# Self-organized spatial patterns on intertidal mudflats: Do they affect ecosystem functioning?

**Bachelor thesis (2012)**

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# Abstract

Self-organized spatial patterning is a common phenomenon in all ecosystems and is often associated with a positive effect on ecosystem functioning. Also on intertidal mudflats, dominating organisms form regular spatial patterns of different sizes and persistence. The main species who organise themselves in spatial patterns on intertidal mudflats are the blue mussel (*Mytilus edulis* L.), dwarf eelgrass (*Zostera noltii*) and benthic diatoms. In this thesis three case studies will be presented considering these species and their spatial self-organisation. Overall it turns out that the underlying mechanism in all three species is the same, although specific interactions differ. In this mechanism, the so-called scale-dependent feedback model, a short-scale positive feedback and a large-scale negative feedback operate on the community, thereby creating spatial patterns. The effect of those patterns on ecosystem functioning is still under debate, but most evidence leads to the conclusion that self-organized spatial patterns increase resilience and productivity of the ecosystem. A future management application of understanding self-organised spatial patterns is their ability to predict ecosystem health and current stress levels.

# Content

# Introduction

Intertidal mudflats are muddy or sandy coastal ecosystems that get flooded twice a day because of the tide. This creates a very unique habitat for sessile organisms, which have to be able to live both without water at low tide and immersed in seawater at high tide. Nevertheless, intertidal mudflats are teeming with life. Many organisms have adapted to the tidal way of living and the intertidal ecosystem provides many valuable human services and goods.

Urbanization has a huge impact on coastal ecosystems, including intertidal mudflats. Since living near the sea has lots of benefits (fishing, transport etc.), approximately 40 % of the human population lives in the coastal zone (Independent World Commission on the Oceans 1998). This has led to high levels of exploitation and degradation of coastal ecosystems worldwide. Nevertheless, the coast still serves us with many ecosystem services like flood control, food production and recreational areas. Furthermore the coast is estimated to be responsible for about 10% of the world's primary production (Kaiser et al 2005). For conservation and restoration of degraded coastal areas we need a better understanding of coastal ecosystem function.

Intertidal soft sediment ecosystems are dominated by organisms that modify their habitat. The reason they modify the soft sediment is not only because it is easy to modify but also to reduce the high stress levels or improve their access to food. Species that modify their own habitat are called ecosystem engineers. By modifying their habitat, ecosystem engineers may create spatial patterns. The three main ecosystem engineering species that form self-organized spatial patterns on intertidal mudflats are the blue mussel, dwarf seagrass and benthic diatoms.

In this thesis I discuss the importance of self-organized spatial patterns for the functioning of intertidal mudflat ecosystems. First I will present a general overview of spatial patterning followed by discussing three case studies of self-organized spatial patterning in three important species groups on the intertidal mudflat. I will specifically address the following questions:

- What is the universal mechanism behind spatial patterning?
- What are the involved feedbacks for different species to form spatial patterns?
- What effect do the spatial patterns have on ecosystem functioning?

The goal of this framework is to gain more insight in why different species groups are organized into spatial patterns and what effect this patterning has on ecosystem functioning.

# 1. Spatial patterning

On mudflats, many dominating organisms with different life-histories and evolutionary histories form regular spatial patterns. For example, bivalve reefs form banded patterns that are several meters wide and up to 30-40 meters long; while diatom communities form elevated patches of circa 1 meter. However, spatial patterning is a common phenomenon present in many biotic as well as abiotic systems, with examples as vegetation patterns on land, ripples formed by waves, and even chemical reactions in morphogenesis. In this review, I am more interested in spatial patterns by sessile marine organisms, but looking at other systems can be helpful in explaining patterns on intertidal mudflats.

In 1952 Turing described the now so-called activator-inhibitor principle. This principle was based upon a chemical reaction in morphogenesis, but can be regarded as a basic principle in biology. The activator-inhibitor principle predicts regular spatial patterns when a chemical substance activates itself to generate more of itself on short scale (the activator), but also generates another chemical substance that inhibits this production (the inhibitor). The inhibitor has to diffuse faster than the activator, so the activator will only spread locally and thereby creates patterns (Fig. 1a, Turing 1952 in: Rietkerk and van de Koppel 2008).

In ecology this phenomenon is described as scale-dependent feedback. This feedback consists of a short-term facilitative feedback and a long-term competitive feedback (Fig. 1b, Rietkerk et al. 2004), comparable with the activator and inhibitor principle of Turing. An important factor in this model is that the positive and negative effects occur at different spatial or temporal scales (Rietkerk et al. 2008). A study on marsh tussocks in Main, USA, pointed out that short distance positive feedback was not essential for regular pattern formation. The scale-dependent feedback in this ecosystem consisted only of a long distance negative feedback. This long distance negative feedback, where seedlings around the tussocks are shaded by the wrack layer of the plants, was essential for the creation of the patterns (van de Koppel and Crain 2006).

This scale dependent feedback mechanism also seems to be the underlying driver in regular pattern formation in arid ecosystems (Rietkerk et al. 2002), savanna ecosystems (Lejeune et al. 2002), wetland ecosystems (Rietkerk et al. 2004) and many more. The patterns in those ecosystems cannot be traced back to the underlying abiotic soil; there are no differences in composition or height. When this is the case spatial patterns are so called self- organized; they emerge from disordered initial conditions and originate from the organism itself (Weerman et al. 2010). Possibly, if there wasn't as much abiotic heterogeneity in most ecosystems regular spatial patterns would be more common.

