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

NIOZ Royal Netherlands Institute for Sea Research

NWO
Netherlands Organisation for Scientific Research

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Chapter 1

1

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

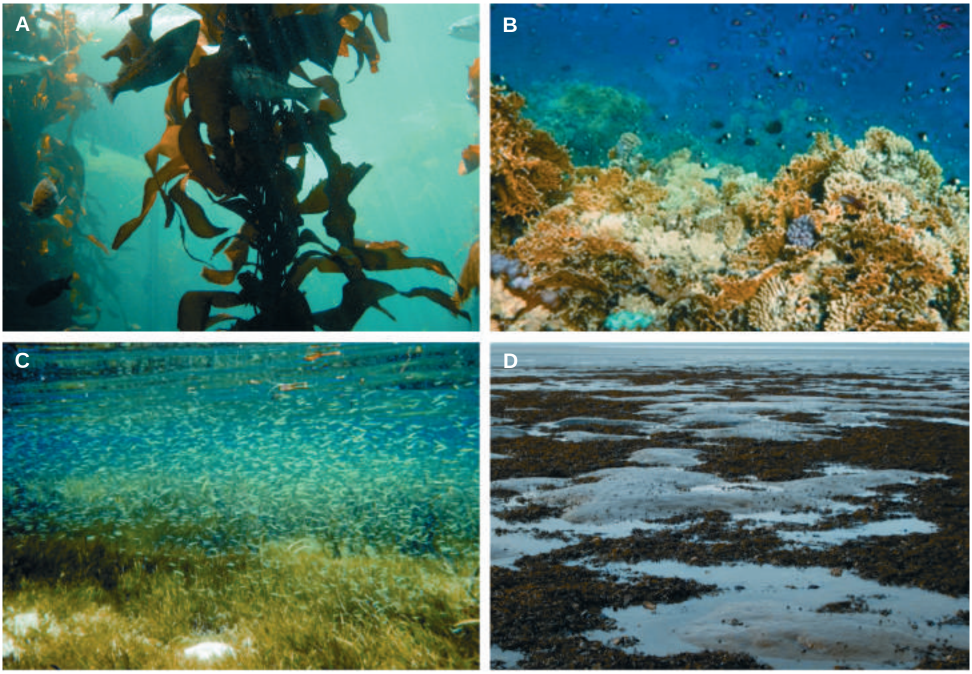

Figure 1.1 Examples of marine habitats created by ecosystem engineers: kelp forest (**A**), coral reef (**B**), seagrass meadow (**C**), and mussel reef (**D**). Photographs reproduced with permission from S. Maruch (A), S. Donadi (B), M. Christianen (C) and E. Weerman (D).

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^2 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

Olff *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; Olff *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

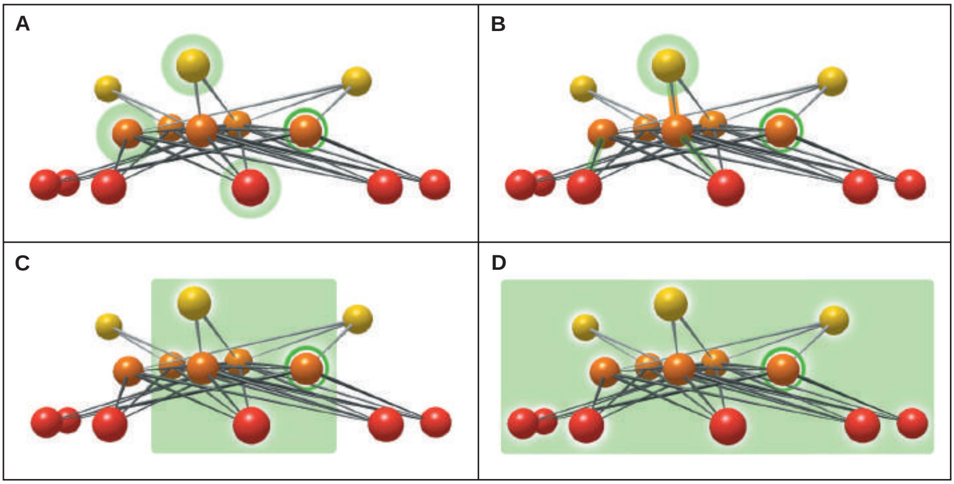

Figure 1.2 Schematic overview of the impacts of ecosystem engineering on the structure and dynamics of interaction webs. The ecosystem engineer in each web is indicated by a green circle and the green shaded areas represent its engineering effect. They can affect the interaction web by affecting species 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^2 of intertidal flats, 412 km^2 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^2) 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

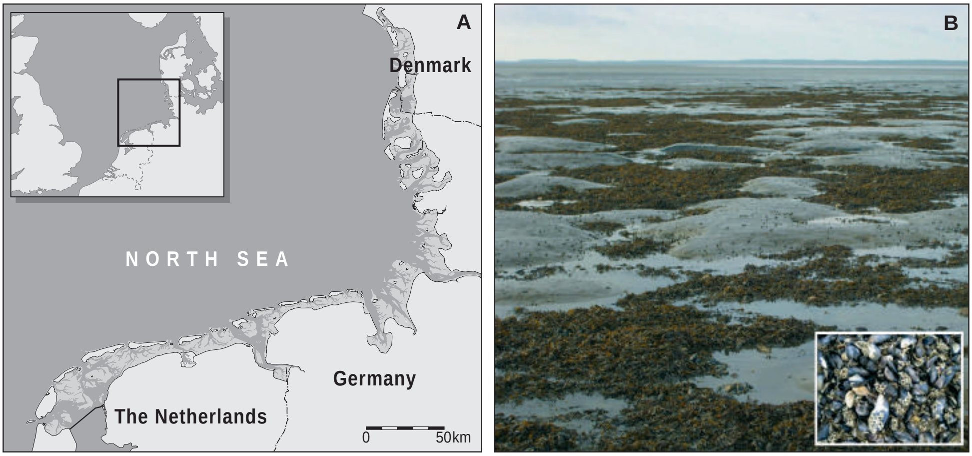

Figure 1.3 The Wadden Sea area, covering the estuaries and the coastal waters inside the barrier islands in the Southeastern part of the North Sea (**A**) and a blue mussel bed during low tide (**B**) (Photo credits: E.J. Weerman).

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).

