Restoring mussel bed

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Synthesis
Nowadays, about 40% of the human population lives near or along the shore (Nicholls and Small 2002, Martínez et al. 2007), and their increasing numbers and activities have dramatically intensified anthropogenic pressure on coastal ecosystems (Valiela et al. 2001, Lotze et al. 2006, Orth et al. 2006). Pollution, habitat destruction and fragmentation, introduction of exotic species, and overexploitation of resources have all contributed to severe declines of habitat-structuring foundation species, such as reef-building bivalves, seagrass meadows, coral reefs and mangrove forests (Ellison and Stoddart 1991, Jackson et al. 2001, Adam 2002, Duarte 2002, Bellwood et al. 2004, Lotze et al. 2006, Orth et al. 2006). This decline in turn has resulted in ecosystem degradation of the loss of ecosystem services such as flood protection, nutrient cycling, carbon storage, water quality and biodiversity enhancement. To conserve and restore coastal ecosystems and their services, both protection and active ecosystem restoration are increasingly attempted to halt and reverse coastal ecosystem degradation (Costanza et al. 1992, Ehrenfeld and Toth 1997, Young 2000, Mitsch and Jørgensen 2004, Aronson and Alexander 2013).

The establishment of Marine Protected Areas (MPA’s) have recently become a popular measure to limit anthropogenic activities in threatened areas and protect important and/or iconic species (Agardy 1994, Edgar et al. 2007). Although MPA’s are successful in many areas (Babcock et al. 1999, Castilla 1999, Mumby et al. 2006, Edgar et al. 2009, Babcoek et al. 2010), protection measures have proven insufficient to allow the ecosystem to recover in other areas because the internal dynamics of the system are insufficiently understood and thus not taken into account (Rius and Zabala 2008, Christianen et al. 2014). For instance, Christianen et al (2014) demonstrated that protection of green turtles in Indonesian MPA’s was initially very successful, but became endangered because overpopulation of turtles within the MPA lead to overgrazing of the seagrass meadows in the area. Furthermore, the mere implementation of MPA’s may be insufficient if re-establishment of habitat-modifying foundation species with strong self-facilitating density-dependent feedbacks is required. This is because
during the re-establishment phase, the habitat modifier density often remains below a critical threshold required to induce the extent of habitat modification needed to generate a sufficiently strong positive feedback. In such cases, active re-introduction may be needed for successful ecosystem recovery.

Because most of habitat-modifying coastal foundation species are typically not only facilitating their own growth and survival, but also provide a refuge and hard substrate for many associated species, they are increasingly considered as priority species in restoration program (Fortes 1991, Clark and Edwards 1995, Peterson et al. 1996, Southworth and Mann 1998, Carls et al. 2004, Brumbaugh et al. 2006, Byers et al. 2006, Crain and Bertness 2006, Brumbaugh and Coen 2009). For instance, active restoration has been attempted to facilitate recovery of coral reefs, meadows, saltmarshes, mangroves and shellfish beds, using an array of different techniques. Transplantation of adult organisms and introduction of offspring or seedling are widely used techniques. In addition, provision of natural substrate for establishment, growth or survival can be used, and if this is not sufficient, the use of artificial material, such as concrete or coir mat can be considered (Bartol and Mann 1997, Fonseca et al. 1998, Clark and Edwards 1999). Moreover, harnessing positive interactions among species may also greatly improve restoration success (Halpern et al. 2007, Silliman et al. 2015, de Fouw et al. 2016).

