

# Soft-bottom intertidal ecosystems shaped by ecosystem engineers

Consequences for trophic structure



Els van der Zee

# **Soft-bottom intertidal ecosystems shaped by ecosystem engineers:**

Consequences for trophic structure



Research presented in this thesis was conducted at the Department of Marine Ecology (MEE), Royal Netherlands Institute for Sea Research (NIOZ) and the Department of Animal Ecology, Centre for Ecological and Evolutionary Studies (CEES), University of Groningen. The research was funded by a grant from the Netherlands Organization for Scientific Research (NWO-ZKO: 839.08.310). The printing of this thesis was funded by the Royal Netherlands Institute for Sea Research (NIOZ) and the Faculty of Mathematics and Natural Sciences of the University of Groningen.

*This thesis should be cited as:*

van der Zee, E.M. (2014). Soft-bottom intertidal ecosystems shaped by ecosystem engineers: consequences for trophic structure. PhD Thesis, University of Groningen, Groningen, The Netherlands

Cover design:	Roelant Snoek & Els van der Zee
Lay-out & figures:	Dick Visser
Photographs:	Serena Donadi (cover Chapter 1, 2, 3, Samenvatting), Minze de Boer (cover Chapter 4), Sander Holthuijsen (cover Chapter 5), Maarten Schrama (cover Chapter 6), Jeroen Onrust (cover Chapter 7, 8, Summary), Laura Govers (cover Chapter 9, Thesis) Jim de Fouw (cover Acknowledgements, Thesis) Marjolijn Christianen (cover Thesis) Roelant Snoek (cover Thesis) Ellen Weerman (cover Thesis)

Printed by: GVO drukkers & vormgevers B.V., Ede

ISBN: 978-90-367-6773-6

ISBN: 978-90-367-6772-9 (electronic version)



rijksuniversiteit  
 groningen

# **Soft-bottom intertidal ecosystems shaped by ecosystem engineers:**

## **Consequences for trophic structure**

### **Proefschrift**

ter verkrijging van de graad van doctor aan de  
Rijksuniversiteit Groningen  
op gezag van de  
rector magnificus, prof. dr. E. Sterken  
en volgens besluit van het College voor Promoties.

De openbare verdediging zal plaatsvinden op

vrijdag 28 maart 2014 om 16:15 uur

door

**Elsbeth Merith van der Zee**

geboren op 20 augustus 1983  
te Leek

**Promotor**

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# Chapter 1



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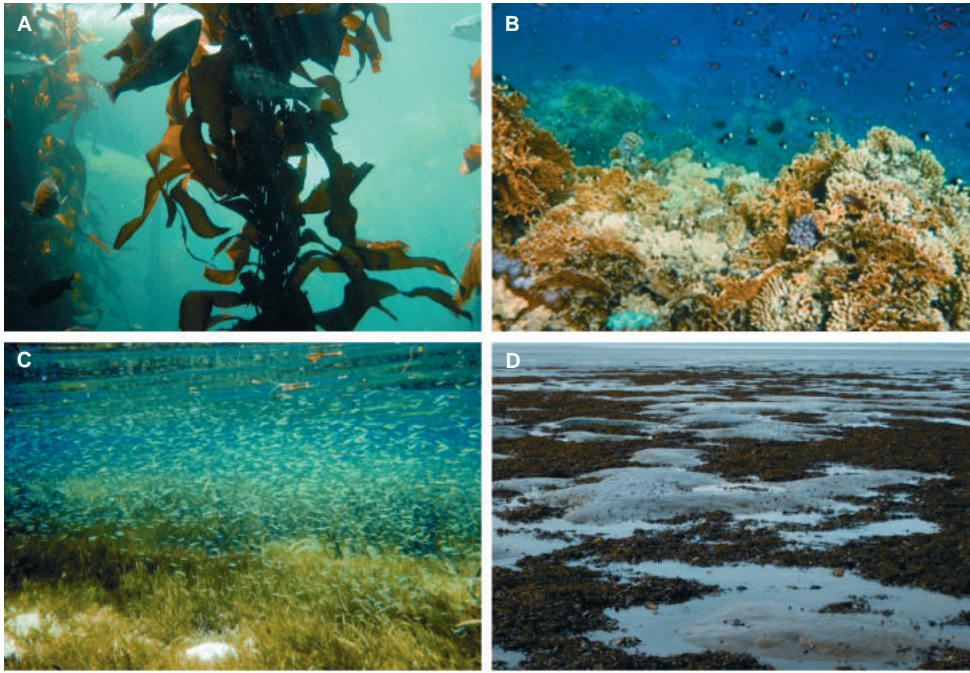
## Introduction

## The concept of species as Ecosystem Engineers

A substantial part of ecological theory concerns the role of interactions between organisms in determining species abundance and distribution (e.g. Andrewartha 1961; Begon *et al.* 1996). Among these interactions, biotic processes such as predation and competition, received most attention, as they are believed to be crucial in structuring natural communities (e.g. Paine 1966; Schoener 1983; Chase *et al.* 2002). However, organisms can also affect each other indirectly by way of abiotic processes. Darwin (1881) already noted that certain species are able to modify the abiotic environment and Dayton (1972) coined the term “foundation species”: organisms that moderate abiotic conditions to other species through their own physical structure. In the 1990s, the role of species in modifying habitats became more systematically defined when Jones *et al.* (1994, 1997) introduced the concept of “ecosystem engineers”: organisms that directly or indirectly alter the availability of resources to other organisms by modifying the abiotic environment.

Jones *et al.* (1994) classified ecosystem engineers as ‘allogenic’ and ‘autogenic’. Allogenic engineers change their abiotic environment by transforming living or non-living materials from one physical state to another through their behavior and activity. A classic example of such an engineer is the beaver. By building dams, beavers create extensive wetlands that support species not found in the surrounding unmodified area (Naiman *et al.* 1988; Wright *et al.* 2002). In contrast, autogenic engineers or foundation species change their abiotic environment through their own physical structure. In many coastal marine ecosystems, habitats are created by the presence of these autogenic engineers, such as kelp, corals, seagrasses and reef-building bivalves (Fig. 1.1)(e.g. Orth 1977; Goreau *et al.* 1979; Foster and Schiel 1985; Bruno and Bertness 2001; Gutierrez *et al.* 2003). By providing structure, these species can form habitats to sessile organisms and provide a refuge to environmental stress and/or predation (e.g. Orth *et al.* 1984; Foster and Schiel 1985; Gutierrez *et al.* 2003; Idjadi and Edmunds 2006).

The concept of ecosystem engineering explicitly includes the relationship between organisms and their abiotic environment, separately from biotic processes such as predation and competition (Jones *et al.* 1994; Jones *et al.* 1997). In addition, although all organisms can affect their abiotic environment to a certain extent, ecosystem engineers are regarded as species that have disproportionally strong effects on their habitat and their modifications typically persist on time scales longer than their own lifespan (Hastings *et al.* 2007 and references therein). The classic example of such a modification is the beaver dam. Beavers can be active at a site for approximately 5 years and when the dam is abandoned, ponds typically drain and form beaver meadows (Wright *et al.* 2004). These meadows can persist for over 70 years and rarely convert back into the original riparian zone (Remillard *et al.* 1987). In addition to the effects on long time scales, ecosystem engineers can also



**Figure 1.1** Examples of marine habitats created by ecosystem engineers: kelp forest (A), coral reef (B), seagrass meadow (C), and mussel reef (D). Photographs reproduced with permission from S. Maruch (A), S. Donadi (B), M. Christianen (C) and E. Weerman (D).

have strong effects at both small and large spatial scales, where scale is defined relative to the dimension of the engineer. An example of an effect on a much larger spatial scale than the organism itself, are mounds built by termites. These mounds or nests can be 4 meters high, cover an area of up to 50 m<sup>2</sup> and the abundance of multiple colonies creates mosaics at a landscape scale (Dangerfield *et al.* 1998 and references therein). In general, ecosystem engineering results in community composition shifts at a local scale, because the modified abiotic conditions can either facilitate or inhibit species (Jones *et al.* 1997). However, at a landscape scale, a mosaic of engineered and unengineered habitats enhances species diversity by increasing habitat heterogeneity (e.g. Jones *et al.* 1997; Wright *et al.* 2002).

## The role of ecosystem engineers in complex ecological networks

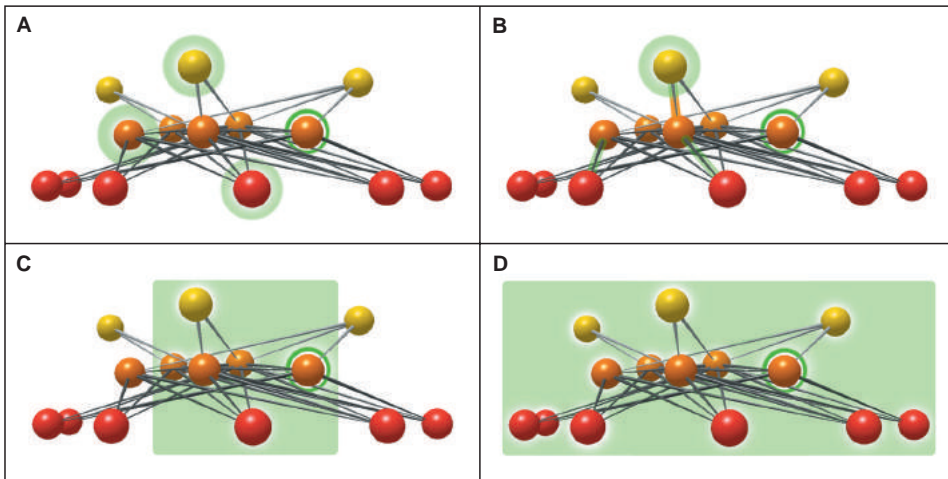
Ecosystems often contain a wide variety of species that interact with each other in multiple ways, forming complex ecological networks of various types of interactions such as predation, competition, mutualism and ecosystem engineering (reviewed by



Oloff *et al.* 2009). Ecosystem engineering effects within these networks can be highly complex, since ecosystem engineers are able to affect other species in multiple ways (e.g. Sanders *et al.* 2013).

By modifying the abiotic environment, ecosystem engineers can alter resource availability (e.g. Stephens and Bertness 1991; Badano *et al.* 2006; Norling and Kautsky 2007). By doing so, they affect their own distribution and abundance and that of other species (e.g. Wright *et al.* 2002; van de Koppel *et al.* 2005; Norling and Kautsky 2007; van der Heide *et al.* 2007), which can influence the structure of ecological interaction networks (Fig. 1.2. A). Next, by affecting the abiotic environment, ecosystem engineers can directly affect the number and strength of biotic interactions among species (Fig. 1.2.B: green links). Structural heterogeneity provided by floating macrophytes for instance, reduces predation efficiency (Padial *et al.* 2009), while termite-induced habitat heterogeneity can facilitate competitive coexistence when species differ in their ability to exploit resource-rich vs. resource-poor conditions (Palmer 2003). By affecting species abundance and distribution, ecosystem engineers can also indirectly affect the number and strength of biotic interactions among species (e.g. Aguiar and Sala 1994; Arkema *et al.* 2009)(Fig. 1.2.B: orange links). In addition, as being a member of the interaction web itself, ecosystem engineers can interact with other species as ecosystem engineers and as, for instance, predators or competitors simultaneously (e.g. Wilby *et al.* 2001; Sanders and van Veen 2011). Finally, besides influencing one or more species within or across trophic levels, ecosystem engineers can also affect food web-compartments or entire food webs by creating new types of habitats within an ecosystem (Fig. 1.2. C & D). However, it is unlikely that food webs in newly created habitats are completely isolated. For instance, juveniles of coral reef fish can migrate between corals and nearby habitats such as mangroves or seagrass meadows to feed (Nagelkerken *et al.* 2000).

Previous studies revealed that ecosystem engineers can affect multiple trophic levels up to whole-communities (e.g. Graham 2004; Silliman *et al.* 2011; Angelini and Silliman 2014), suggesting that they can strongly affect food web dynamics. However, the multi-trophic structure of natural food webs is often studied in ignorance of non-trophic interactions such as ecosystem engineering (as emphasized by Berlow 2004; Ings *et al.* 2009; Oloff *et al.* 2009). Although integration of trophic and non-trophic interactions into a single framework has recently been gaining attention, the studies addressing this issue have remained of a theoretical nature (Arditi *et al.* 2005; Goudard and Loreau 2008; Kefi *et al.* 2012; Sanders *et al.* 2013). Furthermore, it is increasingly recognized that understanding the assembly of food webs or ecological networks requires the inclusion of temporal dynamics (e.g. Blonder *et al.* 2012), since food web structure is often not static, but changes over time due to for instance succession (Schoenly and Cohen 1991; Neutel *et al.* 2007; Schrama *et al.* 2012). Besides succession, ecosystem engineering also has the potential to affect



**Figure 1.2** Schematic overview of the impacts of ecosystem engineering on the structure and dynamics of interaction webs. The ecosystem engineer in each web is indicated by a green circle and the green shaded areas represent its engineering effect. They can affect the interaction web by affecting species abundance at different trophic levels (A), by directly (green link) and indirectly (orange link; via species abundance) affecting the interplay of biotic interactions among species (B) and by affecting food web-subsets (C) or the entire food web (D) through the creation of new habitats within an ecosystems. Nodes (red-yellow gradient as resource-consumer gradient) represent species and grey lines represent their interactions within the network. Images are partly based on Sanders *et al.* (2013) and made with Network3D (Yoon *et al.* 2004; Williams 2010).

food web structure over time by altering abiotic conditions (Hastings *et al.* 2007), especially when multiple habitat modifying species act hierarchical over time in the form of a facilitation cascade (Altieri *et al.* 2007; Thomsen *et al.* 2010; Angelini and Silliman 2014). Despite the potential importance of both ecosystem engineering and temporal dynamics in structuring food webs, empirical studies that integrated food web assembly with ecosystem engineering in a temporally explicit manner are lacking to my knowledge.

### **Ecosystem engineers in intertidal soft-bottom systems – study systems and species**

Organisms in intertidal soft-bottom ecosystems live in sandy environments between the low and high water level, which means that they are emerged during low tide and submerged during high tide. Consequently, organisms living in this area have to cope with highly dynamic and hostile environmental conditions, such as drought, high temperatures and sediment erosion (e.g. Waugh 1975; Leuschner *et al.* 1998;

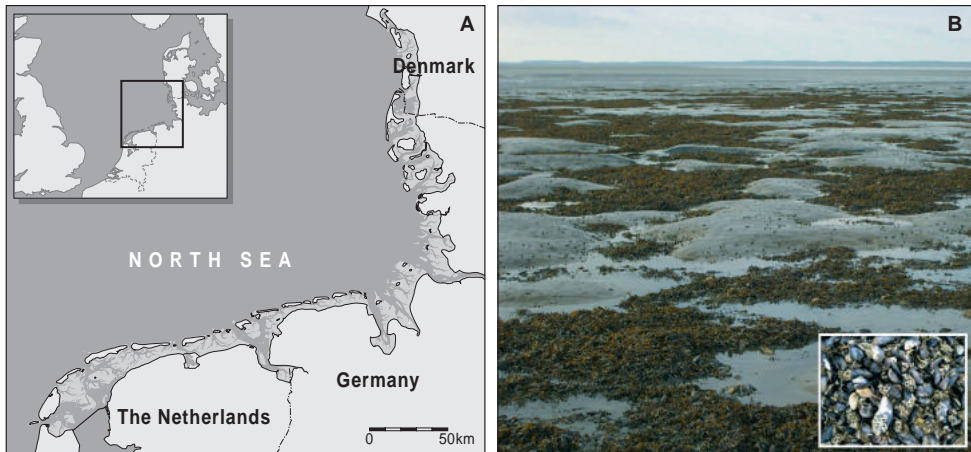
Widdows and Brinsley 2002). Especially in these systems, the group of ecosystem engineers that provide structure such as reef-building bivalves and seagrasses (e.g. Orth *et al.* 1984; Gutierrez *et al.* 2003), can have a significant impact on the associated community, since natural 'hard' substrate and structure are almost exclusively provided by these species in the otherwise sandy environment.

In this thesis, I investigated the role of ecosystem engineers in structuring the intertidal soft-bottom community of the Wadden Sea (The Netherlands) and the Banc d'Arguin (Mauritania). The Wadden Sea is an intense by humans disturbed system and it is proposed that overexploitation and habitat destruction caused a shift from a historical state where the community was structured by abiotic conditions, structure-providing and sediment-stabilizing ecosystem engineers and top-predators, to a modern state where only abiotic conditions structure the community (see section below; Eriksson *et al.* 2010). In contrast, the Banc d'Arguin is still relatively pristine and the presence of extensive seagrass meadows (out of 491 km<sup>2</sup> of intertidal flats, 412 km<sup>2</sup> are covered by seagrasses; see section below) suggests that the community in this system is still strongly structured by structure-providing and sediment-stabilizing species. In order to get a better understanding of how important ecosystem engineers are in structuring intertidal communities and how important they are to conservation management, I investigated their effects in both systems by focusing on reef-building bivalves and seagrasses, relatively common structure-providing and sediment-stabilizing species in the Wadden Sea and Banc d'Arguin, respectively (van Zweeden *et al.* 2010; Brummelhuis *et al.* 2012; Folmer *et al.* 2012).

### **Study system – The Wadden Sea**

The Wadden Sea is a coastal ecosystem, situated in the Southeastern part of the North Sea (Fig. 1.3.A). It is characterized by highly dynamic and productive tidal flats (Herman *et al.* 1999) and is considered as one of the largest (8000 km<sup>2</sup>) and most important intertidal ecosystems in the world (Wolff 1983; Reise 2005). Due to its productivity, the Wadden Sea support large numbers of invertebrates, fish and shorebirds (Zijlstra 1972; Beukema 1976; Wolff 1983; van de Kam *et al.* 2004). The main ecosystem engineers that interrupt and shape the extensive sandy intertidal flats are structure-providing and sediment-stabilizing reef-building bivalves and seagrasses, together with sediment-reworking lugworms (Cadée 1976; Dankers and Zuidema 1995; van der Heide *et al.* 2007; Reise and Kohlus 2008; Markert *et al.* 2009).

Nowadays, the Wadden Sea is under protection by international agreements such as the Ramsar Convention on Wetlands (1971), the joined Declaration of the protection of the Wadden Sea (1982) and Natura 2000 (2003). Recently, the Wadden Sea became one of the UNESCO Natural World Heritage sites (2009). However, despite these conservation frameworks, the Wadden Sea has a history of destructive human



**Figure 1.3** The Wadden Sea area, covering the estuaries and the coastal waters inside the barrier islands in the Southeastern part of the North Sea (A) and a blue mussel bed during low tide (B) (Photo credits: E.J. Weerman).

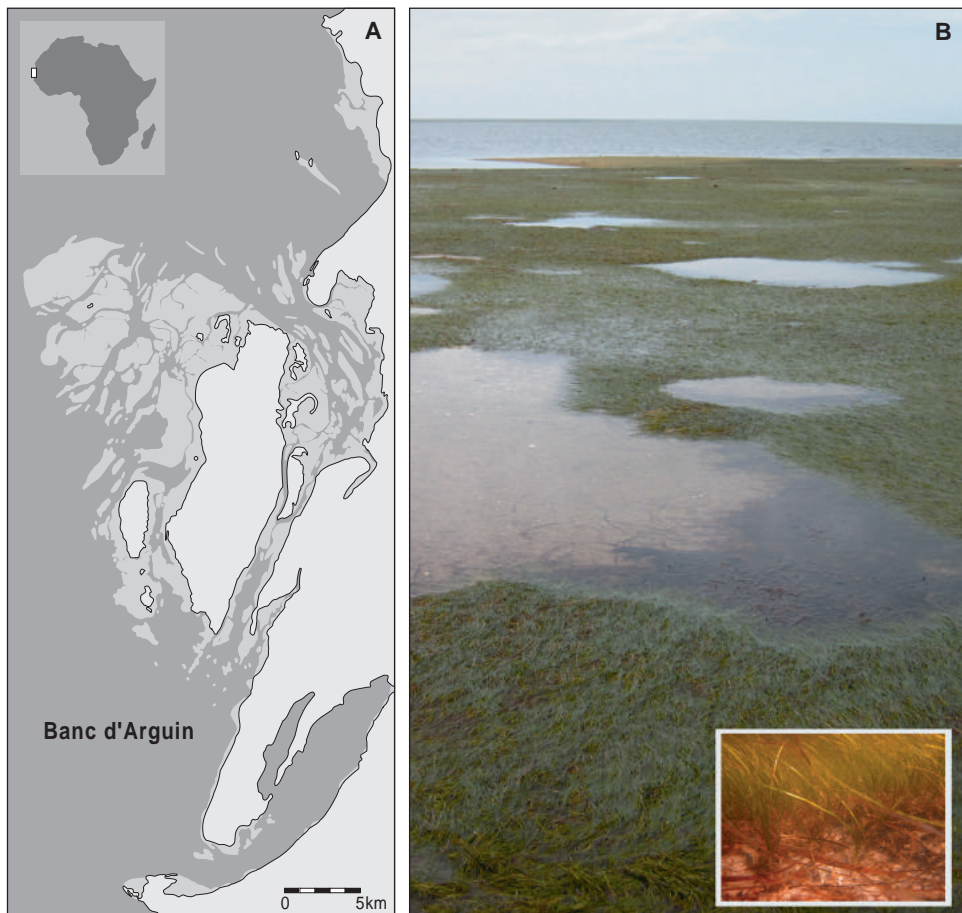
impacts (Lotze 2005; Lotze *et al.* 2006; Boere and Piersma 2012). At the moment, the Wadden Sea is ranked among the most degraded coastal seas worldwide (Lotze *et al.* 2006) due to overexploitation and habitat destruction (Wolff 2000; Lotze *et al.* 2005; Wolff 2005; Lotze *et al.* 2006). Coinciding with the overall degradation, structure-providing and sediment-stabilizing ecosystem engineers have strongly declined as well. First, European oyster reefs (*Ostrea edulis*) completely disappeared around the 1900s due to overfishing (Lotze 2005). Second, seagrass abundance (*Zostera marina* and *Z. noltii*) was severely reduced in the 1930s by a combination of the wasting disease (den Hartog 1987; Vergeer and den Hartog 1994) and changes in hydrodynamics caused by altered water flow (e.g. due to the construction of a large dams)(Giesen *et al.* 1990). Third, mussel reefs (*Mytilus edulis*) have strongly declined since the 1970s, largely due to overfishing by mechanical dredging (Beukema and Cadee 1996; Lotze 2005). European oysters and subtidal seagrass beds never reestablished, intertidal seagrass beds occur nowadays in sparse densities and, despite several bans on mechanical dredging for bivalves, it took over a decade for mussels to start re-establishing in substantial densities in some areas (reviewed by Lotze 2005).

### Study species – Reef-building bivalves

Blue mussels (*Mytilus edulis*) and Pacific oysters (*Crassostrea gigas*) are suspension-feeding reef-building bivalves that form dense aggregations in the intertidal to subtidal littoral zone (Fig. 1.3.B).



The structure of living bivalves and dead shells provide hard substrate for the settlement of epibenthic species and form refuges for many different invertebrates (Gutierrez *et al.* 2003; Norling and Kautsky 2007; Commito *et al.* 2008). By forming reefs, reef-building bivalves reduce the near-bed hydrodynamic stress (Widdows *et al.* 1998; Gutierrez *et al.* 2003), thereby enhancing the accumulation of fine, organic matter rich sediments. Reef-building bivalves further increase the sediment organic and silt content by depositing large amounts of faeces and pseudofaeces (Kröncke 1996; Graf and Rosenberg 1997). Besides serving as a food source to deposit feeders (Norkko *et al.* 2001), biodeposition can inhibit surrounding infaunal species by resulting in low oxygen and high sulfide and ammonia levels (Hartstein and Rowden 2004; Norling and Kautsky 2008).