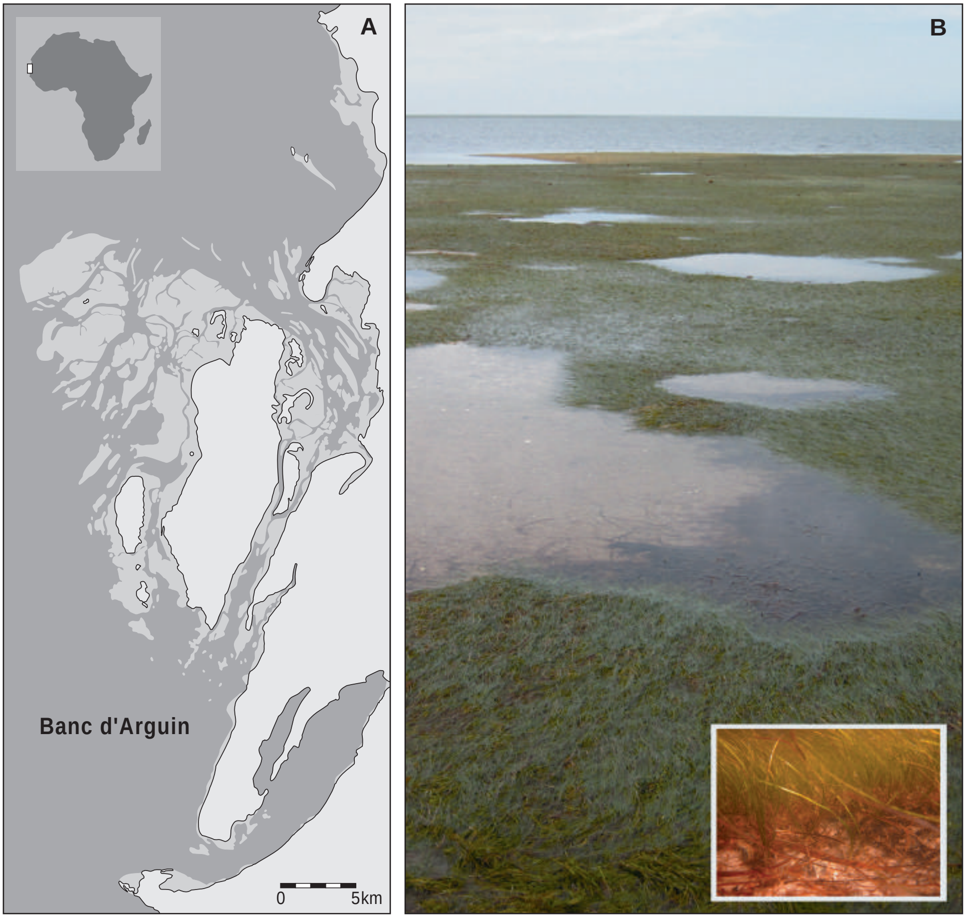

Figure 1.4 The Banc d'Arguin (**A**) and a Dwarf eelgrass meadow during low tide (**B**). Photo credits: L. Govers).

Study system – the Banc d’ Arguin

The Banc d' Arguin is located on the Atlantic coast of Mauritania (West-Africa) and covers and area of more than 10,000 km^2 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^2 of the 491 km^2 of intertidal flats are covered by seagrasses (Altenburg *et al.* 1982; Wolff and Smit 1990). Consequentially, 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^2 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

2

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

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Johan S. Eklöf, Johan van de Koppel, Ellen J. Weerman,
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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.

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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 (Frechétte *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 (Eijkelkamp 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 μm) 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°C) 0–5 cm samples as Loss On Ignition (LOI; 5 h, 550°C).

In May 2011, we performed additional surveys at two other mussel beds (53°28'2" N, 6°10'59" E; 53°29'44" N, 6°19'20" E) and corresponding areas without mussels (53°28'7" N, 6°11'33" E; 53°29'51" N, 6°19'48" 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 1×1 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 0.9×0.9 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):

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

where L_1 and L_2 are respectively the initial and final lengths and Δt is the time elapsed between L_1 and L_2. The parameter Δt was assigned a value of 0.8 year because the experiments were carried out during the growth season. The parameters L_∞ 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^{-1} (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 locations 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 ± 62.53 SE individuals/m^2), 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 (± 7.74 SE) % and 6.98 (± 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 (± 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).

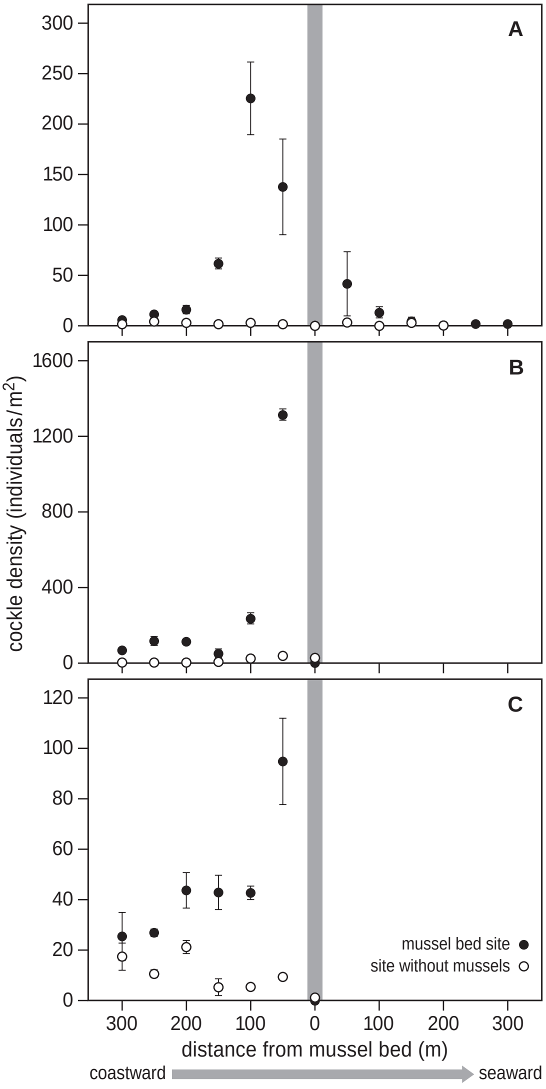

Figure 2.1 Cockle density along transects perpendicular to the coast across three intertidal mussel beds (closed circles) and three corresponding areas without mussels at the same tidal elevation (open circles) in 2009 (**A**) and 2011 (**B**, **C**) in Schiermonnikoog. The x axis represents the distance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

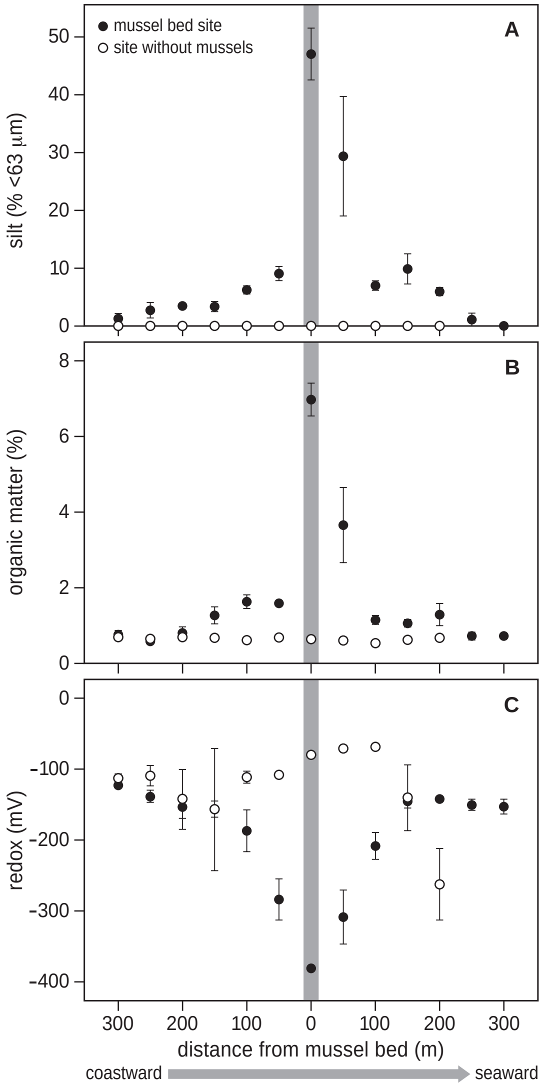

Figure 2.2 **A**) Silt content, (**B**) organic matter content and (**C**) redox potential along transects perpendicular to the coast across an intertidal mussel bed (closed circles) and a corresponding area without mussels at the same tidal elevation (open circles). The x axis represents the distance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

