observed a clear decrease of both individual and overall dry biomass from the edge to the center of the mussel bed. While the density of the mussels did not change significantly from the edge to the center of the mussel bed (Figure 5.1b; $F_{1,9} = 1.512$, $P = 0.25$), mussels near the edge contained more flesh (Figure 5.1c; one-way ANOVA, $F_{1,9} = 9.78$, $P < 0.01$) and showed a higher net dry biomass per square meter (Figure 5.1d; one-way ANOVA, $F_{1,9} = 8.03$, $P < 0.01$) compared to mussels near the center. These findings suggest that a large-scale spatial gradient in algal availability
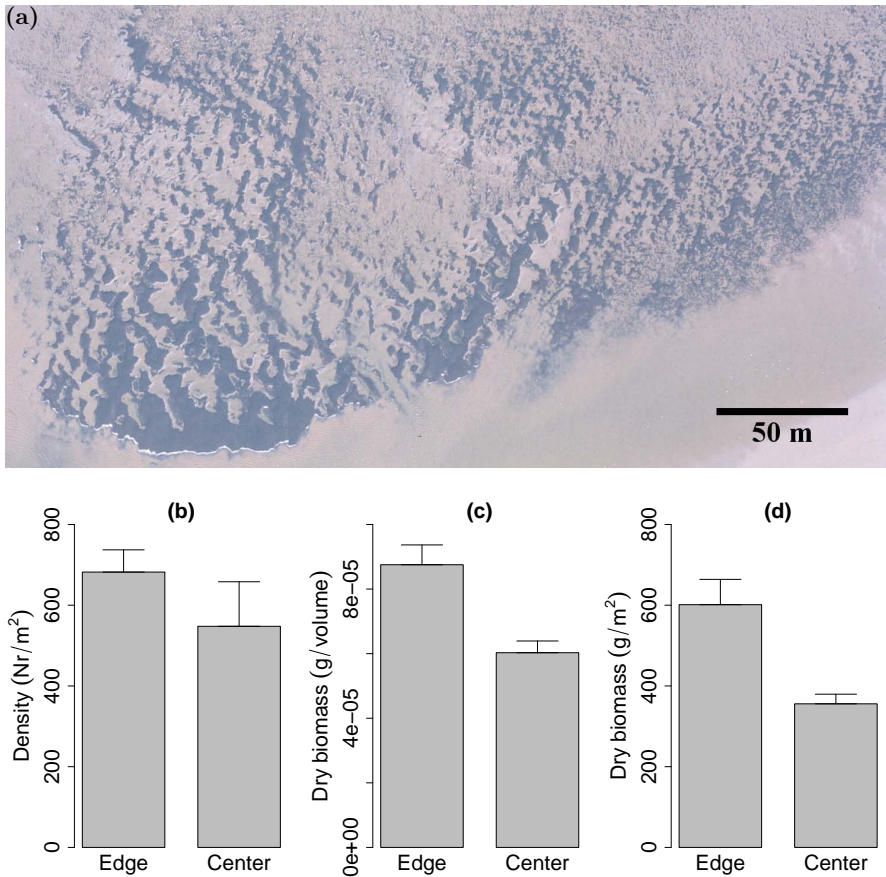
Figure 5.1: *A mussel bed in the Wadden Sea and the effect of position on the properties of the mussels (a) Aerial photographs clearly show gradients in mussel cover over a mussel bed, suggesting depletion of algae at large spatial scale. Within the patches, edge-to-center gradients in mussel density per unit area (b), dry biomass for individual mussel (c) and dry soft tissue biomass per unit area (d) between the edge and center position, respectively; error bars denote ±SE.*

occurs over the mussel bed, which is reflected in heavier individual mussels and higher net dry biomass per square meter near the edge of the mussel bed. As the density of the mussels does not change significantly, it is unlikely that predation is an important factor. Hence, under the assumption that mussels are the main consumers of algae over the bed, our results support the hypothesis that mussels at the center have less food to consume than the mussels at the edge due to large-scale depletion of algae.