**Figure 1.4** The Banc d'Arguin (A) and a Dwarf eelgrass meadow during low tide (B). Photo credits: L. Govers).

### Study system – the Banc d'Arguin

The Banc d'Arguin is located on the Atlantic coast of Mauritania (West-Africa) and covers an area of more than 10,000 km<sup>2</sup> of intertidal flats and shallow inshore waters, stretched from Nouamghar in the south to Nouadhibou in the north (Fig. 1.4.A)(Wolff *et al.* 1993). The area borders the Sahara and the intertidal flats consist mainly of soft sediments. In general, the intertidal flats are characterized by extensive areas covered with seagrasses and muddy sediments (Fig. 1.4), alternated with sandy unvegetated areas. Approximately, 412 km<sup>2</sup> of the 491 km<sup>2</sup> of intertidal flats are covered by seagrasses (Altenburg *et al.* 1982; Wolff and Smit 1990). Consequently, the main ecosystem engineers that shape the intertidal flats of the Banc d'Arguin are seagrasses (see section below; Fig. 1.4.B). Dwarf eelgrass (*Zostera noltii*) is the most dominant species although other species such as shoalgrass (*Halodule wrightii*) and little Neptune seagrass (*Cymodocea nodosa*) are also observed (Wolff *et al.* 1993 and references therein). Furthermore, the Banc d'Arguin provides a habitat to extreme high numbers of birds, despite relatively low biomasses of the macrobenthos (Altenburg *et al.* 1982; Engelmoer *et al.* 1984; Wolff and Smit 1990). It is the most important wintering site for shorebirds migrating along the eastern coastal zone of the Atlantic Ocean by sustaining over 2 million of waders (Altenburg *et al.* 1982; Engelmoer *et al.* 1984; Smit and Piersma 1989). In 1976, 12,000 km<sup>2</sup> of shallow water, tidal flats and adjacent desert were assigned as the Parc National du Banc d'Arguin (PNBA). This national park was established to protect both the natural resources and the valuable fisheries (Hoffmann 1988). In 1989, the Banc d'Arguin became one of the UNESCO Natural World Heritage sites. Although the establishment of the national park and the World Heritage site were used in order to protect this unique and pristine area, overfishing by international fleets in the offshore waters just outside Parc National du Banc d'Arguin is depleting fish resources (ter Hofstede and Dickey-Collas 2006; Nagel and Gray 2012) and may cause strong biodiversity losses within the park in the near future.

### Study species – Seagrasses

Seagrasses are aquatic flowering plants that can form extensive meadows in the intertidal to subtidal littoral zone and are widely distributed along temperate and tropical coastal areas (den Hartog 1970; Green and Short 2003). They are important ecological components of coastal zones worldwide that serve as key-habitats for many different species including large numbers of bivalves, gastropods, shrimp, fish and waterbirds (Beck *et al.* 2001; Orth 2006). Seagrasses are ecosystem engineers in the sense that they modify the abiotic environment by providing structure and reducing flow velocities with their shoots. By forming extensive meadows, seagrasses can strongly attenuate currents and waves, thereby reducing hydrodynamic stress (Gambi *et al.* 1990; Fonseca and Cahalan 1992; Hemminga and Duarte 2000). Consequentially, they trap suspended sediments and organic particles that

results in increased sediment accretion, sediment silt content and water transparency (e.g. Ward *et al.* 1984; Gacia and Duarte 2001; Bos *et al.* 2007; van der Heide *et al.* 2007).

In addition to the structural component of seagrass, nutrient uptake by seagrasses can lower nutrient levels in the water column (Moore 2004), thereby reducing growth of epiphytes, macroalgae and phytoplankton and increasing water transparency even more (Nielsen *et al.* 2002; Kemp *et al.* 2005). The presence of seagrass meadows is known to enhance biodiversity and faunal abundance compared to unvegetated areas (e.g. Orth *et al.* 1984; Edgar *et al.* 1994; Hemminga and Duarte 2000; Honkoop *et al.* 2008) and the main mechanisms behind this are: i) decreased predation efficiency due to habitat complexity (Orth *et al.* 1984; Farina *et al.* 2009), ii) habitat preference of species as refuge from predation (Orth *et al.* 1984; Nagelkerken *et al.* 2000), iii) stabilization of sediments (Orth 1977; Fonseca and Fisher 1986) and iv) alterations of the food supply to associated species (Brun *et al.* 2009; Fredriksen *et al.* 2010).

## **Objective and outline of this thesis**

The main objective of this thesis is to investigate how and to what extent ecosystem engineers can affect the (trophic) structure of intertidal soft-bottom communities. Questions that arose during this investigating where: At what temporal and spatial scales are ecosystem engineering effects still visible? What happens to species richness and food web structure if engineers are removed or added? Which part of the effects of an ecosystem engineer on the associated community is due to its engineering versus its trophic effects? And how does ecosystem engineering interact with other ecological interactions such as competition and predation? By answering these questions, I tried to contribute to a better understanding of the role of ecosystem engineers in structuring communities and ecological networks and to determine their importance for conservation management.

First, the effects of spatially extended engineering by reef-building bivalves on the intertidal community of the Wadden Sea were examined. Cross-habitat interactions between reef-building bivalves and benthic organisms are discussed in chapter 2, where it is hypothesized that reef-building bivalves can enhance the abundances of cockles along a spatial gradient from the reefs. This was investigated by using data from transects across three intertidal mussel reefs and three nearby areas without reefs, in combination with data from field experiments. Additionally, in chapter 3, I investigated the importance of spatial extended engineering by reef-builders in explaining the distribution of four avian predators and their benthic prey in the Wadden Sea. Structural Equation Modeling (SEM) was applied to identify important direct and indirect interactions between the different components of the system.

Results from these two chapters were then used to develop an experiment to investigate the role of multiple interactions types in structuring an intertidal bivalve population in the Wadden Sea. In chapter 4, I tested the hypothesis that ecosystem engineering by mussels can strongly interfere with predation and competition by modifying the quality of the environment. The interactive effects of ecosystem engineering, predation and competition on common cockle (*Cerastoderma edule*) recruitment, growth and survival were tested by manipulating cockle densities within a predator-exclosure experiment at a site engineered by a blue mussel bed (*Mytilus edulis*) and at a sandy control site.

In chapter 5, I empirically tested the hypothesis that recovery of stable sediments and aboveground structure provided by ecosystem engineers such as mussels and tube worms will increase species and trophic diversity of the benthic community by facilitating both infaunal and epifaunal species in the Wadden Sea. In a large-scale experiment, we applied anti-erosion mats to simulate sediment stabilization and added adult mussels to test for the effects of habitat modification. The experiment was carried out at two different sites in order to generalize the treatment effects. One site was located in the western part of the Dutch Wadden Sea, south of the island Terschelling, and one in the eastern part of the Dutch Wadden Sea, south of the island Schiermonnikoog.

Additionally, in chapter 6 it was hypothesized that bivalve recruitment failure in intertidal soft-bottom ecosystems is due to (anthropogenically-) increased predation and loss of facilitation mechanisms. On top of the large-scale experiment described in chapter 5, the interactive effects of predation and habitat modification on bivalve recruitment were investigated. Within this experiment, shrimp and crab predation were manipulated using exclosures on the anti-erosion mats and mussels treatments.

Furthermore, since ecosystem engineers might strongly affect food web dynamics, the effects of ecosystem engineering on food web assembly were investigated in a temporally explicit manner in chapter 7. Using a unique combination of remote sensing, field surveys, and stable isotopes, the effects of hierarchical habitat modification by seagrasses and burrowing crabs over long timescales were explored. Finally, the main results are synthesized in Chapter 8. I discuss the findings and implications from earlier chapters in relation to the existing literature and provide ideas for conservation and management strategies.





## *Chapter 2*

## Cross-habitat interactions among bivalve species control community structure on intertidal flats

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### Abstract

Increasing evidence shows that spatial interactions between sedentary organisms can structure communities and promote landscape complexity in many ecosystems. Here we tested the hypothesis that reef-forming mussels (*Mytilus edulis* L.), a dominant intertidal ecosystem engineer in the Wadden Sea, promote abundances of the burrowing bivalve *Cerastoderma edule* L. (cockle) in neighboring habitats at relatively long distances coastward from mussel beds. Field surveys within and around three mussel beds showed a peak in cockle densities at 50–100 m towards the coast from the mussel bed, while cockle abundances elsewhere in the study area were very low. Field transplantation of cockles showed higher survival of young cockles (2–3 yr old) and increased spat fall coastward of the mussel bed compared to within the bed and to areas without mussels, whereas growth decreased within and coastward of the mussel bed. Our measurements suggest that the observed spatial patterns in cockle numbers resulted from (1) inhibition effects by the mussels close to the beds, due to preemptive algal depletion and deteriorated sediment conditions, and (2) facilitation effects by the mussels further away from the beds, due to reduction of wave energy. Our results imply that these spatial, scale-dependent interactions between reef-forming ecosystem engineers and surrounding communities of sedentary benthic organisms can be an important determinant of the large-scale community structure in intertidal ecosystems. Understanding this interplay between neighboring communities of sedentary species is therefore essential for effective conservation and restoration of soft-bottom intertidal communities.

## Introduction

In the last two decades, studies from a wide range of terrestrial and marine ecosystems have demonstrated that interactions between sedentary organisms can generate spatial patterns at a landscape level (e.g. Connell 1961, Paine 1974, Dayton 1975, Maron and Harrison 1997; Klausmeier 1999, Guichard *et al.* 2003). The interplay between small-scale facilitation and long-range inhibition of organisms generate regularly patterned ecosystems, a form of spatial self-organization (Rietkerk and van de Koppel 2008). An opposite interplay between local competition and large-scale facilitation has been observed on cobble beaches, where various forbs species were facilitated behind stands of the cordgrass *Spartina alterniflora* Loisel. (Bruno 2000), but were outcompeted within the dense *Spartina* beds (van de Koppel *et al.* 2006). These studies have in common that intra- and interspecific interactions between sedentary species are scale-dependent, as they change in intensity and even sign with distance among the organisms under consideration.

The concept of scale-dependent interactions has mainly been used to explain spatial patterns of vegetation. Little is known about the importance of scale-dependent interactions between sedentary animals (van de Koppel *et al.* 2005). Moreover, to what extent such interactions determine the structure of neighboring communities has rarely been investigated. Nevertheless, understanding such spatial interactions may be necessary for the ecological conservation of ecosystems in which the structure of the community living in one habitat depends on interspecific interactions with species in neighboring habitats (Gaines and Roughgarden 1987, Rilov and Schiel 2011).

In this study, we investigated whether negative effects on food availability and sediment properties combined with positive effects on hydrodynamic conditions by reef-forming blue mussels (*Mytilus edulis*) result in scale-dependent effects of mussel beds on edible cockles (*Cerastoderma edule*) on intertidal mudflats in the Dutch Wadden Sea. Blue mussels are well-known ecosystem engineers that decrease near-bed hydrodynamic stress (Widdows *et al.* 1998, Widdows and Brinsley 2002, Widdows *et al.* 2002, Gutierrez *et al.* 2003) and increase sediment organic content through production and deposition of faeces and pseudofaeces; processes that affect both the mussel bed itself and the surrounding tidal flat (Graf and Rosenberg 1997, Bergfeld 1999, van der Zee *et al.* 2012). While cockle recruitment and persistence may be positively affected by decreased hydrodynamic stress (Bouma *et al.* 2001), cockle survival may be negatively affected by adverse low-oxygen sediment conditions created by the accumulation of organic material (Wegeberg and Jensen 1999). Furthermore, by their filter-feeding, mussels locally reduce algae concentrations in the benthic boundary layer (Fréchette *et al.* 1989). As cockles are also filter-feeders, blue mussels can compete with cockles for food over larger distances due to the directional flow of water in intertidal habitats (Asmus *et al.* 1992, Kamermans



1993). There is a rich literature on the formation of spatial patterns within mussel beds due to the scale-dependent interplay of facilitation and competition between mussels (Gascoigne *et al.* 2005, van de Koppel *et al.* 2005, van de Koppel *et al.* 2008). However, no study has reported on how scale-dependent effects extent beyond the boundaries of mussel bed to affect neighboring communities at larger distances.

We hypothesized that cockle abundances may be enhanced at a distance from mussel beds because mussel beds: 1) inhibit cockle growth locally by competition for food and by creating adverse sediment conditions (anoxia), and 2) promote the settlement of cockle spat at larger distances through reduction of hydrodynamic stress. As the size and protective status of mussel beds precludes manipulative experiments on the effects on their surroundings, we apply a comparative approach in which we confront our hypotheses with multiple lines of evidence, following Hollings "Adaptive inference" methodology (Holling and Allen 2002). To test our hypotheses, we measured cockle abundances and abiotic variables along transects across three intertidal mussel beds and nearby areas without mussels. At one of the sites where these patterns were observed, we carried out field transplantations of cockles where we investigated if cockle settlement, survival and growth rates within and close to the mussel reef correlated to changes in food availability, sediment chemistry and hydrodynamic conditions. Our results suggest that an interplay between local inhibition and longer-range facilitation result in maximal cockle abundance at a distance from mussel beds where positive effects on larval settlement outweigh negative effects on cockle growth and survival.

## Methods

### Field surveys

The first field survey was conducted in April–May 2009 in the intertidal zone of the Dutch Eastern Wadden Sea, just south of the island of Schiermonnikoog. The intertidal mudflats in the area are mostly dominated by the bioturbating lugworm (*Arenicola marina*), but also harbor several large mussel beds (each >1 ha). To study the effect of blue mussels on cockles, we first sampled three transects perpendicular to the coast across a 100×150 m mussel bed (53°28'8" N, 6°13'27" E) and three additional transects at the same elevation in a nearby area without mussels (53°28'7" N, 6°13'52" E) without mussel beds. Along each transect, we measured cockle (*Cerastoderma edule*) abundance, sediment characteristics and sediment pore water every 50 m. Local cockle abundances were determined by counting individuals within a 0.5×0.5 m frame, and sediment samples were collected for two depth ranges (0–1 and 0–5 cm) using a PVC corer (with an internal diameter of 3 cm). Pore water samples were collected in airtight 50 ml syringes using ceramic soil moisture samplers (Eijkelpkamp Agrisearch Equipment, The Netherlands). Within two hours



after collection, pore water reduction-oxidation potential (RedOx) was measured with a Sentix ORP probe connected to a Multi 340i voltmeter (WTW, Germany). Silt content of the 0–1 cm sediment samples (fraction  $<63\ \mu\text{m}$ ) was determined with a Malvern particle size analyzer (Malvern Particle Sizer 2000, United Kingdom) following freeze-drying of the sediment samples. Organic matter content was estimated from oven-dried (48 h,  $95^{\circ}\text{C}$ ) 0–5 cm samples as Loss On Ignition (LOI; 5 h,  $550^{\circ}\text{C}$ ).

In May 2011, we performed additional surveys at two other mussel beds ( $53^{\circ}28'2''\text{ N}$ ,  $6^{\circ}10'59''\text{ E}$ ;  $53^{\circ}29'44''\text{ N}$ ,  $6^{\circ}19'20''\text{ E}$ ) and corresponding areas without mussels ( $53^{\circ}28'7''\text{ N}$ ,  $6^{\circ}11'33''\text{ E}$ ;  $53^{\circ}29'51''\text{ N}$ ,  $6^{\circ}19'48''\text{ E}$ ) in Schiermonnikoog to test the generality of the observed patterns. In each survey, variation in cockle abundances was determined as described above along three transects from each mussel bed towards the coast and three transects at the same elevation in a nearby area without mussel beds.

### Field transplantation experiments

The initial field surveys showed a peak in cockle abundance at about 100 m coastward from the mussel bed, while cockle abundances within the mussel bed and in the area without mussels were extremely low (see Results). To test if this pattern was caused by scale-dependent effects of mussels on cockles, a field transplantation experiment was carried out following the field surveys. Due to logistical constraints, we had to limit our experiment to a single mussel bed. We chose four experimental locations: (1) "mussel bed" (bare patches between the mussel aggregations inside the mussel bed), (2) "coastward of the mussel bed", at a distance of approximately 100 m coastward from the mussel bed, where we determined the peak in cockle abundance, and, in a sandy area without mussels, (3) at the same elevation as the mussel bed ("lower sandy site"), and (4) at the same elevation relative to mean sea level as the area of the cockle peak ("upper sandy site"). At each location we randomly designated four  $1\times 1\text{ m}$  experimental plots (Appendix A). Naturally occurring densities of *Cerastoderma edule* varied greatly among sites. We found an average density of 225 cockles per square meter ( $n = 20$ ) coastward of the mussel bed, while in all other locations densities were lower than 1 per square meter. In order to minimize potential density-dependent effects due to the presence of cockles (e.g. competition for space, settlement facilitation/inhibition), 225 adult cockles were transplanted in May 2009 from the area coastward of the mussel bed to the plots at each of the two sandy sites and inside the mussel bed. Persistence of high density of cockles in the plots was checked and confirmed at the end of the experiments.

To test whether the vicinity of mussels affected cockle growth and survival, we added 10 tagged cockles to the  $0.9\times 0.9\text{ m}$  center area of each plot at the end of May 2009. Young cockles (2 to 3 yr. old; 12 to 26 mm shell length) were collected from a nearby mudflat, transferred to the lab, measured (shell length, using a vernier

calliper), tagged with a plastic label glued to the shell with cyanoacrilate and added to the experimental plots. Nearly four months later (September 2009), all cockles were collected by hand-raking. To avoid edge effects, only the 0.9×0.9 m center area of each plot was sampled. The number of recaptured tagged cockles was used to compare *in situ* survival of juveniles, while cockle spat (3–12 mm long individuals), which settle in the Wadden Sea from end of May until end of June (van der Veer *et al.* 1998; R. Dekker, personal observation), were counted to examine effects on recruitment and settlement success.

### **Measurements of chlorophyll *a* content and hydrodynamic conditions**

Since mussel beds may facilitate settlement of cockle spat in the wake of the reef through reduction of water flow velocities, we investigated the effect of the mussel bed on hydrodynamic conditions. For this, we simultaneously measured current velocity at the site coastward of mussels (at 100 m from the reef) and in its corresponding site without mussels (upper sandy site), at 5 cm above the sediment bed in 1 Hz intervals during four consecutive tidal cycles in July. For this purpose, we fixed two Acoustic Doppler Current Profilers (ADCP; Nortek Aquadopp, Norway) in the sediment with a stainless steel frame.

Furthermore, we measured water chlorophyll *a* content as a proxy for concentrations of suspended algae and suspended sediment at each site. Water samples were taken at 10 cm above the sediment in the middle of incoming tide, when water speed was highest. In total, we simultaneously sampled both sites three times across a two-week period in August. After collection, each sample was filtered over two pre-combusted (3 h; 450°C), pre-weighed GF/F glass-fiber filter (Whatman, United Kingdom) in standardized aliquots in a dark room. Suspended sediment concentrations were determined from the first filter as the weight difference between the initial filter and the dried filter sample (24 h; 70°C). Chlorophyll *a* content was determined from the second filter by acetone extraction following Jeffrey and Humphrey (1975).

### **Measurements of sediment erosion and cockle spat abundance**

Reduction of water flow velocity coastward of mussel reefs in the study area was confirmed in March 2012 by additional measurements of plaster dissolution along four transects perpendicular to the coast across a mussel bed and four transects at the same elevation in a sandy area without mussels. Dissolution cylinders (6.3 cm long; 2.4 cm diameter) were molded with model plaster (Knauf Modelgips, Knauf B.V., Utrecht, Netherlands), dried, weighted and placed in the field for four tidal cycles (about 46 h), after which they were retrieved and dried until constant weight. To account for difference in the exposure time between sites, plaster weight loss values were divided by the average tidal submersion time of each site estimated by means of Sensus Ultra pressure loggers (Reefnet, Missisauga, Canada). Cockle spat

abundances along the transects were measured by counting individuals (3–12 mm long) within a 0.5×0.5 m frame.

### Statistical analyses

The effect of site on the number of recaptures and cockle recruits was analyzed by fitting Generalized Linear Models (GLM). Error distributions were selected based on the lowest AIC or on the comparison of residual patterns. We assumed Poisson and Negative Binomial error distributions for the number of recaptures and spat fall densities, respectively, both with log-link functions. When possible, multiple comparisons were performed via contrast coefficients through the “glht” function from the Multcomp package in R.

To compare growth rate of recaptured tagged cockles, the effect of initial size on growth was removed by fitting an equation to the pooled data set of initial and final lengths and residuals were calculated. We used the von Bertalanffy growth model as modified by Ramón (2003):

$$L_2 = L_1 + (L_\infty - L_1) \cdot [1 - e^{-k\Delta t}]$$

where  $L_1$  and  $L_2$  are respectively the initial and final lengths and  $\Delta t$  is the time elapsed between  $L_1$  and  $L_2$ . The parameter  $\Delta t$  was assigned a value of 0.8 year because the experiments were carried out during the growth season. The parameters  $L_\infty$  and  $k$  were estimated by a non-linear least-squares method using the Gauss-Newton algorithm, that yielded  $L_\infty = 29.711$  mm and  $k = 1.423$  year<sup>-1</sup> ( $n = 28$ , Residual Sum of Squares = 8.599,  $r = 0.945$ ). Residual averages of each plot were compared by one-factor analysis of variance (ANOVA) to investigate effects of site on cockle growth and Tukey’s HSD test was used for post-hoc comparisons. As tagged cockles in the Lower Control were recaptured in only one plot, this site was excluded from the analysis (see Results).

Effects of site and sampling time on chlorophyll *a* content, suspended sediment matter and water current velocity were tested in three separate models. The direction of the water current (incoming vs. outgoing) was also included as explanatory variable when analyzing water current velocity data. Independence of observations taken at the same site or time interval was tested by comparing GLS (Generalized Least Squares) models with and without a residual correlation structure (Zuur *et al.* 2009). For current velocity data, a significant correlation (Likelihood Ratio Test statistic = 14.06610,  $P < 0.05$ ) was found between values observed within the same time interval. We calculated an intraclass correlation of 0.96 and used this value to calculate the design effect and the effective sample size (Snijders and Bosker 1999).

To confirm the effect of mussel reefs on hydrodynamic conditions, a one-way ANOVA was used to compare values of plaster dissolution measured in four loca-

tions along transects: at 100 m seaward of the mussel bed, at 50 m coastward of the mussel bed (where a peak in cockle abundance was previously observed) and in the sandy site without mussels at the same elevation respectively. Tukey's HSD test was used for post-hoc comparisons. The relationship between plaster weight loss and cockle spat abundance in the absence of mussel beds was investigated for data collected in the site without mussels by means of a quantile regression on the natural-log transformed data.