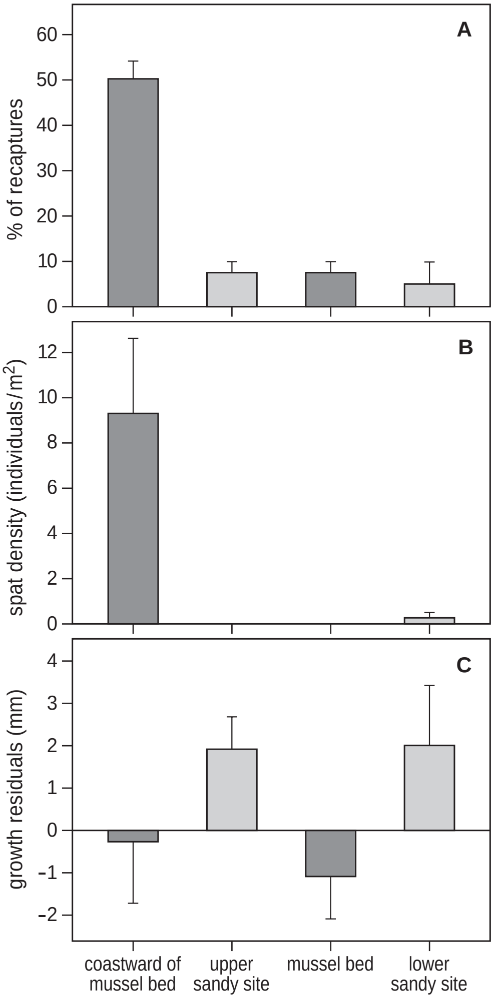

Figure 2.3 **A**) Percentage of recaptured tagged cockles, (**B**) spat density and (**C**) growth residuals measured coastward of the mussel bed, at a comparable tidal elevation in the area without mussels (upper sandy site), within the mussel bed and at a comparable tidal elevation in the area without mussels (lower sandy site). Mean ± 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 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

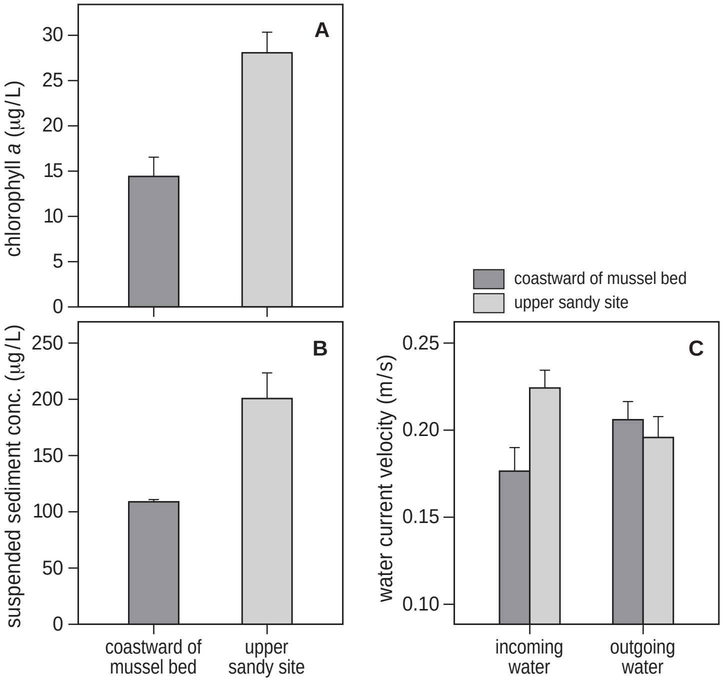

Figure 2.4 **A**) Chlorophyll *a* content and (**B**) suspended sediment concentration in the water column coastward of the mussel bed and at a comparable tidal elevation (upper sandy site). (**C**) Water current velocity measured during incoming and outgoing water coastward of the mussel bed and at a comparable tidal elevation (upper sandy site). Mean ± 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 ± 1.60 SE % plaster weight loss) and higher than the values observed coastward of the mussel bed (32.30 ± 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 influence 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 patters 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-kilometer 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.

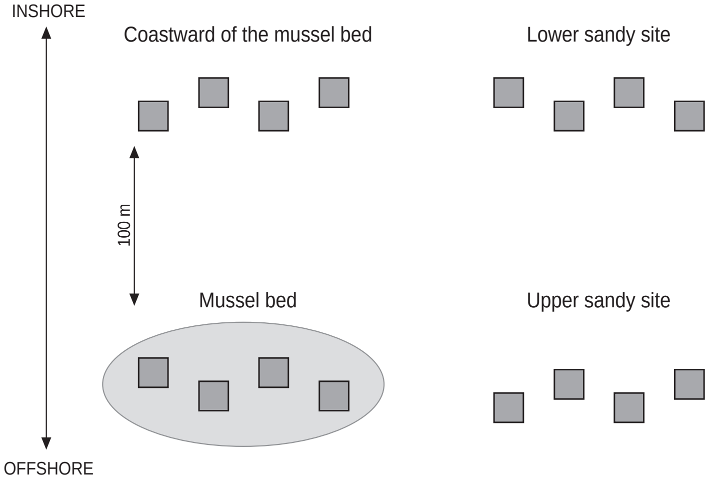

Figure 2.A Schematic showing the four sites of the field transplantation where four 1×1 m plots were randomly assigned. Distance between plots was at least 5 m.

Appendix B

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

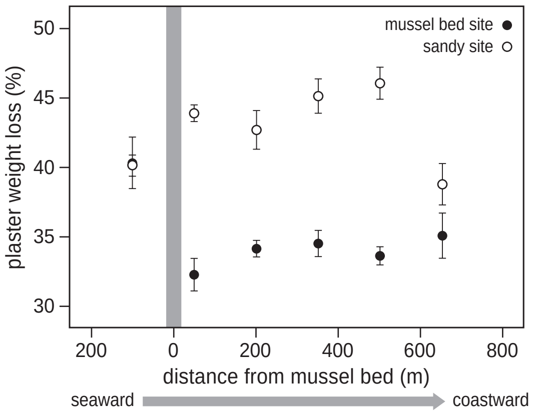

Figure 2.B Plaster weight loss along transects perpendicular to the coast across a mussel bed (closed circles) and in a sandy site without mussels at the same tidal elevation. The x axis represents the distance from the mussel ereef along the mussel-bed transects. Grey area indicates the position of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

Appendix C

Relationship between cockle spat densities and plaster weight loss.

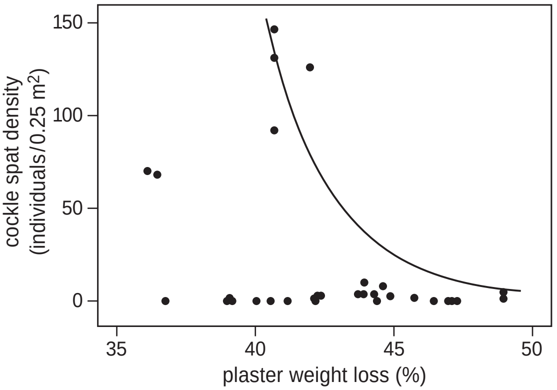

Figure 2.C Scatter plot of cockle spat densities and plaster weight loss measured along transects perpendicular to the coast in an area without mussel beds (n = 32). The line indicates regression for quantile 0.909 (*P* = 0.023)

Chapter 3

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.