Analysis of aerial photographs 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 5.2; linear regression, $P < 0.001$, $R^2 = 0.905$), 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.
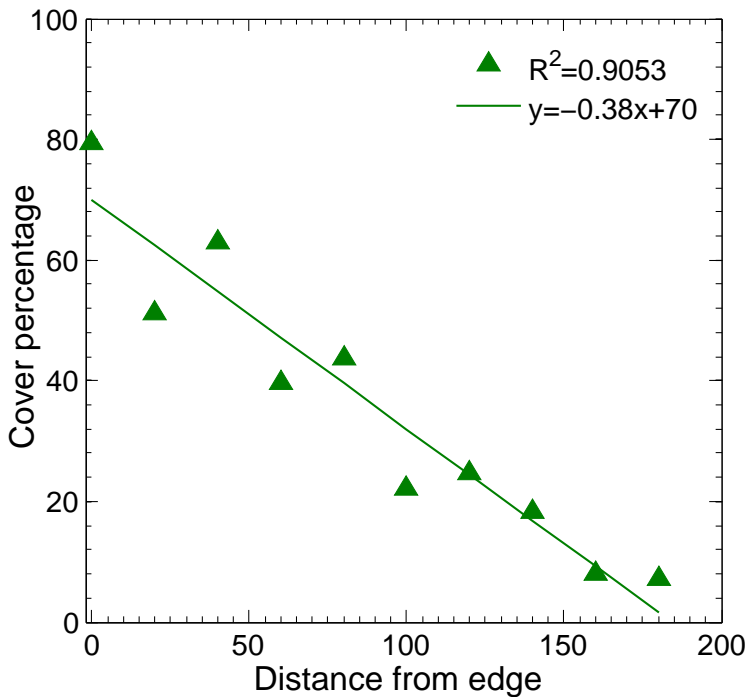

Figure 5.2: *Relationships between the cover of mussels on the bed and the distance from the boundary edge, as obtained from aerial photographs.*

Models

(a) Model description

In previous papers (van de Koppel et al., 2005; Liu et al., 2012), we identified that the formation of self-organized spatial patterns depends crucially on

two important ecological processes. 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, inhibiting their growth. This process acts over a larger distance than hummock formation, which is a critical element for pattern formation.

Below, we will present an extended version of the model of Liu et al. (2012), in which we analyze 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. (2012) 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 employ a fixed upstream boundary concentration of algae. As a consequence, this model induces a heterogeneous environment for pattern formation where the overall availability of algae declines 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 5.3a).

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 due to the predation of mussels; concentration change of algae in middle layers only occurs by diffuion and advection processes. The relations between horizontal advection and diffusion, vertical diffusion and consumption can

be expressed as:

$$\frac{\partial A}{\partial t} = -V(z)\frac{\partial A}{\partial x} + D_h\left(\frac{\partial^2 A}{\partial x^2} + \frac{\partial^2 A}{\partial y^2}\right) + D_z\frac{\partial^2 A}{\partial z^2}, \tag{5.1}$$

with the following boundary condtions: 1) a fixed upstream concentration, $A\mid_{x=0}= A_s$; 2) a no-gradient downstream concentration, $\frac{\partial A}{\partial x} = 0$ at $x = x_{max}$; 3) periodic boundary conditions in y-direction; 4) No-flux upper boundary condition, $\frac{\partial A}{\partial z} = 0$ at $z = H$; and 5) a grazing flux at lower boundary conditions, $-D\frac{\partial A}{\partial z} = -cA_0 M\left(\frac{S+k_s g}{S+k_s}\right)\left(1 - \frac{M}{K}\right)$.

Here, we denote algal concentration, mussel biomass, and sediment elevation by variables A, M, and S, respectively. x is the horizontal coordinate parallel to the tidal current, y is the perpendicular horizontal coordinate, z is the vertical coordinate. The algae influx from the seaward boundary is driven by advection induced by tidal currents with velocity $V(z)$ (a linear function of z). Horizontal diffusion of algae is given by the Laplacian operator multiplied by diffusion constant D_a. The third term describes the vertical mixing of algae between the upper and lower layers, with vertical diffusion constant D_z. For the lowest boundary layer, algae face consumption by filter feeding mussels; hence, the boundary formulation describes the predating processes by filtering mussels, where c represents the maximal consumption rate, k_s is sediment level at which consumption is half maximal, g represents the minimal consumption as a fraction of the maximal, and K is the carrying capacity of the mussels, as set by other factors than food. K is introduced in the model to eliminate unrealistically high growth of mussels at the seaward boundary.