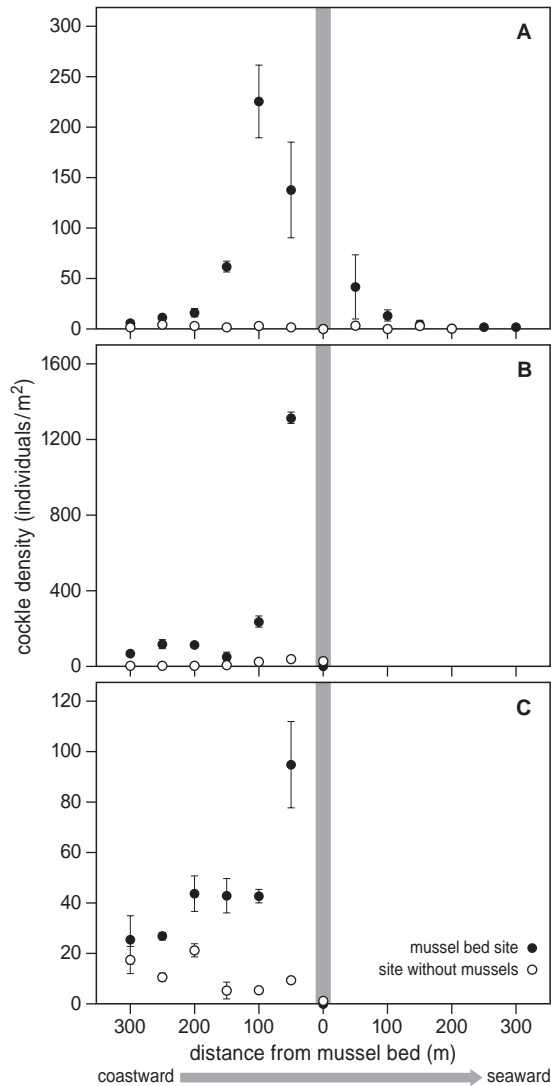
When needed, normality assumption was checked using both a normal quantile plot and Shapiro-Wilks test ( $P = 0.05$ ) and homoscedasticity was assessed by comparing GLS models with different residual variance structures (Zuur *et al.* 2009). All statistical calculations were carried out in R (CRAN, R: A language and environment for statistical computing. 2010. R Foundation for Statistical computing. Vienna, Austria).

## Results

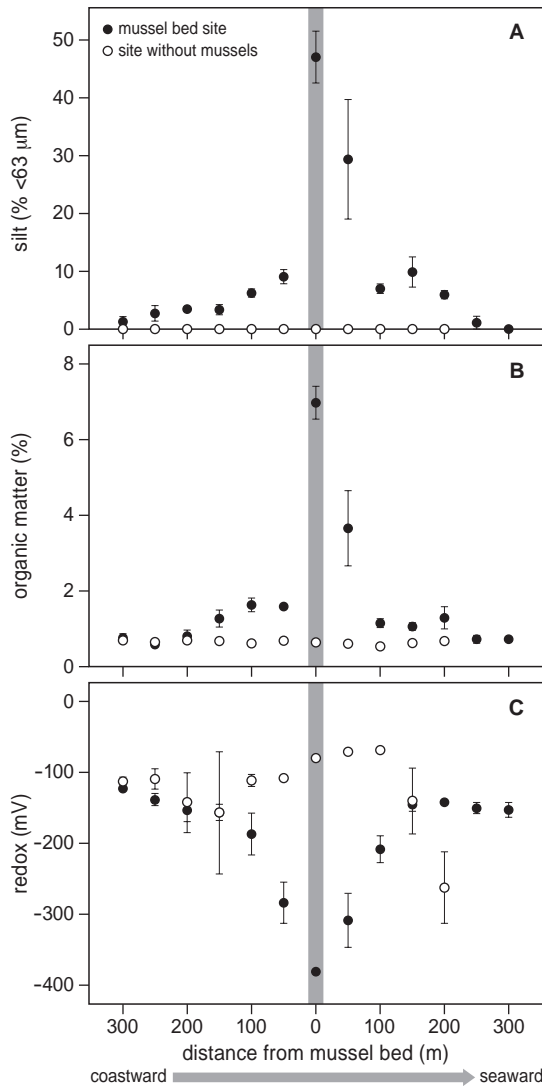
### Field surveys: spatial pattern of abiotic parameters and cockle abundance

The combined surveys from 2009 and 2011 strongly suggested that the mussel bed affected the structure of the intertidal community both at the site of the bed and on its surroundings. Most importantly, the presence of the mussel bed was associated with the occurrence of cockle beds at a distance; the survey of 2009 showed that cockle densities in the mussel bed transects peaked 100 m coastward from the bed (at  $225 \pm 62.53$  SE individuals/m<sup>2</sup>), sharply declined to zero within the bed, and then slightly increased seaward from the bed (Fig. 2.1A). In contrast, cockle abundance along the transects in the area without mussels did not change with distance from land. The spatial pattern in cockle distribution relative to the mussel bed was confirmed by the surveys conducted in 2011 at two other mussel beds (Fig. 2.1B & C). In both mussel areas, cockle abundance peaked at 50 m coastward from the beds, while little variation was observed in the corresponding areas without mussels. Hence, our surveys suggested a spatial covariation of mussels and cockles between neighboring communities of these sedentary species.

A clear difference in abiotic parameters was found between the mussel transects and the area without mussels. We found a strong increase in silt content and organic matter towards the mussel bed with maximum values inside of  $46.92 (\pm 7.74$  SE) % and  $6.98 (\pm 0.74$  SE) %, respectively (Fig. 2.2.A & B). In contrast, sediment pore water redox decreased sharply towards the mussel bed with a minimum value of  $-382 (\pm 6.08$  SE) mV inside the bed (Fig. 2.2.C). Silt content, organic matter and redox showed little variability in the area without mussels (Fig. 2.2.A-C).



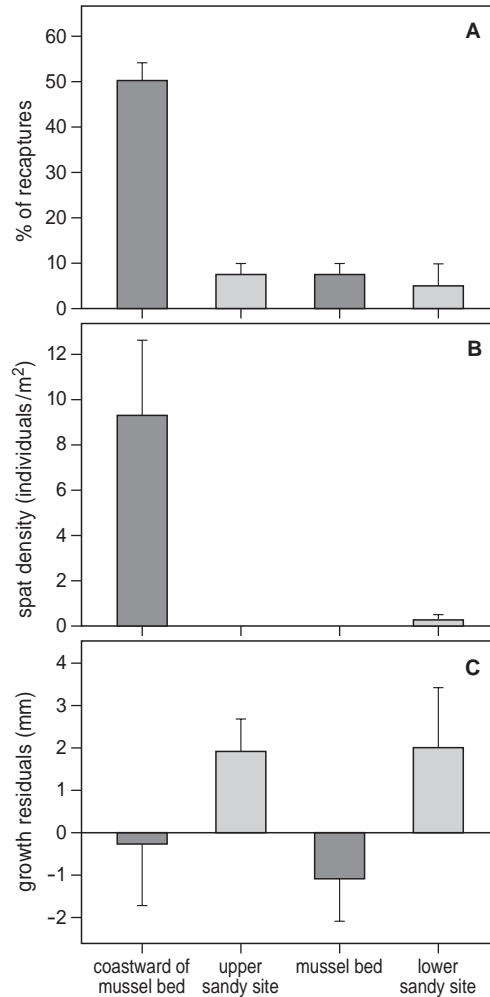
**Figure 2.1** Cockle density along transects perpendicular to the coast across three intertidal mussel beds (closed circles) and three corresponding areas without mussels at the same tidal elevation (open circles) in 2009 (A) and 2011 (B, C) in Schiermonnikoog. The x axis represents the distance from the mussel reef along the mussel-bed transects. Grey area indicates the position of the mussel bed. Mean  $\pm$  SE (n = 3).



**Figure 2.2** A) Silt content, (B) organic matter content and (C) redox potential along transects perpendicular to the coast across an intertidal mussel bed (closed circles) and a corresponding area without mussels at the same tidal elevation (open circles). The x axis represents the distance from the mussel reef along the mussel-bed transects. Grey area indicates the position of the mussel bed. Mean  $\pm$  SE ( $n = 3$ ).

### Field transplatation of cockles: effects on cockle growth and survival

Our experiments show that survival and recruitment of cockles were higher on the coastward side of the mussel bed, compared to within the bed or in any of the sandy areas without mussels. Over 50% of the tagged cockles were found back coastward of the mussel bed, while  $\leq 8\%$  in the mussel bed or in any of the sandy sites (Site effect, Likelihood Ratio test statistic = 26.81,  $df = 3$ ,  $P < 0.001$ ; Fig. 2.3.A). Likewise, we found higher densities of recruits (juvenile cockles of 3–12 mm) coastward of the

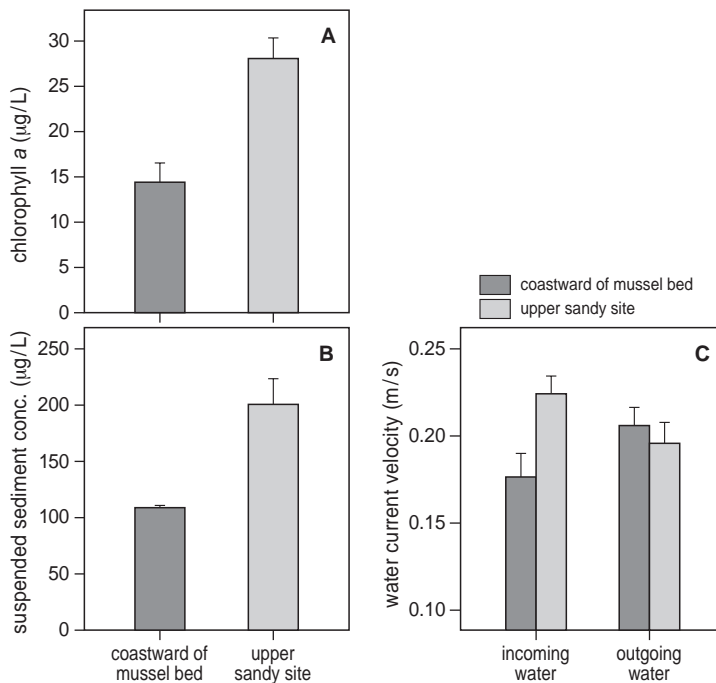


**Figure 2.3** A) Percentage of recaptured tagged cockles, (B) spat density and (C) growth residuals measured coastward of the mussel bed, at a comparable tidal elevation in the area without mussels (upper sandy site), within the mussel bed and at a comparable tidal elevation in the area without mussels (lower sandy site). Mean  $\pm$  SE (A and B:  $n = 4$ . C:  $n = 20$  coastward of the mussel bed,  $n = 3$  in the upper sandy site,  $n = 3$  within the mussel bed,  $n = 2$  in the lower sandy site).

mussel bed (ca.  $10 \text{ m}^{-2}$ ) compared to the other sites, where hardly any juveniles were collected (Site effect, Likelihood Ratio test statistic = 64.00,  $df = 3$ ,  $P < 0.001$ ; Fig. 2.3.B). Contrastingly, cockle growth was generally negatively affected by the mussel bed. Analysis of variance of mean growth residuals revealed a significant effect of site ( $F_{2,7} = 8.23$ ,  $P < 0.015$ ), such that growth in the upper sandy site was significantly higher compared both to coastward of the mussel bed (Tukey's HSD post-hoc test;  $P = 0.046$ ) and inside the mussel bed (Tukey's HSD post-hoc test;  $P = 0.014$ ; Fig. 2.3.C). This suggests that improved survival of cockles at the spat or juvenile stage is the main driver of the high abundance that we observed coastward of the mussel beds.

### Variation in chlorophyll a content and hydrodynamic conditions

We found that the mussel bed likely influenced both food availability for other filter feeders and hydrodynamic conditions. Chlorophyll *a* content ( $F_{1,4} = 17.17$ ,  $P = 0.014$ ), suspended sediment concentration ( $F_{1,4} = 17.08$ ,  $P = 0.014$ ) and water current velocity ( $F_{1,6} = 69.05$ ,  $P < 0.001$ ) were lower coastward of the mussel bed



**Figure 2.4** A) Chlorophyll *a* content and (B) suspended sediment concentration in the water column coastward of the mussel bed and at a comparable tidal elevation (upper sandy site). (C) Water current velocity measured during incoming and outgoing water coastward of the mussel bed and at a comparable tidal elevation (upper sandy site). Mean  $\pm$  SE (A and B:  $n = 3$ . C:  $n = 4$ ).



than in the site without mussels (Fig. 2.4.A, B & C), and no differences were observed between sampling times (main effect and interactions of time were not significant;  $P < 0.05$ ). For current velocity, we found an interaction between site and water current direction ( $F_{1,6} = 167.90$ ,  $P < 0.001$ ), revealing a 21% lower current velocity coastward of the mussel bed compared to the area without mussels with rising tide, but no significant difference during outgoing water. Our results therefore imply that mussels may affect cockle survival in two opposite directions, by depleting food availability in the water column and by providing shelter to new recruits from waves and water currents.

### **Sediment erosion and cockle spat abundance**

Reduction of hydrodynamic forces coastward of mussel beds in the study area was confirmed by data collected along transects: plaster weight loss measured at 50 m coastward of the reef (where a peak in cockle abundance was previously observed) was decreased by 20% compared to seaward of the reef (significant one-way ANOVA result,  $F_{3,12} = 16.18$ ,  $P < 0.001$ ; Tukey's HSD post-hoc test;  $P = 0.001$ ) and by 21% compared to the same tidal elevation in the sandy site (Tukey's HSD post-hoc test;  $P < 0.001$ ; Appendix B). Our measurements strongly suggest that cockle spat settlement and survival observed in an area without mussels are affected by hydrodynamic stress and sediment erosion: we found a negative relationship between high spat densities (quantile 0.90) and plaster weight loss ( $n = 32$ ,  $P = 0.023$ ), with high spat densities never occurring at high values of sediment erosion (Appendix C). This indicates that cockle bed settlement and survival may be possible only below a certain threshold of hydrodynamic stress, which is lower than the values measured in the area without mussels ( $43.91 \pm 1.60$  SE % plaster weight loss) and higher than the values observed coastward of the mussel bed ( $32.30 \pm 1.16$  SE % plaster weight loss).

## **Discussion**

We found that cross-habitat interactions can play an important role in determining the community structure of sedentary species in soft-bottom intertidal systems. Enhanced densities of cockles were observed coastward of reef-forming mussels, but not within the reef itself or in the areas without mussels. Our experiments suggest that this pattern of cockle distribution is caused by a scale-dependent influence of the mussel bed on the survival and growth of cockles: cockles experienced strong competition for food by mussels within the mussel bed, while spat fall and juvenile survival were profiting from reduced hydrodynamics stress coastward of the mussel bed. These results emphasize the importance of mussels as ecosystem engineers that shape soft-bottom intertidal communities, and reveal that their influ-

ence may extend well beyond the boundaries of the actual reefs. Moreover, it emphasizes that intertidal ecosystems can be structured by long-distance interactions, suggesting that protection of specific intertidal habitats requires consideration of its linkages to other habitats in the surrounding.

When studying the effects of mussel reefs on the surroundings, strong inference methods, implying replicated experimental removal of entire beds, are not feasible because of the scale and protective status of mussel reefs. Therefore, we confronted our hypotheses to multiple lines of supportive evidence, following Hollings "Adaptive inference" approach. First, we found a decline in Chlorophyll *a* and low oxygen content in the sediment within and coastward of the mussel bed, relative to the site without mussels at the same tidal elevation. This points at the proposed short-range negative effects of mussels on cockles imposed by the combined effects of intense competition for food and deteriorated sediment conditions. These observations are in close agreement with other studies revealing reduced cockle growth close to mussel beds due to algal depletion (Kamermans 1993, Ramón 1996). Also, deteriorated sediment conditions (e.g. low oxygen content, high organic matter) have been previously reported to hinder survival of many benthic species (Pearson and Rosenberg 1978, Diaz and Rosenberg 1995, Gray *et al.* 2002, Hyland *et al.* 2005, Magni *et al.* 2008).

A striking opposite effect of mussels on cockles appears to occur at a larger spatial scale. Our results show that cockle densities were greatly enhanced coastward of mussel beds, compared to sites without mussels, and that this may be explained by reduced hydrodynamics stress caused by the mussel bed. Hydrodynamic forces are known to have a strong influence on the settlement and recruitment of larvae, though in contrasting ways. Flow speed can have positive effects on larval settlement (i.e. by increasing larval supply and the contact rate with the substrate) (Judge and Craig 1997, De Montaudouin *et al.* 2003). However, evidence from the field often showed opposite results (Armonies and Hellwig-Armonies 1992; Bouma *et al.* 2001, Jonsson *et al.* 2004). High flow speed decreases the time available for larval adhesion and increase the drag force detaching the larvae from the substrate (Abelson and Denny 1997). Reef-forming mussel beds can enhance the settlement of larvae and post-larvae by alleviating hydrodynamic stress imposed by waves and water flow (Widdows and Brinsley 2002, Gutierrez *et al.* 2003, Commito *et al.* 2005). In agreement with these studies, we measured higher recapture rates of tagged cockles and spat densities at 100 m coastward of a mussel bed, where field measurements revealed a peak in cockle abundance and reduced water flow, suggesting an increased survival relative to the sites without mussels. Hence, at a larger spatial scale, the positive effects of reduced wave action on spat fall seem to outweigh the negative effects of increased competition, explaining the high densities of cockles coastward of the mussel bed.

An alternative explanation for the observed high cockle survival in the wake of the mussel bed is that predation by birds, flatfishes and crustaceans (Sanchezsalazar

*et al.* 1987, Norris and Johnstone 1998, van der Veer *et al.* 1998) is reduced here for some reason. Yet, we documented much higher abundances of cockle predators, such as oystercatchers (*Haematopus ostralegus*) and crabs (*Carcinus maenas*), within and coastward of the mussel bed (van der Zee *et al.* 2012) rather than in the area without mussels, where numbers of cockles recaptured and spat fall were lower. This leaves the alleviation of hydrodynamic stress as the best explanation for enhanced cockle settlement and survival in the larger neighborhood of mussel beds. However, our conclusions remain to be confirmed by further studies providing conclusive experimental evidence of the mechanisms investigated.

When these lines of evidence are put together, our results strongly suggest that the interactions between mussels and cockles are scale-dependent: competition dominates at a small scale, while facilitation predominates at larger scales. A similar type of interaction has previously been proposed to explain zonation on cobble beaches (van de Koppel *et al.* 2006), where forbs were facilitated by dense stands of *Spartina alterniflora*, but only in their wake, at a distance up to 10 meters. Within the dense *S. alterniflora* stands, competition predominated, and no forbs could persist. Our results now suggest that such scale-dependent interactions can also structure soft-bottom intertidal communities at scales up to 250 meters, linking mussel bed habitats to the cockle-dominated tidal flat that lies in their wake. In this way, long-range effects of reef builders may allow the persistence of productive intertidal communities under conditions that would normally not support such a high spatial complexity and associated biodiversity.

Scale dependence has been proposed as the basic mechanism causing self-organized, regular spatial patterns in ecosystems all over the world, ranging from arid bushlands to boreal peat bogs (see review in Rietkerk and van de Koppel 2008). Self-organization is a process whereby spatial patterns at the global level of a system emerge solely from local interactions among the components of a system (Camazine *et al.* 2001). Even within mussel beds, regular spatial patterns are found, both at sub-meter scale (van de Koppel *et al.* 2008) and at 10 meter scale (van de Koppel *et al.* 2005), that seem crucial in minimizing competition, promoting mussel biomass and increasing mussel bed resilience. Other studies have found self-organized spatial patterns in other intertidal habitats such as mudflats (Van der Heide *et al.* 2010), tidal freshwater wetlands (van de Koppel and Crain 2006) and salt marshes (van Wesenbeeck *et al.* 2008). The current study shows that effects of spatial self-organization may scale up to much larger spatial scales than previously shown, affecting the presence and distribution of sedentary communities and species across distances up to several hundred meters. Although at this scale regularity is not prevalent, it emphasizes the importance and reach of self-organization processes in intertidal ecosystems, determining distribution patterns of individuals at meter scale (van de Koppel *et al.* 2008) to habitats (e.g. cockle beds) at sub-kilo-meter scale.

Our study suggests that reef forming organisms can change the balance between abiotic and biotic control over species settlement, growth and survival over different spatial scales. In the sites without mussels, adverse hydrodynamic conditions likely caused low settlement of juvenile cockles, explaining the lack of cockles in these locations. This confirms that reef builders are indeed important ecosystem engineers that alter hydrodynamic energy and sedimentation processes, both locally (within the reef) and at the tidal flat that lies in their wake (Kroncke 1996, Graf and Rosenberg 1997, Gutierrez *et al.* 2003). Hence, while abiotic stress potentially inhibits cockles in the absence of the mussel reef, biological processes, such as competition for food and interactions through ecosystem engineering, may dominate within and coastward of the mussel bed.

Our results point to the importance of spatial interactions among neighboring communities. As a consequence, intertidal ecosystems can be particularly vulnerable to disturbances that destroy such spatial interactions and the resulting structures (Weerman *et al.* 2011). Because intertidal communities seem to rely on a spatial network of facilitative and competitive interactions at different scales, human perturbations (e.g. the overfishing of ecosystem engineers) can cascade through the ecosystem, leading to unexpected and drastic changes on large spatial and temporal scales (Lotze 2005, Eriksson *et al.* 2010). On the other hand, our results suggest that successful restoration of soft-bottom ecosystem engineers can have beneficial cascading effects on ecosystem over large areas, increasing spatial complexity and associated biodiversity. Therefore, better understanding of cross-scale interactions among neighboring habitats is essential for effective conservation and restoration of intertidal ecosystems, such as the Wadden Sea.

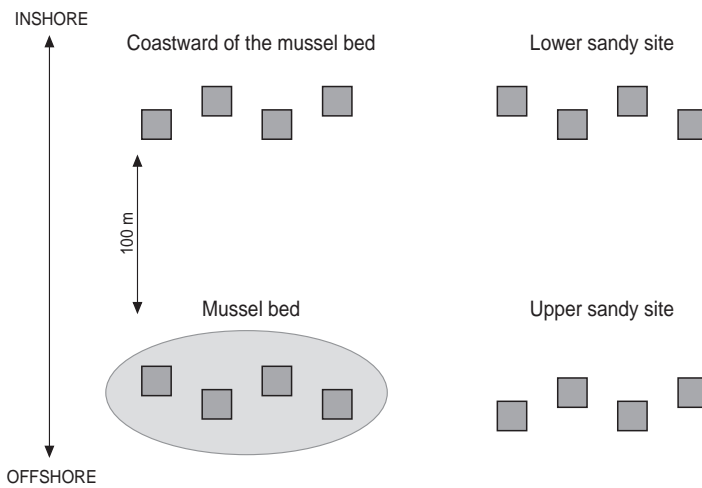
## Acknowledgements

This study was financed by a grant from the ZKO program of the Netherlands Organization of Scientific Research (NWO) to BKE, TvdH, EW, SD, HO and EvdZ (grant no. 839.08.310), and by a post-doctoral grant from FORMAS to JSE (grant no. 2008-839). We thank two anonymous reviewers for helpful comments on the text.

## Supplemental material

### Appendix A

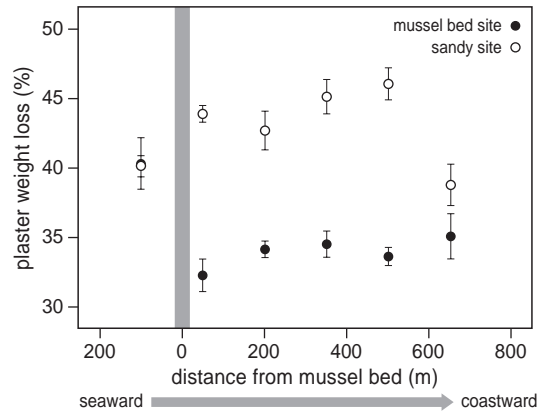
Schematic overview of the field transplantation design.



**Figure 2.A** Schematic showing the four sites of the field transplantation where four 1×1 m plots were randomly assigned. Distance between plots was at least 5 m.