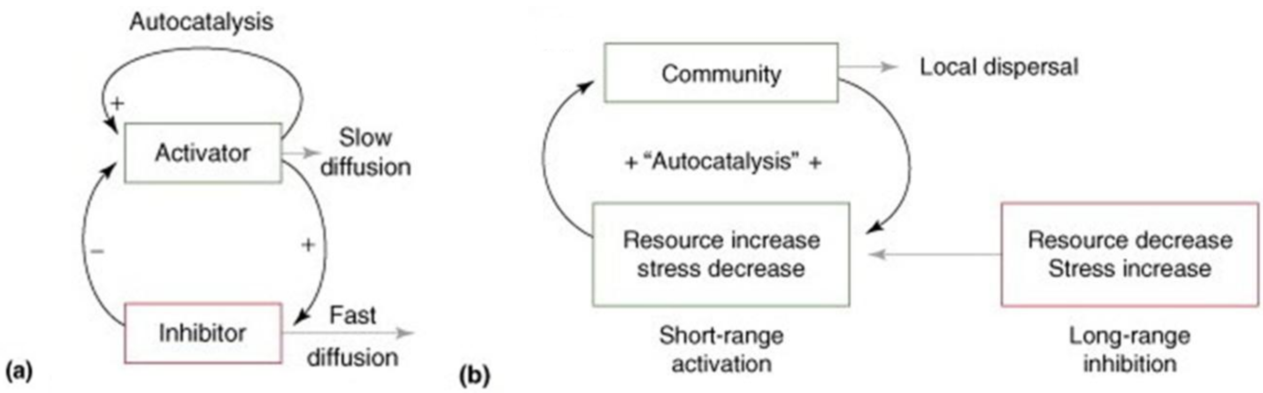


Figure 1: Overview of interactions in (a) the activator-inhibitor principle of Turing, where the activator activates itself by autocatalysis and diffuses slowly. The inhibitor, also produced by the activator, diffuses fast and inhibits the activator.
(b) shows the interactions in scale-dependent feedback, following the same principles. The community facilitates itself via autocatalysis in a short-range activation, but is also inhibited by a long-range inhibition (Rietkerk and van de Koppel 2008).

On mudflats, hydrodynamic conditions determine the large-scale distribution of sediment and thereby form large-scale patterns. Created patterns are for instance channels, creeks and gullies. These channels perform a drainage function on the mudflat and continue to flow long after the tide has receded (Whitehouse et al. 2000). Other bedforms on the mudflat are ridges and runnels, oriented perpendicular to the shore with a width of 0.5 to 1 meter and a height of tens of centimeters. They are a result of wave-induced erosion of the sediment (O'Brien et al. 2000). The third form of patterning on the mudflat consists of ripples, which are regular small-scale wave-like features, they are also oriented perpendicular to the water flow and caused by waves and currents. They mainly exist in non-cohesive sediment (Whitehouse et al. 2000)

There are several indications that cases of local patterning are caused by self-organization through scale-dependent feedback, rather than hydrodynamic processes. First, because scale-dependent feedback causes similar spatial patterns in ecosystems where hydrodynamics are not involved (Rietkerk et al. 2008). Second, if wave action causes a pattern, the pattern should decrease with distance because of diminishing current strength, which is often not observed in local patterning on mudflats (van de Koppel et al. 2005). Third, to explain patterns arising from megaripples with a wavelength of more than 8 meters, which is common in mussel beds, it would require current velocities where organisms would be unable to sustain (Amos and King 1984). Finally, spatial patterns also occur in the laboratory without currents; uniformly spread mussels developed spatial patterns in only one day (van de Koppel et al. 2008).

One of the reasons why spatial self-organization is considered an important phenomenon in ecology is their link with catastrophic shifts. Catastrophic shifts cause an ecosystem to switch between two alternative stable states, for instance from a heterogeneous to a homogeneous state. This can drastically change composition and function of an ecosystem. Typical of alternative stable states is a high resilience to environmental changes until a certain threshold. Once the system passes this threshold it shifts to an alternative stable state with a different structure and function. If the system does not switch back to the former state when original conditions are restored it may depend on the fact that the second alternative state has to pass beyond a different environmental threshold to go back to the first state; this is called hysteresis (Fig. 2, Rietkerk et al. 2004, Eriksson et al. 2010). The shape of self-organized patterns of organisms can give an indication of the health of an ecosystem; when the pattern changes from a banded pattern to a patchier pattern this can for instance indicate an increased stress-level and thereby an increased risk of an approaching catastrophic shift (Fig. 2). Thus, patterning may predict an upcoming catastrophic shift, which makes it a possible very important indicator for conservation and management of ecosystems.

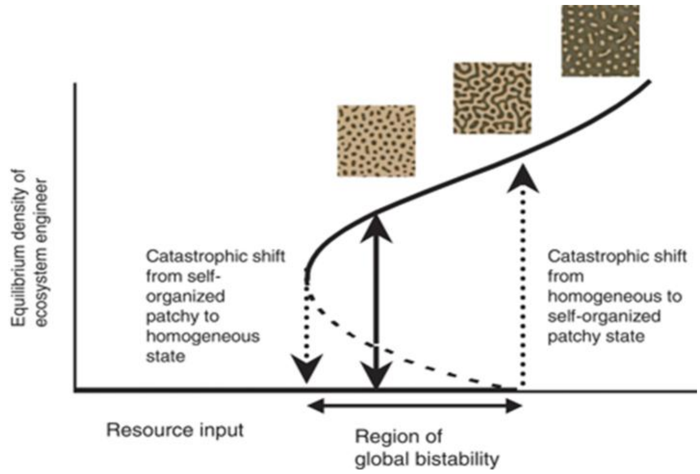


**Figure 2:** Model showing how patterns may change with fluctuating resource input (dark colours in inset represent high density). Thick solid lines represent mean equilibrium density of the ecosystem engineer. Dotted arrows represent catastrophic shifts between self-organized patchy states and homogeneous states, and vice versa. At the solid arrow initial ecosystem engineer densities determines towards which state the system develops (Rietkerk et al. 2004)