In this thesis, I have focused on the restoration of beds of the Blue Mussels (Mytilus edulis) as a key species in intertidal soft-sediment coastal ecosystems. By building large epi-benthic reefs, they attenuate currents and waves, provide solid substrate for attachment in an otherwise sandy environment, and provide refuge for associated many species (Norling and Kautsky 2008, Bouma et al. 2009). In addition, by their filtering activities, they are able to filter and clarify the water, and increase local sediment nutrient levels through the deposition of pseudofaeces (Pohle et al. 1991, Newell 2004, van der Zee et al. 2012, Donadi et al. 2013). Despite their
ecological and societal importance, this key component of coastal ecosystems is under threat worldwide (Higler et al. 1998, Brinkman et al. 2002, Smith et al. 2008, Fariñas-Franco et al. 2016). Although many protection measures have been attempted to aid mussel beds recovery, restoration techniques are often unsuccessful, and the reasons for this have been poorly documented (Carls et al. 2004, van der Heide et al. 2014, Fariñas-Franco et al. 2016). The objectives of this study was to identify the mechanisms underlying mussel bed persistence and resilience, and to find novel techniques for mussel bed restoration on intertidal mudflats.

**Mechanisms underlying intertidal mussel bed persistence and resilience**

**Mussels morphology and behavior**

In the Wadden Sea, large beds of blue mussels can be found in both subtidal and intertidal areas. Sub- and intertidal mussels are of the same species, and likely also of the same population, as both gametes, eggs and larvae are mixed in the water column before the mussels find a place to settle. After settlement, however, conditions for sub- and intertidal mussels are very different. In the intertidal area, low-tide exposure and wave exposure during high tide are important abiotic stressors for mussels (Porter et al. 2000, Eklof et al. 2011), whereas subtidal areas mussels are continuously under water and wind-driven waves typically do not reach the bottom. In addition, predation in both habitats is also very different. In the intertidal area, birds and crabs are considered as being the main predators of mussels (Elner 1978, Hilgerloh et al. 1997, Smallegange et al. 2009, van der Zee et al. 2012), while predation by starfish is most important in the subtidal (Saier 2001).

Mussels from sub- and intertidal mudflats develop a number of contrasting adaptations regarding their behavior and morphological features (Figure S.1). First of all, I found that intertidal mussels have a
much stronger, thicker shell compared to subtidal mussels (chapter 5). The relatively thick shell of intertidal mussels is likely important to survive predation by birds and crabs that typically predate on mussels by cracking the shell (Elner 1978). Moreover, the heavier shell also decreases buoyancy and might reduce the risk for the mussels to be flushed away by waves and currents. Compared to intertidal mussels, subtidal mussels have more flesh than intertidal mussels (chapter 5). Most likely, this results in a stronger adductor muscle which may increase resistance against starfish predation.

![Figure 1: Morphological differences between a subtidal (A) and an intertidal mussel (B). The shell of intertidal mussels was found to be 3 times thicker than the shell of subtidal mussels.](image)

Compared to endo-benthic bivalves such as cockles (*Cerastoderma edulis*), American razor clams (*Ensis americanus*) or Baltic tellins (*Macoma baltica*), mussels have developed a unique adaptation to survive strong currents and waves. Rather than seeking refuge from by burying themselves in the sediment (Drew 1907, Richardson et al. 1993), mussels remain epibenthic and use byssal threads – a protein filament – to attach to solid surfaces in order to resist strong hydrodynamics and predation (Bell and Gosline 1996, Brenner and Buck 2010). On rocky shores, solid surfaces
are amply provided by the rocks, and conspecifics provide only a secondary opportunity for attachment. In soft-sediment systems, where rocky surfaces are absent, mussels mainly attach to shells of conspecifics and other dead or live bivalves such as cockles. In this thesis (chapter 5), I found that subtidal mussels primarily attach to each other. On the other hand, in my laboratory experiments, intertidal mussels demonstrated much stronger attachment to abiotic substrate, resulting in a stronger resistance against hydrodynamics.