Appendix B

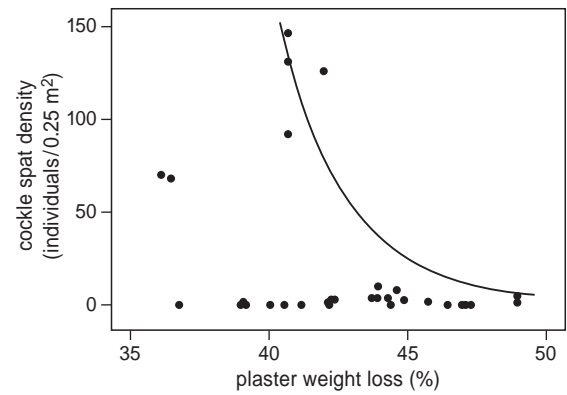
Plaster weight loss along transects across a mussel bed and in an area with no mussel beds.



**Figure 2.B** Plaster weight loss along transects perpendicular to the coast across a mussel bed (closed circles) and in a sandy site without mussels at the same tidal elevation. The x axis represents the distance from the mussel reef along the mussel-bed transects. Grey area indicates the position of the mussel bed. Mean  $\pm$  SE ( $n = 4$ ).

Appendix C

Relationship between cockle spat densities and plaster weight loss.



**Figure 2.C** Scatter plot of cockle spat densities and plaster weight loss measured along transects perpendicular to the coast in an area without mussel beds ( $n = 32$ ). The line indicates regression for quantile 0.909 ( $P = 0.023$ )



# Chapter 3



## Spatially extended habitat modification by intertidal reef-building bivalves has implications for consumer-resource interactions

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### Abstract

Ecosystem engineers can strongly modify habitat structure and resource availability across space. In theory this should alter the spatial distributions of trophically interacting species. Here, we empirically investigated the importance of spatial extended habitat modification by reef-builders in explaining the distribution of four avian predators and their benthic prey in the Wadden Sea – one of the world's largest intertidal soft-sediment ecosystems. We applied Structural Equation Modeling (SEM) to identify important direct and indirect interactions between the different components of the system. We found strong spatial gradients in sediment properties into the surrounding area of mixed blue mussel (*Mytilus edulis*) and Pacific oyster (*Crassostrea gigas*) reefs, indicating large-scale (100s of m) engineering effects. The benthic community was significantly affected by these gradients, with the abundance of several important invertebrate prey species increasing with sediment organic matter and decreasing with distance to the reefs. Distance from the reef, sediment properties and benthic food abundance simultaneously explained significant parts of the distribution of oystercatchers (*Haematopus ostralegus*), Eurasian curlews (*Numenius arquata*) and bar-tailed godwits (*Limosa lapponica*). The distribution of black-headed gulls (*Chroicocephalus ridibundus*) – a versatile species with many diet options – appeared unaffected by the reefs. These results suggest that intertidal reef builders can affect consumer-resource dynamics far beyond their own boundaries, emphasizing their importance in intertidal soft-bottom ecosystems like the Wadden Sea.



## Introduction

Over the last decades it has become well established that some organisms can have disproportionally strong effects on their abiotic environment, indirectly affecting other species. Such species, often called ‘ecosystem engineers’ by Jones *et al.* (1994), typically promote their own preferred conditions at the local (‘patch’) scale (Bertness and Leonard 1997; Rietkerk *et al.* 2004 and references therein). However, ecosystem engineering is often not only important locally, but may also have strong impacts at landscape scales (Wright *et al.* 2002; Kefi *et al.* 2007; Scanlon *et al.* 2007). Apart from altering the spatial structure of the environment, ecosystem engineers may affect the spatial distribution and abundance of their resources (e.g. nutrients, water, light). This also alters resource availability for other species (Gutierrez *et al.* 2003; van de Koppel *et al.* 2006), which should in turn affect the spatial distribution of their consumers (e.g. Hassell and May 1974; Folmer *et al.* 2010; Piersma 2012). Although effects of prey-patchiness and ecosystem engineering on the distribution of species have been documented separately (e.g. Hassell and May 1974; Wright *et al.* 2002), assessments of the spatially extended effects of ecosystem engineers on resources and its consumers have remained largely theoretical (Bagdassarian *et al.* 2007; Olff *et al.* 2009).

Reef-builders like blue mussel (*Mytilus edulis*) and Pacific oyster (*Crassostrea gigas*) are striking examples of ecosystem engineers that impact their environment through habitat modification (Kröncke 1996; Gutierrez *et al.* 2003; Kochmann *et al.* 2008). At a local scale, mussels and oysters create hard substrate and increase habitat complexity, reduce hydrodynamics, and modify the sediment by depositing large amounts of pseudo-feces and other fine particles (Kröncke 1996; Hild and Günther 1999; Gutierrez *et al.* 2003). However, in soft-bottom systems, their effects on sediment conditions typically extend beyond the direct surroundings of the reefs and may be detectable up to several hundreds of meters (Kröncke 1996; Bergfeld 1999). Many studies have demonstrated that reef builders have an important effect on the local benthic community (Dittmann 1990; Norling and Kautsky 2008; Markert *et al.* 2009) and that the reefs themselves are important foraging grounds for avian consumers (e.g. Nehls *et al.* 1997; Caldow *et al.* 2003). However, the spatially extended effects of such reef builders on this community remain largely unstudied.

Furthermore, possible implications of such spatially extended habitat modification on the community may also be important from a management perspective. In many intertidal soft-bottom systems, like the Wadden Sea, ecosystem engineers have disappeared due to multiple anthropogenic disturbances and many associated species disappeared with them (Piersma *et al.* 2001; Lotze *et al.* 2005; Kraan *et al.* 2007; Eriksson *et al.* 2010). For instance, in the Wadden Sea, 150 km<sup>2</sup> of seagrasses disappeared in the 1930s (van der Heide *et al.* 2007) and mussel beds were almost

completely removed in the beginning of the 1990s and have only partly recovered thus far (Beukema and Cadée 1996). If spatial effects of ecosystem engineers are not recognized, such dramatic changes might result in unexpectedly strong losses in these ecosystems.

Here we investigate the effects of spatial habitat modification by mixed blue mussel and Pacific oyster reefs on the distribution of benthic prey and their consumers (shorebirds) at a sandy intertidal flat. We collected spatially explicit data on important abiotic variables and the biota in and around two reefs in the Dutch Wadden Sea. We used Structural Equation Modeling (SEM) to infer the relative importance of ecosystem engineering on the spatial distribution of resources and consumers. Based on sediment and benthos data of 119 sampling stations at varying distances from the reefs and the spatial mapping of shorebirds, we constructed default models for four of the most commonly observed bird species that included all possible interactions between the birds and their environment. Next, we determined the relative importance of each interaction, using an approach with stepwise exclusion of variables.

## Material and Methods

### Study area

Our study area covered about 44 ha of intertidal mudflats, south of the island of Schiermonnikoog in the eastern Dutch Wadden Sea (53°28'15.75" N, 6°13'20.06" E). These intertidal flats contain a variety of macrobenthic invertebrate species (Beukema 1976) that are accessible to shorebirds twice a day (van de Kam *et al.* 2004; van Gils *et al.* 2006). The area contained two mixed reefs of blue mussels and Pacific oysters, established in 2002 (Goudswaard *et al.* 2007 and unpublished data of our research group). The main cohort of bivalves was 7 years old, with several younger cohorts. Prior to the establishment of the two reefs, our study area consisted of a sandy intertidal flat without patches of hard substrata (van de Pol 2006 and unpublished data of our research group). The spatial relationships of the reef builders with the local and surrounding benthic community and associated shorebirds was examined at two adjacent study areas of 22 ha each (see Fig. 3.2).

### Benthic sampling

Sediment, pore water and benthic samples were collected in August 2009 on a predetermined 100 m grid with 46 additional random points. In total, 119 station points were sampled across the two study sites. All stations were identified during low tide using a handheld GPS. At each sampling station, we sampled and pooled three 5 cm deep sediment cores with a PVC corer with area of 7.1 cm<sup>2</sup>. Sediment organic matter content in dried sediment (24 h, 70°C) was estimated as weight Loss

On Ignition (LOI; 5 h, 550°C). Silt content (% sediment fraction < 63µm) was determined by a Particle size Analyzer (Malvern). Redox potential was measured immediately after sampling with a multi-probe meter (556 MPS, YSI) in pore water that was extracted from the sediment with a ceramic cup into a vacuumized 50 ml syringe. Benthic samples were taken with a stainless steel core with area of 179 cm<sup>2</sup> down to a depth of 20–25 cm. Samples were sieved over a 1 mm mesh and all fauna fixed in 4% formalin. In the laboratory, samples were stained with Rose Bengal and fauna was identified to species level. Ash free dry mass (AFDM) of each species was determined by Loss On Ignition (5 h, 550°C) after drying for 48 h in a stove at 60°C.

### **Bird mapping**

A 3.2 m high observation platform was constructed 100 m away from each of the two study sites in such a way that the platforms covered the respective sampling grids, i.e. a reef and the associated gradient towards a sandy area, all within a radius of 500 m. The spatial distribution of shorebirds was determined during four tidal cycles between 18 August and 8 September 2009. Positions of individual birds were determined using the newly developed Telescope-Mounted Angulator (TMA) described by van der Heide *et al.* (2011). This was done from an hour before to an hour after time of low water, i.e. when the areas were completely exposed and tidal movement would not affect their spatial distribution. With the TMA, using trigonometry, we were able to determine a bird's spatial position with high accuracy (maximum prediction error of 8.7 m at 500 m; van der Heide *et al.* 2011).

We mapped the spatial distribution of four common shorebird species: oystercatcher (*Haematopus ostralegus*), Eurasian curlew (*Numenius arquata*), bar-tailed godwit (*Limosa lapponica*) and black-headed gull (*Chroicocephalus ridibundus*). These focal species were chosen for three reasons. First, due to their body size, all four species are easy to follow and clearly visible which prevented double counting and inaccurate positioning (van der Heide *et al.* 2011). Second, all four species form sparse flocks, a feature that represents a degree of sensitivity to interference of conspecifics (Goss-Custard 1980; Piersma 1985). In contrast to social and interference-insensitive species, the distribution of such interference-sensitive species should mostly be determined by the distribution of food resources (Folmer *et al.* 2010). Thirdly, each of these species should differ in its degree of association with mussel and oyster reefs. For example, as blue mussels form a substantial part of their diet, oystercatchers tend to be highly associated with reef builders (Goss-Custard 1996). Eurasian curlew typically respond to an increased abundance of crabs and shrimps in and near reefs compared to sandy intertidal flats, but they also feed on bare mudflats (Goss-Custard and Jones 1976; Petersen and Exo 1999). The degree of association for bar-tailed godwits is probably lower, since they feed on a large variety of benthic animals often along the edge of the receding and advancing tide (Goss-Custard *et al.* 1977; Scheiffarth 2001). Black-headed gulls feed on a large

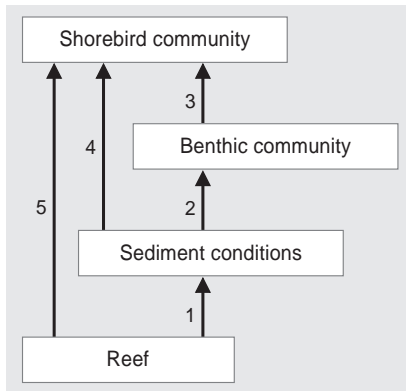
variety of prey and can be found in many different habitats (Dernedde 1994; Kubetzki and Garthe 2003).

### Data analysis

Both study sites were subdivided by Thiessen polygons (Thiessen 1911) in ArcGIS (Environmental Systems Research Institute, Redlands, California, USA). Each polygon defines a discrete area around each sampling station (both random and predetermined) in such a way that any location inside the polygon is closer to that point than to any of the neighboring points. No great differences were detected between shorebird numbers during the four tidal cycles, so data were pooled to calculated densities. Densities of each bird species (# ind. m<sup>-2</sup>) were calculated for each polygon and merged into a single master dataset that now contained data on abiotic variables (sediment organic matter, silt and redox), biomass of all benthic species and bird densities for each sampling station. To approach a normal distribution for analyzed variables, organic matter content was reciprocally transformed ( $y = 1/x$ ), redox potential was log transformed ( $y = \log_{10}(x)$ ) and all other variables were square root transformed ( $y = \sqrt{x}$ ).

Next, we used Structural Equation Modelling (SEM; in Amos v18) to test the spatial effects of the reefs on abiotics and the possible direct and indirect effects on the distribution of macrobenthic and bird species. For each bird species, we created default models that included all potentially important causal relationships between straight-line distance to the centre of the reef (calculated in ArcGIS), directional effects that may arise from strong winds or currents (calculated in ArcGIS as the deviation of each station from the north-south axis through the centre of the reef), sediment conditions (organic matter, silt fraction & redox), macrobenthos biomass and bird density (Fig. 3.1). These models focus on explaining shorebird distribution from information on underlying resources. Therefore, each model only included macrobenthos species that are known prey items for that particular bird species (Table 3.1). Apart from modelling the effect of prey density on shorebird distribution, the models also tested for possible relationships between sediment variables, distance to the reef, and bird density. Sediment conditions can, directly or indirectly, affect bird distribution (Myers *et al.* 1980; Yates *et al.* 1993; Johnstone and Norris 2000). Furthermore, distance to the reef might influence bird distribution because birds may be attracted to these areas in anticipation of altered sediment conditions and prey densities. In summary, all four default models include (Fig. 3.1): (1) effect of distance and direction to the reef on sediment variables, (2) the effect of sediment variables on macrobenthos, (3) effects of macrobenthos variables on bird density, (4) direct effects of sediment variables on bird density, and (5) effect of distance to the reef on bird density.

To test whether the identified relationships extended beyond the reefs themselves, we analysed each model twice – once with all data points included (119



**Figure 3.1** The conceptual path analysis model. Arrows depict direct effects of one variable (boxes) on another. Numbers represent specific mechanisms described in *Materials & Methods: Data analysis*.

**Table 3.1** Variables included in the model to test the default model for each focal bird species. General prey preference of the four common shorebird species (Dernedde 1994; Kubetzki and Garthe 2003; Folmer *et al.* 2010 and references therein) used in SEM is listed together with sediment conditions and distance and direction to the centre of a reef. Shore crabs (*Carcinus maenas*) and brown shrimps (*Crangon crangon*) were clustered as crustaceans.

Prey species	Model			
	Oystercatcher	Curlew	Bar-tailed godwit	Black-headed gull
<i>Arenicola marina</i>		+	+	+
<i>Lanice conchilega</i>		+	+	
<i>Hediste diversicolor</i>	+	+	+	+
<i>Heteromastus filiformis</i>			+	
<i>Scoloplos armiger</i>			+	+
<i>Cerastoderma edule</i>	+			+
<i>Macoma balthica</i>	+	+	+	+
<i>Mytilus edulis</i>	+			
<i>Scrobicularia plana</i>	+	+		
Crustaceans ( <i>Carcinus maenas</i> & <i>Crangon crangon</i> )		+	+	+
<b>Sediment conditions</b>				
Organic matter	+	+	+	+
Silt	+	+	+	+
Redox	+	+	+	+
<b>Reef builder presence</b>				
Distance to centre of reef	+	+	+	+
Direction to centre of reef	+	+	+	+

stations) and a second time with the stations inside the reefs excluded (111 stations). Models were analysed with stepwise backward elimination of relations included in the default model (threshold significance for elimination:  $P < 0.05$ ). After each elimination step, we used the c2 test (probability level  $> 0.05$ ) to test for an adequate fit (i.e. that observed data did not differ significantly from those predicted by the model), and compared the model to previous models using Akaike's Information Criterion (AIC). Unidentified models were excluded from the results. We also excluded macrobenthic species from the model if they were not correlated with the modeled bird species, while sediment conditions were omitted if they were not related with either macrobenthic species or bird density. Furthermore, when abiotic or benthic variables exhibited strong significant collinearity ( $r > 0.4$ ) without one explaining the other (e.g., different proxy's for sediment conditions), we only included the variable with the highest explained variation in our models. The latter was done because SEM models become notoriously unreliable when relations with very strong covariance are included (Petraitis *et al.* 1996; Grewal *et al.* 2004).

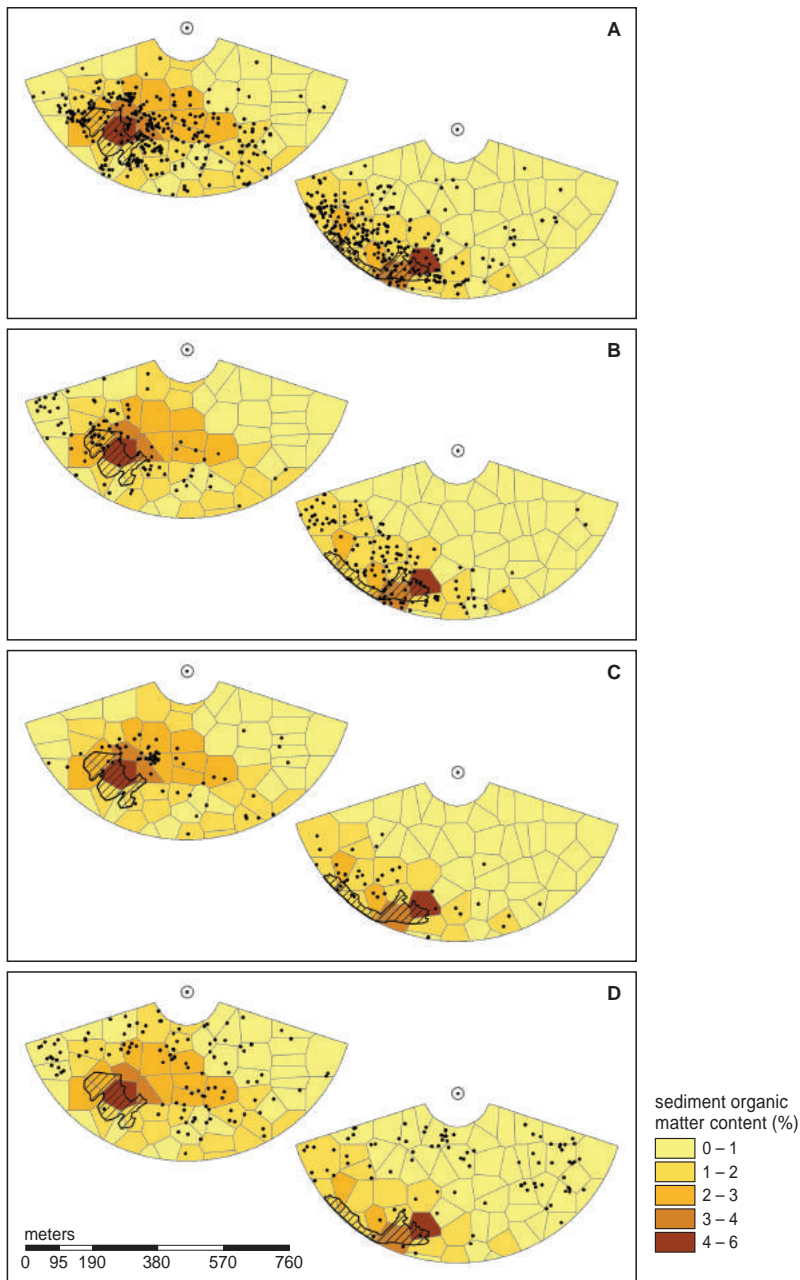
## Results

Organic matter, silt content and redox were all highly correlated ( $r$ -values for OM-silt, OM-redox and silt-redox were 0.9, 0.5, and 0.5 respectively) and exhibited strong spatial gradients, with organic matter and silt increasing and redox decreasing in the direction of the reef. A map overlay of organic matter and the distribution of the four shorebird species suggest that oystercatchers, and to a lesser extent also curlews and bar-tailed godwits, tend to aggregate in these organic matter-rich areas in and around the reefs (Fig. 3.2). In contrast, the spatial distribution by black-headed gulls appears much less affected by the presence of the reefs.

Organic matter was included as a proxy for sediment conditions in the SEM models instead of silt content or redox because of its highest explained variation ( $R^2$ 's were 0.45, 0.31 and 0.43 respectively). The distributions of several macrobenthic species were strongly affected by sediment organic matter, which in turn explained a significant part of the distribution of all four shorebirds (Fig. 3.3, Appendix A & B). The correlations suggest that organic matter had a positive effect on the biomass of *Lanice conchilega*, *Hediste diversicolor*, *Cerastoderma edule* and crustaceans (explaining 7%, 12%, 39% and 11% of their variance, respectively).

All default models based on the fully saturated model (Fig. 3.1) and species-specific feeding relations (Table 3.1) demonstrated poor model-data fits (Table 3.2). After stepwise backward elimination and removal of non-significant relations, all final models demonstrated a strong fit. In contrast to the default models, final models demonstrated low Chi-square values, a probability level above 0.05 and low AIC's (Table 3.2 & Appendix A). After removing the sampling stations within the





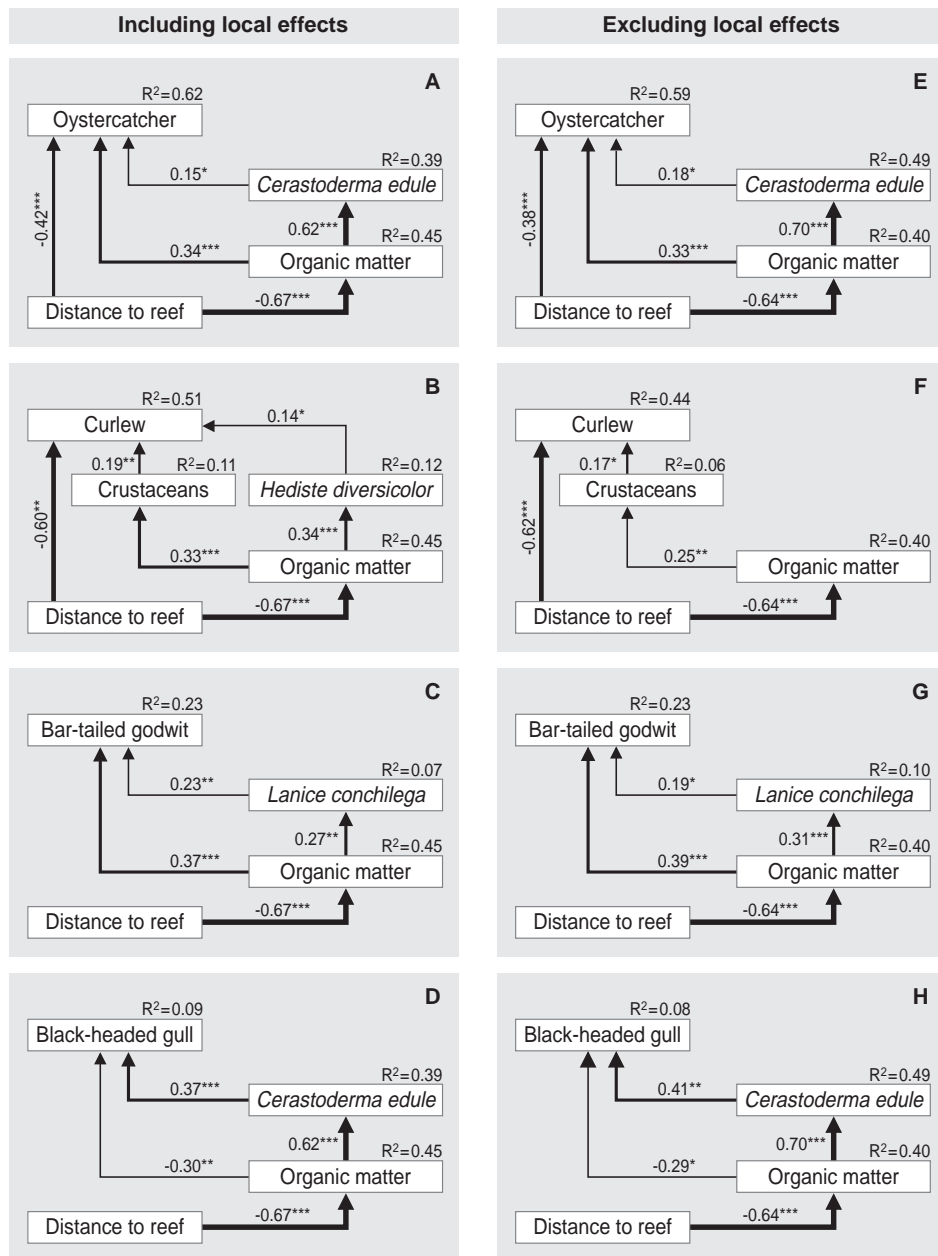
**Figure 3.2** Overview of the two reefs and their surrounding intertidal flats, showing Thiessen polygons (each polygon contains one sampling station), the position of the reefs (striped black areas) and the distribution of sediment organic matter content in relation to the distribution of (A) oystercatchers (B) curlews, (C) bar-tailed godwits and (D) black-headed gulls. Black dots represent the positions of the birds. Circles with a black dot indicate the position of the observation platforms.

reefs from the dataset, all final models still had an adequate fit and the structure of the models remained nearly identical (Table 3.2 & Fig. 3.3). The models including the sampling stations on the reefs yielded a slightly better fit for oystercatchers, bar-tailed godwits and black-headed gulls, whereas the model for curlews improved after removing the reef stations.

