The emergent properties of spatial self-organization
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Chapter 3

Phase separation explains a new class of self-organized spatial patterns in ecological systems

Self-organization is a process in which pattern at the global level of a system emerges solely from numerous interactions among the lower-level components of the system. Moreover, the rules specifying interactions among the systems components are executed using only local information, without reference to the global pattern.

According to Scott Camazine et al. (2003)

Abstract

Turing’s activator-inhibitor principle has been the central paradigm for explaining regular, self-organized spatial patterns in ecology. According to this principle, local activation combined with long-range inhibition of growth and survival is an essential prerequisite for the formation of regular ecological patterns. Here, we reveal density-dependent motion of animals as a new mechanism for self-organization in ecology, and show that it conforms to the principle of phase separation in physics. The basis of this mechanism is a switch from dispersal to aggregation with increasing density. First, using experiments with self-organizing mussel beds, we derive an empirical relation between animal movement speed and local animal density. Second, we incorporate this relation in a partial differential equation, and show that this model corresponds mathematically to the well-known Cahn-Hilliard equation for phase separation in physics. Third, we show that the assumptions and predictions of this model with regard to development of patterns are in close agreement with the results of our experiments and field observations. Hence, our results uncover a new principle for ecological self-organization, where motion rather than activation and inhibition processes explains spatial pattern formation.
Introduction

The activator-inhibitor principle, originally conceived by Turing in 1952 (Turing, 1952), and further developed by Belousov (Belousov, 1959), Zhabotinsky (Zhabotinsky, 1964) and Meinhardt (Meinhardt, 1982) provided a potential theoretical explanation for the occurrence of regular patterns in biology (Murray, 2002; Kondo and Miura, 2010; Maini, 2003) and chemistry (Zhabotinsky, 1964; Castets et al., 1990; Ouyang and Swinney, 1991). In the past decades, this principle has been applied to a wide range of ecological systems, including arid bush lands (Klausmeier, 1999; van de Koppel and Crain, 2006; von Hardenberg et al., 2001; Rietkerk et al., 2002; Borgogno et al., 2009), mussel beds (van de Koppel et al., 2005; Liu et al., 2012), and boreal peat lands (Eppinga et al., 2009; Rietkerk and Van de Koppel, 2008). The activator-inhibitor principle, where a local positive, activating feedback interacts with large-scale inhibitory feedback to drive spatial differences in growth, birth, mortality, respiration or decay, explains the spontaneous emergence of regular spatial patterns. These patterns may have important emergent effects on the functioning of ecosystems, such as increased growth efficiency, resource utilization and ecosystem resilience, independent of the organizational level (Liu et al., 2012; Pringle et al., 2010; Kondo and Miura, 2010; Rohani et al., 1997; Sole and Bascompte, 2006).

Physical theory offers an alternative mechanism for pattern formation, proposed by Cahn and Hilliard in 1958 (Cahn and Hilliard, 1958). They pointed at the possibility that density-dependent rates of dispersal would lead to separation of a mixed fluid into two phases that are separated in distinct spatial regions, subsequently leading to pattern formation. The principle of density-dependent dispersal, switching between dispersion and aggregation as local density increases, has become a central mathematical explanation for phase separation in many fields (Bray, 2002) such as multiphase fluid flow (Falk, 1992), mineral exsolution and growth (Kuhl and Schmid, 2007), and biological applications (Cohen and Murray, 1981; Chomaz et al., 2004; Khain and Sander, 2008; Cates et al., 2010; Liu et al., 2011). However, while aggregation due to individual motion is a commonly observed phenomenon within ecology, application of the Cahn-Hilliard (CH) framework to explain pattern formation in ecological systems is absent both in terms of theory and experiments (Cohen and Murray, 1981; Cates et al., 2010).
Here, we apply the concept of phase separation to the formation of spatial patterns in the distribution of aggregating mussels. On intertidal flats, establishing mussel beds exhibit spatial self-organization by forming a pattern of regularly spaced clumps. By so doing, they balance optimal protection against predation with optimal access to food, as demonstrated in a field experiment (van de Koppel et al., 2008). This self-organization process has been attributed to the dependence of the speed of movement on local mussel density (van de Koppel et al., 2008). Mussels move at high speed when they occur in low density and decrease their speed of movement once they are included in small clusters. However, when occurring in large and dense clusters, they tend to move faster again, due to food shortage. Mussel pattern formation is a fast process, giving rise to stable patterning within the course of a few hours, and clearly is independent from birth or death processes (Figure 3.1A and B). Although mussel pattern formation at centimeter scale was successfully reproduced by an empirical individual-based model (van de Koppel et al., 2008), to date no satisfactory continuous model has been reported that can identify the underlying principle in a general theoretical context.

