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### Restoring mussel bed

de Paoli, H el ene Claudine

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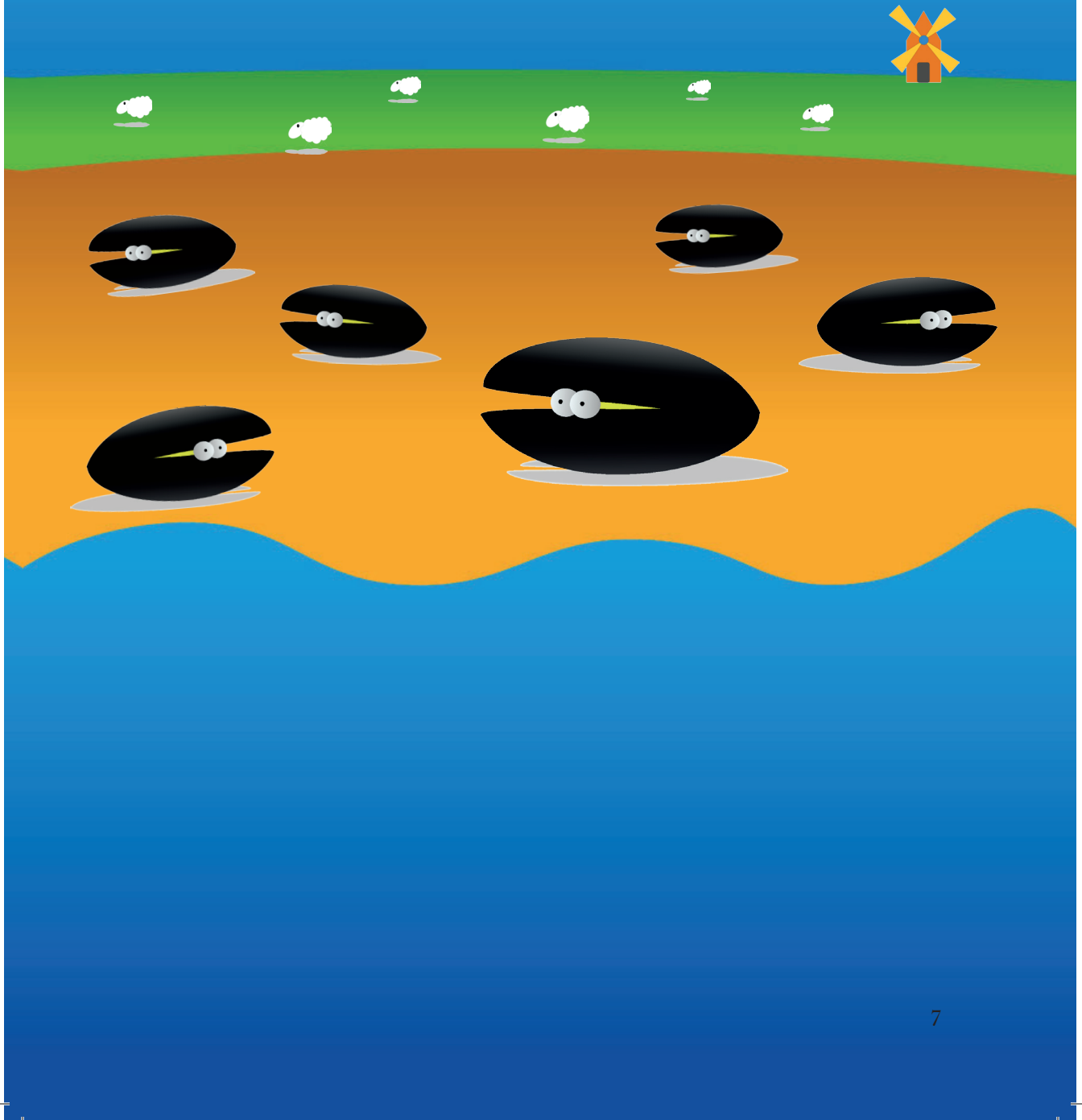
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# Chapter 1: General introduction