The final models for each bird species revealed significant correlations with macrobenthic species, but also with abiotic variables. Distance to the reef, organic matter and *Cerastoderma edule*, were significant predictors of oystercatcher density (Fig. 3.3A & E), with the final model explaining 62 (including local effects) to 59 (excluding local effects) % of the variance. The standardized effect of distance to the reef on oystercatcher density (−0.417 to −0.380) was stronger than the effect of organic matter (0.338 to 0.331) and biomass of *Cerastoderma edule* (0.152 to 0.179). For curlews (51 to 44% of the variance explained), crustaceans and distance to the reef were significant predictors for both models (Fig. 3.3B), while *Hediste diversicolor* was dropped in the model that excluded the reef effect (Fig. 3.3F). The standardized effect of distance to the reef on curlew density (−0.597 to −0.617) was larger than the effect of crustacean biomass (0.195 to 0.168) and biomass of *Hediste diversicolor* (0.141, only in the model which included local effects). *Lanice conchilega* and organic matter were the two significant predictors of densities of bar-tailed godwits (Fig. 3.3C & G). The standardized effect of organic matter on bird density (0.370 to 0.386) was larger than that of the biomass of *Lanice conchilega* (0.227 to

**Table 3.2** Model fit summary from SEM for the default model and the final modified model for the dataset with all sampling stations included and for the dataset wherein the sampling stations inside the reefs were excluded.

	Oystercatcher		Curlew		Bar-tailed godwit		Black-headed gull	
	default	final	default	final	default	final	default	final
<b>All stations</b>								
$\chi^2$	46.383	0.220	70.176	3.753	113.654	0.937	97.784	0.767
$df$	11	1	28	4	38	2	31	2
Probability level	<0.001	0.639	<0.001	0.441	<0.001	0.626	<0.001	0.682
AIC	96.383	18.220	146.176	25.753	193.654	16.937	167.784	16.767
<b>Stations inside reefs excluded</b>								
$\chi^2$	32.494	1.378	46.505	1.210	92.908	1.742	72.309	1.387
$df$	11	1	28	2	38	2	31	2
Probability level	0.001	0.240	0.015	0.546	<0.001	0.419	<0.001	0.500
AIC	82.494	19.378	122.505	17.210	172.908	17.742	142.309	17.387



**Figure 3.3** Diagram of the SEM results with all sampling stations for oystercatchers, curlews, bar-tailed godwits and black-headed gulls (A to D) and the sampling stations inside the reefs excluded for the same bird species (E to H). Straight arrows indicate significant direct effects. The line thickness of each arrow indicates the magnitude of the standardized path coefficient, which is presented numerically next to each path. The  $R^2$  values adjacent to the boxes represent the total variance explained by all significant predictors (\*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ ).

0.187) and the final models both explained 23% of the observed variance. Finally, for black-headed gulls, organic matter and *Cerastoderma edule* were significant predictors of density (Fig. 3.3D & H). The standardized effect of *Cerastoderma edule* on black-headed gull density (0.372 to 0.405) was larger than the effect of organic matter (−0.303 to −0.289). The final models explained 9 to 8% of the variance.

## Discussion

Although ecosystem engineering can determine the spatial distribution of resources (e.g. Gutierrez *et al.* 2003; van de Koppel *et al.* 2006) and resources in turn importantly control the distribution of consumers (e.g. Nachman 2006; Folmer *et al.* 2010; Piersma 2012), the interaction between these two processes so far has rarely been examined (Olf *et al.* 2009). Here we demonstrate that ecosystem engineers can affect consumer-resource interactions far beyond their own physical spatial boundaries in intertidal soft-sediment systems. Reef building bivalves like mussels and oysters cover a relatively small part of the intertidal mudflats of the Wadden Sea ( $\pm 1\%$ ). Our results, however, imply that their ecological impact is much larger than their size may suggest.

We found strong spatial gradients of increasing sediment organic matter and silt fraction and decreasing redox potential in the direction of mixed mussel-and-oyster reefs, which in turn affected the distribution of benthic species. Moreover, distance from the reefs, sediment characteristics, and prey abundance simultaneously affected the distribution of the three studied species that have more or less specific prey requirements (oystercatchers, curlews and bar-tailed godwits). This is most likely because the birds feed in the modified areas in anticipation of higher prey abundances. Black-headed gulls, the only species that did not cluster on and around the reefs, are versatile foragers with many diet options and this may explain why the reefs and the modified areas did not affect their spatial distribution. When the data points for the reefs themselves were excluded from the statistical analysis, the outcomes did not change, thus emphasizing the importance of the spatial extended effects of reefs. Only the ragworm *Hediste diversicolor* was excluded from the model as predictor for the distribution of curlews. This was, however, understandable as ragworms were mostly found in muddy sediments in and around the mixed reefs.

Community structure alteration by ecosystem engineers through spatially extended habitat modification seems to occur in many different ecosystems including beaver-inhabited wetlands (Wright *et al.* 2002) and cordgrass-inhabited cobble beaches (Bruno 2000). However, the relevance of habitat modification by ecosystem engineers on its surrounding and higher trophic levels may vary with environmental conditions. For instance, while our results show that habitat modification by reef-builders can be pronounced and exceed the spatial boundaries of the

reefs themselves, spatial engineering effects by the same species on rocky shores are typically more limited. In these systems, blue mussels modify environmental conditions mainly by providing structural protection for associated fauna (Thiel and Ullrich 2002; Gutierrez *et al.* 2003). Hard substrate is already present and fine particles produced by mussels (faeces and pseudofaeces) are washed away by more intense hydrodynamics, resulting in more limited modifications at larger spatial scales (Thiel and Ullrich 2002). Furthermore, the effect of habitat modification by reef builders may also interact with the presence of other ecosystem engineers. For example, the tube-worm *Lanince conchilega* is also considered as an ecosystem engineer in soft-sediment systems, as their tubes provide substrate and facilitate the deposition of fine sediments (Friedrichs *et al.* 2000; Zühlke 2001). Since the presence of *L. conchilega* is positively correlated with the abundance and richness of the benthic community (Zühlke 2001; Callaway 2006; Godet *et al.* 2011), *L. conchilega* may locally enhance the engineering effect of the reefs on the benthic and shorebird community.

In our study, Structural Equation Modeling proved to be a useful tool for disentangling the relative importance of consumer-resource interactions and spatial habitat modification by ecosystem engineers. Using stepwise backward elimination of significant relations, we obtained models with reliable fits of multiple ecologically relevant variables. The method is correlative and does therefore not provide any direct evidence. Ideally, this method should be complemented with other, more direct approaches like smaller-scale manipulative experiments. However, before the reefs established themselves seven years ago the study the area was sandy and homogeneous, and in this respect the study reported here can be regarded as experimental (but in want of detailed description of the re- establishment situation).

In conclusion, our results indicate that consumer-resource interactions can be affected by reef-builders far beyond the spatial boundaries of the reefs. This implies that these reefs have a much larger ecological impact on the intertidal community than their actual size suggests, which in turn means that loss of ecosystem engineers may result in disproportionately large consequences for biodiversity values in protected intertidal areas, like the Wadden Sea. Although the Pacific oyster is an alien species that invaded the Wadden Sea in the late 1970s (Troost 2010 and references therein), recent studies showed that oyster reefs might compensate for the large loss of mussels in 1990-1991 by replacing the ecological function of blue mussel reefs (Kochmann *et al.* 2008; Markert *et al.* 2009; Troost 2010). Nevertheless, the effects of Pacific oysters on the intertidal community and trophic interactions should be further investigated. Overall, our study emphasizes that conservation and restoration of reef builders should be considered a crucial step in the restoration of such systems.

## **Acknowledgements**

We thank R.C. Snoek and W. van der Heide for their help in the field. R.C. Snoek, E.J. Weerman, P. Herman, J.A. van Gils and two anonymous referees for their valuable comments on preliminary drafts of this manuscript. This study was financed by NWO grant 839.08.310 of the 'Nationaal Programma Zee- en Kustonderzoek'. Johan S Eklöf was funded by FORMAS (post-doc grant no. 2008-839).



## Supplemental material

### Appendix A

**Table 3.A** Results from structural equation modeling after stepwise backward elimination of relations for each shorebird model. All sampling stations were included in these models. Distance represents distance to the centre of a reef.

	Model			
	Oystercatcher	Curlew	Bar-tailed godwit	Black-headed gull
Squared multiple correlations ( $R^2$ )				
Organic matter	0.450	0.450	0.450	0.450
<i>Lanice conchilega</i>			0.072	
<i>Hediste diversicolor</i>		0.117		
<i>Cerastoderma edule</i>	0.387			0.387
Crustaceans		0.111		
Oystercatcher	0.616			
Curlew		0.511		
Bar-tailed godwit			0.233	
Black headed gull				0.090
Standardized regression weights ( $P$ -value)				
Distance > Organic matter	-0.671 (<0.000)	-0.671 (<0.000)	-0.671 (<0.000)	-0.671 (<0.000)
Organic matter > <i>L. conchilega</i>			0.268 (0.003)	
Organic matter > <i>H. diversicolor</i>		0.342 (<0.000)		
Organic matter > <i>C. edule</i>	0.622 (<0.000)			0.622 (<0.000)
Organic matter > Crustaceans		0.333 (<0.000)		
<i>L. conchilega</i> > Bar-tailed godwit			0.227 (0.007)	
<i>H. diversicolor</i> > Curlew		0.141 (0.033)		
<i>C. edule</i> > Oystercatcher	0.152 (0.037)			
<i>C. edule</i> > Black headed gull				0.372 (0.007)
Crustaceans > Curlew		0.195 (0.003)		
Distance > Oystercatcher	-0.417 (<0.000)			
Distance > Curlew		-0.597 (<0.000)		
Organic matter > Oystercatcher	0.338 (<0.000)			
Organic matter > Bar-tailed godwit			0.370 (<0.000)	
Organic matter > Black headed gull				-0.303 (0.007)

## Appendix B

**Table 3.B** Results from structural equation modeling after stepwise backward elimination of relations for each shorebird model. All sampling stations were included in these models. Distance represents distance to the centre of a reef.

	Model			
	Oystercatcher	Curlew	Bar-tailed godwit	Black-headed gull
Squared multiple correlations ( $R^2$ )				
Organic matter	0.404	0.404	0.404	0.404
<i>Lanice conchilega</i>			0.097	
<i>Cerastoderma edule</i>	0.495			0.495
Crustaceans		0.060		
Oystercatcher	0.590			
Curlew		0.441		
Bar-tailed godwit			0.229	
Black headed gull				0.083
Standardized regression weights ( $P$ -value)				
Distance > Organic matter	-0.636 (<0.000)	-0.636 (<0.000)	-0.636 (<0.000)	-0.636 (<0.000)
Organic matter > <i>L. conchilega</i>			0.311 (0.003)	
Organic matter > <i>C. edule</i>	0.704 (<0.000)			0.704 (<0.000)
Organic matter > Crustaceans		0.245 (<0.008)		
<i>L. conchilega</i> > Bar-tailed godwit			0.187 (0.034)	
<i>C. edule</i> > Oystercatcher	0.179 (0.037)			
<i>C. edule</i> > Black headed gull				0.405 (0.002)
Crustaceans > Curlew		0.168 (0.020)		
Distance > Oystercatcher	-0.380 (<0.000)			
Distance > Curlew		-0.617 (<0.000)		
Organic matter > Oystercatcher	0.331 (<0.000)			
Organic matter > Bar-tailed godwit			0.386 (<0.000)	-0.289(0.025)
Organic matter > Black headed gull				

# Chapter 6



# Predation and habitat modification interact to control bivalve recruitment on intertidal mudflats

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Abstract

Bivalves are key components of coastal ecosystems that link pelagic and benthic food webs, and shape the landscape through habitat modification. Nevertheless, many bivalve stocks have dramatically declined, and recruitment failure due to (anthropogenically-)increased predation by mesopredators and loss of facilitation mechanisms have been separately hypothesized as potential underlying causes. Here, we tested the interactive effects of predation and habitat modification on bivalve recruitment in a large-scale experiment in the Wadden Sea, one of the world's largest intertidal soft-sediment ecosystems. We applied anti-erosion mats to simulate biotic attachment and substrate stabilization by commonly found tubeworm beds, crossed this with addition of adult mussels, and manipulated shrimp and crab predation using exclosures within these treatments. Results show that both the anti-erosion mat and adult mussels facilitated epibenthic mussel recruits, whereas three out of four endobenthic species were facilitated by the mat, but inhibited by mussels. Contrastingly, invasive surf-dwelling American razor clams were inhibited by both substrate manipulations, indicating their preference for unstable sediments. The observed facilitation and inhibition effects, however, only clearly emerged when predators were excluded, demonstrating strong synergistic effects between predation and habitat modification. Our findings suggest that disturbance of trophic interactions and loss of habitat modifying species can severely affect bivalve recruitment dynamics in coastal ecosystems. We conclude that conservation and restoration of bivalves should focus on simultaneously protecting and restoring internal facilitation mechanisms and reducing excessive predation by mesopredators by restoring natural food web dynamics.

## Introduction

Over the last decades, about 30% to 50% of the Earth's coastal ecosystems have become severely degraded due to human impact, and losses are still continuing (Lotze *et al.* 2006; Barbier *et al.* 2008). Even though these areas make up only 4% of the Earth's surface, they are of great importance to marine biodiversity and human society (Costanza *et al.* 1997; Barbier *et al.* 2008). Bivalves are an important component for the functioning of these ecosystems. Reef-building species like mussels and oysters strongly modify their environment by creating complex structures that serve as a key-habitat for many species, attenuating currents and waves, enhancing water quality by filtering out large amounts of suspended particles and altering sediment conditions by depositing pseudofeces (Gutierrez *et al.* 2003; Schulte, Burke & Lipcius 2009; van der Zee *et al.* 2012). Furthermore, both reef-building and free-living bivalves are important food sources for a wide range of animal species, like crustaceans, starfish, fish and birds (Hiddink *et al.* 2002; Beukema & Dekker 2005; van Gils *et al.* 2006; Harley 2011; van der Zee *et al.* 2012).

In conjunction with coastal ecosystems in general, various important bivalve species have declined or are under threat in a wide array of ecosystems, often with dramatic implications for associated species and overall biodiversity (Jackson *et al.* 2001; van Gils *et al.* 2006; Schulte, Burke & Lipcius 2009; Eriksson *et al.* 2010). Natural recovery of bivalves – particularly those of epibenthic bivalves like mussels and oysters – is often slow, unpredictable or absent, and even active restoration has been proven difficult (Jackson *et al.* 2001; Schulte, Burke & Lipcius 2009; Eriksson *et al.* 2010). This may in part be directly related to changes in abiotic conditions (Philippart *et al.* 2003), but altered biotic interactions may also play a major role in failing bivalve recovery. One potentially important biotic factor is increased predation by crustaceans (e.g., shrimp, crab) on bivalve spat. Outbreaks of crustaceans can for instance occur due to climate change (Philippart *et al.* 2003) or overfishing of predatory fish that prey on crustaceans – co-called meso-predator release (Worm & Myers 2003). Second, declines of reef-forming species like mussels and oysters may reduce inter- and intraspecific facilitation mechanisms, further hampering bivalve recovery (Brinkman, Dankers & van Stralen 2002; Schulte, Burke & Lipcius 2009; Troost 2010; Donadi *et al.* 2013).

In this study, we investigated the importance of predation, habitat modification and their interplay in explaining bivalve recruitment dynamics in the Wadden Sea, one of the world's largest intertidal soft-sediment ecosystems. Predation during high tide by brown shrimp (*Crangon crangon*) and shore crab (*Carcinus maenas*) has been suggested to have a strong negative effect on bivalve recruitment in soft-sediment systems (van der Veer *et al.* 1998; Strasser 2002). Next to predation, biotic habitat modification could be an important driver for recruitment as well, because such mechanisms can cause strong facilitation effects in coastal ecosystems (Bruno,

Stachowicz & Bertness 2003; Eriksson *et al.* 2010). Intraspecific facilitation may be especially important for epibenthic reef-building bivalves like mussels and oysters, as mussel and oyster beds provide both stable settlement substrate and protection from predators for their larvae in an otherwise unstable, sandy area (Brinkman, Dankers & van Stralen 2002; Schulte, Burke & Lipcius 2009; Troost 2010). Still, there are also indications that substrate stabilization and aboveground structure provided by other species like the tubeworms *Lanice conchilega* and *Pygospio elegans* enhance settlement of mussels (*Mytilus edulis*), cockles (*Cerastoderma edule*), Baltic tellins (*Macoma balthica*) and sand gapers (*Mya arenaria*) (Armonies & Hellwigarmonies 1992; Brinkman, Dankers & van Stralen 2002; Bolam & Fernandes 2003; Volkenborn, Robertson & Reise 2009; Donadi *et al.* 2013).

To test the interactive effects of predation and habitat modification on intertidal bivalve recruitment we manipulated predation pressure, substrate conditions, and presence/absence of adult epibenthic bivalves in a full factorial large-scale field experiment that was set up in the Dutch Wadden Sea just before the start of the reproductive season. We crossed the application of anti-erosion mats (to mimic commonly found tubeworm beds) with the addition of adult mussels in twelve large 20×20 m plots. Within these plots, we designated uncaged control areas and manipulated predation by placing enclosure cages. To test for possible cage effects, we also placed cage controls. After 21½ months, we ended the experiment and determined recruitment success of all bivalve species found.

## Materials and methods

**Experimental setup.** The experiment was conducted in 2011 on an intertidal mudflat at 0.5 m below mean water level (low water exposure time ~30%) in the eastern Dutch Wadden Sea, south of the island of Schiermonnikoog (53°28'3.43"N, 6°14'13.40"E). The site itself was characterized by bare sandy sediment, but was located relatively close (~500–1000 m) to three natural intertidal mussel beds with a similar depth and exposure time. In the study area, we set up twelve 20×20 m plots in a line parallel to the gully (distance from the gully ~100–150 m), with a distance of about 20 m between plots. The plots were divided over three blocks, with four plots within each block. Within each block we randomly designated one of four treatments to the plots: (1) control, (2) enhanced sediment stabilization and aboveground structure by application of a coco coir mat on the sediment surface, (3) addition of adult mussels, and (4) application of coir mat followed by addition of adult mussels (Fig. 6.1A).

We used coir mats to mimic sediment stabilization and habitat structure provided by tubeworm beds – a biotic structure that is common and often serves as settlement substrate for bivalves in the Wadden Sea. The mats consisted completely





**Figure 6.1** (A) The experiment was set up in three blocks that included four treatments, with cage treatments (control, cage control and enclosure cage) nested within these treatments. (B) Coir mat and adults mussels on the 20×20 m plots were added by hand. (C) The 30-cm high cages were pushed 17 cm into the sediment.

out of coconut fibre and are commonly used to prevent erosion of sediment and seeds on bare soil (e.g. on hill slopes, dikes). To still allow endobenthic burrowing bivalves to dig into the sediment, we selected coir mats with mesh size of  $\sim 2$  cm. The mats were applied by hand, fixated along the edges by digging it in to a depth of  $\sim 20$  cm (Fig. 6.1B) and in the middle by 15-cm long biodegradable pins. To prevent complete burial of the anti-erosion mats by deposition of suspended sediments, we added 128 knotted burlap balls (diameter  $\sim 10$  cm) to each plot at regular distances underneath the mat, yielding small hummocks on which the mat was exposed and available as attachment substrate. Two-year old live mussels (shell length:  $54 \pm 6$  mm;  $n = 456$ ) were obtained from a natural subtidal mussel bed by mechanical dredging and transported to the site in the beginning of May. Within two days after fishing, 25 circular mussel patches with a  $\sim 2.5$ -m diameter were created by hand at regular distances from each other within each plot, yielding a total cover of around 30% – a cover commonly found in natural mussel beds in the Wadden Sea.

After a two-week adjustment period, we designated a control (uncaged) area and set up one enclosure and one partial (control) cage within each plot. Cages were similar in design as those used by Strasser (2002) near Sylt in the German Wadden Sea, but with a larger surface area. The cages were cylindrical with a 32-cm diameter and a height of 30 cm. The frame of the cages consisted out of three regularly interspaced 1.5-cm high pvc rings that were connected with three, regularly interspaced 2-cm wide pvc strips. The sides of the enclosures were completely covered with 1-mm mesh made out of pvc covered glass fibre, while 1/3 of the sides of the partial cages were left open. The tops of all cages were fit with removable lids that consisted of a 1.5-cm pvc ring and 1-mm mesh. Cages were pushed about 17 cm into the sediment, in such a way that the middle ring was completely beneath the sediment surface (Fig. 6.1C). To minimize differences between control and enclosure cages, control cages were placed in such a way that the openings were located on side of the cage that was most sheltered from currents and waves (north-east side). Because cages in coir mat plots were placed in areas without burlap balls, we added a small  $5 \times 5$  cm piece of wood in underneath the mat in the middle of the cages (and control areas) to prevent complete burial of the coir mat.

Over the course of the experiment, cages were cleaned and checked at least once every two weeks. Fouling on the cages turned out to be minimal and we found no evidence of breached or disturbed cages during the experiment. 21/2 Months after placement of the cages, the upper 15-cm layer of sediment in all cages and control areas was collected and passed through a 1-mm sieve. Everything remaining in the sieve, including adult mussels and coir mat, was stored in 4% formaldehyde solution for later analyses. Finally, we randomly collected sediment samples (top 5 cm) in each plot to determine the effects of adult mussels and coir mat on sediment grain size and organic matter content. Burial depth of the anti-erosion mats was determined with a ruler by 10 random measurements on each plot in areas without burlap balls.

Sieved samples were stained with Rose Bengal in the laboratory. All fauna were identified to species level and all bivalves were counted. Sediment organic matter content in dried sediments (24 h at 70°C) was estimated as weight loss on ignition (5 h at 550°C). Silt (<63 µm) content of the sediment was measured on freeze-dried samples by laser diffraction on a Beckman Coulter particle size analyser.

