The emergent properties of spatial self-organization

Liu, Quan-Xing

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

Document Version
Publisher's PDF, also known as Version of record

Publication date:
2013

Link to publication in University of Groningen/UMCG research database

Citation for published version (APA):

Copyright
Other than for strictly personal use, it is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), unless the work is under an open content license (like Creative Commons).

Take-down policy
If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Downloaded from the University of Groningen/UMCG research database (Pure): http://www.rug.nl/research/portal. For technical reasons the number of authors shown on this cover page is limited to 10 maximum.
Chapter 4

Spatial pattern formation at multiple scales drives the resilience of mussel bed ecosystems

Understanding how biological function arises through the integration of processes interacting on very different spatial and temporal scales is perhaps the greatest challenge facing developmental biology this century.

According to Philip K. Maini (2013)

This chapter is based on the manuscript: Q.-X. Liu, W. Mooij, P.M.J. Herman, M. Scheffer, J. Huisman, H. Olff, and J. v.d. Koppel – “Spatial pattern formation at multiple scales drives the resilience of mussel bed ecosystems,” (in preparation).
Complexity occurs at all levels of biological organization, i.e. from the organization of the cell to the structure of ecological communities (Par-rish and Edelstein-Keshet, 1999; Camazine et al., 2003; Waal and Tyack, 2003; Currie et al., 2010; Viswanathan et al., 2011). Spatial complexity, in the form of self-organized mosaics of different communities, is an important aspect of ecological complexity, and a driver of productivity, biodiversity, and vulnerability (Klausmeier, 1999; van de Koppel et al., 2005; Rietkerk and Van de Koppel, 2008). Little is known on how complex processes at multiple levels of organization influence each other and determine the outcome for ecosystem dynamics. Here we report on the interplay of two organizational levels, behavioral and demographic, in the spatial complexity of mussel beds. Mussel beds exhibit self-organized spatial patterns at a large scale due to the interplay of facilitation and competition (van de Koppel et al., 2005), leading to death and growth at demographic level, and at a small scale due to behavioral aggregation (van de Koppel et al., 2008; Liu et al., 2013). Analysis of a nested mathematical model representing both processes reveals a striking interaction effect of the different levels of biological complexity on ecosystem resilience. Our model demonstrates that mussel beds are less vulnerable to disturbances, have a higher resistance to deteriorating feeding conditions, are less vulnerable to tipping points, and experience a smaller magnitude of change at eventual tipping points, when they are more complex. Moreover, the mussel bed experienced a smaller loss of resilience when approaching a tipping point (i.e., a phenomenon called critical slowing down) when multiple processes driving ecosystem complexity were interacting. Our analysis highlights that complexity occurring at multiple organizational levels (or spatial scales) can be an important determinant of the resilience of ecosystems.


Chapter 4

Introduction

One of the most striking features of biological systems is the bewildering complexity at all organizational levels, ranging from the structure of organic molecules to the spatial organization of ecosystems. Untangling this biological complexity has developed into a separate line of research, which is highly interdisciplinary in nature, and involving concepts that cut across many different fields (Sole and Bascompte, 2006; Parrish and Edelstein-Keshet, 1999; Camazine et al., 2003; Waal and Tyack, 2003; Currie et al., 2010; Viswanathan et al., 2011). Yet, most studies of the mechanisms that generate complexity only look at a single organizational level or process. For instance, the spatial complexity of ecosystems is shaped by behavioral processes at individual level (movement) when aggregation incurs benefits from shelter, improved mate choice, or sharing of information (Viswanathan et al., 2011; Ioannou et al., 2012; van de Koppel et al., 2008), and by demographic processes at population level that create variation in predation pressure (Murray, 2002; Sherratt et al., 2002), resource availability (Klausmeier, 1999; Rietkerk et al., 2002; Anderson et al., 2012), and other processes affecting local population growth. However, little is known about how complex interactions between these levels of organization, also involving different spatial scales, determine ecosystem functioning.