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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^2 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 Cadee 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 recourses 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^2. 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 $< 63\mu$m) 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^2 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^{-2}) 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

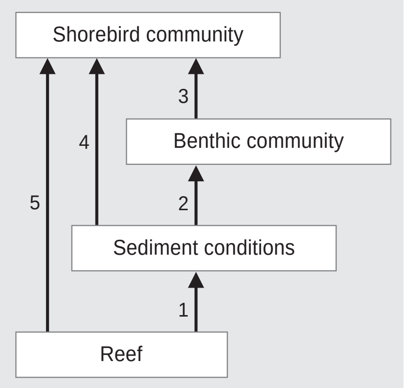

Figure 3.1 The conceptual path analysis model. Arrows depict direct effects of one variable (boxes) on another. Numbers represent specific mechanisms described in *Materials & Methods*: *Data analysis*.

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 maenus*) and brown shrimps (*Crangon crangon*) were clustered as crustaceans.

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

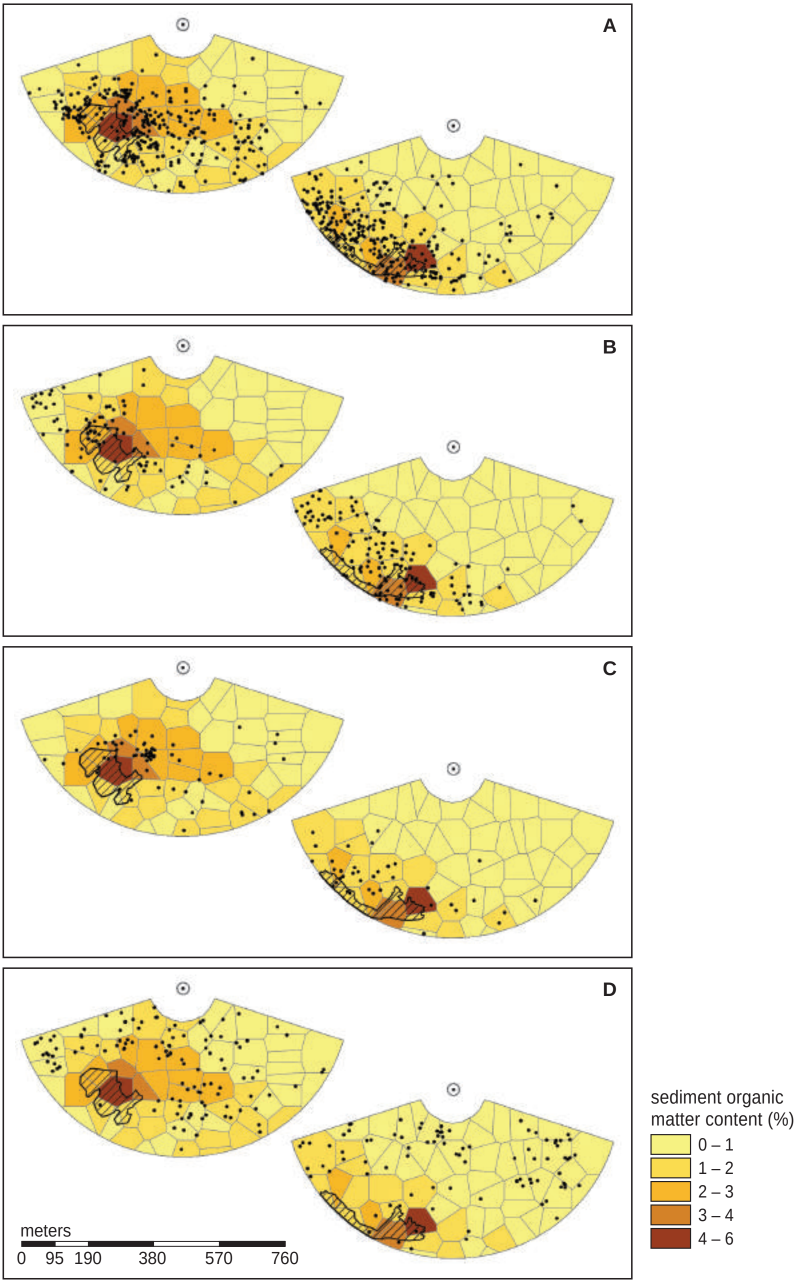

Figure 3.2 Overview of the two reefs and their surrounding intertidal flats, showing Thiessen polygons (each polygon contains one sampling station), the position of the reefs (striped black areas) and the distribution of sediment organic matter content in relation to the distribution of (**A**) oystercatchers (**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
All stations								
χ^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
Stations inside reefs excluded								
χ^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