Increases in human populations and associated pressures on the ecosystems are leading to a worldwide decline of keystone species, of biodiversity and of ecosystem services (Balmford and Bond 2005, Duarte et al. 2008). Global climate change (Peters and Lovejoy 1992, Blaustein et al. 1994), pollution (Colborn et al. 1993, Schindler 1998), introduction of exotic species (Lövei 1997), overuse of resources (Botsford et al. 1997, Pauly et al. 1998, Pauly et al. 2005), expanding land use (Elliott and Hemingway 2008), and fragmentation of habitats (Pimm and Raven 2000, Fahrig 2003) are threatening biological diversity, particularly in species-rich ecosystems, such as coral reefs or tropical forests. Nowadays, species numbers are decreasing so fast that 25% or more of all species currently alive are predicted to become extinct during the next 50 years (Ehrlich 1991, Chivian 2001, Baillie et al. 2004).

Human populations tend to concentrate in the Earth's coastal zones. These areas host more than 40% of the global human population, and 70% of the world's megacities (Nicholls and Small 2002, Martínez et al. 2007). Moreover, this proportion is increasing, as a result of population growth and migration toward the coasts (Curran et al. 2002). Coastal ecosystems offer a plethora of economic and ecological services (Orth et al. 2006, Barbier et al. 2008). Habitats created by coastal ecosystem engineers, such as mangrove roots, shellfish beds, seagrass beds, saltmarshes or coral reefs are used as nursery by many fish species, and play an essential role in fish stock renewal (Primavera 1998, Nagelkerken et al. 2000, Beck et al. 2001). Moreover, by attenuating wind and waves, these ecosystem engineers do not only protect the associated organisms from strong hydrodynamics, but also protect human populations along the coast during extreme weather events (Fonseca and Cahalan 1992, Möller et al. 1996, Möller and Spencer 2002, Adger et al. 2005, Donadi et al. 2013). A dramatic illustration of this was provided in 2004, when a tsunami hit the coast of Southeast Asia, and villages that were not protected by mangroves were much more severely impacted than villages in the shelter of mangrove forests (Kathiresan and Rajendran 2005).

Anthropogenic pressures have led to high loss of coastal ecosystem engineers worldwide (Valiela et al. 2001, Lotze et al. 2006, Orth et al. 2006). These pressures are multiple, and include land reclamation, coastal development, sediment resuspension, overfishing, invasion by exotic species, intensive aquaculture, and global warming. These impacts have led to coral reef declines, degradation of seagrass meadows, major losses of salt-marshes and epibenthic shellfish reefs such as mussel and oyster beds, as well as a major decrease of biodiversity associated to these habitats (Ellison and Stoddart 1991, Jackson 2001, Adam 2002, Duarte 2002, Bellwood et al. 2004, Lotze et al. 2006, Orth et al. 2006). At present, the global loss of ecosystem engineers is so high that if loss rates remain the same for another 50 years, only 15% of the surface covered by engineers within coastal ecosystems as was present in the 1950's will remain (Duarte et al. 2008).

Growing concerns about declines of coastal ecosystems, and about the consequences of these losses have recently spawned two major initiatives in ecosystem protection and restoration (Costanza et al. 1992, Ehrenfeld and Toth 1997, Young 2000, Mitsch and Jørgensen 2004, Aronson and Alexander 2013). The number of marine reserves and marine protected areas has greatly increased for the broad purpose of conservation and sustainable use (Agardy 1994, Edgar et al. 2007). By limiting most of the anthropogenic activities, ecosystems may in some cases recover naturally. Some examples show a clear gain of biodiversity after the creation of protected areas (Babcock et al. 1999, Castilla 1999, Mumby et al. 2006, Edgar et al. 2009, Babcock et al. 2010). However, in many other cases, these simple protection measures are insufficient to facilitate ecosystem recovery (Rius and Zabala 2008, Christianen et al. 2014), and more active measures, such as ecosystem restoration, thus need to be considered.