Here we report on the interplay of behavioral and demographic mechanisms of pattern formation in self-organizing intertidal mussel beds. In mussels, patterns develop at two distinctly separate scales, in the form of large-scale banded patterns occurring at ecosystem-level (see Figure 4.1A and B), and small-scale net-shaped patterns at the scale of individual mussels (Figure 4.1C). Pattern formation at the ecosystem level is driven by the interplay of two scale-dependent demographic processes. Mussels compete for algae at large spatial scales, but facilitate each other at the small scale by accumulating sediment, which improves feeding efficiency (Liu et al., 2012). At the individual level, mussels actively aggregate to form small-scale strands using byssus threads, providing protection against predation and dislodgement. Being a behavioral process, pattern formation at individual level is strikingly fast, occurring within days, while ecosystem-level patterns require more than a month to develop. Hence, mussel beds may provide a unique opportunity to investigate how different processes,
one at the behavioral level, and another at the demographic level, affect the functioning of ecosystems.

Figure 4.1: Schematic representation of self-organized spatial patterns in a real mussel bed at two spatial scales, nested within one another. (A) Aerial view of a mussel bed on an intertidal flat, representing a width of approximately 200 meters. (B) Self-organized banded patterns within this bed, where the distance between successive mussel bands varies between 2 and 20 meters. (C) Small-scale clusters less than 20 cm in scale embedded within the mussel bands.

The Model

We constructed an individual-based model that integrates aggregative movement of mussels with the demographic processes of mussel facilitation and large-scale competition for algae. The movement process follows a random Brownian walk with an evenly distributed angle and a step size that obeys a statistical model (van de Koppel et al., 2008) derived in a previous
paper, where the movement step length of mussels follows an exponential distribution, \( h(x, \beta) = 1/\beta \exp(-x/\beta) \), with parameter \( \beta = 1/(p_0 + p_1 L_1 - p_2 L_2) \) (see Appendix 4.A for detailed interpretation and values). This function expresses a scale-dependent feedback of mussel density on movement, where \( L_1 \) and \( L_2 \) represent the density of other mussels in the neighborhood at a scale of \( x \) and \( y \) cm in polar coordinate, respectively.

The demographic processes are represented as partial differential equations, describing the local growth and mortality of mussels as determined by algal consumption and a density-dependent mortality rate (van de Koppel et al., 2005, 2008; Liu et al., 2012). The demographic part of the model is given by:

\[
\frac{\partial A}{\partial t} = f(A_{up} - A) - c \frac{k_s g}{k_s + S} A M - V \nabla_x A,
\]

\[
\frac{\partial M}{\partial t} = e c \frac{k_s g}{k_s + S} A M - d_m \frac{k_m}{k_m + M} M + \nabla^2 M, 
\]

\[
\frac{\partial S}{\partial t} = k_1 M - d_s S + D_s \nabla^2 S, 
\]

where variable \( A(x, t) \) describes the algal concentration, \( M(x, t) \) describes mussel density, and \( S(x, t) \) represents the sediment elevation at location vector \( x \) and time \( t \). Here the tidal advection is represented by the term \( \nabla_x A \) with velocity \( V \). The spread of sediment is modeled by the diffusion term \( D_s \nabla^2 S \). To account for the movement of mussels, we use the form \( \nabla^2 M \) to express mussel movement, which is modeled explicitly as a Brownian walk (see van de Koppel et al., 2008, for the detailed description).

Local changes in mussel density are translated into the IBM model by random mortality of a fraction of the local individuals when net change is negative, or mussels are added randomly if local change is positive. The detailed model formulation and simulation methods are described in the Appendix 4.A.

The model accurately predicts the formation of nested spatial patterns in mussel beds, consisting of clumped patterns at centimeter (about 10 cm) scale and banded patterns at meter scale (about 5-10 m in Figure 4.1). We compared our model simulation results with the observed development of a mussel bed under natural conditions. Here, photographs taken at various developmental stages describe the development of a young mussel bed starting from a uniform bed approximately 2 months after settlement to a strongly patterned bed of about 2 years of age. At first, behavioral
aggregation leads to the development of a spatial pattern at small spatial scales (Figure 4.2 A/D), while the bed remains relatively homogeneous at larger scales. As time progresses, patterns develop also at larger spatial scales due to differential mortality and further movement, and increased sedimentation triggered by mussel feeding leads to the development of hummocks underneath mussel patches, which become elevated (Figure 4.2 B/E). This leads in the long run to the development of a mature mussel bed, which exhibits clear spatial patterns at two spatial scales as long as they are not disturbed by storm activity (Figure 4.2C/D). For all stages, the model results reveal a striking similarity between predicted patterns and those observed in the field, as is confirmed by spectral analysis of the spatial patterns revealing two steady-state wavelengths at scales of 0.15 m and 3.2 m respectively (Figure 4.A1). This indicates that model (4.1) can well explain the emergence of nested patterns in mussel beds.