# 2. Case studies

To understand more about the patterns occurring on the intertidal mudflat I present three case studies. Those three case studies contain three organisms known to modify their environment into regular spatial patterns; the blue mussel (*Mytilus edulis* L.), dwarf seagrass (*Zostera noltii* L.) and benthic diatoms (Figs 3, 4 and 5). In the following chapters I will present a review of the species, why they organize themselves in regular spatial patterns and what their effects are on ecosystem functioning.

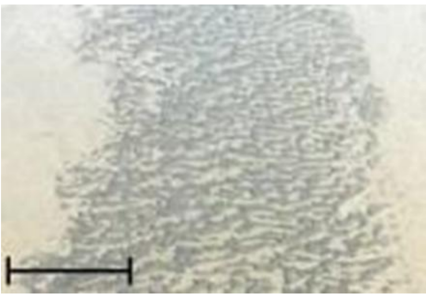

**Figure 3**: A mussel bed in the Waddensea, the Netherlands, showing a self-organized spatial pattern, scale = 50 m (van de Koppel et al. 2005)

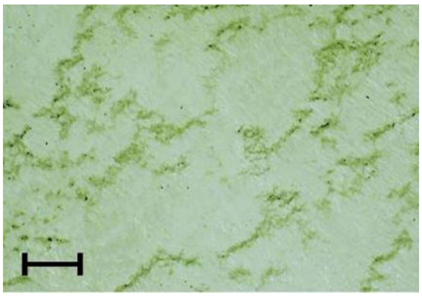

**Figure 4**: A seagrass meadow in the Saint Efflam Bay, France, showing a self-organized spatial pattern, scale = 5 m (van der Heide et al. 2010)

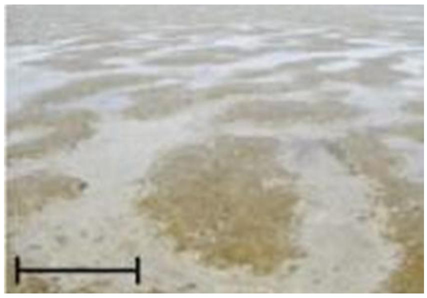

**Figure 5**: An intertidal mudflat In the Netherlands showing self-organized spatial patterns caused by marine benthic diatoms, scale = 1 m (Rietkerk et al. 2007)

# 3. Case study I: Blue mussel

## 3.1 General description

Blue mussels are marine bivalves and belong to the family of mytilidae. They have separated sexes and reproduce by releasing sperm and eggs in the water. Hence, large proportions of the eggs are never fertilized and only 1 percent of the larvae reach adulthood, mainly because of predation (Kaiser et al. 2005). Blue mussels are very efficient filter feeders with high filtration rates. They filter a large part of the water column for algae and also filter out the fine sediments. The indigestible parts are excreted as (pseudo-)pellets. This formation of biodeposits, containing fine sediment, nutrients and carbon, decreases eutrophication and regenerates a large amount of the nutrient demand for pelagic primary production (Kautsky and Evans 1987).

Mussels attach themself to hard substrates with byssal threads, and if hard substrates are unavailable they clump together. Attaching together reduces predatory losses and the probability of washing away due to wave disturbance (Bertness et al. 1985). By clumping together, blue mussels create epi-benthic reefs which have a large impact on hydrodynamic conditions, sediment stabilization and they create heterogeneity on mud flats. Blue mussels live in the intertidal zones and shallow subtidal zones in the eastern Atlantic from southern Norway to tropical Mauritania, throughout the Mediterranean, Black, Azov and Caspian Seas.

## 3.2 Self-organized patterns

Blue mussels organize themselves in large aggregations called mussel beds which can grow to up to thousands square kilometers in size. On mud flats some of the intertidal mussel beds show clear patterning in the form of regular bands perpendicular to the flow of the water (Fig 3; van de Koppel et al. 2005). We can make a distinction between two types of pattern formation in mussel beds; in young mussel beds patterns consist of regularly spaced clusters of 5-10 cm (van de Koppel et al. 2008) in older mussel beds patterns can be up to tens of meters in length, a couple of meters in width and about 30 cm in height due to sediment accumulation (Liu et al. 2012). In between these

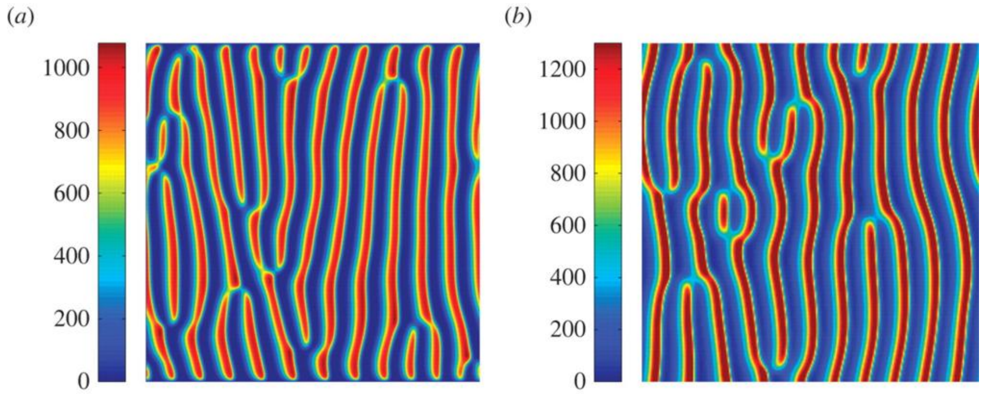


**Figure 6:** model simulating mussel banding, representing an aerial view of the mussel bed on a square mudflat of 50 × 50 m. (a) shows the decreased losses feedback model and (b) shows the sediment accumulation feedback model (Liu, 2012)

bands is always a mussel free area. Due to ice wreckage and washing away, older mussel beds usually get patchier (van de Koppel et al. 2005).