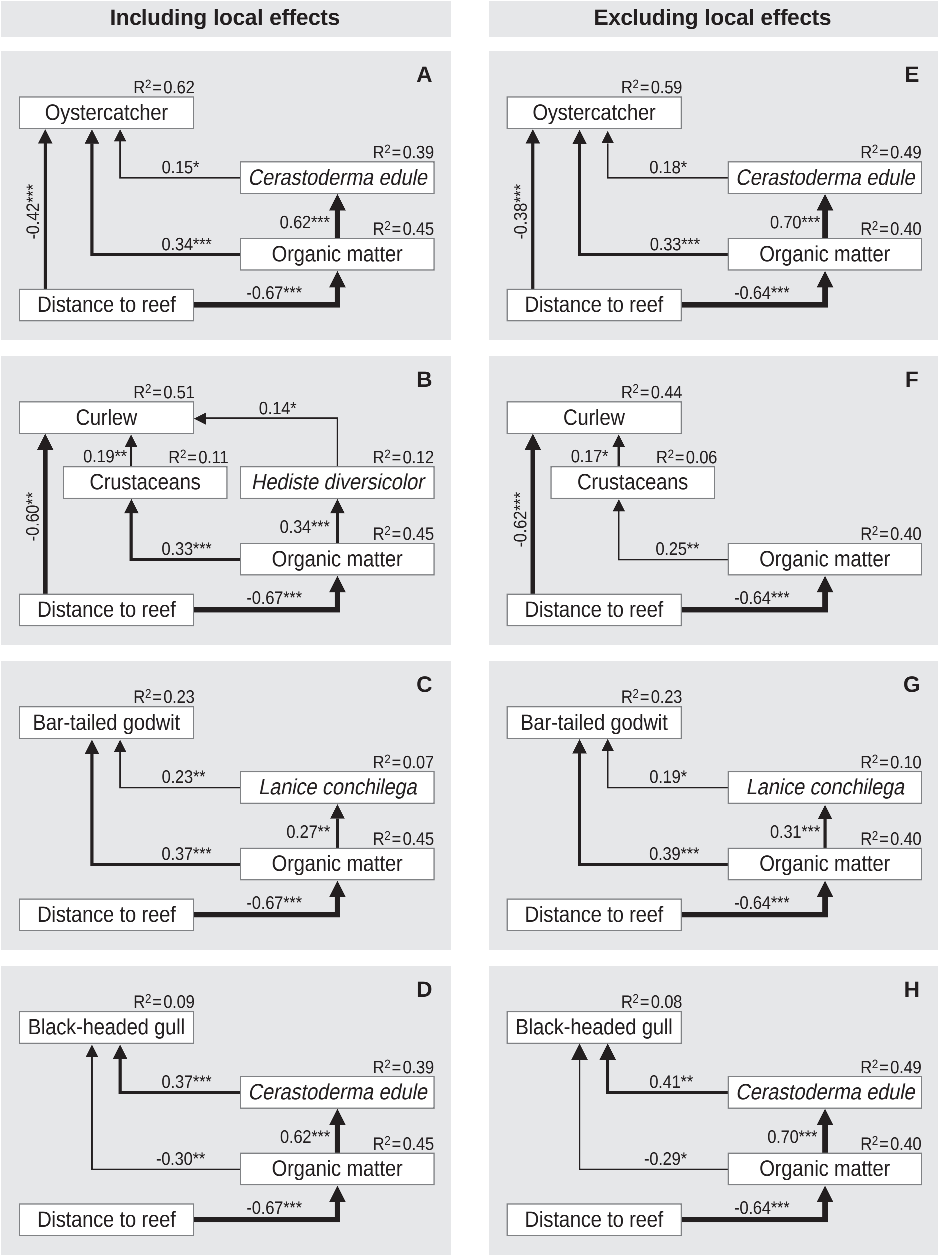

Figure 3.3 Diagram of the SEM results with all sampling stations for oystercatchers, curlews, bar-tailed godwits and black-headed gulls (**A** to **D**) and the sampling stations inside the reefs excluded for the same bird species (**E** to **H**). Straight arrows indicate significant direct effects. 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 (Olff *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 (± 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 disproportionally 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.

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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
Lanice conchilega			0.072	
Hediste diversicolor		0.117		
Cerastoderma edule	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 > *L. conchilega*			0.268 (0.003)	
Organic matter > *H. diversicolor*		0.342 (<0.000)		
Organic matter > *C. edule*	0.622 (<0.000)			0.622 (<0.000)
Organic matter > Crustaceans		0.333 (<0.000)		
L. conchilega > Bar-tailed godwit			0.227 (0.007)	
H. diversicolor > Curlew		0.141 (0.033)		
C. edule > Oystercatcher	0.152 (0.037)			
C. edule > 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
Lanice conchilega			0.097	
Cerastoderma edule	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 > *L. conchilega*			0.311 (0.003)	
Organic matter > *C. edule*	0.704 (<0.000)			0.704 (<0.000)
Organic matter > Crustaceans		0.245 (<0.008)		
L. conchilega > Bar-tailed godwit			0.187 (0.034)	
C. edule > Oystercatcher	0.179 (0.037)			
C. edule > 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 4

4

Caught in the middle: How predation, competition and ecosystem engineering interactively structure an intertidal bivalve population

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Abstract

Trophic interactions, competition and ecosystem engineering - the biotic modification of the physical environment - can all severely affect population dynamics. How these three mechanisms interact to shape ecological communities is, however, still unclear. Here, we studied the interactive effects of predation, competition and ecosystem engineering on common cockle (*Cerastoderma edule*) recruitment, growth and survival in the Wadden Sea, one of the world's largest intertidal ecosystems. In a predator-exclosure experiment, we manipulated cockle densities (100 vs. 1000 individuals m^{-2}) and shorebird predation at a site engineered by blue mussels (*Mytilus edulis*) and at a sandy control site. We hypothesized that by facilitating high cockle numbers, mussels may alleviate predation-induced effects on cockle survival, and that this in turn may negatively affect competition among cockles. We found that bird predation strongly reduced recruit density, while mussels strongly facilitated recruits by reducing hydrodynamic stress. Cockle growth was reduced near mussels, but also in the high cockle density treatment outside exclosures. Adult cockle survival was enhanced near the mussel bed, while high cockle densities decreased adult cockle survival. Bird predation also decreased adult survival, but only at the control site. We conclude that ecosystem engineering by mussel beds can enhance cockle densities by reducing hydrodynamics and predation across different life stages, but may also reduce cockle growth, most likely by reducing hydrodynamics and by increasing inter-specific competition for food. Our study emphasizes the importance of ecosystem engineers in structuring intertidal communities and the necessity to integrate multiple interaction types into a single framework.

Submitted for publication

Introduction

A substantial part of ecological theory concerns the role of interactions between organisms in determining population dynamics. Out of these interactions, predation, competition and their interactive effects 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 through ecosystem engineering – the biotic modification of the physical environment (Jones *et al.* 1994) –, a type of interaction that has more recently been advanced as a critical interaction in many ecosystems as well (Bruno *et al.* 2003; Wright and Jones 2006). Therefore, it might be expected that ecological communities are often structured by an interplay of multiple interactions types (as emphasized by Olff *et al.* 2009).

Until now, most work on integrating ecosystem engineering into ecological interactions has focused on coupling ecosystem engineering to either trophic or competitive interactions among species. Previous studies revealed that ecosystem engineers can affect multiple trophic levels (e.g. Graham 2004; van der Zee *et al.* 2012), are able to modify predatory impact among other species (e.g. Grabowski 2004; Ransom 2011) and that ecosystem engineering and trophic processes are closely associated when a single species act as a predator and an engineer simultaneously (e.g. Wilby *et al.* 2001). Furthermore, facilitation through ecosystem engineering has been shown to affect competition as well (e.g. Palmer 2003; Ransom 2011). 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 to our knowledge.

Here we studied the interactive effects of ecosystem engineering by blue mussels (*Mytilus edulis*), predation by molluscivore shorebirds and competition on survival, recruitment and growth of the common cockle (*Cerastoderma edule*) in the Dutch Wadden Sea – one of the largest intertidal ecosystems in the world (Wolff 1983). Blue mussels are well-known ecosystem engineers that create hard substrate, reduce hydrodynamics and modify sediment conditions by depositing large amounts of (pseudo-)faeces (Kröncke 1996; Donadi *et al.* 2013). Especially in soft-bottom ecosystems like the Wadden Sea, effects on hydrodynamics and sediment conditions can extend far beyond the bed itself, up to distances of several hundreds of meters (Kröncke 1996; van der Zee *et al.* 2012; Donadi *et al.* 2013). In this surrounding area, cockle recruitment can be enhanced due to reduced hydrodynamic stress, yielding higher cockles densities (Donadi *et al.* 2013). Because recruitment is facilitated, cockles may experience enhanced competition for food with conspecifics due to increased densities (Jensen 1993), but also with the nearby mussel bed (Donadi *et al.* 2013). Additionally, the elevated cockle densities can lead to increased aggregation of molluscivore shorebirds, such as oystercatchers (*Haematopus ostralegus*)(van der Zee *et al.* 2012) and red knots (*Calidris canutus*)(van Gils *et al.* 2005). Although higher bird densities can enhance predation pressure, the high cockle density and the presence of mussels as an alternative prey in the engineered area may at the same time mitigate the effects of increased bird densities by increasing giving up densities (GUDs) of predators on their prey (Charnov 1976; Brown 1988; Olsson and Molokwu 2007).