As mentioned previously, we assume that algae enter the system with the tidal water flow from the seaward boundary. Therefore, we assume fixed boundary conditions with respect to the algal concentration. The initial conditions are given by

$$A_i(x, y, z) = \begin{cases} \frac{A_s}{2} & \text{if } x \neq 0, \\ A_s & \text{if } x = 0. \end{cases} \tag{5.2}$$

Mussel growth and mortality on soft-sediment are for a large part determined by the combination of algal availability and by losses imposed by wave dislodgment and predation. Mussel biomass per unit area

$(M, g/m^2)$ is described by

$$\frac{\partial M}{\partial t} = ecA_0 M\Big(\frac{S + k_s g}{S + k_s}\Big)\Big(1 - \frac{M}{K}\Big) - d_m M + D_m\Big(\frac{\partial^2 M}{\partial x^2} + \frac{\partial^2 M}{\partial y^2}\Big), \quad (5.3)$$

where A_0 denotes the boundary concentration of algae at $z = 0$. We assume that sediment accumulation positively affects the feeding rate. Hence, this results in a positive feedback between sediment accumulation and mussel growth (Liu et al., 2012). We assume that the movement of mussels is random in any horizontal direction and therefore we adopt the classical diffusion approximation, using the Laplacian operator. e describes the conversion constant of ingested algae to mussel biomass. Finally, the parameter d_m represents the loss rate of mussels, combining the effects of respiration, predation and wave dislodgment.

We consider that net sediment accumulation is determined by the balance of excretion of fine-grained sediment particles by mussels and sediment erosion processes. Sediment excretion by mussels occurs in the form of pseudofaeces that are produced in response to the involuntary consumption of inorganic sediment from the water column, while erosion is proportional to the amount of sediment present. Thus the simplified version of the sediment equation reads

$$\frac{\partial S}{\partial t} = k_1 M - d_s S + D_s\Big(\frac{\partial^2 S}{\partial x^2} + \frac{\partial^2 S}{\partial y^2}\Big). \quad (5.4)$$

Here S is defined as the sediment elevation on the top of the pre-existing tidal flat surface, k_1 describes the deposition of sediment in the form of pseudofaeces per mussel, while d_s describes the erosion rate of the sediment. Sediment is assumed to disperse in a diffusive manner, where the diffusion is proportional to the diffusion coefficient D_s. Here, D_s is very small compared to the other diffusion constants in the model. This diffusion process is caused by water flow and hydrodynamic processes.

We consider the variation of sediment height as a result of pseudofaeces accumulation small in comparison with the height of the water column, and have not incorporated it into the geometric layout of the model. Thus, the height of the water column is assumed homogeneous throughout. 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 due to tide either.

Equations (5.1)-(5.4) 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 appendix 5.A, we provide the units and explanations on the parameters that were used in the model.

(b) Model analyses

The development of mussel beds is simulated numerically with forward Euler integration of the differential equations (5.1)-(5.4) using the Compute Unified Device Architecture (CUDA) 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 by 1024 by 8 points representing a natural length of 400 by 400 by 1 meter in the real world. The used algorithm was based on an existing 2D model for mussel pattern formation (van de Koppel et al., 2011) and further extended to allow 3d 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.