Results

We now used the model to investigate how these nested patterns, one originating from a behavioral self-organization process, the other from a demographic self-organization process, affects the functioning of self-organized ecosystems. To do this, we used a full factorial design, where we switched off 1) the behavioral self-organization process, 2) the demographic self-organization process, and 3) all forms of self-organization, and compared the predicted properties of the equilibria with that of the full self-organizing model. To do this, we either switched off density-dependence of mussel movement (i.e. we set \( h(x) = \text{const.} \)), switched off large-scale spatial patterning by choosing the value of dispersion coefficient for sediment outside the domain of pattern formation, or combined both. Note that this method does not affect any of the demographic processes directly, making it possible to compare the effects of loss of self-organization on ecosystem dynamics and equilibrium mussel density. To do this, we simulated changes in the equilibrium states along a gradient in algal availability in the inflowing water \( A_{up} \), one of the most important drivers of the establishment and growth of mussel beds (van de Koppel et al., 2005).

The results of the full-factorial, numerical analysis revealed that the
Figure 4.2: Development of self-organized spatial patterns at two spatial scales within mussel beds, where (A–C) represent the development of spatial patterns in the field and (D–F) the prediction by the model. (A and B) depict the development of a mussel bed 2 and 4 months after larval settlement in July 2009, at a tidal flat near Cocksedorp, Texel, The Netherlands. (C) depicts a mature, undisturbed mussel bed in the Menai strait. (D–F), The results of the model providing the predicted development of self-organized spatial patterns at two spatial scales, nested within one another, similar to what is found in the field. Parameter values used in the simulation are listed in Table 4.A1. The insets show a magnified view of the nested patterns.
Figure 4.3: The effects of the increasing spatial complexity on ecosystem functioning in terms of production and resilience. (A) Bifurcation diagram representing the relation of average mussel density with the algal availability in the overlying water, $A_{up}$, for 4 versions of the model, in which either behavioral self-organization and demographic self-organization has been switch off in a full-factoral setting. (B) The average mussel density at the tipping point (marked by down-arrows in A). (C) the change of the size of the bistable domain, and (D) the rate of pattern formation, for all four complexity treatments. Because simulations have been starting from the same initial conditions, we can calculate the rate of pattern formation as the time required to reach 95% of the average density that characterizes a steady state pattern. Here, the abbreviation S-S and L-S represent small-scale pattern and large-scale pattern respectively.
interplay of behavioral and demographic self-organization has far-reaching implications for the resilience of this ecosystem. When we switched off all forms of self-organization, we found that the model exhibited alternate stable states along a broad range of $A_{up}$. When $A_{up}$ is very high, a single stable state is found, characterized by a homogeneous, dense mussel bed. When algal availability is very low, no mussel can survive, and a bare domain devoid of mussels is predicted. At intermediate values in between 0.68 and 1.80, two stable states occur, one with ample mussels and a low mortality rate due to mutual protection, the other bare, with mortality rates being too high for mussel establishment Figure 4.3(A). A tipping point exists at a relatively high algal availability of $A_{up} = 0.68$, at which a sudden dramatic collapse can occur of a mussel bed characterized by a, for natural conditions, high mussel density. Hence, without self-organization, mussel beds are predicted to develop only at high algal availability, and have an extensive range where they are vulnerable to perturbations that push them to the alternate, degraded state.