Johan van de Koppel et al (2005) predicted that the patterning of intertidal mussel beds depended on spatial self-organisation caused by a tradeoff between competition for food and facilitation by clumping together. He argued that at the front of a mussel band there is high wave exposure, so a big risk of washing away, but there is also high food availability. On the back of the band the algae are depleted but there is only small wave exposure, so they have to invest less in byssal threads. In between bands is a region with total algal depletion where mussels will be unable to live. In this mussel free region lower water layers mix with the upper water layers until there is again enough algae in the water to support a new mussel band. In 2008, van de Koppel et al (2008) tested this empirically and found that higher density of blue mussels indeed increased survival rate. Dense near-homogeneous beds had the same survival rate as patterned beds, but in near-homogeneous beds, mussels had grown significantly less than mussels in the patterned bed. Thus, patterned beds where the most favourable distribution both for survival and growth (van de Koppel et al. 2008).

Quan-Xing Liu et al (2012) designed an alternative model that also explains patterning in blue mussel beds successfully (Fig. 6). In both models, the large-scale negative feedback is caused by algal depletion due to competition, but the short-term positive feedback differs. The alternative model is based upon the fact that mussel accumulate sediment underneath their bands, creating hummocks. The short-term positive feedback consists of an increased access to algae on top of the band because the decreased water depth increases water flow (Liu et al. 2012). This theory is supported by his empirical observations where he indeed found a significant higher mussel density and mussel biomass on top of the bands compared with the edges of the band. (Liu et al. 2012). In his article Liu referred to van de Koppel's model as the 'decreased losses feedback' and to his own as the 'sediment accumulation feedback' (Fig. 7).

The existence of two different fitting models for the same phenomenon can be explained by the fact that the models are operational on different scales. Where empirical evidence for the decreased losses feedback is based upon experiments using aggregations of about 5 to 10 cm, the sediment accumulation feedback is based on the bands of 5 to 10 meter (with a height of 30 cm). This might imply a combination of models. In young mussel beds aggregation is one of the major drivers, since the risk of washing away is high. Furthermore, in young mussel beds there are no height differences yet, making the sediment accumulation feedback unsuitable. In mature mussel beds the sediment accumulation feedback is more likely, since mussel beds will be more densely populated and competition for food will be stronger.
In addition, intraspecific interactions do not only occur on a spatial scale but also at a temporal scale

(Gascoigne et al. 2005). Gascoigne et al (2005) suggested that competition for food was the most important driver for self-organisation during the summer. In the winter, however, mussels were growing faster where mussel density was high, implying that facilitation of clumping together to prevent washing away was the most important driver during the winter (Gascoigne et al. 2005). This indicates that the decreased losses feedback and the sediment accumulation might be both working on the same system but in different time periods.

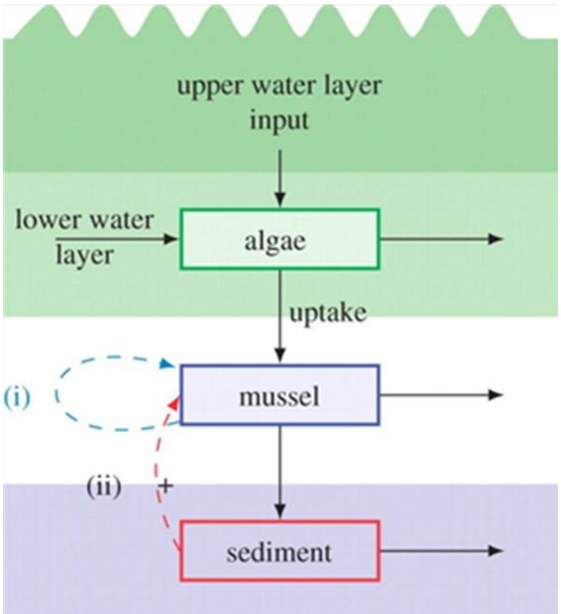


**Figure 7:** Schematic of the models of Johan van de Koppel (2005) and Quan-Xing Liu (2012) giving an overview of the interactions in the models. (i) Indicating the positive feedback of aggregation as in the decreased losses feedback and (ii) indicating the positive feedback of sediment accumulation as in the sediment accumulation feedback.

## 3.3 Effect of self-organized patterns on the ecosystem

Blue mussel beds have an important role in the intertidal ecosystem. They increase the total annual deposition of carbon, nitrogen and phosphorus with 10%, thereby functioning as an eutrophication control and a connecting link between benthic and pelagic ecosystems (Kautsky and Evans 1987). Moreover, mussel beds provide habitat and shelter for many small intertidal species (Tsuchiya and Nishihira 1985) and create heterogeneity on mudflats which increases biodiversity.