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 intrinsic depletion gradients affect the emergent properties of spatial patterns in mussel beds, in terms of mussel productivity and alternative stable states.
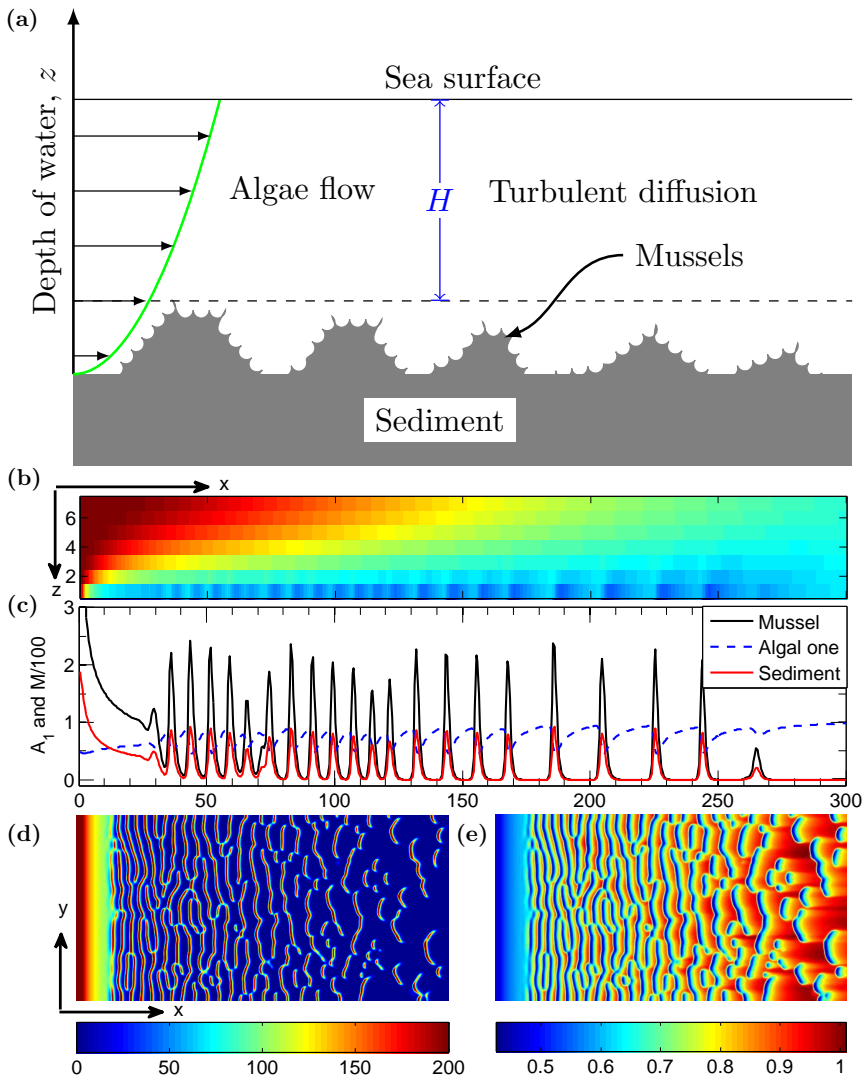
Figure 5.3: *Schematic representation in the (x, z) plane of the algal flow model and the results of a simulation with this model of the development of spatial patterns on a mussel bed. The algae's supply by the tidal flow is indicated by the arrows, where the velocity decreases to close to zero as the bottom is approached (a). Snapshot of the algal profile (b) and the density of the mussels and the sediment elevation (c) at a cross-section in (x, z) plane. (d) and (e) show the spatial patterns of the mussels and the algae respectively in (x, y) plane with periodic boundary conditions in y-direction.*

(a) Development of self-organized patterns

Using the parameters presented in Table 5.A1 in Appendix 5.A, model simulations predict that a large-scale, spatially heterogeneous pattern can develop due 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 5.3d). Comparison of the predictions of the model with field observations reveals similar spatial features in terms of the decrease of cover (cf. Figure 5.1a and Figure 5.3d), 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.

We analyzed how changes in the properties of the incoming tidal water, in terms of its algal content and its flow velocity, affect the properties of the beds. Increase of the algal concentration clearly increased the size of the bed and the total biomass of mussels that it sustains (see Figure 5.4). 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.