Hence, we hypothesize that by facilitating high numbers of cockles, mussels can alleviate predation-induced effects on cockle survival. Both processes can in turn negatively affect inter- and intraspecific competition among cockles. Consequently, cockles are caught between the positive and negative effects of ecosystem engineering: cockle densities and survival are enhanced by reduced hydrodynamic stress and predation, but cockle growth is reduced due to interspecific competition with mussels and both growth and survival are reduced due to increased intraspecific competition among cockles. To test our hypothesis, we carried out a manipulative field experiment on the intertidal flats of Schiermonnikoog at a site engineered by a mussel bed and at a sandy control site. At both sites, we crossed two adult cockle densities with shorebird exclosure treatments, and added tagged cockles to monitor growth. After 1 year, we ended the experiment and determined cockle survival, recruitment and growth.

Materials and methods

Experimental design

The study was conducted at 0.5 m below mean water level (exposed during low tide for ~30% of time) in the eastern Dutch Wadden Sea, south of the island of Schiermonnikoog. The first out of two study sites was situated 100 meters coastward of a mussel bed (site Mussel, 53°28.127 N - 6°13.463′ E). This area was characterized by silty organic matter-rich sediment, and reduced hydrodynamic conditions (Donadi *et al.* 2013). The other site was located at ~500 m from the first site with the same tidal elevation, but out of the influence range of the mussel bed, and was therefore typified by sandy sediments and served as a control site (site Sand, 53°28.117 N - 6°13.938′ E) (Donadi *et al.* 2013). Both sites were chosen based on previous studies that demonstrate that this area is highly suitable to investigate the effects of ecosystem engineering by blue mussels on multiple interaction types (van der Zee *et al.* 2012; Donadi *et al.* 2013). At the start of the experiment in May 2010, the mean background cockle density was 65 n m^{-2} at the mussel site and 0 n m^{-2} at the sandy control site.

We manipulated predation pressure by establishing 12 1-m^2 bird exclosures and 12 control plots at both sites. Exclosure and control plots were paired with a distance of 4 m between pairs and a distance of 10 m between replicates. Each exclosure consisted of 8 PVC-poles (0.5 m long) that were inserted in the sediment to a depth of 0.4 m and aligned in a square of 1 m^2. A nylon rope connected the tops of the poles thereby acting as a fence (Fig. 4.1A). Control plots were marked by two small PVC-poles. The plots were checked regularly in the following year and macroalgae and other fouling was removed if present.

Next, we crossed the exclosure treatments with two cockle densities by adding either 75 or 925 adult cockles (Fig. 4.1B) to each plot in May 2010, yielding a total of 6 replicates of each treatment per site. Cockles for the addition (> 3 yr old; > 25 mm shell length) were collected from a nearby mudflat by hand-raking. To monitor cockle growth, we also added 25 tagged young cockles to each plot, yielding a total of 100 and 1000 cockles m^{-2} for both density treatments. The 1200 young cockles (~2 yr old; 12 to 26 mm shell length) needed for tagging were collected by hand-raking and immediately transferred to tanks with aerated natural seawater in the laboratory. Here, shell length of each individual was measured to the nearest 0.01 mm with a vernier caliper, and tagged with a polyethylene label (Hallprint glue-on shellfish tags, Australia; Fig. 4.1C) glued to the shell with cyanoacrylate glue. The tagged cockles were added to the experimental plots within 24 hours after collection.

One year after the start of the experiment (May 2011), all cockles were re-collected by hand-raking and afterwards the sediment of the plot was sieved over a 1 mm mesh. Shell length of recaptured tagged cockles was again measured to nearest 0.01 mm. Untagged individuals were divided into two age-classes – recruits (cockle juveniles that survived their first winter after settlement in 2010) and adults (>3 yr old) – after which they were counted.

Although experimental setups with similar constructions have proven to work very well in excluding birds without changing abiotic conditions in the Dutch Wadden Sea (van Gils *et al.* 2003), we nevertheless tested for possible effects on hydrodynamic conditions by measuring % weight loss of plaster dissolution cylinders (Donadi *et al.* 2013). Next to possible exclosure effects, the placement of plaster cylinders on all treatments also allowed for the testing of cockle density and site effects. Cylinders (6.3 cm long, 2.4 cm diameter) were made by molding plaster (Knauf B.V., Utrecht, The Netherlands) around steel nails after which they were dried, weighted, and placed in the field for four consecutive tidal cycles in September 2010. Cylinders were placed randomly in the middle of four out of six plots per treatment. After collection, cylinders were again dried (24h, 30°C) and weighed. The loss of dry weight was used as a relative measure of hydrodynamic stress (Donadi *et al.* 2013).

Finally, molluscivore shorebird abundance was measured in a 25×100 m plot, surrounding each experimental study site. The two areas were marked with PVC poles and birds were counted from a distance of 150 m, using a telescope (zoom

Figure 4.1 Overview of a shorebird exclosure (**A**), treatment densities: 100 and 1000 cockles m^{-2} (**B**) and the added tagged cockles (**C**).

ocular 20–60 ×; ATM 80 HD, Swarovski, Absam, Austria). By counting half an hour after the water retreated from the plots until half an hour before the water inundated the plots again, we excluded shorebirds that foraged on pelagic or epibenthic species (i.e. shrimp, fish) and thereby focused only on endobenthic species as prey item. The number of feeding shorebirds was scored every 15 minutes during low water. Based on literature (Goss-Custard *et al.* 1977; Zwarts *et al.* 1996; Kubetzki and Garthe 2003; Folmer *et al.* 2010; Duijns *et al.* 2013) and personal observations (E. M. van der Zee), shorebirds species with cockles in their diet were divided in groups that prefer either adult cockles (>12 mm; oystercatchers (*Haematopus ostralegus*), herring gulls (*Larus argentatus*), common gull (*Larus canus*) and black headed gulls (*Larus ridibundus*)) or cockle recruits (<12 mm; red knots (*Calidris canutus*), dunlins (*Calidris alpina*), bar-tailed godwits (*Limosa lapponica*) and curlews (*Numenius arquata*)). Birds were counted during 8 tidal cycles between June 2010 and May 2011.

Statistical analysis

For statistical comparisons, changes in adult cockles numbers were expressed as proportions relative to the initial numbers at the start of the experiment. To compare growth rate of cockles, we used the Bertalanffy's growth function (Von Bertalanffy 1938). In this function, growth rate $d\mathrm{H}_t/dt$ declines with an increase in size Ht (the shell height in 2010) in the following way:

$$d\mathrm{H}_t/dt = k\,(\mathrm{H}\infty - \mathrm{H}_t) \qquad (1)$$

where H∞ is the mean maximum size and k is the growth constant. For each individual cockle we estimated k by taking $d\mathrm{H}_t/dt$ as the difference in shell length between May 2011 and May 2010, H_t as shell height in May 2010 and H∞ as 45 mm (Cardoso *et al.* 2006). To deal with pseudoreplication (for having multiple cockles per exclosure) we averaged the growth constant k of cockles per plot.

To test for the effects of predation, density and site, we used general and generalized linear models. Prior to model fitting, all data were checked for normality and homogeneity of variance using Shapiro-Wilk tests ($P = 0.05$) and Bartlett's tests ($P = 0.05$) respectively. Therefore, we applied models with a Gaussian residual error distribution to changes in adult density, growth rate and plaster loss. Changes in adult cockle density were logit-transformed to obtain normality. Cockle recruitment could not be fitted to a Gaussian model. These data were therefore fitted to a Poisson regression model and a negative binomial model after which we selected the first model based on AIC comparisons. Furthermore, to test for significance of the random effect the exclosure-control pairs, we first ran all above analyses with linear mixed-effects models (GLMM's) and repeated these procedures with linear models (GLM's) without the random effect pair. We selected models without random effects for all response variables based on AIC comparisons. For adult density, growth rate and plaster loss, we than used ANOVA tests. When applicable, we applied Tukey's HSD for post-hoc comparisons. Finally, bird observation data were analyzed with Chi-square tests.