If we successively include behavioral and demographic self-organization, we observe a striking, progressive improvement of the resilience of the mussel bed. The range at which alternate stable states occur, and where the bed is vulnerable to disturbances, becomes progressively smaller when behavioral self-organization is allowed (18%), when demographic self-organization is allowed (20%), but most significantly when both self-organization processes are allowed to interact (60%, Figure 4.3B). Moreover, mussel beds are able to survive at progressively lower values when the interacting forms of self-organization are introduced, up to a 3 fold reduction in algal availability when behavioral and demographic self-organization are interacting (Figure 4.3C). This allows mussel density to decrease to much lower values before catastrophic shift occurs, mediating the severity of the collapse in density (Figure 4.3C). Finally, the time required to develop the bed is lowest when both types of self-organization are interacting (see Figure 4.3D). These results provide a striking illustration of the importance of the interaction of different levels of self-organization and the complexity that emerges from it for the stability, persistence and productivity of self-organized ecosystems.

We investigated the consequences of the interacting levels of spatial complexity for the resilience of mussel bed systems to disturbances. We
imposed a disturbance to a mussel bed at its equilibrium state, in which the density of the mussels was reduced to 50%, and studied the time it required to return to equilibrium. We compared the recovery time to this perturbation in four simulation runs that correspond to the factorial setup described above. We found that the simulations with only small-scale patterns and the no-self-organization setup had a much slower recovery to their former states (see Figure 4.4) compared to the other two. The large-scale spatial self-organization patterns and complex nested patterns recovered much more quickly to their former states, in which the complex nested patterns reveal a remarkable improvement relative to the one with only large-scale patterns (Figure 4.4B). Hence, similar to the results from the bifurcation analysis, spatial complexity proved an important determinant of the vulnerability of mussel beds to disturbances.

This study highlights that the functioning and resilience of ecosystems is shaped by the interaction of several levels of self-organization, caused by behavioral, demographic and eco-engineering processes. In many ecosystems, spatial self-organization results from organisms improving their growth conditions by moving, modifying their environment, or lowering predation risks. Mussel beds are a unique ecosystem in that
different processes of self-organization create conspicuous regular patterns at distinctly different scales, nested within one another. Although nested regular patterns are also observed in other ecosystems (for instance seagrass, corals), they are not a common phenomenon. Yet, in many ecosystems, spatial organization develops due to a range of different processes. In many estuaries, spatial self-organization occurs due to biogeomorphological processes shaping the landscape (Anderson et al., 2010), plant-herbivore interaction creating patchiness, biological processes shaping population distribution (van de Koppel et al., 1996), and collective animal behavior affecting behavioral distributions. How these processes interact has, so far, not been a dominant topic in the study of complexity of ecosystems.

Positive feedback has long been recognized as an important driver of the occurrence of alternate stable states in ecosystems, resulting in the presence of catastrophic shifts, where sudden switches between ecosystem states can occur. Our study highlights that natural ecosystems where several processes of self-organization are interacting, exhibiting complexity at different spatial scales and organizational levels, may be less likely to experience catastrophic shifts. In these systems, processes such as behavioral aggregation and spatial differentiation in growth conditions may allow for persistence in the face of increasing stress, and recovery in the face of disturbances, while ecosystems that lack self-organization are unable to overcome such adversities and collapse to an alternate, often degraded state. As human influence often results in homogenization of natural ecosystems, and often impairs the movement and dispersal of organisms. This reduces the opportunity for pattern formation at different spatial scales. Our study demonstrates that this makes this ecosystem more vulnerable to disturbances and increases potential for catastrophic collapse. Allowing pattern formation at multiple spatial scales will improve the natural ability of ecosystems to withstand the runaway effects of positive feedback leading to collapse to degraded state. We have to allow ecosystems to develop their full natural complexity at multiple spatial scales. Future studies of complexity in other ecosystems may elucidate the generality of this hypothesis.
Appendix 4.A

Description of the model

We propose a model that combines a large-scale mussel patterning model (Liu et al., 2012), and an individual-based mussel movement model (van de Koppel et al., 2008). This is a deliberately generic and simple spatial model for the study of multi-scale dynamics in ecosystems. Both small-scale interaction and large-scale competition are included.