(b) 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 tipping point (Rietkerk et al., 2004; van de Koppel and Crain, 2006; Kéfi et al., 2010). Under homogeneous conditions, this property also holds for the model in the absence of gradients in algal availability (Liu et al., 2012, Figure 5.5b). Here, the model exhibits alternate stable state 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 (see Figure 5.5a). 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
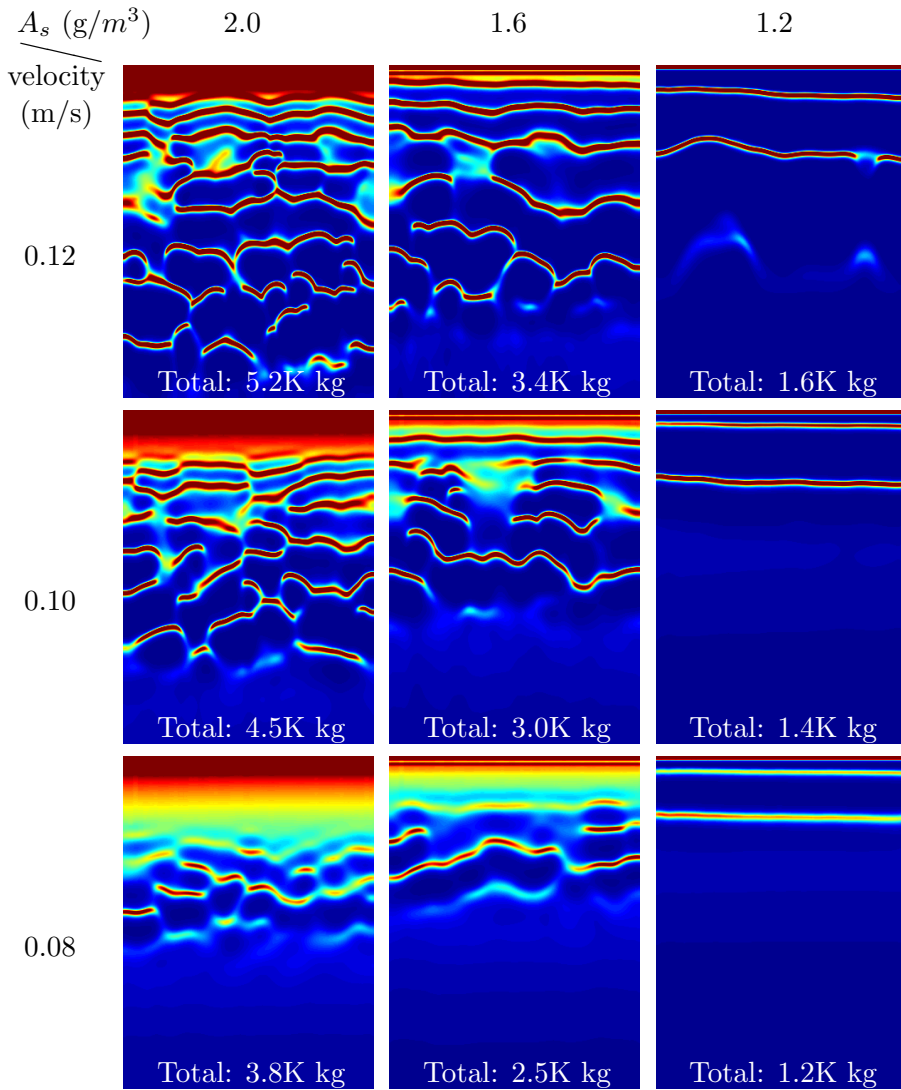
Figure 5.4: *The effect of changes in advective velocity (V) and the algal concentration in the inflowing water (A_s) input algae on the development of a mussel bed, where the inset numbers indicate the total biomass.*

are present, independent of parameter settings. 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 basis of standard self-organization models operating under homogeneous
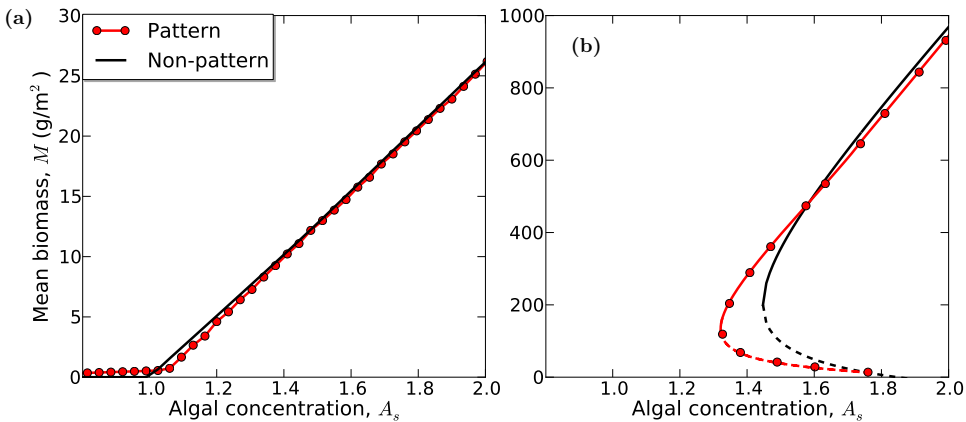
conditions.