**Spatial pattern formation**

The movement of mussels leads to the formation of clumps and spatial patterns. Spatial patterns can be found in many different ecosystems, ranging from terrestrial ecosystems (Foster et al. 1983, Rietkerk et al. 2004, Scanlon et al. 2007, Bekker and Malanson 2008, Eppinga et al. 2009, Pringle et al. 2010) to coastal ecosystems (van de Koppel and Crain 2006, van de Koppel et al. 2008, Weerman et al. 2011). In blue mussel beds, self-organization can be found at two different scales (van de Koppel et al. 2005). At a largest scale, mussels aggregate in bands of 3-5m wide hummock as a result of scale-dependent feedback. At the local scale, aggregation is stimulated as this reduces losses from predation and hydrodynamics, whereas mussels are driven apart at a longer range due to competition for the suspended algae that they feed on (Van de Koppel et al, 2005). At a smaller-scale, they aggregate in clumps and strings (5-10cm). Recent model studies from various ecosystems including mussel beds have shown that spatial patterns have beneficial effects in terms of resilience, productivity and food availability (van de Koppel et al. 2005, van de Koppel et al. 2008, Liu et al. 2014). However, a lack of experimental studies thus far limited the application of self-organization in restoration projects.

**Aggregation**

Experiments presented in chapter 2 revealed that self-organization in the form of both small- and large-scale patterns improves survival of
mussels on artificial beds. Mussels that were experimentally organized in small-scale aggregations displayed much higher survival than mussels that were in plots where they were randomly added. Moreover, I found survival in plots with large-scale aggregations to be similar to plots with small-scale aggregations and with both small- and large-scale aggregations. An important consequence of the large-scale bands was that they increase local density. By increasing density, the average distance between mussels is reduced, which in turn improves the possibility for mussels to form small-scale clumps. If mussels are too far apart, my experiments revealed that their movement on soft substrate is limited by the lack of anchoring points around them. In accordance with my experimental findings, earlier theoretical and experimental studies have suggested that mussels in clumps show a better survival than mussels that are unattached (van de Koppel et al. 2008, Liu et al. 2014). Hence, as large-scale aggregation improves the formation of small-scale clumps, and small-scale clumps in turn increase resistance to hydrodynamics, I conclude that pattern formation indeed increases resilience of natural and artificial mussel beds as suggested in earlier theoretical work.

**Hummocks**

Both the experiments that I presented in chapter 3, as well as earlier theoretical work, have demonstrated that self-organization by mussels facilitates mussel beds resistance to hydrodynamic stress and predation. An important consequence, however, is that underneath aggregations of mussels faeces and pseudofaeces, as well as external materials such as shells tend to accumulate. To prevent being buried, and to be able to survive and feed, mussels continuously improve their position by crawling on the top of the accumulated sediment (Brumbaugh and Coen 2009). In the Wadden Sea, this organizational process leads to the formation of hummocks, from 15 to 40 cm when sufficient sediment is available, provided that the beds are sufficiently stable, and tidal amplitudes are sufficiently high (Donker 2015).
By forming a large elevated and solid structure, mussel hummocks typically attenuate waves and alter water current patterns (Liu et al. 2012, Donker 2015). Field and flume studies have shown that flow velocity and wave attack is higher on the top of the hummock (Chapter 3). This increase in hydrodynamic forcing can enhance physical stress, but also food availability on the hummock. The experiments presented in chapter 3 showed that on a newly established mussel bed, hummocks negatively affect mussel survival. Experimental mussel beds built on artificial hummocks had a lower persistence than beds built on a flat surface, probably as a result of enhanced mussel dislodgements due to an increase in flow velocity. In contrast to newly established beds, hummock formation was found to be beneficial for mussel growth on older, natural mussel beds, as expressed in both mussel condition and in their density. Most likely, this is because the increased current velocity increases food availability for the mussels. As a result, mussels on the top of the hummock can grow in higher density and their shell is also stronger. Thus, I conclude that depending on the life stage and local environmental conditions, hummock formation can have either negative or positive effects on mussel growth and survival. In my experiments, the negative effects obviously prevailed, as the mussels were placed in unstable conditions. In existing hummocks, where mussels are closely packed and well protected against wave action, the positive effects likely predominate, leading to high density of mussels, particularly on the top of the beds.