In this paper, we present the derivation and analysis of a partial differential equation model based on an empirical description of density-dependent movement in mussels (van de Koppel et al., 2008), and demonstrate that it is mathematically equivalent to the original model of phase separation by Cahn and Hilliard (Cahn and Hilliard, 1958). We then compare the predictions of this model with observations from real mussel beds and experiments with mussel pattern formation in the laboratory.

**Results**

**Model Description**

Mussel speed of movement was observed to initially decrease with increasing mussel density, but to increase when the density exceeded that typically observed in nature (Figure 3.1C). We analyzed the experimental data of movement speed as a function of mussel density statistically with two different models.
Figure 3.1: Pattern formation in mussels and statistical properties of the density-dependent movement of mussels under experimental laboratory conditions. (A) and (B), Mussels that were laid out evenly under controlled conditions on a homogeneous substrate developed spatial patterns similar to ‘labyrinth-like’ after 24 hours (images represent a surface of 60 cm by 80 cm). (C), Relation between movement speed and density within clusters of 1, 2, 4, 6, 8, 16, 24, 32, 64, 80, 104, and 128 mussels (mussel density is rescaled, where 128 equals to 1). The blue line describes the rescaled second order polynomial fit with Eq. (3.1). The red line depicts the effective diffusion \( g(m) \) of mussels as a function of the local densities according to the diffusion-drift theory. The circles show the original experiment data. (D), The numerical simulation of Eq. (3.4) implemented with parameters \( \beta = 1.89 \), \( D_0 = 1.0 \), and \( \kappa_1 = 0.1 \), simulating the development of spatial patterns from a near-uniform initial state.

The movement speed data was fitted to the equation

\[
\mathcal{V}(M) = aM^2 - bM + c
\]

with \( a = 2.211 \), \( b = 2.102 \) and \( c = 0.6208 \) (Figure 3.1C; blue line). A linear
model proved not significant \((P = 0.778)\). The quadratic model was overall significant \((P < 0.001)\), where the coefficient for the second-order term was highly significant \((t = 4.732, P < 0.0001)\), and the AIC-test showed that the quadratic model was highly preferable over the linear one (see Table 3.A1 for details).

Based on this formulation, we now derive an equation for the changes in local density \(M\) of a population of mussels, in a 2-dimensional space. As the model describes pattern formation at time scales shorter than 24 hours, growth and mortality (as factors affecting local mussel density) can be ignored. Local fluxes of mussels at any specific location can therefore be described by the generic conservation equation:

\[
\frac{\partial M}{\partial t} = -\nabla \cdot J.
\]  

(3.2)

Here \(J\) is the net flux of mussels, and \(\nabla = (\partial_x, \partial_y)\) is the gradient in two dimensions. To derive the net flux \(J\), we assume that mussel movement can be described as a random, step-wise walk with a step size \(V\) that is a function of mussel density, and a random, uncorrelated reorientation. In the case of density-dependent movement, the net flux arising from the local gradient in mussel density can be expressed as (see Appendix 3.A)

\[
J_v = -\frac{1}{2\tau} \left( V (V + M \frac{\partial V}{\partial M}) \right) \nabla M,
\]  

(3.3)

where \(\tau\) is the turning rate (Schnitzer, 1993, see equation (4.14)). The “drift” term \(M \partial V / \partial M\) accounts for the effect of spatial variation in local mussel density on the spatial flux of mussels. This term does not appear in the case of density-independent movement, but its contribution is crucial when up-scaling the density-dependent movement of individuals to the population level.

Following earlier treatments of biological diffusion as a result of individual movement (Murray, 2002, see p.408-416 for details), we complement this linear diffusion term representing local movement by including higher-order (non-local) diffusion as \(J_{nl} = \nabla (\kappa \Delta M)\) with nonlocal diffusion coefficient \(\kappa\). The non-local diffusion process has a relatively low intensity, and hence parameter \(\kappa\) is much smaller in magnitude than the local movement coefficient in Eq.(3.3). We can now gather both fluxes into the
total net flux rate in Eq.(3.2) to define the general rescaled conservation equation (see text in Appendix 3.A):

$$\frac{\partial m}{\partial t} = D_0 \nabla [g(m) \nabla m - \kappa_1 \nabla (\Delta m)].$$  

(3.4)