Consequences of spatial self-organization for the function of intertidal mussel beds and associated communities are not well understood. The 'decreased losses feedback' model of van de Koppel et al (2005) predicted that mussel beds with self-organized spatial patterns have a higher productivity and a higher resilience against environmental stress than homogeneous mussel beds. The patterning also allowed mussels to sustain at algal concentrations that would not be able to support homogeneous beds (van de Koppel et al. 2005). Furthermore, field evidence showed that pattern formation affected ecosystem-level processes by improved growth and higher survival rates (van de Koppel et al. 2008). In contrast, the 'sediment accumulation feedback' model of Liu et al (2012) predicted no increase in total blue mussel biomass due to self-organization. This also concerned the resilience of the bed, which did not increase due to self-organized spatial patterning. Thus, whether self-organized patterns themselves contribute to ecosystem functioning still remains unclear.

# 4. Case study II: Seagrass

## 4.1 General description

Seagrasses are flowering, marine plants. They are a polyphyletic group, so they have evolved multiple times in different lineages. Nevertheless, they are generally assigned to the family of the Potamogetonaceae and the Hydrocharitaceae, of which neither is related to terrestrial grasses (Kaiser et al. 2005). They reproduce sexually by flowering and spreading seeds. However, seagrasses also grow vegetative and when conditions are stable enough they grow almost endlessly; the largest known clone covers a total area of 6400 m$^2$ and is over 1000 years old (Reusch et al. 1999). Since seagrasses need light for photosynthesis, they are restricted to the photic zone and are very sensitive to eutrophication and changes in water transparency. Eutrophication enhances algae growth and may thereby decrease visibility. If average visibility decreases below a certain threshold, seagrasses are unable to sustain growth and survival. Seagrasses distinguish themselves from macroalgae by their more complex reproductive systems, flowers, and specialized functional structures like roots, stems and leaves with veins.

Seagrasses are found in all the world coastal seas, except in the polar regions and cover approximately 0.1 -0.2 % of the global ocean (Duarte 2002). In this review I focus on dwarf seagrass (*Zostera Noltii*) which is an intertidal seagrass with clear examples of spatial patterning. Dwarf seagrass is restricted to the Eastern Atlantic from southern Norway to tropical Mauritania, throughout the Mediterranean, Black, Azov and Caspian Seas.

## 4.2 Self-organized patterns

*Zostera noltii* meadows are known to organize themselves in regular interspaced banded patterns. The bands they organize themselves in are typically perpendicular to the current and wave direction and have a mean patch size between 0.1 and 0.9 square meters (Fig. 4; van der Heide et al. 2010). Van der Heide et al (2010) suggests that this self-organization occurs because of a trade-off between a short-term positive effect and a long term negative effect, again following the principles of scale-dependent feedback (Rietkerk et al. 2004). High root density decreases the risk of uprooting because of increased sediment stability and better anchoring, this facilitation functions as the short-term positive feedback (Peralta et al. 2005). The negative, long term feedback takes place above ground. The seagrass shoots interact with hydrodynamics which causes scouring of the sediment on the coast side, which results in an asymmetric depression in front of the seagrass band (Fig. 8A). This depression is approximately the same depth as seagrass rooting depth, causing an increased shoot erosion on the coast side of the bands (Fig. 8B). The scour depth increases with plot width and shoot density (Fig. 8C), which works as a long-term negative feedback when the depth of the band or the shoot density increases.

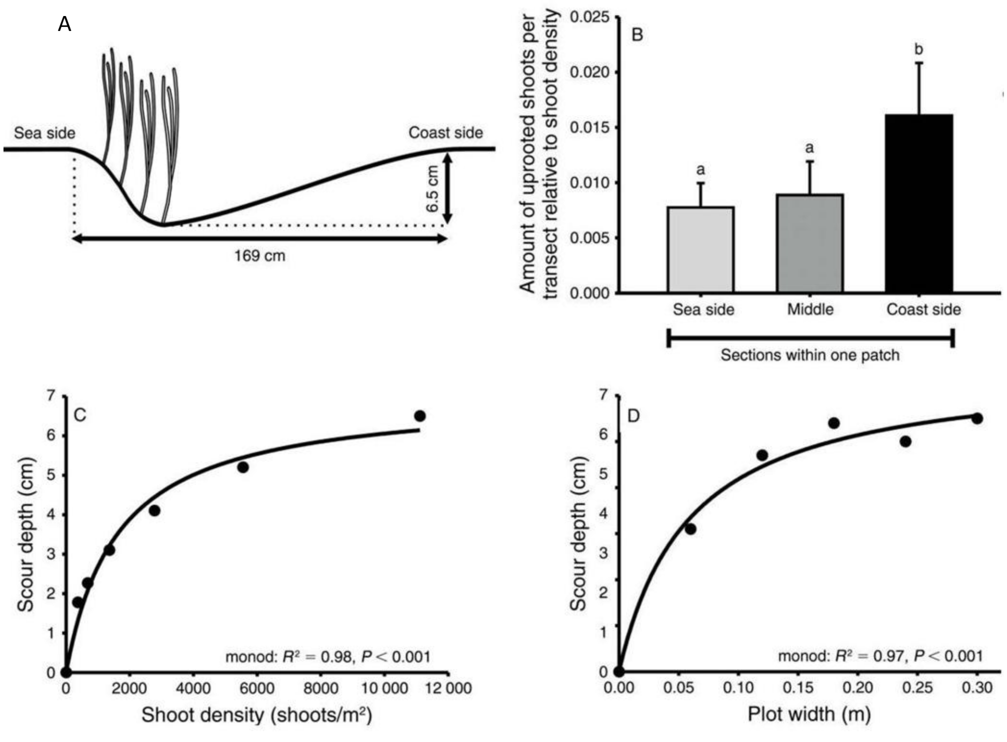


**Figure 8:** (A) schematic view of a seagrass band with an asymmetric depression on the coast side (B) Graph showing a significantly higher amount of uprooted shoots on the coast side (C) Graph showing increased scour depth with increasing shoot density and (D) with increasing plot width (van der Heide et al. 2010).