Implications for mussel bed restoration

Transplantation or reintroduction of organisms into degraded areas is an often-applied mitigation and restoration method, applied to restore natural populations across many ecosystems worldwide (Griffith et al. 1989, Kleiman 1989, Clark et al. 2002, Ripple and Beschta 2012, Hinton et al. 2013). The results presented in this thesis, however, illustrate that it is key to first understand the processes that control the population dynamics of the organisms to be restored.
Chapter 2, combined with earlier theoretical work (van de Koppel et al. 2008), clearly shows that aggregation of mussels into spatial patterns improves their survival as they reduce loss by strong hydrodynamics and predation. Hence, when aiming to restore mussel beds through transplantation, it is important to choose a sufficiently high density of mussels in order to allow them to aggregate. If the density is too low, it will be difficult for mussels to find conspecific and form clumps (Chapter 2). Although a high density increases the survival of mussels under hydrodynamic stress and high predation pressure, it also increases competition between mussels for food. Therefore, an excessively high density may lower mussel condition and survival on the longer term. Thus, in mussel restoration, it is important to find balance between the positive effects of aggregation on survival, and the negative effect of aggregation on food competition.

Natural mussel beds do not have a homogenous spatial cover, but are characterized by a mosaic of mussel hummocks alternating with bare hollows. These patterns develop as a consequence of the aggregative behavior of individual mussels in interaction with local accumulation of faeces and pseudofaeces (see previous section “Spatial patterns - Hummocks”). Although I observed that mussels on the hummocks were of better condition, mussels that I transplanted on artificial hummocks actually showed lower survival due to increased hydrodynamic stress. Therefore, when restoring intertidal mussel beds, I suggest to do this on a flat, unmodified intertidal flat, rather than on artificial hummocks. If successful, the developing mussel bed will develop those hummocks itself, similar to what has been observed in naturally established beds.

In 2011, I set up a large mussel bed restoration experiment on three islands (Terschelling, Ameland, Schiermonnikoog) in the Dutch Wadden Sea (Chapter 4, Figure S2). Similar to earlier restoration attempts of intertidal mussel beds in this area, I transplanted subtidal mussels onto intertidal mudflat, South of the islands. A major difference, however, was that within individual 20x20 m² plots, I clustered mussels into 25 circular 5-
The rapid collapse of the transplanted beds turned out to be caused by my use of subtidal mussels (Chapter 2). Although I could not find any genetic distinction between sub- and intertidal mussels, both populations display major morphological and behavioral differences. Because subtidal mussels have a much weaker shell, and attach much less strongly to the substrate, their losses in the intertidal due to both predation by birds and strong hydrodynamics are much higher compared to transplanted intertidal mussels. In my transplantation experiment, the rapid collapse could not be explained by predation only (Chapter 4). Compared to intertidal mussels, subtidal mussels have a much weaker anchoring (Chapters 4 and 5). Although, they still form clumps by attaching to each other, subtidal mussels hardly attach to the underlying substrate, and are therefore easily flushed away by waves and current (Chapter 5). In my large transplant experiment, the mussels were primarily lost from patches on the outside borders of the plots, suggesting that waves and current were the dominant factors driving the high losses in my case. Overall, my results combined with the results of earlier failed transplantation experiments (Ens and Alting 1997, Pelt et al. 2003, Ens et al. 2004) strongly suggest that subtidal mussels do not form a suitable source population for the restoration of intertidal mussel beds by means of transplantation.