Here, $g(m) = v(m) \left( v(m) + m \frac{\partial v(m)}{\partial m} \right)$, where $v(m) = m^2 - \beta m + 1$ is a rescaled speed. $D_0$ is a rescaled diffusion coefficient that describes the average mussel movement, and $\kappa_1$ is the rescaled non-local diffusion coefficient. Rescaling at the basis of equation (3.4) is given by the following relations: $g(m) = (m^2 - \beta m + 1)(3m^2 - 2\beta m + 1)$ with $m = \sqrt{a/c}M$, $D_0 = \frac{c^2}{2\tau}$, $\kappa_1 = \frac{2\tau \kappa}{c^2}$, and $\beta = b/\sqrt{ac}$. Here, $\beta$ captures the depression of diffusion at intermediate densities in a single parameter. In this model, spatial patterns develop once the inequalities $\beta > \sqrt{3}$ and $\beta < 2$ are satisfied, leading to a negative effective diffusion (aggregation) $g(m)$ at intermediate mussel densities. Thus, if mussel movement is significantly depressed at intermediate density, then effective diffusion $g(m)$ becomes negative, mussels aggregate, and patterns emerge. If the depression of mussel movement speed at intermediate mussel density is weak, then $g(m)$ remains positive, and no aggregation occurs at intermediate biomass (see Figure 3.A4). Under these conditions, no patterns emerge. The fitted values for $a$, $b$ and $c$ reveal that the effective diffusion clearly can become negative (as $\beta = 1.7901$), as shown in (Figure 3.1C). Equation (3.4) predicts the formation of regular patterns (Figure 3.1D), in close agreement with the patterns as observed in our experiments (Figure 3.1B). Using the precise parameter setting obtained from our experiments we are able to demonstrate that reduced mussel movement $v(m)$ at intermediate mussel density results in an effective diffusion $g(m)$ that can change sign, which leads to the observed formation of patterns.

**A Physical Principle**

We now derive that equation (3.4) is mathematically equivalent to the well-known extended Cahn-Hilliard equation for phase separation in binary fluids (see Appendix 3.A). The original Cahn-Hilliard equation describes the process by which a mixed fluid spontaneously separates to form two pure phases (Cahn and Hilliard, 1958; Chomaz et al., 2004). The Cahn Hilliard
equation follows the general mathematical structure:

\[
\frac{\partial s}{\partial t} = D \nabla^2 [P(s) - \kappa \Delta s] = D \nabla \left[ P'(s) \nabla s - \kappa \nabla (\Delta s) \right],
\]

(3.5)

where \(P(s)\) typically has the form of the cubic \(s^3 - s\). In the Supporting Information, we show that density-dependent functions of \(g(m)\) of Eq.(3.4) and its corresponding expression \(P'(s)\) in Eq. (3.5) have the same mathematical shape (concave upwards) with two zero solutions, provided that movement speed \(V(M)\) remains positive for all values of \(M\), which is inevitably valid for any animal. Hence, in a similar way as described in the Cahn-Hilliard equation, net aggregation of mussels at intermediate densities generates two phases, one being the mussel clump, the other being open space. This occurs due to a decrease in movement speed at intermediate density, leading to net aggregation when \(g(m) < 0\), similar to what is predicted by the Cahn-Hilliard equation. Hence, we find that pattern formation in mussel beds follows a process that is principally similar to phase separation, triggered by a behavioral response of mussels to encounters with conspecifics.

### Comparison of Experimental Results and Model’s Predictions

Equation (3.4) yields a wide variety of spatial patterns with increasing mussel density, which are in close agreement with the patterning observed in the field (Figure 3.2), as well as in laboratory experiments (see Figure 3.A2). Theoretical results demonstrate that with the specific value of \(\beta\) determined in our experiment, four kinds of spatial patterns can emerge, depending on mussel density. When mussel numbers are increased from a low value, a succession of patterns develops from sparsely distributed dots (Fig.3.2E) to a ‘labyrinth pattern’ (Fig.3.2F) and a ‘gapped pattern’ (Fig.3.2G), and finally the patterns weaken before disappearing (Fig.3.2H). Note that the theoretical results closely match the patterns observed in the field (Fig.3.2A-D). Moreover, a similar succession of patterns has been found under controlled experimental conditions (van de Koppel et al., 2008) when the number of mussels is increased (Figure 3.A2). The spatial correlation function of the images obtained during the experiments generally agrees with that of the patterns predicted by equation (3.4), displaying a damped oscillation that is characteristic of regular patterns (see Figure 3.A6 and
Figure 3.2: Pattern formation of mussels in the field and numerical results for 2D simulations with varying densities. (A-D), Mussel patterns in the field varying respectively from isolated clumps, ‘open labyrinth’, ‘gapped patterned’ to a dense, near-homogeneous bed. (E-H), Changes in simulated spatial patterning in response to changing overall density, closely follow the field observed patterns. The color bar shows values of the dimensionless density $m$ of Eq. (3.4). Simulation parameters are the same as for Figure 3.1D apart from the overall density of mussels.