## **Coastal ecosystem restoration**

At present, restoration projects of coastal ecosystems are carried out all around the world. For each management program that includes active restoration, one of the first steps is to identify and quantify the stressors underlying ecosystem degradation, and prevent recovery (Poiani et al. 1998, Salafsky et al. 2002). In coastal zones, loss of suitable habitat, eutrophication, and barriers (e.g. dams, dikes) that cause dispersal limitation of recruits are common limitations that should be overcome prior to any restoration measure. As a second step, habitats that have priority for restoration need to be identified. Coastal ecosystem engineers such as coral reefs, seagrass meadows, salt-marshes or shellfish beds are often considered as a priority species in restoration programs because they provide refuge or suitable settlement substrate for many species of marine plants and animal (Fortes 1991, Carls et al. 2004, Byers et al. 2006, Crain and Bertness 2006, McLeod et al. 2012). Because of this pivotal role in the functioning of healthy coastal zones, many restoration programs aim to restore engineering species using a wide variety of techniques, including active transplantation of the organisms.

### ***Strategies to address recruitment limitation***

An important potential limitation hampering natural recovery of marine species is a lack of recruits due to dispersal limitation or limitation in establishment or survival of recruits. When populations disappear from an area or drop to very low numbers, they may reach a point where recruitment of offspring does not overcome the mortality of adults in the population (Allee effect, Gascoigne and Lipcius (2004)). To assess recruitment limitation, a potential solution is to add adults to increase the production or survival of offspring. This strategy has been used for many different species including both coral and bivalve reefs. However, numbers of potentially limiting factors should be considered prior to engaging in transplantation efforts, ranging from predation on transplanted organisms

(Bisker and Castagna 1989, Eggleston 1990), to genetic constraints (Knapp and Dyer 1998).

Nevertheless, transplantation is a technique widely used in coastal restoration projects (Clark and Edwards 1999, Hashim et al. 2010). Although some of these projects have been successful (Green and Short 2003, Schulte et al. 2009), many others proved unsuccessful, often due to low transplant survival (Fonseca et al. 1998). In such cases, scale is often suggested as a major factor determining restoration project success, but other factors, such as sufficiently high density or spatial organization can also be important (Bos et al. 2007, Cunha et al. 2012, Silliman et al. 2015). In addition, phenotypic plasticity and behavior can also play a role in transplant survival (Snell-Rood 2012, 2013).

### ***Strategies to address habitat loss***

Habitat loss has been pointed as one of the major limitations for ecosystem recovery, as this typically results in recruits/seedling not being able to establish due to lack of suitable habitat (Beukema and Cadée 1996, Lenihan and Peterson 1998, Duarte 2002, Green and Short 2003). A technique widely used to overcome this issue in the marine environment is to add substrate to which recruits or seedlings can establish (Bartol and Mann 1997, Fonseca et al. 1998, Clark and Edwards 1999). Although the use of natural substrate should of course be prioritized above artificial forms, various artificial materials are also applied for this purpose. In coral reefs, for instance, artificial structures such as concrete reef balls and iron rebar have been applied as settlement substrate (Sherman et al. 2002, Harris 2009). In oyster reef restoration, plastic screening is often applied in concert with natural oyster shell fragments (O'Beirn et al. 2000), whereas in salt marshes, application of coir netting is an often-used substrate stabilization measure (Koenig 2001, Moore and Erdmann 2002, Goreau and Trench 2012). Regardless of the material used, the goal of all of these structures is to stabilize and restore topographic complexities in areas in order to stimulate new settlement of recruits or enhance survival of

transplanted organisms. For many ecosystem engineers, both recruitment and availability of suitable habitats are limiting factors. In that case, transplanting adults can not only improve recruitment rates, but also provide a suitable habitat for recruits settlement (van der Heide et al. 2014).