Figure 5.5: *Effects of spatial heterogeneity on the relation between imposed algal boundary concentration and the average biomass in the simulated domain, for a model where the upper water layer can get depleted (a), and a model that presumes a homogeneous, non-depleting upper water layer (b). We plotted the average productivity from pattern states and non-patterned states, where the boundary supply algae model predicts no enhancement of productivity on self-organization patterns. Note that in the model in (a) the boundary condition A_s is imposed at the upstream horizontal boundary, whereas in (b) it is imposed as a fixed concentration in the upper water layer while horizontal boundary conditions are periodic. The average algal biomass in the upper water layers is equal for both models, allowing a comparison of the properties of the pattern.*

Discussion

The formation of regular, self-organized spatial patterns has been widely described in ecosystems ranging from arid bush lands to marine coral reefs (Rietkerk and Van de Koppel, 2008). These patterns have typically been modeled assuming a uniform initial distribution of limiting resources. This assumption, however, is violated in many ecosystems, as clear heterogeneous environmental conditions are more the rule than an exception. Our study reveals that large-scale heterogeneous conditions can fundamentally change the effects 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 alternative stable states, 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.

Real-world self-organized ecosystems develop under complex physical or biological conditions that can lead to spatial heterogeneity. 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 (Kimbro and Grosholz, 2006; Moeser et al., 2006; Donker et al., 2012). However, this possible explanation can be excluded based on field measurement on wave energy, detected from the edges to rear of the mussel bed. Here, no a significant dissipation of wave energy between the edges of mussel beds and the rear of mussel beds was detected, in part due to increased elevation across the bed (Donker et al., 2012). 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 in the lower layer water. 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 receives undepleted water, the potential for alternate stable states is much reduced in this model, and 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 5.5.

In the past decade, a number of studies have highlighted that self-organized spatial patterns can have important emergent implications for the functioning of ecosystems (Rietkerk et al., 2004; van de Koppel et al., 2005; Pringle et al., 2010; Weerman et al., 2010; Liu et al., 2012). However, how large-scale spatial heterogeneity affects the predicted emergent properties is still unknown. Mussel beds are not an 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. 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 question 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, unpublished). Our results highlight that the size of mussel beds is under the control of a number of biotic 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, also the flow rate of the water, a second factor determining the net influx of food, was 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 1) harbor more mussels and 2) occupy more space. Our study thereby highlights the importance of understanding both the physical as well as the biological determinant of mussel bed size.

The phenomenon of alternative stable state (ASS) is a leading concept

in conservation ecology. Generally, positive feedback gives a runaway effect that moves the entire ecosystem into a new state, overwhelming the existing community. Yet, this topic is based on theoretical models that presume conditions that are violated in nearly any real ecosystem. In many ecosystems, mechanisms exists that can buffer against alternate stable states, 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 state 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 alternative stable state, or do spatial heterogeneity within ecosystems provide sufficient buffer against such runaway responses to preclude the possibility of state switches. This crucial question needs to be solved for alternative stable state theory to develop into a mature theory that is applicable in a conservation context.

Appendix 5.A

Model parameters

We present here a table of symbols, interpretation, units, values, and sources of parameters used in our model.

Symbol	Interpretation	Unit	Value	Source
D_m	Diffusion coefficient of mussels	m^2/h	0.0001	Variance
D_s	Diffusion coefficient of sediment	m^2/h	0.0001	Variance
V	Velocity of fluid at boundary layer	m/h	≈ 360	Brinkman et al. (2002)
D_a	Horizontal diffusion coefficient of algae	m^2/h	0.0005	Variance
D_z	Vertical diffusion coefficient of algae	m^2/h	0.0125	Variance
A_s	Algal concentration at seaward	g/m^3	2.0	Cadée and Hegeman (2002)
H	Total height of water layer	m	1.0	Measurement
c	Maximum depletion coefficient	$m^3/g/h$	1.0	Scholten and Smaal (1998); Riisgård (2001)
e	Conversion constant of ingested algae to mussel production	g/g	0.02	(Sukhotin et al., 2002; Cole et al., 1992)
k_s	Half-saturation constant of sediment	cm	20.0	Estimated
K	Carrying capacity of mussels per unit area	g/m^2	1000.0	Measurement
d_m	Maximal mortality rate per unit time	1/h	0.002	Estimated
g	Uptake contrast between flat mussel and hummock	—	0.1	Estimated
k_1	Production of mud per capital mussels	cm/g/h	0.0001	Cole et al. (1992)
d_s	Erosion rate of sediment	1/h	0.005	Widdows et al. (2002)

Table 5.A1: *Symbols, interpretation, units, values, and sources are used in the model.*