Appendix 3.A text).

A similar agreement was found in the emergence and disappearance of spatial patterns with respect to changing mussel numbers when we compared a mathematical bifurcation analysis with an experimental bifurcation analysis. The mathematical analysis predicts that the amplitude of the aggregative pattern (i.e., the maximal density observed in the pattern) dramatically increases with increasing overall mussel densities, but decreases again when approaching a relatively high mussel density (Figure 3.3A). Most significantly, these predictions are qualitatively confirmed by our laboratory experiments, as shown in Figure 3.3B. We observed an increase in the amplitude when the number of mussels in the arena was low, but a rapid decline of the amplitude with increasing overall mussel numbers when mussel numbers were high. It should be noted that while spatial homogeneity can easily be obtained in simulated patterns, the discrete nature of living mussels precludes this in our experiments, especially at low mussel density.

Phase-separation kinetics commonly exhibits a coarsening process, which is referred to as the Lifshitz-Slyozov (LS) law (Lifshitz and Slyozov, 1961; Bray, 2002). Typically, the spatial scale of the patterns, $\ell(t)$, grows in a power-law manner as $\ell(t) \sim t^{\gamma}$, where the growth exponent $\gamma = 1/3$ was found to be characteristic of the Cahn-Hilliard equation (Lifshitz and Slyozov, 1961; Oono and Puri, 1987; Mitchell and Landau, 2006). Interestingly, our experimental results reveal that this scaling law also holds during pattern formation in mussel beds, where we found a scaling exponent very close to $1/3$ during the first 6 hours of self-organization (see Figure 3.4). This behavior is independent of the mussel density. However, the LS scaling law collapses at a later stage as the mussels settle and attach
Figure 3.3: Bifurcation of the amplitude of patterns as a function of mussel density as predicted by the theoretical model (A) and found in the experimental patterns (B). (A), Parameter values are \( \beta = 1.89 \), \( D_0 = 1.0 \), and \( \kappa = 0.1 \), apart from mussel density; letters indicate position on the plot corresponding to the four snapshots E, F, G and H in Figure 3.2. The mussel density represents values of the dimensionless density. (B), Laboratory measurement of patterned amplitudes with different densities on surface of 30 cm by 50 cm, where the number of mussels ranges from 100 to 1400 individuals. Amplitude versus the mean density is depicted as symbol lines with solid squares (■), the red lines depict average density.

to each other with byssus threads. Our theoretical model (3.4) matches this result displaying the same scaling exponent as our experiments (note that as the simulation starts with a very fine-grained random distribution, pattern development takes longer in the model in Figure 3.4).

Discussion

The results reported here establish a new general principle for spatial self-organization in ecological systems that is based on density-dependent movement rather than scale-dependent activator-inhibitor feedback. This phase separation-based process was until now not recognized as a general mechanism for pattern formation in ecology, despite aggregation by individual movement being a commonly described phenomenon in biology (Turchin, 1998; Mittal et al., 2003; Buhl et al., 2006; Liu et al., 2011; Vicsek and Zafeiris, 2012). Recent theoretical studies highlight similar aggregative processes as a possible mechanism behind pattern formation.
Figure 3.4: Scaling properties of the coarsening processes. The relation between wavelength spatial scale versus temporal increasing aton the pattern formation in double logarithmic scale. The colored solid lines indicate the experimental data for different mussel density and theoretical simulation. The red dash lines fit the experimental data with a power law $\ell(t) \sim t^\gamma$ at early stages. We found only a slight deviation from the theoretically expected $\gamma = 1/3$ growth. No dominant wavelength emerges from the spectral analysis for the first minutes of the experiment, and hence no data could be plotted. Note that as the simulation starts with a very fine-grained random distribution, pattern development takes longer in the model.

in microbial systems (Cates et al., 2010; Farrell et al., 2012; Fu et al., 2012), insect migration (Cohen and Murray, 1981), or passive movement as found in stream invertebrates (Anderson et al., 2012). Furthermore, studies on ants and termites have shown that self-organization can result from individuals actively transporting particles, aggregating them onto existing aggregations to form spatial structures ranging from regularly spaced corps piles (Theraulaz et al., 2002) to ant nests (Camazine et al., 2003). Also, a number of studies highlight that beyond food availability (Folmer et al., 2012), behavioral aggregation in response to predator presence is an important determinant of the spatial distribution of birds (Quinn and
Cresswell, 2006). These studies indicate there may be a wide potential for application of the Cahn-Hilliard framework of phase separation in ecology and animal behavior that extends well beyond our mussel case study.