## **The role of spatial organization in restoration**

Many coastal ecosystems display a striking degree of patchiness or even coherent patterns. Here, organisms do not occur dispersed through the potential habitat, but aggregate into concentrated patches. For a number of estuarine ecosystems, studies suggest that the patches and patterns are self-organized, i.e. result from the interaction between organisms and physical and chemical processes, and are not per-se imposed by underlying landscape features. Estuarine examples of such self-organized patterns are mussel beds (van de Koppel et al. 2005, van de Koppel et al. 2008), diatom-covered mudflats (Weerman et al. 2010), salt-marshes (Temmerman et al. 2003), and seagrass beds (van der Heide et al. 2010). Many other examples are found semi-arid ecosystems (Klausmeier 1999, Rietkerk et al. 2002), boreal peat lands (Rietkerk 2004, Eppinga et al. 2009), savanna ecosystems (Scanlon et al. 2007, Pringle et al. 2010), ribbon forest (Bekker and Malanson 2008), or freshwater marshes (Koppel and Crain 2006). Self-organized spatial patterns seem to be a global phenomenon, and represents a universal way for organisms to engineer their environment.

So how do these patterns affect the functioning of estuarine ecosystems? Theoretical models (Rietkerk et al. 2004, Van de Koppel et al. 2005) and a small number of comparative studies (Van de Koppel et al. 2008, Pringle et al. 2010) point at important emergent effects of pattern formation on ecosystem functioning, in terms of increased productivity (van de Koppel et al. 2005, Weerman et al. 2010), resource capture (Van de Koppel et al. 2001), sedimentation (Buschbaum et al. 2009), and higher resilience (Liu et al. 2014). Self-organized ecosystems were shown to be

able to recover better when they are perturbed or affected by diverse external factors, compare to beds that lacked any of patterning. As spatial patterns may improve species resilience and persistence, they could form the basis for more successful restoration and conservation practices that harness the natural spatial structure of ecosystems. However, experimental evidence for the emergent effects of spatial pattern formation for ecosystem functioning is rare (van de Koppel et al. 2008, Lamošová et al. 2010), limiting their integration into the management of real-world ecosystems.

Is it important to take self-organized spatial patterning into account in the restoration of degraded ecosystems? A recent paper on salt marsh restoration highlighted that aggregation of transplanted *Spartina anglica* plants improved the survival and spatial spread of the transplants, thereby improving restoration success (Silliman et al. 2015). However, the spatial planting schemes in that study do not resemble a natural self-organized pattern. To what extent the mimicking of the natural patterns in ecosystems improves restoration success needs to be further investigated.

## **Study system: Mussel beds in the Wadden Sea**

The Wadden Sea is the largest uninterrupted system of intertidal sand and mudflats in the world. It covers a coastal area of about 6000 km<sup>2</sup>, from Den Helder, in the Netherlands, to Esbjerg in Denmark (Reise 2005). It is a relatively flat coastal wetland system, formed by the interactions between physical and biological factors that have built a multitude of different habitats, including tidal channels, sandy shoals, mudflats, and salt marshes (Postma 1961, Cadée and Hegeman 1974, Wang et al. 1995, Tindahl Madsen et al. 2007). With its tidal system, the Wadden Sea is a natural area of exceptional value which in part results from the presence of coastal ecosystem engineers, such as seagrass meadows, mussel and oyster beds, and salt marshes (Reise 2005) that sustain a large number of associated species including a wide variety bird and fish species (Beukema



1976). For instance, over the course of the year, the Wadden Sea is visited by an unparalleled 10-12 million migratory birds for resting and foraging on their flyway as food resources in the form of intertidal benthic macrofauna is 10-20 times higher than in adjacent deeper waters (Beukema 1976).

Today's Wadden Sea is a heavily human-altered ecosystem (Lotze et al. 2005, Lotze et al. 2006). Since its origin about 7500 years ago, humans have increasingly influenced ecosystem structure and functioning. Large-scale habitat transformation of the coastline has altered the dynamics of fresh-water input and reduced terrestrial linkages (Wolff 2000, Lotze et al. 2005, Wolff 2005, Lotze et al. 2006). Overexploitation of resources has led to depletion of many species, including habitat building species and large predators. In the last century, species invasion, eutrophication, pollution and climate change have deeply impacted the Wadden Sea flora and fauna, leading to a loss of biodiversity, filter and storage capacity, and a simplification of the food web structure (Knottnerus 2005, Lotze et al. 2005, Reise 2005, van Beusekom 2005). Depletion and collapse of species and environmental degradation have recently led to intensified conservation, protection and restoration efforts (Lotze et al. 2005).