General conclusion

In this thesis, I showed that even with a good understanding of the mechanisms controlling the settlement and survival of intertidal mussel beds, their restoration remains a challenge (see summary table and figure S.3). Transplantation of subtidal mussels to an intertidal mudflat is not a feasible approach for restoration purposes. Therefore, the only suitable way to restore intertidal mussel beds by means of transplantation would be to use intertidal mussels. Of course this would mean that one has to damage or destroy an intact intertidal mussel bed to restore a bed in a nearby area, which at best seems inefficient.

m² patches. This approach differed from earlier experiments, which scattered mussels randomly in the experimental areas (Ens and Alting 1997, Pelt et al. 2003, Ens et al. 2004). Although the general setup – clustered, but not on hummocks – should be optimal considering my later experiments, the transplanted mussel bed nevertheless persisted only a few months. Moreover, the additional measure of stabilizing the sediment and provision of attachment substrate by coir mats did not yield any clear effect.

Figure S.2: Picture of subtidal mussels transplanted to an intertidal bed on Schiermonnikoog (Netherlands). Mussels were set up in clustered circles to allow mussels to aggregate while limiting competition for food.
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Assuming that transplantation of mussels is not a viable approach for future restoration projects, the next step should perhaps be to focus on increasing natural recruitment of mussels on intertidal flats. Recent work demonstrated that mussel recruitment is largely controlled by an interaction between substrate stability and predation pressure. Recruitment is successful only when stable settlement substrate is provided and predation by shrimp and crab is limited – a process that naturally occurs in beds where settling larvae can attach to the adults and escape from predation between their byssal threads (van der Heide et al. 2014). A possible technique would consist in a structure that may indeed successfully simulate natural mussel bed conditions by serving as attachment substrate and predation shelter for recruits.

From a more general perspective, the results from this thesis illustrate that success transplantation projects first of all depends on the ability of the transplanted organism to survive and adapt to its new environment. Similar to reintroductions of iconic vertebrate species, such as wolves or bears (Weaver 1978, Smith et al. 2003, Dax 2015), I observed that lack of adaptation by subtidal mussels to their new intertidal habitat severely limits restoration success. Hence, I suggest that for any restoration program that encompasses the transplantation of organisms into a different environment, it is pivotal to first determine the potential success rate in pilot transplantations before scaling up.

A second general conclusion that emerges from this thesis is that habitat-modifying organisms such as mussels, seagrasses, salt marsh plants and mangroves can be enhanced when positive interactions are effectively harnessed. This principle was only recently demonstrated for restoration of salt marshes. By applying a simple design change – planting cordgrass transplants in a clustered configuration rather than a dispersed one – the yield of the transplantation was enhanced by over 100% (Silliman et al, PNAS, 2015). Moreover, earlier work suggests that similar results may be obtained when increasing the planting density of intertidal annual seagrasses (Bos and Van Katwijk, 2007). By extension, my work shows that
harnessing spatial self-organization in mussels enhances the persistence of transplanted mussel beds, indicating that, next to simpler positive interactions, this principle should be broader integrated into conservation and restoration practices.
**Summary Table**

<table>
<thead>
<tr>
<th>Question</th>
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<td>2</td>
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**Mussel Bed Restoration**

**Mussel density**
- High density favours aggregation and increases mussel bed persistence.
- DENSITY SHOULD BE SUFFICIENT TO ALLOW MUSSELS TO AGGREGATE.

**Hummocks**
- Increased currents and lower survival in newly settled beds.
- Increased food availability on stable mussel beds.
- BEDS SHOULD BE TRANSPLANTED ON A FLAT SUBSTRATE AND LET MUSSELS FORM A HUMMOCK OVER TIME.

**Subtidal mussels**
- Their weak shell make them an easy prey.
- Weakly attach to substrate, thus, are not able to handle hydrodynamic stress.
- SUBTIDAL MUSSELS ARE NOT SUITABLE FOR INTRITIDAL MUSSELS RESTORATION.

**Alternative substrate**
- Subtidal mussels do not use abiotic substrate.
- ALTERNATIVE SUBSTRATE IS NOT SUITABLE FOR RESTORATION WITH SUBTIDAL MUSSELS.
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