Demographic processes at relatively large scale are described by a partial differential equation model with three variables, $A(x, t)$ for algal concentration in the benthic boundary layer, $M(x, t)$ for mussel density, and $S(x, t)$ for sediment elevation at the location vector $x$ and time $t$. The model can be written as follows,

\[
\frac{\partial A}{\partial t} = f(A_{up} - A) - c \frac{S + k_s g}{k_s + S} AM - V \nabla_x A,
\]

\[
\frac{\partial M}{\partial t} = e c \frac{S + k_s g}{k_s + S} AM - d_m \frac{k_m}{k_m + M} M + \nabla^2 M, \tag{4.A1}
\]

\[
\frac{\partial S}{\partial t} = k_1 M - d_s S + D_s \nabla^2 S,
\]

where tidal advection is represented by the term $\nabla_x A$ with velocity $V$. The spread of sediment is modeled by the diffusion term $\nabla^2 S$. Here $A_{up}$ is the concentration of algae in the surface layer; $f$ is the rate of mass transfer between the benthic boundary layer and the rest of the water column. $c$ 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 maximum. The parameter $e$ describes the conversion constant of ingested algae to mussel biomass; $k_m$ is the value of mussel biomass at which mortality is half maximal, and $d_m$ is the maximal per capita mussel mortality rate. $k_1$ describes the deposition of sediment in the form of psuedofeaces per mussel, while $d_s$ describes the erosion rate of the sediment. To account for the movement of individual mussels we use the form $\nabla^2 M$ to express the mussel movement model (individual based model, see also (Van de Koppel et al., 2008) for a detailed description). Statistical analysis of experimental movement trails revealed that the distances covered by the mussels in one minute followed an
exponential distribution, where the frequency $h$ of occurrence decreased with movement distance $x$; $h(x, \beta) = \frac{1}{\beta} \exp \left( -\frac{x}{\beta} \right)$. Here, the scaling parameter $\beta$ is a function of the densities of mussels in the neighborhood. The multiple generalized linear model (GLM) analysis of the relationship between movement speed and mussel density revealed that this scale parameter $\beta$ is negatively affected by density at a scale of 1.87 cm, but positively affected by density at a scale of 7.5 cm (van de Koppel et al., 2008). The scale-dependent feedback can be expressed as $\beta = \frac{1}{(p_0 + p_1 L_1 - p_2 L_2)}$, where $p_0$ represents an intercept (maximum movement speed at zero density); $L_1$ and $L_2$ indicate the densities at the two different scales, respectively. The coefficients $p_1$ and $p_2$ were obtained from a multiple GLM regression. The values used in this study are listed in Table 4.A1.

**Implementation of the model on a graphics processor**

The implementation of this model (4.A1) consists of three steps. The first step is to calculate mussel growth and mortality, along with algal concentration and sediment elevation using the PDE components of the model, which is implemented on a spatial grid of size 128 by 128. The second step is to update local mussel density in the IBM representation of the mussels, using the local densities predicted by the PDE. When densities decrease locally, a random selection of mussels is removed. When mussel density increases, the additional mussels are randomly added to the grid cell. The last step is to calculate mussel movement at an individual mussel scale. Due to the intensive calculations required to compute mussel movement, the simulation was coded in the NVIDIA Compute Unified Device Architecture (CUDA), a C-like language for Generally Programmable Graphics Processing Units (GPGPU) and computed on multiple NVIDIA Tesla C1060 high performance computing boards. The simulation represents a 50 times 50 meter section of a mussel bed, and contains in between 1000 and 3,000,000 individual mussels. Each simulation run was started with randomized individual positions and local densities in space.
Switching off demographic and behavioral self-organization

A simulation that lacked small-scale, behavioral self-organization was produced by setting the exponential distribution to $\beta = \frac{1}{p_0}$. In this scenario, movement becomes a random Brownian motion, i.e. equivalent to the Laplace operator $\nabla^2 M$.

A simulation that lacked large-scale, demographic patterns was obtained by increasing the value of the diffusion coefficient of sediment to $0.005 \text{ m}^2/\text{h}$, which is outside of the domain allowing large-scale pattern formation. This has no effect on the equilibrium densities predicted by the simulation under homogeneous conditions, allowing for comparison of the emergent effects of pattern formation. The homogeneous state was implemented by setting the advection coefficient equal to zero.