A fundamental difference exists between pattern formation as predicted by Turing’s activator-inhibitor principle and that predicted by Cahn-Hilliard principle for phase separation. Characteristic of Turing patterns is that a homogeneous ‘background state’ becomes unstable with respect to small spatially periodic perturbations: this so-called Turing instability is the driving mechanism behind the generation of spatially periodic Turing patterns. Moreover, the fixed wavelength of these patterns is determined by this instability. In the Cahn-Hilliard equation there is no such ‘unstable background state’ that can be seen as the core from which patterns grow. Moreover, there is no specific wavelength that defines the pattern. Rather, the Cahn-Hilliard equation exhibits a coarsening process: the wavelength slowly grows in time. Hence, Cahn-Hilliard dynamics have the nature of being forced to interpolate between two stable states, or phases, while a Turing instability is ‘driven away from an unstable state’.

Strikingly, in mussels, both processes may occur at the same time. Mussels aggregate because they experience lower mortality due to dislodgement or predation in clumps (van de Koppel et al., 2008). This explains why on the short term, they aggregate in a process that, as we argue in this paper, can be described by Cahn and Hilliard’s model for phase separation. On the long term, however, they settle and attach to other mussels using byssal threads, a process that arrests pattern formation, thereby disabling the coarsening nature of ‘pure’ Cahn-Hilliard dynamics by a biological mechanism that acts on intermediate time scales and has not been taken into account in the present model that focuses on the first 24 hours of the process. Moreover, at an even longer time scale, mortality and individual growth further shapes the spatial structure of mussel beds, unless a disturbance leads to large-scale dislodgement, which is likely to reinitiate aggregative movement. Hence, on the long run, both demographic processes (van de Koppel et al., 2005) and aggregative movement (van de Koppel et al., 2008) shape the patterns that are observed in real mussel beds.

Finally, our results demonstrate that to understand complexity in ecological systems, we need to recognize the importance of movement as a
process that can create coherent spatial structure in ecosystems, rather than just dissipate them. Unlike the growth/mortality based Turing mechanism, the movement-based Cahn-Hilliard mechanism has short time scales. It may thus allow for fast adaptation and generate transient spatial structures in ecosystems. In natural ecosystems, both processes occur, sometimes even within the same ecosystems. How the interplay between these two mechanisms affects the complexity and resilience of natural ecosystems is an important topic for future research.
Appendix 3.A: Materials and Methods

Laboratory setup and mussel sampling

The laboratory setup followed that of a previous study by van de Koppel et al. (2008). Pattern formation by mussels was studied in the laboratory within a 130 cm by 90 cm by 27 cm polyester container filled with seawater. Mussel samples were obtained from wooden wave-breaker poles on the beaches near Vlissingen, the Netherlands (51.458713°N, 3.531643°E). They were kept in containers and fed live cultures of *Phaeodactylum tricornutum* daily. In the experiments, mussels were laid-out evenly on a surface of either concrete tiles or a red PVC sheet. The container was illuminated using fluorescent lamps. Fresh, unfiltered seawater was supplied to the container at a rate of approximately one liter per minute.

Imaging procedures and mussels’ tracking

The movement of individual mussels was recorded by taking an image every minute using a Canon PowerShot D10, which was positioned about 60 cm above the water surface, and attached to a laptop computer. Each image contained the entire experimental domain at a 3000 by 4000 pixels resolution. We tested the effect of increasing mussel densities on movement speed. We set up a series of mussel clusters with 1, 2, 4, 6, 8, 16, 24, 32, 64, 80, 104, and 128 mussels respectively on a red PVC sheet to provide a contrast-rich surface for later analysis (see Figure 3.A1). The movement speed of individual mussels was obtained by measuring the movement distance along the trajectories during one minute. All image analysis and tracking programs are developed in Matlab (R2012a, © The Mathworks, Inc) (www.mathworks.com).

Field photos of mussel patterns

Field photos of mussel patterns with different densities were taken on the tidal flats opposite to Gallows Point (53.245238°N, -4.104166°E) near Menai Bridge, UK, in July 2006.
Figure 3.A1: Two example shots of the experimental setup, with superimposed the trajectories of the tracked mussels.

Pattern amplitude determination

The analysis of the amplitude of the mussel patterns was based on two experimental series. In the first series, 450, 750, 1200, and 1850 mussels were evenly spread over a 60 cm by 80 cm red PVC sheet. In the second series, 100, 200, 400, 600, 1100, and 1400 mussels were evenly spread over a 30 cm by 50 cm sheet. We analysed small-scale variation in mussel density from the image recorded by the webcam after 24 hours using a moving window of 3 cm by 5 cm, in which the mussels were counted. The maximum density was used as the amplitude of the pattern. Four typical images are shown in Figure 3.A2.