All statistical analyses were carried out in R (CRAN, R: A language and environment for statistical computing. 2013. R Foundation for Statistical computing. Vienna, Austria). GLMMs were constructed with the *glmmadmb* function in *glmmADMB* package. GLMs with negative binomial distributions were built with the *glm.nb* function from the *MASS* package. GLMs with Poisson error distributions, ANOVA models, post-hoc comparisons and Chi-squared test were constructed using the *glm*, *aov*, *TukeyHSD* and *chiq.test* functions from the *Stats* package (R Core Team).

Results

Adult cockle survival was significantly reduced by both high densities of cockles and predation by birds (Fig. 4.2A). However, whereas cockle survival was overall lowered by 19% in the high density treatment compared to low density treatment irrespective of both exclosure treatment and site (main effect of density: F = 78.69, n = 24, $P < 0.001$; $\overline{X}_{1000}$±SE = 25.9±5.3% vs. $\overline{X}_{100}$±SE = 44.6±9.1%), predation only negatively affected survival at the sandy site (interaction effect of site×exclosure: F = 5.19, n = 12, $P = 0.03$; Tukey's HSD post-hoc test: site Sand, $P < 0.001$; site Mussel, $P = 0.11$) (Fig. 4.2A).

Growth rate of the tagged cockles was affected by site, density and predation (Fig. 4.2B). Cockle growth was 9% higher at the sandy site compared to the mussel site (main effect of site: F = 19.99, n = 24, $P < 0.001$; $\overline{X}_S$±SE = 0.56±0.01 *k* vs. $\overline{X}_M$±SE = 0.51±0.01 *k*). Growth rates were significantly lower in the 1000 cockle m^{-2} than in the 100 cockle m^{-2} plots, but only in the presence of predation (interaction effect of density×exclosure: F = 10.17, n = 12 $P = 0.003$; Tukey's HSD post-hoc test: predation in control plots, $P = 0.014$; predation in exclosure plots, $P = 0.55$).

Cockle recruitment was significantly correlated with predation and site, but not with density (Fig. 4.2C). Cockle recruit densities were 69% lower in the control than in the exclosure plots (main effect of exclosure: $\chi^2 = 33.2$, df = 1, $P < 0.001$; $\overline{X}_c$±SE = 1.1±0.2 *n* m^{-2} vs. $\overline{X}_{ex}$±SE = 3.6±0.7 *n* m^{-2}) and 63% lower at site Sand compared to site Mussel (main effect of site; $\chi^2 = 26.6$, df = 1, $P < 0.001$; $\overline{X}_S$±SE = 1.3±0.3 *n* m^{-2} vs. $\overline{X}_M$±SE = 3.5±0.7 *n* m^{-2}).

Furthermore, as expected because of differences in exposure to waves and currents (see Donadi *et al.* 2013), the effect of site was significant, with a higher relative weight loss at site Sand compared to site Mussel (main effect of site: F = 28.73, n = 8 $P < 0.001$; $\overline{X}_S$±SE = 44.6±0.4% vs. $\overline{X}_M$±SE = 36.1±0.8 %). We found no

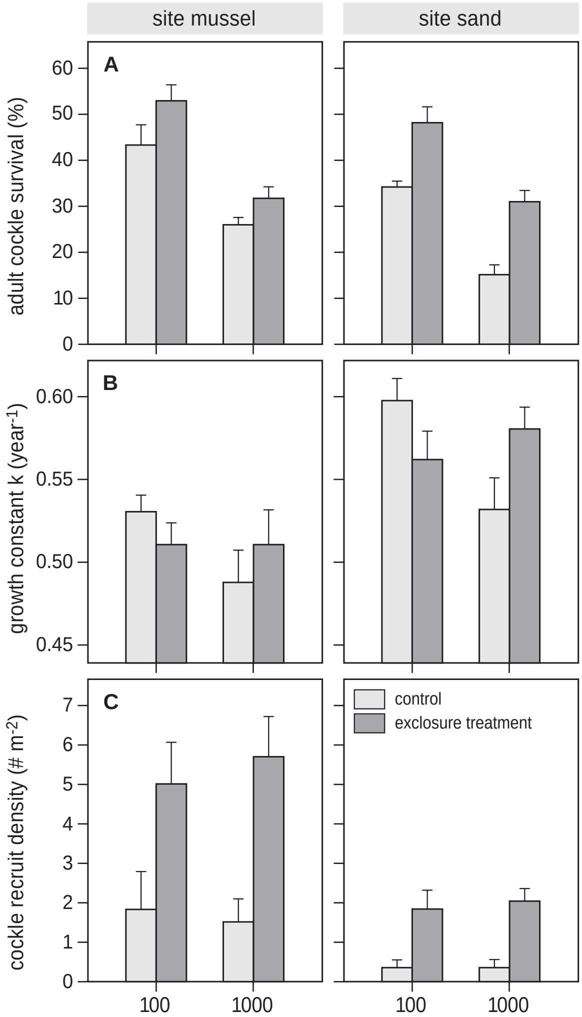

Figure 4.2 Interaction plots showing (**A**) adult cockle survival, (**B**) cockle growth after 1 year and (**C**) cockle recruit density for the treatments: site, density and predation (n = 6 for each group). Representing is the site in the vicinity of a mussel reef (site Mussel) and the site at a sandy intertidal flat (site Sand). Light grey bars represent the control treatment and the dark grey bars represent the exclosure treatment. Means ± 1 S.E.

significant effects on plaster loss of exclosures (main effect of exclosure: F = 0.02, n = 8, $P = 0.89$; $\overline{X}_{c}\pm SE = 40.2\pm1.8\%$ vs. $\overline{X}_{ex}\pm SE = 40.4\pm1.9\%$) and cockle density (main effect of density: F = 0.004, n = 8, $P = 0.954$; $\overline{X}_{100}\pm SE = 40.3\pm1.7\%$ vs. $\overline{X}_{1000}\pm SE = 40.4\pm1.9\%$).

Observations of shorebirds foraging on adult-sized cockles resulted in a cumulative total density of 424 birds ha^{-1} over 8 tides, with a density of 304 birds ha^{-1} (63%

oystercatchers, 32% herring gulls, 1% common gulls and 4% black headed gulls) at the mussel site and a density of 120 birds ha^{-1} (20% oystercatchers, 7% herring gulls, 10% common gulls and 63% black headed gulls) at the sandy site ($\chi^2 = 40.99$, df = 1, $P < 0.001$). The density of shorebirds foraging on recruit-sized cockles was 504 birds ha^{-1}, with a density of 244 birds ha^{-1} (16% red knots, 58% dunlins, 13% curlews and 13% bar-tailed godwits) at the mussel site and 260 birds ha^{-1} (23% red knots, 6% dunlins, 2% curlews and 69% bar-tailed godwits) at the sandy site ($\chi^2 = 0.19$, df = 1, $P = 0.66$).