### Statistical analyses

Prior to model fitting, all data were checked for normality using Shapiro-Wilk tests ( $P = 0.05$ ). Based on this test, sediment organic matter and silt content were analysed using ANOVA models with a Gaussian error distribution and block as random factor. Recruitment data could not be analysed with Gaussian models and these data were therefore fitted to models more suitable for count data. For each bivalve species, we started by comparing uncaged areas with cage controls to identify possible cage effects. Next, when we found no significant differences ( $P < 0.05$ ) between cage treatments (i.e., no cage effect), exclosures were compared to the mean of uncaged areas and partial cages. Exclosure cages were compared to cage controls in case of significant cage effects (Hindell, Jenkins & Keough 2001). The above analyses were first run using Generalized Linear Mixed Models (GLMM) with Poisson and negative binomial distributions, respectively. Blocks were included as random factor with cage treatments nested within plot. To test for significance of the random effects, we repeated the procedure using Generalized Linear Models (GLM). We finally selected negative binomial models without random effects for all bivalve species based on AIC comparisons (using identical AIC algorithms for each model). All analyses were carried out in R 2.15.1 & RStudio 0.96 for Mac. GLMMs were constructed with the *glmmadmb* function in the *glmmADMB* package. Negative binomial GLMs were built with the *glm.nb* function from the *MASS* package. GLMs with Poisson distribution and Gaussian models were constructed using the *glm* and *aov* functions from the *Stats* package, respectively.

## Results

As expected, the anti-erosion mat increased suspended sediment deposition, burying the mat under a  $33 \pm 6$  (mean  $\pm$  SD;  $n = 6$ ) mm layer of sand. The mat only remained available as attachment substrate on small hummocks created by the burlap balls and wooden blocks that were added underneath the mat (Fig. 6.2A). The coir mat did not significantly effect either silt (control:  $4.4 \pm 1.7\%$ ; coir:  $4.8 \pm 2.3\%$ ) or organic matter content (control:  $0.8 \pm 0.2\%$ ; coir:  $0.9 \pm 0.3\%$ ) in the sediment (silt:  $F_{1,6} = 0.5$ ,  $P = 0.516$ ; organic matter:  $F_{1,6} = 1.1$ ,  $P = 0.329$ ).

Apart from providing hard substrate, adult mussels significantly modified sediment conditions. Silt content doubled from  $2.9 \pm 0.8$  (mean  $\pm$  SD;  $n = 6$ ) to  $6.3$

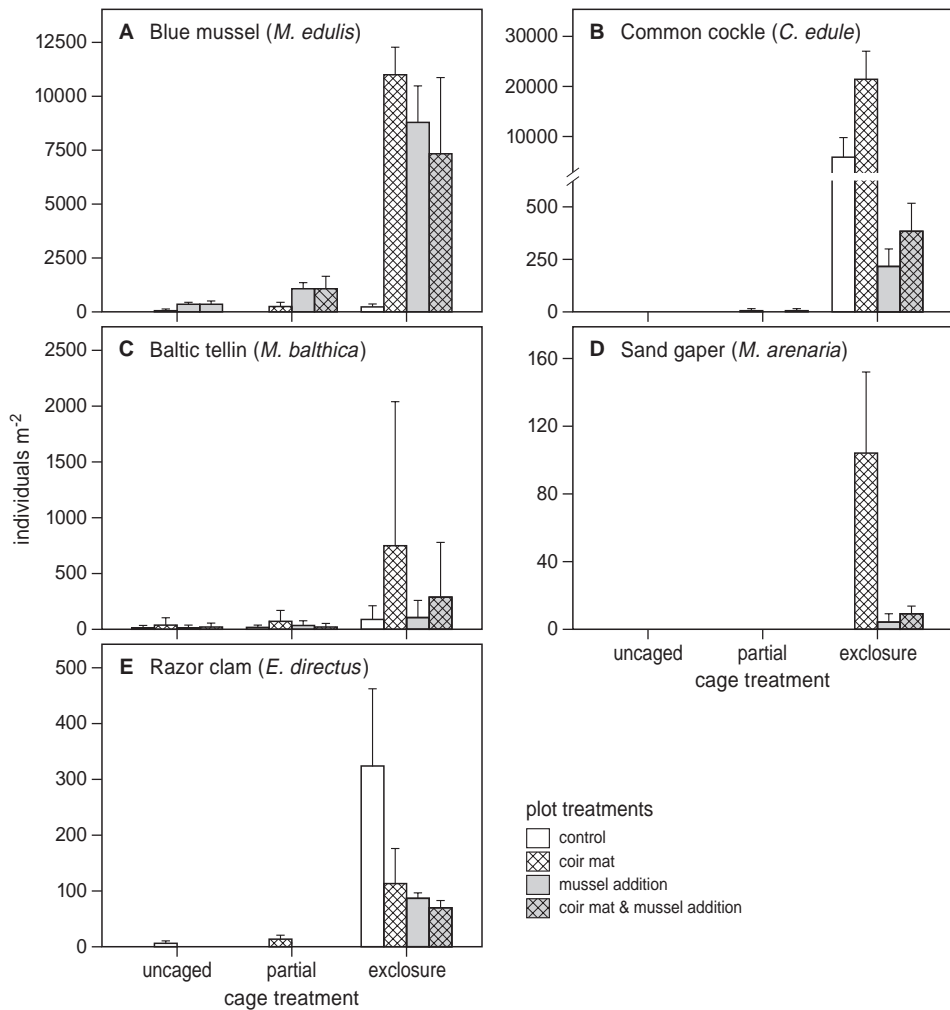


**Figure 6.2** Top views of a control cage (A) and an exclusion cage (B) on a coir mat plot (cage lids removed) at the end of the experimental period. The addition of wooden blocks underneath the mat created small hummocks where the mat remained available as attachment substrate (A). The combination of predator exclusion and substrate stabilization yielded high numbers mussel recruits attached to the mat (black patch in the middle of B) and cockles (white shells) in the surrounding sediment.

$\pm 0.8\%$  ( $F_{1,6} = 44.2$ ,  $P < 0.001$ ), and organic matter increased with a factor 1.6 from  $0.6 \pm 0.1\%$  to  $1.0 \pm 0.2\%$  ( $F_{1,6} = 30.5$ ,  $P = 0.001$ ; no significant interactions with the coir mat treatment). The density of adult transplanted mussels in uncaged areas was  $439 \pm 110$  (mean  $\pm$  SD;  $n = 6$ ) individuals/ $m^2$ , which was lower than in partial cages ( $564 \pm 72$  ind./ $m^2$ ;  $\chi^2 = 7.5$ ,  $P = 0.006$ ). Partial cages, however, did not differ significantly from exclusions ( $576 \pm 78$  ind./ $m^2$ ;  $\chi^2 = 0.1$ ,  $P = 0.798$ ) and we also found no significant effect of the coir mat on adult mussel density ( $\chi^2 = 0.3$ ,  $P = 0.609$ ) or any significant interactions.

We found that 5 bivalve species settled in our plots: blue mussels, common cockles, Baltic tellins, sand gapers, and American razor clams (*Ensis directus*). Of these species, only mussels showed a significant cage effect ( $\chi^2 = 9.6$ ,  $P = 0.002$ ; no significant interactions). However, the increased settlement in the partial cage could only explain between 2% (on bare sediment) to 10% (on coir with mussel addition) of the difference between exclusions and control areas.

Mussel recruits were found almost exclusively attached to either the coir mat or adult mussels and predominately in the predator exclusions (Figs. 6.2 & 6.3; Table 6.1). Similar to mussel recruits, spat numbers of endobenthic, burrowing cockles, Baltic tellins, sand gapers and razor clams were significantly higher in predator exclusions. Cackle densities were highest in sediments of exclusions stabilized by a coir mat ( $\sim 21000\ m^{-2}$ ), but numbers were also high in exclusions on bare sediment



**Figure 6.3** Mean number of recruits per treatment for all five bivalve species found at the end of the experimental period. Error bars denote standard errors.

( $\sim 6000 \text{ m}^{-2}$ ), resulting in a  $\sim 3\text{-cm}$  thick multilayer mat of cockles in these two treatments (Fig. 6.2). In contrast with cockles, Baltic tellins and sand gapers that were all significantly enhanced in coir mat-stabilized sediments, numbers of razor clams were much lower here compared to exclosures on bare sediment (Fig. 6.3). Finally, spat numbers of cockles, sand gapers and razor clams were all significantly lowered by the presence of adult mussels in the exclosures. Baltic tellins were also significantly lowered by adult mussels, but only in the coir mat treatment.



## Discussion

Recruitment failure is an important factor driving bivalve declines in soft-sediment ecosystems and both predation and loss of facilitation mechanisms have been separately suggested as potential underlying causes (Olafsson, Peterson & Ambrose 1994; Gosselin & Qian 1997; Schulte, Burke & Lipcius 2009; Eriksson *et al.* 2010; Donadi *et al.* 2013). In this study, we experimentally show that recruits of the four most important native bivalve species in the Wadden Sea appear strongly, but species-specifically, controlled by the complex interplay between predation, facilitation and interspecific inhibition. Mussel spat was only found in significant amounts in predator enclosure cages attached to either coir mat or adult mussels, illustrating its dependence on both low predation pressure and a suitable attachment substrate. Free-living burrowing cockles, Baltic tellins and sand gapers were similarly dependent on low predation levels, and were facilitated by the anti-erosion mat – most likely due to its sediment stabilizing effects. In contrast to mussel spat, however, adult mussels inhibited settlement of these endobenthic species. Since there is no evidence of selective predation on larvae by filter-feeding mussels (Troost 2010), we suggest that altered sediment conditions caused by pseudofeces deposition inhibited recruitment of these endobenthic bivalves (Diaz & Rosenberg 1995; Graf & Rosenberg 1997). Strikingly, recruitment of invasive razor clams (introduced in the late 1970s) was positively affected by exclusion of predation, but negatively affected by both adult mussels and coir mat, illustrating that these clams may benefit from unstable sediment conditions (Armonies 2001).

Apart from manipulating predation pressure, cages may also alter hydrodynamics and larval settlement because of their physical structure. For instance, lowered hydrodynamic intensity in the cages may lead to reduced sediment distur-

**Table 6.1** Chi-square values and significance levels for all treatments and their interactions per bivalve species.

Treatments	Mytilus	Cerastoderma	Macoma	Mya	Ensis
Coir	14.3 (***)	7.8 (**)	17.4 (***)	16.9 (***)	2.9
Mussels	36.8 (***)	69.0 (***)	1.7	9.1 (**)	10.5 (**)
Predation	63.6 (***)	221.1 (***)	42.7 (***)	25.1 (***)	88.8 (***)
Coir × Mussels	33.8 (***)	0.9	3.8 (*)	4.5 (*)	1.8
Coir × Predation	0.0	1.3	2.0	0.0	6.9 (**)
Mussels × Predation	6.8 (**)	4.9 (*)	0.0	0.0	2.6
Coir × Muss. × Pred.	0.5	0.0	0.0	0.0	0.0

Significance levels: \*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$ . Degrees of freedom: 24 in total; 16 residual.



bance, in turn enhancing larval settlement (Strasser 2002). Nevertheless, our comparison between closed cages and control cages revealed little evidence of cage artefacts. Although we found some evidence for cage effects on mussel spatfall, these effects seem small as the total amount of mussel recruits in the partial cages was only 6% of the number of recruits in the closed cages. Moreover, we found no indication at all for similar artefacts in any of the other bivalve species. Possibly, the byssally attaching mussel larvae used the cage structure as a primary attachment substrate, subsequently allowing recruits to move onto the substrate inside the cages. Also, in the mussel addition treatments, the enhanced mussel recruitment in the partial cages compared to controls may (in part) be explained by increased facilitation due to the somewhat higher adult densities. Overall, however, we conclude that it is unlikely that cage artefacts contributed importantly to our experimental results.

Our findings have important implications for management of soft-sediment ecosystems as they indicate that disturbance of trophic interactions and loss of habitat modifying species can severely hamper bivalve recruitment. Over the last decades, large-scale declines of bivalve stocks occurred in North-America, Australia and Europe (including the Wadden Sea) due to mechanical dredging for commercially exploitable species like oysters, mussels and cockles (Schulte, Burke & Lipcius 2009; Eriksson *et al.* 2010). Apart from the physical removal of adult bivalves, mechanical dredging also removes hard substrates (e.g., dead shells, tubeworm structures) and destabilizes the sediment (Ferns, Rostron & Siman 2000; Piersma *et al.* 2001). Our results show that recruitment of native bivalves in the Wadden Sea is negatively affected by these activities. Contrastingly, the invasive American razor clam, originally an inhabitant of the lower surf-zone, but now strongly increasing in the Wadden Sea, may actually be facilitated as this species profits from unstable sediments (Armonies 2001). Apart from deteriorated substrate conditions, predation pressure by crustaceans is increasing in many coastal areas, often due to overfishing of top-predators resulting in mesopredator release (Worm & Myers 2003). In the Dutch Wadden Sea, shrimp numbers are over twice as high compared to other European coastal waters (Tulp *et al.* 2012), peaking in summer at over 100 individuals/m<sup>2</sup> on intertidal flats (van der Veer *et al.* 1998). Furthermore, shore crab densities increased over 10-fold since 1995, with numbers still rising (Tulp *et al.* 2012). At present, the underlying causes are unknown, but our results suggest that high predator numbers now hamper bivalve recruitment.

Recently, there is an increasing amount of evidence pointing at the key importance of the interplay of habitat modification and biotic interactions in structuring soft-sediment marine ecosystems like mudflats and seagrasses (Weerman, Herman & Van de Koppel 2011; van der Heide *et al.* 2012a; van der Heide *et al.* 2012b). Our study clearly demonstrates that such interactions are equally important for bivalve recruitment dynamics in intertidal soft-sediment ecosystems. Overall, we conclude

that it is of utmost importance to protect existing bivalve beds and conserve their internal facilitation effects. Furthermore, restoration efforts should focus on reducing (anthropogenic) disturbances to both recover lost facilitation mechanisms and restore natural trophic interactions to reduce excessive predation by meso-predators.

### **Acknowledgements**

We are grateful to Natuurmonumenten, Staatsbosbeheer and the many volunteers for their help with setting up the experiment. We thank A. J. P. Smolders for his helpful comments. This study was carried out within project 'Waddensleutels', funded by the 'Waddenfonds'. EZ, EW and BKE were financially supported by grant 839.08.310 of the NWO-ZKO program.



# Chapter 8

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## Synthesis

Research over the last decades has revealed that ecosystem engineering – the modification of the abiotic environment by organisms (Jones *et al.* 1994; 1997) – can be an important structuring interaction in many ecosystems (e.g. Bruno *et al.* 2003; Wright and Jones 2006; Hastings *et al.* 2007; Jones *et al.* 2010). By modifying the availability of resources to themselves and to other species, ecosystem engineers have the potential to alter the structure and dynamics of complex ecological interaction networks (Olf *et al.* 2009). Out of these networks, trophic interactions and the resulting food web have received most attention (e.g. Cohen 1978; Tilman 1982; DeAngelis 1992 ; Polis and Winemiller 1996). However, the multi-trophic structure of natural food webs is often studied in ignorance of non-trophic interactions such as ecosystem engineering (as emphasized by Berlow 2004; Ings *et al.* 2009; Olf *et al.* 2009) and although integration of trophic and non-trophic interactions into a single framework has recently been gaining attention, studies addressing this issue have remained mostly of a theoretical nature (Arditi *et al.* 2005; Goudard and Loreau 2008; Kefi *et al.* 2012; Sanders *et al.* 2013). Additionally, it is increasingly recognized that understanding the effects of ecosystem engineering on complex ecological networks also requires the inclusion of temporal and spatial dynamics, since engineering effects often persist on long time and large spatial scales (Hastings *et al.* 2007 and references therein). Yet, the suggested importance and interplay of these effects has not yet been empirically investigated to my knowledge.

In tidal soft-bottom ecosystems, ecosystems engineers such as reef-building bivalves and seagrasses can significantly affect the associated community by modifying abiotic conditions (e.g. hydrodynamic stress, nutrient availability) and providing natural hard substrate and structure in the otherwise sandy environment (e.g. Orth *et al.* 1984; Gambi *et al.* 1990; Gutierrez *et al.* 2003; Commito *et al.* 2005). However, during the last centuries, tidal soft-bottom systems have become severely degraded worldwide due to human impacts (Jackson *et al.* 2001; Lotze *et al.* 2006). Coinciding with the overall degradation, most ecosystem engineers in these systems, have been overexploited or destroyed (Jackson *et al.* 2001; Lotze 2005; Waycott *et al.* 2009), with potentially dramatic implications for associated species, community structure and overall biodiversity.

The main objective of this thesis is to empirically investigate how and to what extent ecosystem engineers can affect the (trophic) structure and dynamics of intertidal soft-bottom communities. Hence, this thesis provides a deeper insight into the role of ecosystem engineers in structuring ecological networks and their importance for effective conservation management of coastal ecosystems. In this final chapter, the findings and implications from earlier chapters are integrated with the existing literature, and I provide ideas for conservation and management strategies. First, I discuss how ecosystem engineers can affect ecological interaction networks by influencing trophic structure, biotic interactions or entire food webs. Next, the focus is on how these effects can extend in space and time. Finally, implications of the



main findings with regard to the conservation and restoration of intertidal-soft bottom ecosystems are stated.

## **The role of ecosystem engineers in structuring ecological interaction networks**

Ecosystems often contain a wide variety of species that interact with each other in multiple ways, forming complex ecological networks of various types of interactions such as predation, competition and ecosystem engineering (reviewed by Olff *et al.* 2009). The integration of ecosystem engineering within these networks can be highly important and complex, since engineers are able to affect other species in multiple ways (e.g. Sanders *et al.* 2013):

### **The modification of species abundance and distribution**

By modifying the abiotic environment, ecosystem engineers can alter abiotic conditions, such as temperature or moisture (e.g. Orth *et al.* 1984; Badano *et al.* 2006), but they can also alter the availability of trophic and non-trophic resources such as nutrient deposition (e.g. Norling and Kautsky 2007) and refuge to thermal stress (e.g. Stephens and Bertness 1991). By doing so, they affect the network members, i.e. their own distribution and abundance and that of other species (e.g. Wright *et al.* 2002; van de Koppel *et al.* 2005; Norling and Kautsky 2007; van der Heide *et al.* 2007), which in turn influences the overall structure of the ecological interaction network they are part of (Fig. 1.1. A). Up to now, many studies investigated the effects of ecosystem engineering on the community in a general way by looking at species richness and abundance (e.g. Bruno 2000; Wright *et al.* 2002; Lill and Marquis 2003; Badano *et al.* 2006; Commito *et al.* 2008). Relatively few studies specifically investigated the effects of ecosystem engineering on the distribution of competing or trophically interacting species (e.g. Palmer 2003; Graham 2004; Norling and Kautsky 2008; Arkema *et al.* 2009; Sanders and van Veen 2011; Angelini and Silliman 2014), of which so far none were conducted in intertidal soft-bottom ecosystems to my knowledge.

Findings in this thesis, together with those of Donadi *et al.* (2013), demonstrate that ecosystem engineering by intertidal reef-building bivalves can affect the distribution of species within and across multiple trophic levels. Donadi *et al.* (2013) showed that mussels facilitate microphytobenthos abundance in the surrounding area of their reefs. Possible mechanisms behind this microphytobenthos facilitation are enhanced nutrient availability caused by biodeposition (Bracken 2004; Donadi *et al.* 2013; chapter 2 & 3), and increased substrate cohesiveness and light availability through the combined effects of biodeposition and reduced hydrodynamic stress (Widdows and Brinsley 2002; Newell and Koch 2004; Donadi *et al.* 2013). By



strongly modifying structure and nutrient availability and primary producer abundance, it is inevitable that higher trophic levels are also affected by the engineering effect of reef-building bivalves. In Chapters 2, 3 and 5, it is demonstrated that reef-building bivalves also facilitate macrofaunal species across different trophic levels, not only on the reef itself but also in the surrounding area. The observed facilitation effects are most likely caused by (1) increasing nutrient availability to deposit feeders (Norkko *et al.* 2001 chapter 2, 3 & 5), (2) provision of suitable substrate and sediment (Donadi *et al.* submitted; chapter 5 & 6) and (3) provision of refuge to hydrodynamic stress (Widdows and Brinsley 2002; chapter 2 & 4).

By altering the distribution and abundance of macrofaunal benthic species, ecosystem engineering by reef-building bivalves also strongly affected the distribution of three avian predators feeding on these species (Chapter 3). Sediment properties and benthic food abundance simultaneously explained significant parts of the distribution of oystercatchers (*Haematopus ostralegus*), Eurasian curlews (*Numenius arquata*) and bar-tailed godwits (*Limosa lapponica*), with higher densities in the surrounding area of the reef compared to sandy un-engineered tidal flats. Overall, these findings demonstrate that ecosystem engineers can strongly facilitate individual species, which in turn can cascade through multiple trophic levels (Fig. 8.1.A).

### The modification of biotic interactions

By affecting the abiotic environment, ecosystem engineers can directly modify the interaction between species, i.e. the number and strength of biotic interactions (Fig. 1.1.B: green links). Structural heterogeneity provided by floating macrophytes for instance, reduces predation efficiency (Padial *et al.* 2009), while termite-induced habitat heterogeneity can facilitate competitive coexistence when species differ in their ability to exploit resource-rich vs. resource-poor conditions (Palmer 2003). Additionally, by affecting the abundance and distribution of network members, ecosystem engineers can also indirectly affect the number and strength of interactions (e.g. Aguiar and Sala 1994; Arkema *et al.* 2009) (Fig. 1.1.B: orange links). Hence, the interplay of multiple interactions types such as predation, competition and ecosystem engineering are highly important in structuring ecological communities (as emphasized by Berlow 2004; Olff *et al.* 2009; Fontaine *et al.* 2011).

In intertidal soft-bottom ecosystems, for example, recruitment failure is an important factor driving bivalve declines and both predation and loss of ecosystem engineering mechanisms have been suggested as potential underlying causes for this failure (Olafsson *et al.* 1994; Gosselin and Oian 1997; Schulte *et al.* 2009; Eriksson *et al.* 2010; Donadi *et al.* submitted). Experimental evidence in this thesis (Chapter 6), shows that recruits of four important native bivalve species in the Wadden Sea (Blue mussels - *Mytilus edulis*, Edible cockles - *Cerastoderma edule*, Baltic tellins - *Macoma baltica* and Sand gapers - *Mya arenaria*) appear strongly, but species-specifically, controlled by the interplay between predation and ecosystem engi-

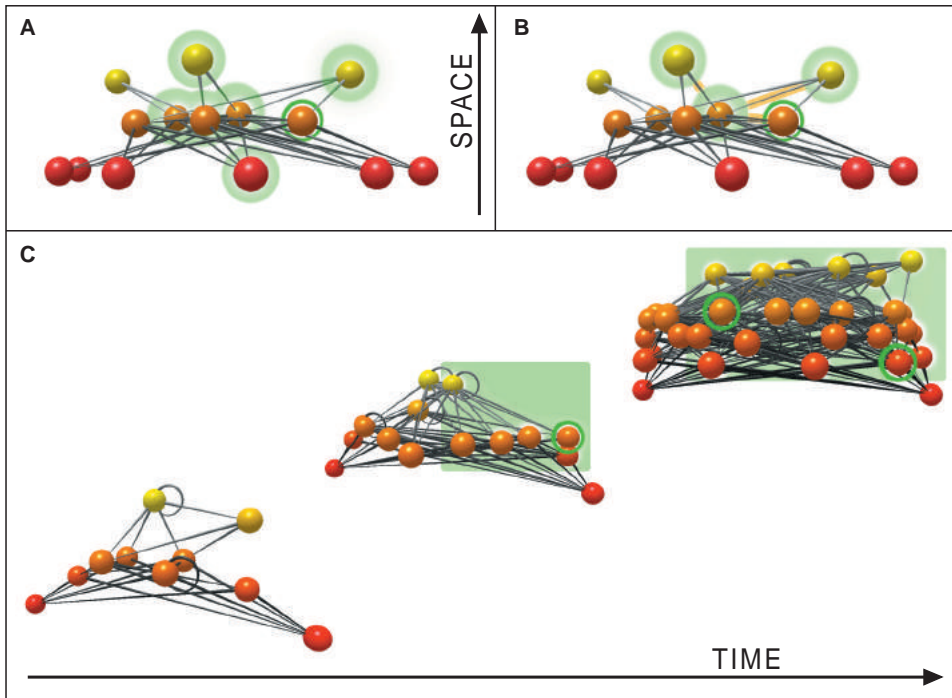
neering. These findings contribute to an increasing amount of evidence that underlines the importance of the interplay of ecosystem engineering and biotic interactions in structuring intertidal soft-bottom ecosystems, like diatom and seagrasses dominated-mudflats (Weerman *et al.* 2011; van der Heide *et al.* 2012).