## 4.3 Effect of self-organized patterns on the ecosystem

Seagrass meadows have strong effect on their surroundings and are so-called ecosystem engineers. They stabilize the sediment by binding the substrate with their roots. Their aboveground biomass increases deposition of fine particles and slows down water flow, which increases visibility of the water (Terrado and Duarte 2000). Also, seagrass meadows create habitat for multiple small organisms; both abundance and species richness is positively correlated with seagrass biomass (Lee et al. 2001). Their net production is about 0.6 * $10^{15}$ g carbon per year (Duarte and Chiscano 1999), and they are responsible for approximately 15 % of the oceans carbon storage (Duarte and Chiscano 1999)

Seagrass loss has been recorded to have major effects on the ecosystem. In Cockburn Sound, Australia, loss of a large proportion of the seagrass meadows because of coastal development and nutrient inputs, led to large-scale sediment resuspension and a decrease in the fish population. Nowadays, if seagrass density gets below a certain level remedial action is obliged by law (Orth et al. 2006).

Consequences of pattern formation in seagrass meadows on ecosystem functioning are still unclear. Nevertheless, self-organized spatial patterns in seagrass meadows are a good indicator for the health of the ecosystem. Properties of self-organisation react predictably to increased stress in the environment (Fig. 9, van der Heide et al. 2010). Along the depth gradient characteristics of the patterns of the seagrass meadow change, with an optimum of both seagrass cover and mean patch size at a depth of 1 meter below mean water level. When seagrass grows shallower than the optimum, desiccation is the main limiting factor for growth. When seagrass grows deeper than the optimum, light availability decreases and thereby sets the lowest limit (Fig. 8). The patterns they organize themselves in when limited by either desiccation or light react predictably and therefore spatial patterning in seagrass meadows can be an important indicator for current stress levels.

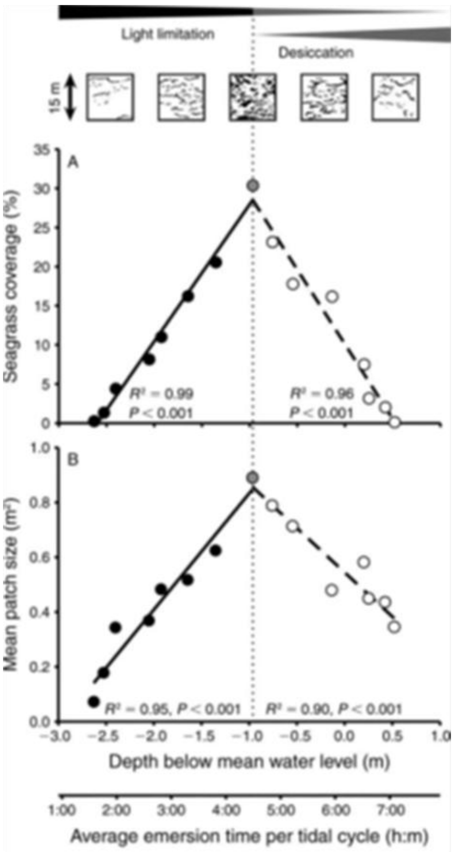


**Figure 9:** Graphs of mean patch size and Seagrass coverage against a depth gradient. Light sets the lower limit while desiccation sets the upper limit, with an optimum at a depth of 1 m. The squares on top show a change in pattern according to stress level (van der Heide, 2010)

In contrast with results from other ecosystems, models of spatial patterns in seagrass do not suggest a potential for catastrophic shift from a vegetated to a bare state. Instead the model predicts a bistability between a stagnant patterned state and a homogeneous, fully covered state at low stress levels. At higher stress levels the only stable state is one of migrating banded patterns (van der Heide et al. 2010). When stress levels increase even further the seagrass cover is predicted to decrease linear towards a complete loss instead of through a sudden shift as predicted in other patterned ecosystems (Rietkerk et al. 2004). But as we have seen in the paper of Liu et al (2012) on mussel beds, different models on the mechanisms behind patterning can predict different outcomes according to ecosystem functioning.

# 5. Case study III: Diatoms

## 5.1 General description

Diatoms are unicellular, photosynthetic algae. The family they belong to, the Bacillariophyce, consists of 300 genera and more than 12,000 species and are thereby the most numerous eukaryotic aquatic organisms in the world. They have a unique silica cell wall, consisting of two petri-dish like frustules. Their life cycle consists of cell division, but, because they have an inflexible cell wall, every cell division reduces their size. When cells become too small, an auxospore is formed, wherein a new diatom cell develops (Kaiser et al. 2005). On the intertidal mudflat diatoms are the dominant group within microphytobenthos (Underwood 1994) which is considered the most important primary producer on the intertidal mudflat (Cariou-Le Gall and Blanchard 1995). Because they are mainly autotrophic organisms, they live in the photic zone either as solitary cells or in colonies. Diatoms occur in nearly every environment that contains water.

## 5.2 Self-organized patterns

Spatial patterning in intertidal diatoms consists of elevated ridges with water-filled runnels in between. The elevated ridges - hummocks - are characterized by a high diatom concentration and little erosion while in the hollows this is opposite (Blanchard et al. 2000). The spatial pattern lies parallel with the primary drainage direction of the intertidal mudflat and perpendicular to the tidal flow direction with a wave length of approximately 1 meter (Weerman et al. 2010). The shape of the patterns depend on the strength of the tidal current; when the current is strong patterns are strongly banded, when the tidal current decreases in strength patterns gets more rounded.