Calculation of the scale of the patterns

The spatial scale of the patterns were obtained quantitatively by determining the wavelength of the patterns from the experimental images. We applied a two-dimensional Fourier transform to obtain the power spectrum within a square, moving window. Local wavelength was identified for each window, and the results averaged for all windows. This straightforward technique is suitable for identifying the wavelength in noisy images with irregular patterning (Penny et al., 2013).

Formulating the model

Derivation of a general equation describing density-dependent movement. We now derive a general equation describing the rate of change
of local density $M$ of a population of organisms, in our case mussels. In principle we consider a general $n$-dimensional case; we will later restrict ourselves to a 2 dimensional space, i.e. where $n = 2$.

We study a population of organisms that perform a random walk with an individual movement speed which is a function of the local density $M$, denoted by $V(M)$. The organisms change direction with a density-dependent turning rate $\tau(M)$. Since the speed of the particles depends on $M$, the flux $J_v$ is given by

$$J_v = -\frac{V(M)}{n\tau(M)} \nabla \left(V(M)M\right),$$

(3.A1)

as derived by Schnitzer (1993). This relation is valid under the assumptions that $V|\nabla \tau| \ll \tau^2$ which states that the fractional change of the turning rate over the typical distance travelled between turning must

Figure 3.A2: Laboratory images of mussels pattern formation on a surface of 30 cm by 50 cm, where the number of mussels equals to 200, 400, 600, and 1100 individuals in the arena from A to D respectively.
be small (Schnitzer, 1993). We also incorporate the effect of non-local movement in the model which results in a second contribution to the flux (Murray, 2002, see p.408-416 for details),

\[ J_{nl} = \kappa \nabla (\Delta M), \quad (3.A2) \]

for some constant \( \kappa > 0 \) (here \( \Delta = \nabla^2 \)). See literature (Cates et al., 2010; Murray, 2002) for a similar approach.

We study the population on relatively short time-scales of maximally one day, at which birth and mortality processes play a relatively minor role. For this reason, we do not consider demographic processes in our model analysis. Combining the above assumptions, changes in the local density of organisms can be described by

\[ \frac{\partial M}{\partial t} = -\nabla (J_v + J_{nl}), \]

in which \( M \) is - by construction - a conserved quantity. Combining (3.A1) and (3.A2), leads to

\[ \frac{\partial M}{\partial t} = \nabla [f(M)\nabla M - \kappa \nabla \Delta M], \quad (3.A3) \]

where \( f(M) = \frac{V}{2\tau} \left( V + M \frac{\partial V}{\partial M} \right) \), and \( V \) and \( \tau \) are, in general, functions of \( M \).

For simplicity, we consider the turning rate \( \tau \) to be independent of \( M \). Moreover, we restrict the problem to two dimensions, and hence \( n = 2 \). Note that since \( V \) is the speed of the organisms in the population, \( V(M) > 0 \), for all \( M \) and since \( f(M) = \frac{V}{2\tau} (V + M \frac{\partial V}{\partial M}) \), the occurrence of zeros in \( f(M) \) is controlled by \( V + M \frac{\partial V}{\partial M} \), and thus by the parameters in \( V \).

The derivation of the mussel movement model (3.4). Based on the data obtained from the experiments and the analysis provided in the main text, we assume a parabolic relation between speed \( V \) and density \( M \):

\[ V(M) = aM^2 - bM + c, \]

where the values of the constants \( a, b, c \) can be obtained from the experimental data.
With this definition of $V$, we can derive function $f(M)$:

$$f(M) = \frac{1}{2\tau}(aM^2 - bM + c)(3aM^2 - 2bM + c),$$

so that by introducing $m = \sqrt{\frac{a}{c}} M$ and $\beta = \frac{b}{\sqrt{ac}}$, (3.A3) can be written as

$$\frac{\partial m}{\partial t} = D_0 \nabla [g(m)\nabla m - \kappa_1 \nabla \cdot \Delta m], \quad (3.A4)$$

where $g(m) = (m^2 - \beta m + 1)(3m^2 - 2\beta m + 1)$, with $D_0 = \frac{c}{2\tau}$, $\kappa_1 = \frac{2\tau \kappa}{c^2}$, and $\beta^2 < 4$ (since $V(m) > 0$).