#### Mussel beds: a valuable habitat

In the Wadden Sea, extensive beds of blue mussels (*Mytilus edulis*) used to form one of the most important components of the benthic ecosystem (Dekker 1989). By building reefs, mussels dramatically alter abiotic conditions and enhance biodiversity. They provide habitat and refuge for many species of marine plants and animals (Norling and Kautsky 2008, Bouma et al. 2009). Moreover, through their feeding activity, they increase water clarity, and facilitating other habitat modifying species such as seagrasses (Pohle et al. 1991, Newell 2004). In addition, due to their attenuating effect on currents and waves, mussel beds also provide shoreline protection. In a country like the Netherlands, where about 30% of the country is situated below sea-level, this ecosystem service can be considered very important. Finally, high numbers of resident and

migrating birds feed on mussel beds, either on the associated community or in mussels directly, thus increasing the biodiversity of the Wadden Sea ecosystem (Brinkman et al. 2002).

### Building a landscape

Mussel beds are highly engineered, reef-like structures. In the Wadden Sea, young beds are developing banded patterns that are aligned perpendicular to the incoming tidal current. These bands have a wavelength of 6-10 meters, and show a high density of mussels (van de Koppel et al. 2005, van Leeuwen 2008) alternating with bare sediment. These patterned landscapes are surrounded by homogeneous sand flat, indicating that their formation is driven by self-organized processes (Van de Koppel et al 2005). Prior work has suggested that the patterns likely result from a scale-dependent interaction that encompasses facilitation between individual mussels at a local scale and competition for algae at a large scale (Van de Koppel et al. 2005). At a smaller scale, another type of self-organization can be observed in mussel beds. Mussels actively aggregate to form clumps or strings of about 5-10cm wide. These small-scale clump-shaped patterns result from behavioral aggregation by mussels. This pattern development is extremely fast, as mussels aggregate into patterns within a few hours (Van de Koppel et al. 2008). Both theoretical models and comparative studies highlight the importance of pattern formation for mussel survival (van de Koppel et al. 2008) and the persistence of mussel beds on tidal flats that are regularly exposed to intense wave action and and predation (Liu et al. 2014, van der Heide et al. 2014).

In the 80's, 23% of the Wadden Sea's intertidal benthic fauna consisted of mussels (Dankers and Koelemaj 1989, Dankers and Zuidema 1995). However, by the end of the 80's, virtually all intertidal mussel beds disappeared due to a combination of overfishing by mechanical dredging, a number of severe storms and poor recruitment (Higler et al. 1998, Brinkman et al. 2002). As a consequence, fishing restrictions have been implemented in 1993 and dredging activities in the intertidal have been

banned in 2004. However, despite these protection measures, mussel beds showed a limited recovery. Nowadays, about half of the mussel population recovered. As a consequence, the food web of the Wadden Sea is considered to be significantly impoverished, as an important habitat-forming species, which is also an important link in the intertidal food chain, has been lost.

### Mussel bed restoration

Bivalve shellfish restoration projects are becoming increasingly common all over the world. However, whereas oyster reef restoration has been widely documented (Brumbaugh et al. 2006, Beck et al. 2011, Brumbaugh and Coen 2009), only few studies have been published on mussel bed restoration efforts (Fariñas-Franco and Roberts 2014). Limitation of mussel bed recovery can be caused by the loss of suitable habitat for mussel settlement due to the destructive nature of mussel fishing techniques (Eriksson et al. 2010). In 2010, two projects, Mosselwad and Waddensleutels, started in the Dutch Wadden Sea with the objective to investigate what the processes limiting mussel bed recovery were, and how to restore intertidal mussel beds.

## **Outline of the thesis: How can we restore mussel beds?**

As mussel bed restoration has been poorly documented, it is important to (1) understand the mechanisms underlying mussel bed persistence and resilience in a natural bed, and (2) investigate different methods to restore intertidal mussel beds in the Wadden Sea.