Sediment accumulation on the hummocks depends on the physiology of the diatoms. Diatoms migrate vertically through the sediment to be at the surface during low tide and retreat back before high tide or when it gets dark (Hay et al. 1993). When they move through the sediment they produce extracellular polymeric substances (EPS; Neumann 1970), thereby creating a brown biofilm. According to Staats et al (2000), this biofilm is not only produced by their movement but also deliberately produced as an overflow metabolism due to nutrient limitation. EPS increases accumulation of sedimentation by increasing sediment cohesion and decreasing bottom roughness (Paterson et al. 1989).

The characteristics of EPS cause a local positive feedback. Because the by EPS accumulated sediment increases the hummock height which lowers the water level and thereby reduce the risk for diatoms to be eroded by the water (Fig. 10A).

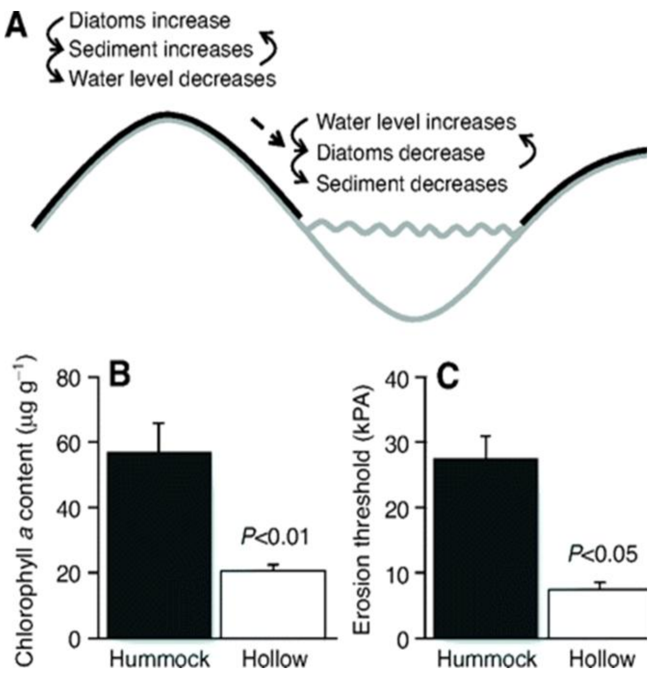


Figure 10: (A) overview of interactions between diatom abundance, sediment accumulation or erosion and water level; a scale-dependent feedback (B) Graph showing higher diatom abundance on the hummock than in the hollows (C) Graph showing sediment stability is higher on the hummock than in the hollows. (van de Koppel et al. 2012, modified from

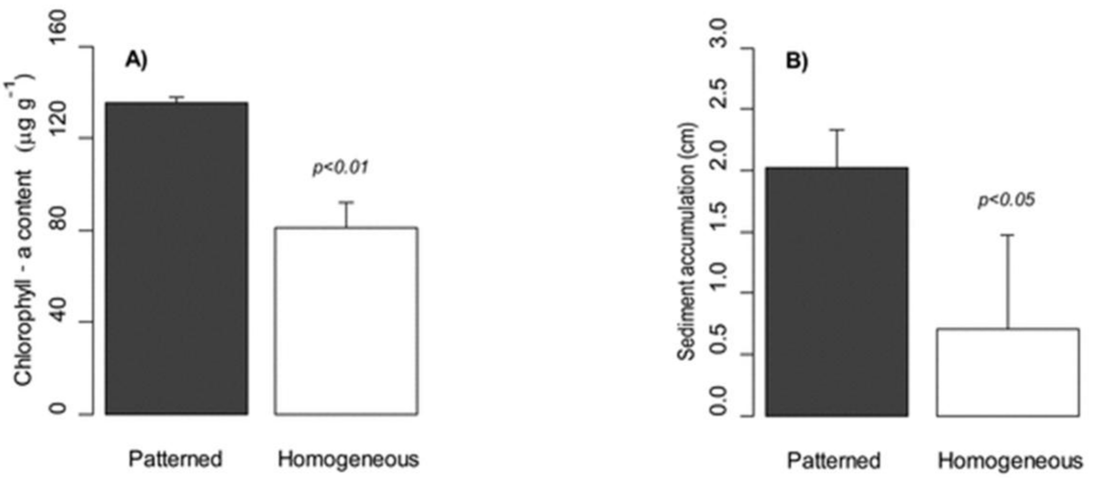


**Figure 11:** Graphs showing that patterning increases both diatom biomass (A) and sediment accumulation (B) (Weerman, 2010)

At larger distances a negative feedback occurs in the runnels. Because the hummocks are higher due to the sediment accumulation water flows into the runnels. This enhanced water level increases the risk for diatoms to be eroded, partly because EPS, which on the hummocks prevents them from being eroded, dissolves in water (Fig. 10A, Rietkerk and van de Koppel 2008). Weerman et al (2010) tested this feedback empirically and could demonstrate a significantly higher diatom abundance and sediment stability on top of the hummocks compared with the hollows (Fig. 10 B), which confirms the model. Thus, also for benthic diatoms, scale-dependent feedback creates spatial patterns on the intertidal mudflat.

## 5.3 Effect of self-organized patterns on the ecosystem

Diatoms have a large impact on the ecosystem, because they are one of the major primary producers on the mudflat (Cariou-Le Gall and Blanchard 1995). This makes them an important food source for both benthic macrofauna (Herman et al. 2000) and for the total planktonic foodweb (de Jonge and van Beusekom 1992). The habitat modification capacity of diatoms is not as strong as for mussel beds or seagrass meadows, but diatom patterns do significantly affect ecosystem functioning.