**The standard Cahn-Hilliard equation.** The original Cahn-Hilliard (from here abbreviated as CH) equation describes the separation of a binary fluid into two phases. Assuming $s$ is the concentration of this fluid, it follows the general structure

$$\frac{\partial s}{\partial t} = D \nabla^2 [\mathcal{P}(s) - \kappa \Delta s], \quad (3.A5)$$

where in the most standard setting, proposed by Cahn-Hilliard in 1958 Cahn and Hilliard (1958), $\mathcal{P}(s) = s^3 - s$, and $D$ is the diffusion coefficient. This equation generates patterns of the type shown in Figure 3.A3, consisting of two phases characterized by $s_+ = 1$ and $s_- = -1$. Mathematically, the values $s_+$ and $s_-$ are given by the minima of the potential function $Q(s)$, where $Q'(s) = \mathcal{P}(s)$. For $\mathcal{P}(s) = s^3 - s$, this potential function is given by $Q(s) = \frac{1}{4}s^4 - \frac{1}{2}s^2 + \frac{1}{4},$ where $Q(s)$ has a symmetric double-well shape. For the generation of CH-type patterns, it is not strictly necessary that $Q(s)$ has the precise standard form given above. The condition needed is that two minima exists in $Q(s)$ (Fife, 2002; Novick-Cohen, 2008), separated by a local maximum that acts as a third, unstable state, $s_0$. This implies that $Q'(s)$ must have three - and no more than three - zeros, at $s_- < s_0 < s_+.$

In the context of model (3.A5), this means that one expects CH-type dynamics in case $\mathcal{P}(s)$ has three zeros. This implies that $\mathcal{P}'(s)$ must have two zeros, and one negative minimum between these points. Vice versa, if $\mathcal{P}'(s)$ does not have zeros, Eq. (3.A5) cannot generate patterns since the associated potential well does not have two preferred stable states.

**Translating the mussel model to an extended Cahn-Hilliard model.** Based
on the data obtained from the experiments given in Fig.1(c) of the main text, we adopted a general form of the relation between movement speed $V(M)$ and mussel density $M$ in which $V(M)$ is minimal at a certain density $M^*$: $V$ increases as $M$ moves away from $M^*$. Hence, we consider $V(M)$ with $V'(M) < 0$ for $M < M^*$ and $V'(M) > 0$ for $M > M^*$. In this case, it can be shown that $f(M)$ has one global minimum. The position of this minimum with respect to $M$ is controlled by the precise structure of $V(M)$. Thus, the general shape of $V(M)$ found in the experiments is such that equation (3.A4) could generate phase separation and spatial patterns, but patterns arise only when the minimum of $f(M)$ is negative.

Equation (3.A4) can be written in the CH-form (3.A5) with $P(m)$ such that $P'(m) = g(m)$ (see Eq. (3.A6) in the remark below for details). Since $g(m)$ is a quartic polynomial with respect to $m$, $P(m)$ will be a quintic: significantly different from the standard CH-case in which $P(m)$ is a cubic polynomial, see section (The standard Cahn-Hilliard equation). However, in the model that we consider, $f(M)$ can have at most one minimum that lies below the axis because of the condition on movement speed that $V(M) > 0$. This can be deduced by straightforward arguments from the

Figure 3.A3: Spatial pattern of CH equation (3.A5) with $\kappa = 0.01$. 

on the data obtained from the experiments given in Fig.1(c) of the main text, we adopted a general form of the relation between movement speed $V(M)$ and mussel density $M$ in which $V(M)$ is minimal at a certain density $M^*$: $V$ increases as $M$ moves away from $M^*$. Hence, we consider $V(M)$ with $V'(M) < 0$ for $M < M^*$ and $V'(M) > 0$ for $M > M^*$. In this case, it can be shown that $f(M)$ has one global minimum. The position of this minimum with respect to $M$ is controlled by the precise structure of $V(M)$. Thus, the general shape of $V(M)$ found in the experiments is such that equation (3.A4) could generate phase separation and spatial patterns, but patterns arise only when the minimum of $f(M)$ is negative.

Equation (3.A4) can be written in the CH-form (3.A5) with $P(m)$ such that $P'(m) = g(m)$ (see Eq. (3.A6) in the remark below for details). Since $g(m)$ is a quartic polynomial with respect to $m$, $P(m)$ will be a quintic: significantly different from the standard CH-case in which $P(m)$ is a cubic polynomial, see section (The standard Cahn-Hilliard equation). However, in the model that we consider, $f(M)$ can have at most one minimum that lies below the axis because of the condition on movement speed that $V(M) > 0$. This can be deduced by straightforward arguments from the
observational fact that \( V(M) \) only has one minimum at \( M = M^* \) (and decreases, respectively increases, for \( M < M^* \), resp. \( M > M^* \)). Thus, in the present model only CH-type patterns may develop. This is also typical behavior if we drop the assumption that the turning rate \( \tau \) is constant, and take it to depend on the mussel concentration \( M \). Since the turning rate must remain positive for all \( M \), it is not possible to create additional zeroes in \( f(M) \) by varying \( \tau \). Hence, also in this more general case, the dynamics generated by (3.A3) remain of CH-type.