## ***Part 1: Mechanisms underlying intertidal mussel bed persistence and resilience***

### Large-scale and small-scale aggregation

Theoretical models (Rietkerk 2004, Van de Koppel et al. 2005) and a small number of comparative studies (Pringle et al. 2010) point at important emergent effects of pattern formation on ecosystem functioning, in terms of higher resilience (Liu et al. 2014). By improving mussel persistence after transplantation, regular spatial patterns could be used as a basis for restoration and management projects. However, experimental evidence for the emergent effects of spatial pattern formation for ecosystem functioning is rare (Van de Koppel et al. 2008, Lamošová et al. 2010), limiting their application for conservation and restoration of natural ecosystems. In this thesis, I experimentally tested the effect of large-scale and small-scale aggregation on mussel bed resilience and persistence.

*Research question 1:* What is the influence of small-scale and large-scale spatial patterns for the persistence of transplanted mussels in restored mussel beds? (Chapter 2)

### Hummock formation

By increasing local mussel density through aggregation, faeces and pseudo-faeces accumulate underneath the mussels (Buschbaum et al. 2009). A model study showed that by their structure, hummocks increase water velocity (Liu et al. 2012). As a result, mussels on the top of hummocks should have more food available. However, experimental evidence of effects of hummock formation on the growth and persistence of mussels on hummocks is still lacking. I experimentally studied the influence of hummocks on the growth and survival of both natural and transplanted mussels.

Research question 2: What is the influence of hummocks on mussel growth and persistence? (Chapter 3)

## ***Part 2: Transplantation of subtidal mussels to restore intertidal beds***

### The use of artificial substrate for mussel bed restoration

In the Wadden Sea, intertidal mussel beds are found on sandy tidal flats that are often subject to strong hydrodynamic forces (Friedland and Denny 1995). To survive on such an unstable substrate, blue mussels attach themselves to various hard structures, such as shell-fragments, or each other through the use of byssal threads (Seed 1969, Bairati and Zuccarello 1976, Suchanek 1978, Dankers and Zuidema 1995, Bell and Gosline 1996, Albrecht 1998, Carrington et al. 2008). As the byssal threads allow mussels to detach and re-attach, individual mussels can reposition themselves to maintain an optimal position on the substrate where attachment and access to planktonic food in the water column are both sufficient. The byssal structure consists of multiple collagenous fibers that are attached to the substrate via a plaque (Waite et al. 1998). In this thesis, I tested whether the use of a stable artificial attachment substrate, such as coir net, could improve restoration of intertidal mussel beds using transplanted subtidal mussels.

Research question 3: Can an artificial substrate improve mussel bed transplantation? (Chapter 4 & 5)

### Limiting environmental factors for survival of transplanted mussels

Survival of both naturally occurring and transplanted mussels is determined by a combination of abiotic and biotic factors. Mudflat are typically exposed to intense hydrodynamic conditions, especially in the intertidal zone where both currents and wave activity can be severe during storms (Bell and Denny 1994, Gaylord et al. 2003). Moreover, intertidal

mussels are heavily predated by birds during low tide and crabs during high tide. For mussel bed transplantation efforts to be successful, identification of the main factors that limit long-term persistence of mussel beds is of crucial importance.

Research question 4: Are predation and/or wave exposure limiting factors for mussel bed transplantation? (Chapter 4)

The use of subtidal mussel transplantation to restore intertidal mussel beds

Transplantation is a technique widely used in restoration projects (Clark and Edwards 1995, Hashmi et al. 2010). Although there are many examples of successful projects (Green and Short 2003, Schulte et al. 2009), many coastal transplantation programs have remained unsuccessful often due to low transplant survival (Fonseca et al. 1998). In the Wadden Sea, blue mussels are found in both subtidal and intertidal habitats, with subtidal mussel beds being much more prevalent. In this thesis, I therefore transplanted subtidal mussels to the intertidal mudflat with the aim of restoring intertidal beds. To study whether or not subtidal mussels can actually survive in the intertidal environment and are thus suitable for restoration, I compared the survival of sub- and intertidal mussels on intertidal mudflats and studied morphological and behavioral differences between both populations.

Research question 5: Is transplantation of subtidal mussels a viable approach for the restoration of intertidal mussel beds? (Chapter 4 & 5)



# PART 1:

## Mechanisms underlying intertidal mussel bed persistence and resilience