Pattern formation has a positive impact on overall diatom biomass (Fig. 11A, Weerman et al. 2010). Chlorophyll *a* concentration (as proxy for diatom abundance) was found to be significantly higher in patterned plots compared to homogeneous plots. Furthermore, sediment capture was positively correlated with spatial patterns. Sediment level increased twice as much in patterned plots compared with homogeneous plots (Fig. 11B; Weerman et al. 2010). Degeneration of self-organized patterning may therefore have major impacts on intertidal mudflats since it could lead to a decrease in diatom abundance which might have cascading effects on higher trophic levels, and lead to resuspension of the sediment. Hence, spatial patterns significantly affects ecosystem functioning on the intertidal mudflat.

**Table 1**: A summary of the scale-dependent feedback mechanisms leading to self-organised spatial patterning on intertidal mudflats that were described in this review.

| Organism | # studies | Short-range positive feedback | Long-range negative feedback | Effect on ecosystem functioning |
|---|---|---|---|---|
| Blue mussel | *3* | 1. Preventing of dislodgement by clumping together 2. Higher food availability on top of bands | Food depletion due to competition | 1. Possible increased resilience and productivity, depending on model 2. Indicator for stress |
| Dwarf seagrass | *1* | Decreased risk of uprooting with high root density | Increased coast side uprooting with increasing shoot density or plot width | Predictor for ecosystem health |
| Diatom communities | *1* | Increased growth rate on the hummock | Washing away in the runnels | 1. Higher productivity 2. Higher sediment capturing |

# Discussion

My review shows that scale-dependent feedback is an important underlying principle that creates spatial patterning on intertidal mudflats. The presented case studies provide empirical evidence of self-organised patterning in three important organism groups on tidal mudflats: mussels, seagrasses and diatom communities. All three organism groups depend on different drivers (Table 1) and even within species there is discussion on their exact feedback mechanisms (van de Koppel et al. 2008, Liu et al. 2012). Still, in all three case studies it is likely that scale-dependent feedbacks cause the described local patterning. In addition, although we lack knowledge of specific effects of spatial patterning for all case studies, we have clear indications from some organism groups that self-organized spatial patterns have a positive influence on ecosystem functioning.

All described specie groups are important for the ecosystem functioning because they are ecosystem engineers. To create patterns they have to be able to modify their surroundings. By modifying their surroundings they create heterogeneity on the mudflat and create a habitat for many other organisms (Tsuchiya, 1985; Lee, 2001). Thus, whether they make patterns or not, they are important for the function of the ecosystem because by modifying their surroundings they change the structure of the ecosystem.

Hydrodynamics are able to create spatial patterns on intertidal mudflats (Whitehouse 2000) but are not able to explain all occurring patterns. Patterns created by hydrodynamics are also oriented perpendicular to the water flow, comparable with the banded patterns in mussel beds, sea grass meadows and diatom patches (van de Koppel 2005, van der Heide 2010, Weerman 2010). And probably the orientations of the existing biotic patterns are structured by hydrodynamics. Nevertheless, hydrodynamics is not the only factor, as the case studies show intraspecific interactions and self-organisation contribute significantly to local patterning.

On the intertidal mudflat scale-dependent feedback is the shared mechanism behind spatial patterning in all three described specie groups. This mechanism consists of a short-term positive feedback and a long-term negative feedback. The specific feedbacks differ among the different specie groups. For the blue mussel access to food is seen as an important driver for spatial self-organization, for diatoms and seagrasses on the other hand food availability is not mentioned at all in any of the studies. Hydrodynamics is generally seen as an important factor, in diatoms and seagrasses both the positive and negative feedback are hydrodynamic related. In musselbeds the importance of hydrodynamics for the creation of patterns is under debate, according to some studies the decreased risk of washing away by clumping together is a positive feedback (van de Koppel et al. 2005), others studies argue that patterns are only based on food availability (Liu et al. 2012).

In general spatial patterns increase productivity and resilience of the described species (Rietkerk et al. 2002). For both mussels and diatoms, biomass increased significantly with patterning (van de Koppel et al. 2008, Weerman et al. 2010). Models of seagrass meadows show that at realistic natural stress levels migrating bands are the only stable community structure (van der Heide 2010). This is also suggested in models about mussel beds, where at low algal concentrations mussels could only survive in patterned beds (van de Koppel et al. 2005).Thus, pattern formation allows species to sustain under circumstances where they wouldn't survive in a homogeneous bed (van de Koppel et al. 2005). Overall, it seems that spatial patterns of the described species increase productivity and resilience of the intertidal mudflat ecosystem.

One of the recurring benefits from spatial patterns in studies of different species is the fact that spatial patterns can be used as an indicator for the health of the ecosystem (Rietkerk et al. 2004). This is supported by empirical data; patterns in seagrass meadows react predictably to changes in stress levels (van der Heide et al. 2010). Because information on the spatial patterns of communities are relatively easy to obtain (aerial photographs or satellite imagery), using spatial patterns as management tool be an improvement on currently used methods for monitoring ecosystem health. In addition, spatial patterns in mussel beds and diatom communities can predict upcoming catastrophic shifts. In the future pressure on our coasts will only become higher, due to the expanding human population and accelerated sea-level rise. Therefore a good understanding on how we can predict possible catastrophic shifts and increased stress levels can be crucial to avoid a total collapse of the ecosystem.

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