It is straightforward to ‘control’ the appearance of zeros of \( g(m) \): \( g(m) > 0 \) for all \( m \) when \( \beta < \sqrt{3} \). As \( \beta \) crosses through \( \sqrt{3} \), two zeros appear: thus, CH-like patterns will appear as \( \beta^2 \) increases through 3. This is confirmed by our simulations in the bifurcation analysis in Figure 3.A4 and the simulated pattern in Fig.1(d).

\[
\frac{\partial m}{\partial t} = D_0 \nabla^2 [P(m) - \kappa_1 \Delta m], \quad (3.A6)
\]

with \( P(m) = \frac{3m^5}{5} - \frac{5\beta m^4}{4} + \frac{(4+2\beta^2)m^3}{3} - \frac{3\beta m^2}{2} + m + \mathcal{H} \). Here, \( \mathcal{H} \in \mathbb{R} \) is a new
Numerical implementation

The continuum equation (3.A4) was simulated on a HP Z800 workstation with an NVidia Tesla C1060 graphics processor. For the two-dimensional spatial patterns, our computation code was implemented in the CUDA extension of the C language (www.nvidia.com/cuda). The spatial fourth-order kernel is implemented in two-dimensional space using the numerical schemes shown in Figure 3.A5. Spatial patterns were obtained by Euler integration of the finite-difference equation with discretization of the diffusion van de Koppel et al. (2011). The model’s predictions were examined for different grid sizes and physical lengths. We adopted periodic boundary conditions for the rectangular spatial grid. Starting conditions consisted of a homogeneous distribution of mussels with a slight random perturbation. All results were obtained by setting $\Delta t = 0.001$ and $\Delta x = 0.15$.

![Figure 3.A5: The kernel $\nabla^4$ in two-dimensional space.](image)

Correlations analysis

The comparison of images obtained from the mussel beds on the tidal flats near Menai Bridge with results of the numerical solution of model (3.A4)
reveals a remarkable similarity of the real mussel beds with the model prediction (see Fig. 2 in main text). Of course, due to the inherent stochastic nature of the real mussel ecological system, the snapshots do not match precisely. To reach a quantitative assessment on the validity of the model (3.A4) to describe the spatial properties of the mussel system in the short-time scale, we have computed spatial correlation function for the system’s spatial patterns.

We consider equal-time spatial correlation functions (in fact, the system displays coarsening at long-time scale, then we must choose the appropriate timescale), which yield information about the size of the emerging patterns. Here, we focus on the correlation function, where 
\[ G(r) = \frac{\langle m(r+r')m(r) \rangle - \langle m(r,t) \rangle^2}{\langle m(r,t)^2 \rangle - \langle m(r,t) \rangle^2}, \]
which expressed how the value at position \( m(r,t) \) is related to data points at some distance \( r' \) (Arfken and Weber, 2005). The spatial correlation function, \( G(r) \), averaged for specie distance classes over the entire density field, reveals the global behavior of the pattern as a function of spatial scale. The position of the first peak gives the mean wavelength of spatial patterns. In Figure 3.A6, we show the spatial correlation function obtained for both field patterns and from the predicted patterns of model (3.A4), after a timescale of about 24 hours, revealing an excellent agreement.
**Figure 3.A6:** Correlation functions of the patterns. The spatial correlation as function of $r$ comes from the experimental aggregation patterns and simulation patterns about 24 hours timescale. Results obtained from experiment in Figure 3.1(B), and numerical solutions of the model (3.A4), and notice an excellent agreement.

**Table 3.A1:** Likelihood ratio test LRT, AIC weights, adjusted $R^2$, and significant level of the fitted functions for mussel movement speed data. The observed data is best fitted by a quadratic function.

<table>
<thead>
<tr>
<th>Model</th>
<th>LRT</th>
<th>AIC weights</th>
<th>Adjusted $R^2$</th>
<th>p-vales</th>
</tr>
</thead>
<tbody>
<tr>
<td>quadratic</td>
<td>3.1836</td>
<td>1.63283</td>
<td>0.3894</td>
<td>0.00001* (t=4.732)</td>
</tr>
<tr>
<td>linear</td>
<td>-6.292</td>
<td>18.4985</td>
<td>0.009474</td>
<td>0.556 (t=-0.595)</td>
</tr>
</tbody>
</table>

*The significant difference is refered to second-order term.*