**Figure 4.A1:** Spatial simulation of the proposed model and the fingerprint of the multi-scale patterning. (A) An illustration of multi-scale patterns generated by the model on a 50 m by 50 m spatial scale. (B) The spatial spectral analysis of the multi-scale patterning. The upper panel in B shows the radial spectrum explained by a cosine of a specific wavelength (x-axis direction) on the multi-scale patterning as was shown in (A) by 50 m by 50 m, where two distinct wavelengths present at 0.15 and 3.2 meters on the semilog plot. Inset shows the spectrum on a linear y-scale. The bottom panel shows the radial spectrum from a small-scale patterning model on a 20 m by 20 m domain, where the inset panel shows a magnified view of the spectrum for small wavelength.
### Model parameter and interpretation

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Interpretation</th>
<th>Unit</th>
<th>Value</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>$k_m$</td>
<td>Half saturation constant of mussel mortality</td>
<td>g/$m^2$</td>
<td>500</td>
<td>van de Koppel et al. (2005)</td>
</tr>
<tr>
<td>$f$</td>
<td>Exchange coefficient between surface and bottom</td>
<td>1/h</td>
<td>100</td>
<td>Estimated</td>
</tr>
<tr>
<td>$A_{up}$</td>
<td>Concentration of algae in the upper water layer</td>
<td>g/$m^3$</td>
<td>0–2.5</td>
<td>Cadée and Hegeman (2002)</td>
</tr>
<tr>
<td>$c$</td>
<td>Maximum depletion coefficient</td>
<td>$m^3/g/h$</td>
<td>1.0</td>
<td>Riisgård (2001); Scholten and Smaal (1998)</td>
</tr>
<tr>
<td>$k_s$</td>
<td>Half-saturation constant of sediment</td>
<td>cm</td>
<td>20.0</td>
<td>Estimated</td>
</tr>
<tr>
<td>$V$</td>
<td>Velocity of tidal flow</td>
<td>m/h</td>
<td>360.0</td>
<td>Brinkman et al. (2002)</td>
</tr>
<tr>
<td>$e$</td>
<td>Conversion constant of ingested algae to mussel production</td>
<td>g/g</td>
<td>0.02</td>
<td>(Sukhotin et al., 2002; Cole et al., 1992)</td>
</tr>
<tr>
<td>$d_m$</td>
<td>Maximal mortality rate per unit time</td>
<td>1/h</td>
<td>0.002</td>
<td>Estimated</td>
</tr>
<tr>
<td>$D_m$</td>
<td>Diffusion coefficient of mussels</td>
<td>$m^2/h$</td>
<td>0</td>
<td>Estimated</td>
</tr>
<tr>
<td>$k_1$</td>
<td>Per capita mud production by mussels</td>
<td>$m^3/g/h$</td>
<td>0.0001</td>
<td>Cole et al. (1992)</td>
</tr>
<tr>
<td>$d_s$</td>
<td>Erosion rate of sediment</td>
<td>1/h</td>
<td>0.005</td>
<td>Widdows et al. (2002)</td>
</tr>
<tr>
<td>$D_s$</td>
<td>Diffusion coefficient of sediment</td>
<td>$m^2/h$</td>
<td>0.0005</td>
<td>Estimated</td>
</tr>
<tr>
<td>$g$</td>
<td>Uptake contrast between flat mussel and hummock</td>
<td>—</td>
<td>0.1</td>
<td>Estimated</td>
</tr>
<tr>
<td>$p_0$</td>
<td>Intercept of the maximum movement speed</td>
<td>cm$^{-1}$</td>
<td>0.5</td>
<td>(van de Koppel et al., 2008)</td>
</tr>
<tr>
<td>$p_1$</td>
<td>Coefficient of the small-scale feedback</td>
<td>cm</td>
<td>100.0</td>
<td>(van de Koppel et al., 2008)</td>
</tr>
<tr>
<td>$p_2$</td>
<td>Coefficient of the large-scale feedback</td>
<td>cm</td>
<td>-80.0</td>
<td>(van de Koppel et al., 2008)</td>
</tr>
</tbody>
</table>

**Table 4.A1:** Symbols, interpretation, units, values, and sources were used in models.