Until now, most work on integrating ecosystem engineering into ecological interactions has focused on the coupling of ecosystem engineering with either trophic or competitive interactions among species. Ecosystem engineers can affect multiple trophic levels (e.g. Graham 2004; Angelini and Silliman 2014; chapter 3) and are able to modify predatory impact among other species (e.g. Farina *et al.* 2009; Ransom 2011; chapter 4 & 6). In addition, ecosystem engineering and trophic processes can also be closely related when a single species act as a predator and an engineer simultaneously (e.g. Wilby *et al.* 2001; Sanders and van Veen 2011). Besides interacting with predation, ecosystem engineering has been shown to affect competition as well (e.g. Palmer 2003; Ransom 2011; chapter 2). However, despite the fact that trophic interactions, competition, ecosystem engineering and their two-way interactions are all recognized as important structuring mechanisms in ecosystems, the combined effects of all three interaction types on population dynamics remain to be investigated. In Chapter 4, it is demonstrated that ecosystem engineering, predation and competition interactively structure an intertidal bivalve population. Ecosystem engineering by mussel reefs enhanced cockle densities by reducing hydrodynamics stress and predation pressure across different life stages, but reduced cockle growth, most likely by reducing seawater flow (Frechette *et al.* 1989) and by indirectly affecting inter-specific competition for food through the facilitation of cockles in the vicinity of the mussel reefs. Overall, these findings demonstrate that multiple interactions types can interactively structure ecological communities (Fig. 8.1.B).

### The modification of food webs

Besides influencing single species or food chains (Fig. 8.1.A; Chapter 2 & 3), ecosystem engineers can also affect food web-compartments or entire food webs by altering abiotic conditions and creating entire new types of habitats within an ecosystem (Fig. 1.1. C & D). This thesis provides empirical evidence that ecosystem engineering affects food web structure by adding new habitats and niches to an ecosystem (Chapter 7). In the Banc d'Arguin, a pristine intertidal soft-bottom ecosystem, hierarchical habitat modification by seagrasses and burrowing crabs transform simple intertidal food webs into a complex mosaic of linked inter- and subtidal food webs, suggesting that ecosystem engineering can be more important in structuring ecological networks than previously thought.

Our results reveal that habitat modifying species, through non-trophic facilitation rather than trophic interactions, dramatically alter basic food web properties, such as species richness, the number of links per species and connectance. Removal of non-trophic effects changed these food web properties by 54% on average,



**Figure 8.1** Schematic overview of the impacts of ecosystem engineering on the structure and dynamics of interaction webs. The ecosystem engineer in each web is indicated by a green circle and the green shaded areas represent its engineering effect. Ecosystem engineering can affect interactions webs by affecting species abundance at different trophic levels at a spatial scale (A), by indirectly affecting the interplay of biotic interactions (orange links) among species (B) and by affecting foodweb-subsets through the creation of new environments within an ecosystems by multiple ecosystem engineers over time (C). Nodes (red-yellow gradient) represent species and grey lines represent their interactions within the network. Food web images were made with Network3D (Yoon *et al.* 2004; Williams 2010). Images are partly based on Sanders *et al.* (2013).

whereas the change in properties resulting from the removal of the trophic effect of crabs and seagrass was an order of magnitude lower; 5% on average. Furthermore, since May (1972) demonstrated that randomly assembled food webs become less robust as their complexity increases, food web structure and stability have been typically analyzed as a function of the properties of the network itself, like the number of species and links, connectance (Williams and Martinez 2000; Dunne *et al.* 2002; Gross *et al.* 2009; Dunne *et al.* 2013) or the strength of trophic loops in the network (Neutel *et al.* 2002). Our findings indicate that food web structure and temporal dynamics can to a large extent be determined by interactions outside the trophic network, yet intrinsic to the species of the system. We therefore conclude that integration of non-trophic interactions into analyses of food web stability and temporal dynamics may be crucial for their empirical reliability and predictive

value. Overall, our findings demonstrate that ecosystem engineering can strongly affect food web composition and dynamics (Fig. 8.1.C), which provides grounds for new approaches to ecological network analyses and ecosystem conservation.

## Ecosystem engineering in space and time

Two typical features of ecosystem engineers are that they affect the abiotic space in which they and other species live and that their effects can be long-lasting (Hastings *et al.* 2007 and references therein). To understand the role of ecosystem engineers in structuring communities and the resulting ecological interaction networks, it is crucial to investigate these two features, especially because ecosystem engineering can act on much larger spatial scales than the engineer itself and persist on time scales much longer than their own lifetime (e.g. Remillard *et al.* 1987; Dangerfield *et al.* 1998),

Over the last decades, studies have demonstrated that the interplay between small-scale facilitation and long-range inhibition of organisms through ecosystem engineering and competition respectively, can generate large-scale spatial patterns in ecosystems (Rietkerk and van de Koppel 2008 and references therein). In contrast, an opposite interplay between local competition and large-scale facilitation through ecosystem engineering has also been observed (Bruno 2000; van de Koppel *et al.* 2006). These studies have in common that facilitation through ecosystem engineering is often scale-dependent. In Chapter 2, it is demonstrated that scale-dependent interactions can also play an important role in structuring the community of sessile species in soft-bottom intertidal ecosystems. Peaks in cockle densities were observed at around 100 meters coastward of reef-forming mussels, but not in the reef itself or in the areas without mussel reefs. This spatial pattern in cockle densities was caused by a combination of the facilitation of cockle recruitment, which prevailed at a distance of 100 m from the mussel reefs, and the inhibition of cockle growth and survival within the reefs. Facilitative effects on cockle recruits were found to be caused by hydrodynamic stress alleviation. Negative effects were due to filter-feeding and biodeposition of mussels, resulting in competition for food and deteriorated sediment conditions. These findings demonstrate that intertidal ecosystems can be structured by short and long-range interactions, of which the latter causes spatial linkages between neighboring communities.

Long-range engineering by reef-building bivalves, however, did not only affect the distribution of cockles, but also affected hydrodynamic and sediment conditions up to several hundreds of meters away from the reefs (Kröncke 1996; Bergfeld 1999; chapter 2 & 3). Along this spatial gradient, the abundance of microphytobenthos and several macrofauna and shorebird species was enhanced with increasing distance to the reefs (Donadi *et al.* 2013; Chapter 2 & 3). These findings demonstrate that reef-

building bivalves can affect multiple trophic levels far beyond their own physical spatial boundaries (Fig. 8.1. A), and have the potential to affect biotic interactions at large spatial scales.

Apart from spatial effects, abiotic modifications by ecosystem engineers can also persist on long time scales – even longer than the lifespan of the engineer itself (Hastings *et al.* 2007 and references therein). For example, the physical structure of autogenic engineers such as corals and shell-reefs (Kidwell 1986), can persist over thousands of years, but also the effects of allogenic engineers such as beaver dams and termite mounds (Remillard *et al.* 1987; Moore and Picker 1991) can persist over long time scales. Since it is increasingly recognized that understanding the assembly of complex ecological interaction networks requires the inclusion of temporal dynamics (Blonder *et al.* 2012), it is very important to investigate this temporal aspect. Succession for instance, strongly changes food web structure over time (Schoenly and Cohen 1991; Neutel *et al.* 2007; Schrama *et al.* 2012), suggesting that ecosystem engineering may have equally important effects (Hastings *et al.* 2007), especially when multiple ecosystem engineers act hierarchical over time in the form of a facilitation cascade (Altieri *et al.* 2007; Thomsen *et al.* 2010; Angelini and Silliman 2014). In Chapter 7, it is demonstrated that colonizing seagrass patches (< 4 years) that accumulate silt and form 3D structures, increased species richness and the number of links per species (L/S) by 1.5 times relative to uncolonized sand flats. On the long term (>37 years), burrowing crabs have created large intertidal pools in the accumulated silt layer which further enhanced species richness and the number of links per species by 2 and 1.5 times, expanding the intertidal foodweb with subtidal species. Connectance (C; defined as  $L/S^2$ ) on the other hand, displayed the opposite trend, decreasing by 0.6 times as the systems matured from bare to colonizing seagrass and long-term stable seagrass meadows. Overall, these findings emphasize that food web assembly and composition can be strongly controlled by ecosystem engineering and that this process can be highly complex in terms of being hierarchical and temporal (Fig. 8.1.C).

## Implications for conservation

In conclusion, results presented in this thesis demonstrate that ecosystem engineering can strongly affect the trophic structure and dynamics of intertidal communities in space and time, thereby emphasizing the importance of ecosystem engineers for ecosystem functioning and integrating multiple ecological interaction types into a single framework.

Despite its protected status, the Wadden Sea is ranked among the most degraded systems and is situated in a state far from its historical baseline (Lotze *et al.* 2006), mostly due to over exploitation and habitat destruction (Wolff 2000; Lotze 2005;

Wolff 2005; Box 1). Coinciding with this overall degradation, structure-providing and sediment-stabilizing ecosystem engineers like reef-building bivalves and seagrasses, have strongly declined in the Wadden Sea (Lotze 2005; Lotze *et al.* 2006). Although it has been acknowledged that the loss of these ecosystem engineers caused a simplification and homogenization of the Wadden Sea landscape (Lotze 2005; Reise 2005), the consequences of their loss for the (trophic) structure of the intertidal community have remained largely unclear.

### **Box 1: The Wadden Sea: protected and heavily exploited at the same time**

The Dutch Wadden Sea has been under various laws of protection by international agreements from the early 1970s, including the Ramsar Convention on Wetlands (1971), the joined Declaration of the protection of the Wadden Sea (1982) and Natura 2000 (2003). More recently, the Dutch and German part of the Wadden Sea even became one of the UNESCO Natural World Heritage sites (2009). However, despite this high-level conservation status, the Wadden Sea has a history of destructive human impacts (Lotze 2005; Lotze *et al.* 2006; Boere and Piersma 2012). How is it possible that a nominally protected nature area like the Wadden Sea could be exposed to intensive fisheries that fully removed all intertidal mussel reefs and nearly all cockle beds in the 1990s and that continued until 2004?

### **Mechanical dredging for shellfish in the Wadden Sea**

- based on Swart and van Andel (2008) -

In the 1970s, the exploitation of mussels and cockles intensified by the introduction of mechanized fisheries. In the early 1990s, the decline of both mussel and cockles as a consequence of this intensification was identified, which increased the public and political awareness about the degradation of the Wadden Sea. In response, the Dutch government announced protection measures (LNV 1993). After five years, in 1998, these measures were assessed by an unpublished ecological evaluation study (EVA I). It was concluded that full recovery after fishing had not taken place. However, because of strong fluctuations in cockle densities and because of the short study period, definitive conclusions could not be made (LNV 1998). Furthermore, it was stated that dredging is unlikely to affect the top layer of the sediment and that hydrological processes cause turbidity and deposition of fine material in the top layer of the sediment (Scholten and Kaag 1998). Based on these findings, the Dutch government concluded that there was no need to ban the mechanized cockle fishing. Only after a second inconclusive evaluation study (EVA II; 1999–2003), the



publication of several studies carried out in full independence of the governmental process (Piersma and Koolhaas 1997; Piersma *et al.* 2001) and an independently organized expert congress at the University of Groningen, the Dutch government finally bought out the destructive cockle dredging industry (for 122 million Euro) in 2004.

That it took over 30 years of ongoing overfishing in a protected natural area before political action, can be explained by the power of vested financial interests and a lack of evidence-based conservation policies. There were strong controversies among stakeholders that slowed down the decision making as exploitation went on. A large part of this problem was due to the fact that ecologists were not in line with each other. Those in charge ignored published effects of dredging on soft-bottom ecosystems and the importance of ecosystem engineers. In fact, a considerable amount of scientific literature on the negative ecological effects of mobile fishing gear on benthic communities was available at the time (Dieter *et al.* 2003; Versteegh 2004). This also applied to the positive effects of ecosystem engineers such as mussels and seagrass on the benthic community (e.g. Orth *et al.* 1984; Dankers and Zuidema 1995; Stewart *et al.* 1998). Instead, abiotic factors such as hydrological processes, severe winters and storms, were put forward as the major forces structuring the Wadden Sea ecosystem (LNV 1998; Scholten and Kaag 1998).

Findings in this thesis and recent literature now demonstrate that biotic processes also play a major role in the structuring the Wadden Sea ecosystem. Ecosystem engineers like mussels, cockles and seagrass have a much larger ecological impact on the intertidal community than their actual size and lifespan suggests and they can generate strong positive feedbacks (e.g. van de Koppel *et al.* 2005; Donadi *et al.* 2013; Donadi *et al.* submitted; this thesis). Loss of ecosystem engineers can therefore result in disproportionately large consequences for biodiversity values in protected intertidal areas such as the Wadden Sea. In management aimed towards sustainable use, the considerable evidence for the key roles of ecosystem engineers should be taken into account in order to restore and conserve the unique values of the Wadden Sea



Cockle dredgers (Photo M. de Jonge) and an aerial view of the sediment after cockle dredging (photo J. de Vlas, note the two people for the scale)

Based on findings in this thesis, I propose that structure-providing and sediment-stabilizing ecosystem engineers can form the foundation for a trophically diverse ecosystem and that the overexploitation of these engineers therefore significantly reduced trophic diversity in the Wadden Sea. This idea is supported by the finding that loss of these engineers may result in disproportionately large consequences for biodiversity values, since they can have a much larger ecological impact on the intertidal community than their actual size and lifespan suggests (Chapter 3 & 7).

In addition to the loss of ecosystem engineers, the loss of top-down processes can also strongly determine the trophic structure and dynamics of coastal systems (e.g. Pinnegar *et al.* 2000; Steneck and Sala 2005; Eriksson *et al.* 2011). Predation pressure by crustaceans for instance, has increased in many marine areas parallel to overfishing of top-predators, causing so-called mesopredator-release – excessive predation on lower trophic levels due to lack of predation on intermediate levels – (Worm and Myers 2003; Eriksson *et al.* 2011). In the Dutch Wadden Sea, shrimp numbers are more than twice as high compared to other European coastal waters (Tulp *et al.* 2012) and shore crab densities increased over 10-fold since 1995, with numbers still rising (Tulp *et al.* 2012), suggesting that loss of top-predators (Wolff 2000; Lotze 2005; Lotze *et al.* 2005) may have resulted in mesopredator release. Findings in this thesis support this notion as crustacean numbers seem to strongly contribute to bivalve declines by hampering bivalve recruitment (Chapter 6). Overall, the findings presented in this thesis indicate that, besides altered abiotic conditions, the Wadden Sea community is likely disrupted from two biotic directions: loss of ecosystem engineering negatively affects its foundation by decreasing (trophic) diversity, while loss of natural trophic interactions negatively affects its top-down regulation.

In contrast to the Wadden Sea, the Banc d'Arguin is still a relatively pristine and undisturbed ecosystem. Here, extensive seagrass meadows shape the intertidal flats, indicating that ecosystem engineers form a solid foundation for the trophic diversity in this system (Chapter 7). Nevertheless, overfishing by international fleets in the offshore waters just outside Parc National du Banc d'Arguin, is depleting fish resources (ter Hofstede and Dickey-Collas 2006; Nagel and Gray 2012), suggesting that disrupted top-down processes may negatively affect trophic structure and dynamics in the Banc d'Arguin as well.

Ecosystem engineers in intertidal soft-bottom ecosystems typically facilitate a large number of associated species, making them an appealing conservation target because by managing a single species, entire communities can be positively affected (Boogert *et al.* 2006; Byers *et al.* 2006; this thesis). Nevertheless, findings in this thesis also illustrate that ecosystem engineering are often entangled in a network of multiple interaction types, illustrating that conservation and restoration efforts should in many cases not only focus on a single species or interaction type. Instead, multiple species should be considered within an integrated network of multiple

interaction types in order to protect or restore these ecosystems. The lack of such an integrated approach may explain why, despite some encouraging results of restoration efforts (e.g. Schulte *et al.* 2009; Lotze *et al.* 2011), large-scale recovery of coastal ecosystems remains difficult (Eriksson *et al.* 2010; Lotze *et al.* 2011). Because of the long-term and large-scale spatial dynamics characterizing ecosystems like the Wadden Sea and the Banc d'Arguin, I expect that only large-scale and long-term management approaches will be successful in order to restore biodiversity, trophic dynamics and substrate conditions in intertidal soft-sediment ecosystems. Examples of measures that could be taken in such an approach, would be (1) long-term (>10 years) closure of large parts (i.e., at a scale of tidal basins) to industrial fisheries and mechanical dredging in combination with (2) large-scale restoration of ecosystem engineers in these areas. Hopefully, the complex ecological structure of these intertidal communities can then be restored and maintained in order to keep their unique values as being among the world's most important intertidal soft-bottom ecosystems.

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Summary  
Samenvatting

# Summary



Ecosystem engineers are organisms that directly or indirectly alter the availability of resources to themselves and to other organisms by modifying the abiotic environment. By doing so, they affect their own distribution and that of other species, which can influence community composition. Moreover, by affecting the abiotic environment and species distribution, ecosystem engineers can also affect the number and strength of biotic interactions among species, such as predation and competition. Together with the notion that engineering effects often persist on long time and large spatial scales, this leads to the suggestion that ecosystem engineers have the potential to alter the structure and dynamics of ecological interaction networks in space and time.

In soft-bottom intertidal ecosystems like the Wadden Sea and the Banc d'Arguin, the group of ecosystem engineers that provide structure such as reef-building bivalves and seagrasses, can have a significant impact on the associated community, since natural 'hard' substrate and structure are almost exclusively provided by these species in the otherwise sandy environment. Unfortunately, soft-bottom coastal ecosystems have become severely degraded worldwide during the last centuries due to human impacts and most ecosystem engineers in these systems have strongly declined, with potentially dramatic implications for associated species, community structure and overall biodiversity.

The main objective of this thesis is to empirically investigate how and to what extent ecosystem engineers affect the (trophic) structure and dynamics of intertidal soft-bottom communities. Hence, this thesis provides a better understanding of the role of ecosystem engineers in assembling and structuring ecological interaction networks and their importance for effective conservation management of coastal ecosystems.

In chapter 2 and 3, we demonstrate that ecosystem engineering effects of reef-building bivalves are spatially extended and act on multiple trophic levels. In the Dutch Wadden Sea, transects across three mussel reefs and three nearby sandy areas without reefs showed a peak in cockle densities at ~100 meters coastward from the mussel reef, while cockle abundances within the reefs and in the nearby sandy areas were very low. Additionally, transplantation of tagged cockles showed higher survival of cockles and higher juvenile cockle densities in the area close to the mussel reef compared to areas without mussels, whereas cockle growth was lower close to the reef. This spatial pattern was caused by scale-dependent effects of mussel reefs: in the mussel-reef, cockle survival was reduced by deteriorated sediment conditions through biodeposition and by algal depletion, while further away from the mussel reefs, cockle survival was facilitated due to the reduction of water flow velocity. Next, we demonstrate with a field survey that a comparable spatial pattern is visible in other benthic species and that these effects on their spatial distribution cascade through multiple trophic levels. Distance from the reef,

sediment properties and benthic food abundance simultaneously explained significant parts of the distribution of Oystercatchers (*Haematopus ostralegus*), Eurasian Curlews (*Numenius arquata*) and Bar-tailed Godwits (*Limosa lapponica*), with higher densities of these shorebirds in the surrounding area of the reef compared to sandy un-engineered tidal flats.

Results from these two chapters were then used to develop an experiment to investigate the interactive role of ecosystem engineering, predation and competition in structuring an intertidal bivalve population in the Wadden Sea (chapter 4). In a predator-exclosure experiment, we manipulated cockle densities (100 vs. 1000 individuals  $\text{m}^{-2}$ ) and shorebird predation at a site engineered by a blue mussel bed (*Mytilus edulis*) and at a sandy control site. We conclude that cockles are caught in the middle. Ecosystem engineering by mussel beds can enhance cockle densities by reducing hydrodynamic stress and predation across different life stages, but can reduce cockle growth by reducing seawater flow and by affecting inter-specific competition for food. This study emphasizes the importance of ecosystem engineers in structuring intertidal communities and the necessity to integrate multiple interaction types into a single framework.

In chapter 5, we empirically tested the hypothesis that recovery of aboveground structure and stable sediments provided by ecosystem engineers facilitates the intertidal benthic community by influencing species composition and trophic structure. In a large-scale experiment at two different sites in the Dutch Wadden Sea (West vs. East), we applied anti-erosion mats and added adult mussels to test for the effects of sediment stabilization and habitat modification, respectively. The anti-erosion mats mainly enhanced species and trophic diversity of the infaunal community, while the addition of mussels mainly enhanced species and trophic diversity of the epifaunal community, irrespective of location. In this chapter, we conclude that structure-providing and sediment-stabilizing species such as mussels play an important role in facilitating the benthic community throughout the Wadden Sea by influencing species composition and trophic structure. On top of this large-scale experiment, the interactive effects of ecosystem engineering and predation on bivalve recruitment were investigated (chapter 6). Results show that both adult mussels and the anti-erosion mat facilitated epibenthic mussel recruits, whereas three other endobenthic bivalve species were facilitated by the mat, but inhibited by mussels. However, these observed facilitation and inhibition effects, only emerged when predators were excluded, demonstrating strong interactive effects between ecosystem engineering and predation. Our findings suggest that loss of ecosystem engineers and disturbance of trophic interactions can strongly hinder bivalve recruitment in coastal ecosystems

Finally, the effects of ecosystem engineering by seagrass and burrowing crabs on food web assembly were studied (chapter 7). Using a unique combination of remote sensing, field surveys, and stable isotopes, we reveal that hierarchical habitat modification by seagrasses and burrowing crabs transform simple intertidal food webs into a complex mosaic of linked inter- and subtidal food webs over long timescales. We found that seagrass and burrowing crabs dramatically alter food web structure, composition and its temporal development by accumulating silt and creating large intertidal pools in the accumulated silt layer, respectively. Our empirical findings show that ecosystem engineering is strongly interwoven with trophic networks by changing food web composition over time.

Concluding, results presented in this thesis demonstrate that ecosystem engineering can strongly affect the trophic structure and dynamics of intertidal communities and that ecosystem engineers have a much larger ecological impact on the intertidal community than their actual size and lifespan suggests. Ecosystem engineers in intertidal soft-bottom ecosystems are therefore appealing conservation targets because by managing a single species, entire communities can be positively affected. Nevertheless, findings in this thesis also illustrate that ecosystem engineering are often entangled in a network of multiple interaction types, illustrating that conservation and restoration efforts should focus on multiple species within an integrated network of interaction types. Additionally, due to long-term and large-scale dynamics characterizing ecosystems like the Wadden Sea and the Banc d'Arguin, it is expected that only long-term and large-scale management approaches, such as prolonged closure of large parts to industrial fisheries and mechanical dredging, will be successful in order to restore and protect the unique values of these important intertidal soft-bottom ecosystems.



# *Samenvatting*





Biobouwers zijn organismen die de beschikbaarheid van bronnen zoals voedsel en beschutting, voor zichzelf en voor andere organismen kunnen beïnvloeden door hun abiotische omgeving te veranderen. Hierdoor hebben ze invloed op hun eigen verspreiding, maar ook op die van andere soorten waarmee ze de samenstelling van de gemeenschap kunnen beïnvloeden. Ze kunnen bovendien ook nog eens invloed hebben op het aantal en de sterkte van biotische interacties tussen soorten, zoals predatie en competitie, doordat ze hun abiotische omgeving en de verspreiding van soorten veranderen. In combinatie met het gegeven dat biobouwer-effecten vaak voor lang tijd en op grote schaal aanhouden, leidt dit tot de suggestie dat biobouwers de potentie hebben om de structuur en dynamiek van ecologische interactie-netwerken sterk te veranderen in ruimte en tijd.

In inter-getijdse kustecosystemen met een zandige bodem zoals de Waddenzee en de Banc d'Arguin, kan de groep biobouwers die structuur bieden, zoals rifbouwende schelpdieren en zeegrassen, een aanzienlijk effect hebben op de gemeenschap. Dit komt doordat deze soorten bijna uitsluitend de natuurlijke 'harde' structuur verstrekken in deze anders zo zandige omgeving. Helaas zijn tijdens de laatste decennia wereldwijd veel kustecosystemen ernstig aangetast door menselijke handelen. Parallel aan deze aantasting, zijn in veel kustgebieden ook de biobouwers sterk in aantal gedaald. Dit kan dramatische gevolgen hebben voor aanverwante soorten, structuur van de gemeenschap en algemene biodiversiteit.

Het doel van dit proefschrift is om te onderzoeken hoe en in welke mate biobouwers invloed hebben op de (trofische) structuur en dynamiek van de gemeenschap in inter-getijdse gebieden. Dit proefschrift draagt bij aan een beter begrip van de rol die biobouwers spelen in het structureren van ecologische interacties en van hun belang voor het behoud van deze gebieden.

In hoofdstuk 2 en 3 tonen we aan dat rifbouwende schelpdieren zoals mosselen (*Mytilus edulis*), een groot ruimtelijk effect hebben op hun omgeving en dat dit effect meerdere trofische niveaus kan beïnvloeden. Transecten over mosselbanken en nabijgelegen gebieden zonder banken laten een piek zien in kokkel (*Cerastoderma edule*) dichtheden op een afstand van ongeveer 100 meter van de mosselbanken, terwijl kokkel dichtheden in de banken zelf en in de nabijgelegen gebieden juist erg laag zijn. Dit ruimtelijke patroon wordt veroorzaakt door schaalafhankelijke effecten van een mosselbank: in de bank zelf is kokkeloverleving laag door slechte sedimentcondities veroorzaakt door biodepositie van de mossels, maar rond de bank is de kokkeloverleving hoger omdat de stroomsnelheid van het water gereduceerd wordt door de bank en kokkels daardoor minder snel weg spoelen. De groei van kokkels is echter wel lager in de buurt van de mosselbank door competitie om voedsel. In hoofdstuk 3 laten we vervolgens zien dat een vergelijkbaar ruimtelijke patroon ook zichtbaar is bij hogere trofische niveaus. Dichtheden van een aantal bentische soorten die onderdeel uitmaken van het dieet van Scholeksters (*Haema-*

*topus ostralegus*), Wulpen (*Numenius arquata*) en Rosse grutto's (*Limosa lapponica*), en dichtheden van de vogelsoorten zelf zijn hoger rond de mosselbanken in vergelijking tot op de banken en in de nabij gelegen zandige gebieden zonder banken.

De resultaten van deze twee hoofdstukken zijn vervolgens gebruikt om een experiment op te zetten waarmee de interactieve effecten van biobouwers, predatie en competitie op een kokkelpopulatie in de Waddenzee onderzocht worden (hoofdstuk 4). In dit experiment hebben we kokkeldichtheden (100 vs. 1000 individuen per m<sup>2</sup>) en predatie door wadvogels gemanipuleerd. Dit gebeurde op twee verschillende plaatsen: in de buurt van een mosselbank en op een zandige nabije wadplaat. De resultaten laten zien dat biobouwer-effecten van mosselen zorgen voor hogere kokkeldichtheden in de omgeving van de bank doordat ze de stroomsnelheid van het water reduceren en predatie beïnvloeden tijdens verschillende levensfasen van de kokkel, maar daarnaast ook competitie beïnvloeden. Dit hoofdstuk benadrukt dat biobouwers een belangrijke rol spelen in het structureren van inter-getijde gemeenschappen en dat het belangrijk is om verschillende interactietypes te integreren.

In hoofdstuk 5 hebben we onderzocht hoe sediment-stabiliserende- en structuur-biedende biobouwers de soortensamenstelling en trofische structuur van benthische inter-getijde gemeenschappen kunnen beïnvloeden. In een grootschalig experiment op twee verschillende locaties in de Nederlandse Waddenzee (West en Oost), hebben we anti-erosiematten van kokos op de bodem geplaatst en volwassen mosselen toegevoegd om de effecten van sedimentstabilisatie en biobouwen te onderzoeken. De anti-erosiematten verbeterden voornamelijk de soort- en trofische diversiteit van de endobenthische gemeenschap, terwijl de toevoeging van mosselen voornamelijk de soort- en trofische diversiteit van de epibenthische gemeenschap verbeterden. In dit hoofdstuk concluderen we dat sediment-stabiliserende en structuur-biedende soorten zoals mosselen, een belangrijke rol kunnen spelen bij het verhogen van de benthische diversiteit in de gehele Waddenzee.

Binnen dit grootschalige experiment werden ook de interactieve effecten van biobouwers en predatie door garnalen en krabben op de broedval van schelpdieren onderzocht (hoofdstuk 6). De resultaten laten zien dat zowel de volwassen mosselen als anti-erosiematten de broedval van epibenthische mosselen bevorderen, terwijl de broedval van drie andere endobenthische schelpdieren werd bevorderd door de anti-erosiematten, maar juist geremd werd door de aanwezigheid van mosselen. Deze faciliterende en remmende effecten ontstaan echter alleen als garnalen en krabben werden buiten gesloten. Dit laat sterke interactie-effecten tussen biobouwers en predatie zien. Onze bevindingen suggereren dat het verlies van biobouwers en de verstoring van trofische interacties, de broedval van schelpdieren sterk kan hinderen.

Als laatste hebben we de biobouwer-effecten van zeegras en gravende krabben op de voedselweb-structuur onderzocht (hoofdstuk 7). Met behulp van een unieke combinatie van remote sensing, veldonderzoek en stabiele isotopen, laten we zien dat zeegras en gravende krabben er samen voor zorgen dat een eenvoudige voedselketen over de tijd verandert in een mozaïek van gekoppelde inter- en sub-getijdse voedselketens. Onze bevindingen in het veld tonen aan dat biobouwen sterk is verweven met trofische netwerken doordat biobouwers de voedselweb-samenstelling en de temporele ontwikkeling hiervan kunnen veranderen.

Concluderend, de resultaten in dit proefschrift laten zien dat biobouwers een sterke invloed kunnen hebben op de trofische structuur en dynamiek van inter-getijdse gemeenschappen en dat biobouwers een veel groter ecologisch effect hierop hebben dan hun werkelijke grootte en levensduur suggereert. Biobouwers in inter-getijdse gebieden met een zandige bodem zijn daarom erg aantrekkelijk als beheerdoel. Door het beheer van een enkele soort, kunnen hele gemeenschappen positief beïnvloed worden. Toch laten bevindingen in dit proefschrift ook zien dat biobouwers onderdeel uitmaken van een complex netwerk van meerdere interacties, wat suggereert dat behoud en herstelinspanningen gericht moeten zijn op meerdere soorten binnen een geïntegreerd netwerk van interacties. Bovendien, als gevolg van de langdurige en grootschalige dynamiek die ecosystemen zoals de Waddenzee en de Banc d'Arguin karakteriseert, is de kans groot dat ook grootschalig en langdurig beheer, zoals het langdurige sluiten van grote gebieden voor visserij en mechanische baggerwerkzaamheden, nodig is om de unieke waarden van deze belangrijke inter-getijdse gebieden te herstellen en te beschermen.

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# Acknowledgements



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## Acknowledgements



Op de piste in Oostenrijk werd ik gebeld door Henk: het startsein van mijn promotie-onderzoek aan biobouwers in de Waddenzee. Nu precies vijf jaar later zit ik hier weer en leg de laatste hand aan mijn proefschrift. Het waren vijf mooie jaren en na urenlang rondlopen in de modder, werken in het lab, gegevens verwerken en eindeloos schrijven aan stukken tekst, is 'het boekje' eindelijk klaar! Tijd om iedereen die in welke vorm dan ook heeft bijgedragen te bedanken!

Tjisse, jou wil ik als eerste bedanken. Zonder jou had dit proefschrift er niet in deze vorm gelegen!! Ik heb een enorme bewondering voor je passie voor de wetenschap, je gedrevenheid, brede interesse en onuitputtelijke energie. Het eerste veldseizoen op Schier was even wennen toen jij en Johan, Serena en mij op sleeptouw namen. Dubbele getijden werken en mijn weg vinden binnen "Wadden Engine" met drie PhD's, een Postdoc en vijf begeleiders zorgden af en toe voor wat strubbelingen. Maar onze gezamenlijke inspanning in dat ene veldseizoen leidde wel tot vijf artikelen met nog één in de pijplijn! Dat veldwerkseizoen was dan ook een goede basis voor een mooie samenwerking☺. We zaten vanaf het begin op een lijn en ik heb veel aan je gehad bij al het werk en keuzes tijdens mijn promotieonderzoek. Ook tijdens de laatste zware loodjes heb je me enorm geholpen! Ik hoop dat ons BdA-RI manuscript een mooie beloning wordt voor al onze inspanningen. Ik heb veel van je geleerd en hoop in de toekomst nog met je te blijven samenwerken!

Theunis en Henk, heel erg bedankt voor het vertrouwen en de vrijheid die jullie mij gegeven hebben! Vooral toen duidelijk werd dat Tjisse en ik een goed team vormden en hij min of meer de 'dagelijkse begeleiding' overnam, hebben jullie mij in al mijn keuzes gesteund. Ik wil jullie uiteraard ook bedanken voor de begeleiding van mijn promotieonderzoek en het altijd snel lezen van mijn manuscripten. Jullie passie voor de wetenschap en de ecologie van de Waddenzee was enorm inspirerend en dat nog wel op twee heel verschillende onderwerpen (wadvogels en vissen). En niet te vergeten: ik wil jullie graag bedanken voor de kans die jullie mij gegeven hebben om naar de Banc d'Arguin te gaan, dit prachtige inter-getijde gebied te ontdekken en ook hier de effecten van biobouwers te onderzoeken! Het begon met het bijwonen van een symposium over de Banc d'Arguin op Texel in juni 2010 en in januari 2011 ging ik mee met de expeditie van Jan, Jim en Thomas. Wat een fantastische ervaring en geweldig dat ik in januari 2012 nog een keer mee mocht gaan! Mijn doel is om aan de Waddenzee te blijven werken en ik hoop in de toekomst ook met jullie nog te kunnen samenwerken. Klemens, bedankt voor je begeleiding, hulp bij het analyseren en schrijven, en voor het onder je hoede nemen van mij tijdens de start van het project. Als NIOZ-MEEër en RuG-Dierecoloog was ik bij MarBEE van harte welkom. We hebben een hoop gepresteerd als "Wadden Engine" team! Jan, bedankt voor al je hulp bij het enclosure-experiment, het opzetten en uitvoeren van mijn Banc d'Arguin veldwerk en hulp bij het schrijven. Je positieve vibe, creativiteit en werklust waren enorm inspirerend en motiverend. Han,

bedankt voor de inhoudelijke discussies, je commentaar op manuscripten en je creatieve inbreng.

Naast mijn begeleiders zijn er ook een heleboel andere mensen die direct of indirect hebben bijgedragen aan dit boekje. Leuke collega's zorgden voor een goede werksfeer. Serena, it was fun meeting you! I enjoyed the discussions with you about work and life, with or without wine and beer ☺. I am glad that we could work together on this project, spending time at the Herdershut and experiencing the ups and downs of life as a PhD! It has been tough with the long fieldwork days (I especially remember the \*#@\* blue -killoff - sheets) and the large number of people involved, but we both made it!! I wish you all the best and when I am in Italy you have to show me your best diving spots! Johan, thanks for all your help in the field during our first field season. Ellen, jij werd pas halverwege Wadden Engine mijn collega toen je Tjisse's postdoc-positie overnam. Jammer dat je er niet al eerder bij betrokken was, want we hebben een hoop lol gehad! Voetbal kijken en dansen in de Tox Bar op Schier, een zeker persoon rondleiden op het wad met een kater, uit eten naar een lange dag veldwerk (bij Van der Werff of de McDonalds), de koffiepauzes en Bernoulliburgers op de universiteit, New York op de fiets verkennen en de Benthic Ecology Meeting in Virginia bijwonen. Een hoop gedaan in een korte tijd ☺. En je hebt me ook nog eens goed geholpen met mijn veldwerk en onderzoek! Ik hoop dat we zo af en toe nog een bakkie thee blijven doen om bij te kletsen. Jim, bedankt voor de leuke samenwerking! Halverwege mijn PhD begon jij aan jouw PhD en vanaf dat moment hebben we veel samen opgetrokken. Ik heb genoten van ons gezamenlijk veldwerk en de vele inhoudelijke en persoonlijke gesprekken. Bedankt ook voor alle klusjes die je voor mij deed op het NIOZ zodat het mij een reis naar Texel bespaarde. We spreken elkaar ongetwijfeld nog! Laura en Marjolijn, bedankt voor jullie bijdrage aan dit proefschrift en de leuke samenwerking!

Tijdens mijn veldwerk op Schier vormde de Herdershut een thuisbasis. Het was een tijd van hard werken, maar ook een van een hoop gezelligheid. Bedankt Maarten, Kelly, Elske, Judith, Marc, Imke, Tom, Alma, Harm, Quan-Xing, Roel, Kees, Hacen en alle anderen voor de leuke tijd, lekkere etentjes en spelletjes avonden. Uiteraard wil ik ook 'mijn' drie Master-studenten Tom, Alma en Daan bedanken voor hun bijdrage aan dit proefschrift! Pour la facilitation de mon travail dans le Parc National du Banc 'd Arguin et de l'hospitalité mauritanienne, je tiens à remercier Lemhaba Ould Yarba, Antonio Araujo, Sidi Ould Ely, Amadou Abderahmane Sall, Hassan, Mohamed Camera, Mubarek, Baba et Hacen. I also want to thank Christine, Andrew and Brian for all their help in the final stage of my PhD. The follow-up version of chapter 7 looks great, let's hope for the best!

Bij het Wadden Engine project waren meerdere vakgroepen betrokken. Tijdens de start van het project begonnen Tjisse, Serena en ik bij MarBEE. Klemens, Karin, Katrin, Stella, Jan en Jim bedankt voor de hulp, lunches en koffiepauzes. Officieel was ik NIOZ MEE-er, maar door al het veldwerk op Schier was Groningen een betere

uitvalsbasis. Toch was het altijd heel leuk om een dagje naar het NIOZ op Texel te gaan. Theunis, Petra, Henk, Jan (van Gils), Jan (Drent), Pieterella, David, Andreas, Jeremy, Rob (Dekker), Thomas, Jim, Matthijs, Eelke, Roeland, Allert, Tamar, Roos, Jeltje, Sander, Job, Maarten, Anne, Anita, Bernard, Piet, Sjoerd, Lodewijk, Arno en Maaïke, bedankt voor het welkome gevoel dat kreeg als ik weer eens op het NIOZ was! Bij de verhuizing van het BC naar het CvL, verhuisde ik van MarBEE naar de afdeling Dierecologie. Door veldwerk, veel thuiswerken in de schrijffase en mijn zwangerschap was ik niet vaak aanwezig, maar de koffie/lunchpauzes en lunchmeetings waren gezellig en interessant. Janne, Claudia, Jildau, Arne en alle andere dierecologen, bedankt!

Jolanda Evers, Joke Mulder, Rob Dapper, Hilde Kooyman, Hans van Tuinen, Joyce Rietveld en Ingeborg Jansen, bedankt voor het regelwerk waar jullie mij mee hebben geholpen! Dick Visser, bedankt voor de prachtige lay-out van mijn boekje. Geniet van je pensioen straks.

Hoewel ik mijn leesversie al had in geleverd voordat ik bij AGW aan het werk ging en dus dacht dat ik het vrijwel 'af' had, was het laatste regel- en schrijfwerk nog een flink stuk lood. Eddy, Wibe, Leo en alle andere collega's, bedankt voor de tijd en hulp die ik gekregen heb tijdens het afronden.

Zonder de nodige afleiding naast het werk, had ik het zeker niet gered. Emilie, Saskia, Feikje, alle Ruige Beren, Henk & Emma, Roeland & Nelleke, bedankt voor jullie vriendschap. Fijn dat ik de mooie momenten met jullie kon delen of juist lekker kon klagen, maar vooral ook om even niet aan werk te denken! De bezoekjes, bakkies thee, etentjes, weekendjes weg en gezamenlijke vakanties waren heerlijk ontspannend en gezellig. Ook was het na een tijd van veldwerk altijd heerlijk thuis-komen in Luinjeberd-city. Het is nog steeds elke dag genieten om er te wonen. Door het prachtige uitzicht, maar ook door de goeie sfeer, bedankt buurtjes!

Aart, Anne-Marie, Aernout, Elina, Marijn, Henri en Marieke, wat zijn jullie een geweldige schoonfamilie! Bedankt voor de interesse, steun en afleiding! Het was vaak moeilijk het werk helemaal los te laten en ik zat dan ook regelmatig nog met de laptop op schoot in de 'kuil' als we een dagje in Loozen waren, maar de snelle discussies en drukte in huize Snoek zorgden er wel voor dat ik even moest stoppen. De jaarlijkse wintersport was een terugkerend rustpunt om heerlijk te ontspannen en te genieten van de prachtige natuur en het goede gezelschap. Helemaal dit laatste jaar, nu ook de drie kleine muiers Koen, Floris en Thúr voor het eerst mee waren.

Lieve familie, bedankt voor alles! Anne-Marije, Merijn en Jacqueline, bedankt voor al jullie steun en interesse! Mijn 'hobby-project' met verre reisjes is nu toch echt klaar! Dit boekje laat wel zien waar ik de afgelopen jaren zo druk mee was en jullie kleine zusje heeft het geflikt, de eerste Doctor in de familie! Anne, ik vind het dan ook heel leuk dat je mijn paranimf bent (komt toch aardig in buurt van toga's in de rechtbank ☺). Papa en mama, bedankt voor jullie onvoorwaardelijke steun,

kansen en vrijheid die jullie mij gegeven hebben. Een landbouwmecanicien, advocaat en mariene ecooloog in de familie. Die diversiteit laat wel zien hoe vrij jullie ons hebben gelaten in het maken van keuzes. Ik wil jullie ook enorm bedanken voor de vele klussen in en om ons huis waar we zelf door alle drukte niet altijd aan toe kwamen en uiteraard voor alle zorg voor Thúr!! Mijn 'mama-dag' is er vaak bij ingeschoten tijdens de laatste maanden en elke keer stonden jullie weer klaar om op te passen, geweldig fijn dat we altijd op jullie konden terug vallen!

Als laatste en allerbelangrijkste, wil ik Roelant bedanken. Zonder jou had dit proefschrift er überhaupt niet gelegen! Je bent mijn grote liefde, steun en maatje, al bijna 11 jaar lang! De start van mijn promotieonderzoek en jouw baan bij Arcadis zorgden voor een hoop verandering. Van ons kleine schippershuisje aan het Damsterdiep in Groningen verhuisden we samen met Bracca naar een net zo klein huisje in Luinjeberd op het Friese platteland. Een hoop mensen verklaarden ons vast voor gek, maar ik heb nog geen minuut spijt gehad! Al snel versterkte Teske het team en hadden we twee (on)gecontroleerde projectielen in huis. Maar wat zorgen ze voor een hoop lol en afleiding!! Je hebt niet alleen bijgedragen aan dit proefschrift door mij onvoorwaardelijk te steunen en te motiveren, je hebt ook nog eens bijgedragen door mee te helpen op Schier, ingenieuze en praktische oplossingen te verzinnen voor het veldwerk, manuscripten te lezen, computerproblemen op te lossen en een deel van de plaatjes en lay-out van mijn proefschrift te maken. Het was een mooie tijd, helemaal na de geboorte van ons zoontje Thúr, maar het was af en toe ook zwaar. Je hebt een hoop alleen moeten doen als ik weer eens weken voor veldwerk weg was of tot in de late uurtjes zat te schrijven. De afgelopen maanden waren extra zwaar. Het was behoorlijk aanpoten met een nieuwe baan, het proefschrift afronden, de hoofdstukken publiceren, zorgen voor ons kleine mannetje en een goeie partner voor jou en baas voor de honden zijn. We hebben het samen geflikt en ik hoop nog veel mooie dingen samen met jou, Thúr en de hondjes mee te maken!!

Els van der Zee



Aschau im Zillertal, Oostenrijk  
28 december 2013

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# List of publications

## Peer reviewed publications

- Donadi, S., Westra, J., Weerman, E.J., van der Heide, T., **van der Zee, E.M.**, van de Koppel, J., Olff, H., Piersma, T., van der Veer H.W. & Eriksson, B.K. (2013). Non-trophic interactions control benthic producers on intertidal flats. *Ecosystems* 16: 1325-1335.
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- Van der Heide, T., Eklöf, J.S., van Nes, E.H., **van der Zee, E.M.**, Donadi, S., Weerman, E.J., Olff, H. & Eriksson, B.K. (2012). Ecosystem engineering by seagrasses interacts with grazing to shape an intertidal landscape. *Plos One* 7: e42060.
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- Van der Heide, T., Tielens, E., **van der Zee, E.M.**, Weerman, E.J., Holthuijsen, S., Eriksson, B.K., Piersma, T., van de Koppel, J. & Olff, H. Predation and habitat modification interact to control bivalve recruitment on intertidal mudflats. *Biological Conservation*.
- Van der Zee, E.M.**, de Fouw, J., van Gils, J.A., Eriksson, B.K., Weerman, E.J., Donadi, S., van der Veer, H.W., Olff, H., Piersma, T. & van der Heide, T. Caught in the middle: How predation, competition and ecosystem engineering interactively structure an intertidal bivalve population. *Oikos*.
- Donadi, S., **van der Zee, E.M.**, van der Heide, T., Weerman, E. J., Piersma, T., van de Koppel, J., Olff, H., Bartelds, M., van Gerwen, I & Eriksson, B.K. The bivalve loop: the role of positive feedbacks for recovery of exploited populations. *Limnology and Oceanography*.
- Eklöf, J.S., Donadi, S., van der Heide, T., **van der Zee, E.M.** & Eriksson, B.K. Using traits to understand contrasting effects of ecosystem engineers on associated-communities. *Oikos*.

## Media

Weblog Zeeinzicht.nl:

Tropische zusje van de Wadden Sea

<http://www.zeeinzicht.nl/nieuws2/?p=628>

Mega-kokkelverhuizing

<http://www.zeeinzicht.nl/php/?target=nieuwsblogs&link=20100714>

Natuurbericht.nl - Belang mosselbanken in de Waddenzee veel groter dan vermoed

<http://www.natuurbericht.nl/?id=8144>

Vroege Vogels TV - Goede mosselpoep

[http://vroegevogels.vara.nl/Fragment.202.0.html?tx\\_ttnews%5Btt\\_news%5D=360622](http://vroegevogels.vara.nl/Fragment.202.0.html?tx_ttnews%5Btt_news%5D=360622)



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