Discussion

Although trophic interactions, competition and ecosystem engineering and their two-way interactions have been recognized as important structuring mechanisms in ecosystems, the interplay between the three types of interaction on population dynamics have not been investigated to our knowledge. In this study, we demonstrate that cockles, one of the most common and trophically important bivalve species in the Wadden Sea (e.g. Verwey 1981; van Gils *et al.* 2006; Compton *et al.* 2013), are caught between ecosystem engineering-induced processes that affect survival, growth and predation risk across different life stages. Our experimental results show that cockles have higher recruit and adult survival in the vicinity of mussels, most likely due to reduced hydrodynamics (see also Donadi *et al.* 2013). Moreover, despite the generally higher abundance of shorebirds foraging on adult cockles at the mussel site, high adult cockle densities (i.e., caused by the enhanced recruitment and adult survival) in combination with high densities of other potential prey (i.e., mussels) at this site seem to mitigate potential predation effects of this increased shorebird abundance, resulting in a lower predation pressure on adult cockles at the mussel site. Apart from these positive effects, ecosystem engineering by mussels negatively affected relative growth rates of cockles, an effect that is most likely caused by reduced water flow (and hence lower food availability) (Frechette *et al.* 1989) and by indirectly affecting inter-specific competition for food (Donadi *et al.* 2013) through the facilitation of cockles.

The low impact of predation on adult cockles at the mussel site compared to the control site can be explained by earlier studies arguing (Charnov 1976; Olsson and Molokwu 2007) or showing (Brown 1988) that predators have higher GUDs in higher quality foraging environments. At the mussel site, with high cockle densities and mussels nearby as an alternative prey for molluscivore shorebird that forage on adult-sized cockles, higher intake rates may induce higher GUDs and a reduced predation effect compared to the site not affected by mussel beds. Our results corresponds to this explanation by showing that numbers of remaining cockles in the control plots at the mussel site were higher for both manipulated densities ($\overline{X}_{100}$±SE

= 43±4 and $\bar{X}_{1000}$±SE = 260±16 n m^{-2}; see Fig. 4.2A) compared to numbers of remaining cockles in the control plots at the sandy site ($\bar{X}_{100}$±SE=34±1 and $\bar{X}_{1000}$±SE=150±23 n m^{-2}; see Fig. 4.2A). However, since oystercatchers, the main avian predator of adult-sized cockles, can have very low GUDs for adult cockles (<25 n m^{-2}; Zwarts *et al.* 1996), it is suggested that the actual GUD may not be reached yet for both sites, especially not in the high density treatments.

In contrast to predation on adult cockles, we found no significant site effect of predation on recruits (i.e. no interaction between site and exclosure on recruit densities). As the number of cockle recruits were relatively low at both sites, it seems likely that a lack of alternative prey for birds specifically feeding on this size class, results in lower GUDs at both sites, causing the observed differential result between recruits and adult cockles. Another explanation for this result might be that red knots, which are important avian predators of small cockles, have much larger home ranges (van Gils and Piersma 1999), than oystercatchers (Schwemmer and Garthe 2011). This suggests that the notion that environments differ between both sites may only hold for oystercatchers and not for red knots. For this reason, one would only expect a differential predation effect between sites for adult cockles, but not for recruits. The overall low densities of cockle recruits further indicates low survival during the first months after settlement, most likely due to predation by crustaceans (crabs and shrimps) that were able to enter the exclosures and are known to strongly reduce cockle spat numbers (e.g. Strasser 2002).

Apart from apparent interspecific competition for food between mussels and cockles (Donadi *et al.* 2013), we found a significant effect of cockle density on adult cockle survival and growth. The lower survival of adult cockles in the high density treatments is most likely caused by intraspecific interference competition for space (Peterson and Andre 1980) and/or by density-dependent predation by crabs (Seitz *et al.* 2001) and not by density-dependent predation by shorebirds because we did not detect a difference in density-dependent survival between the exclosure and control plots. The density-dependent effect on growth under normal condition (i.e. including predation), however, cannot solely be explained by intraspecific competition for food. The lack of a density-effect in predator exclosures indicates that the 1-m^2 plots were probably too small to cause significant differences in food depletion between the high and low density treatment (Kamermans *et al.* 1992, but see for example Peterson 1982) or that treatment densities were too low to see an effect of food depletion (Jensen 1992; 1993). We therefore suggest that the density-dependent effect on growth in the presence of predators and the lack of this effect in the absence of predators is a behavioural mechanism in response to predators (Brown and Kotler 2004 and references therein) rather than an effect of food depletion. Possibly, cockles in the exclosure plots burry less deeply, as there is no need to escape predation (but see Zwarts and Wanink 1989; Griffiths and Richardson 2006) A more shallow position would make it easier to filter-feed and by reducing burrowing activities, less encounters with conspecifics would occur, resulting in longer feeding times (Peterson and Andre 1980). This effect can especially increase growth rate in the high densities plots with high encounter rates, thereby neutralizing the density-dependent effect of 1000 versus 100 cockles per m^2. Other behavioural responses of cockles to shorebird predation might be an extension of their valve closure time during low tide and/or the investment in thicker shelves (Irlandi and Peterson 1991; Smith and Jennings 2000). The absence of these responses when avian predators are excluded might neutralize the density-dependent effect on growth as well, but only if shorebird predation is density-dependent. For this hypothesis, however, we did not find evidence, since density-dependent survival did not differ between the exclosure and control plots (but see for example Goss-Custard 1977). Overall, we demonstrate that predation increases the strength of intraspecific competition.

Recently, integration of multiple interaction types into so-called "interaction networks" has been gaining attention, but the studies addressing this issue have mostly remained of a theoretical nature (e.g. Goudard and Loreau 2008; Kefi *et al.* 2012). Our empirical results clearly show that predation, competition and ecosystem engineering can interactively control population dynamics in a real ecosystem, which emphasizes the need to integrate multiple ecological interaction types into a single framework (Olff *et al.* 2009). Finally, our study shows that communities in intertidal soft-sediment ecosystem can be strongly structured by ecosystem engineers. We therefore argue that conservation and restoration of habitat-forming species like mussels, oysters and seagrasses is crucial for protecting the health and overall functioning of these ecosystems.

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Chapter 5

5

Biotic structure and sediment stability facilitate benthic species and trophic diversity in an intertidal soft-bottom ecosystem

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Abstract

In intertidal soft-bottom ecosystems, reef-building bivalves have strong effects on the associated community both by providing habitat structure and by stabilizing the sediment. However, these species have declined dramatically in the past centuries and consequences of their loss for the trophic structure of the intertidal benthic communities remain largely unclear. In this study, we empirically tested the hypothesis that recovery of above-ground structure and stable sediments are both important ecosystem functions provided by ecosystem engineers that facilitate distinctly different intertidal benthic communities. In a large-scale experiment at two different sites, one in the Eastern and one in the Western Dutch Wadden Sea, we applied anti-erosion mats and created adult mussel beds to test for separate effects of sediment stabilisation and biotic structure, 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. The effect size of mussel addition, however, was larger at the site in the Western part compared to the Eastern part of the Dutch Wadden Sea, probably due to higher abiotic stress alleviation in the latter area. We conclude that structure-providing and sediment-stabilizing species such as reef-building bivalves, and most likely also seagrasses and tube-worms, can play a crucial role in structuring the benthic community throughout the Wadden Sea by affecting species composition and trophic structure. These species are therefore of great value for intertidal soft-bottom ecosystems and restoration attempts can be beneficial for overall biodiversity.

In preparation for publication

Introduction

Coastal ecosystems are of great importance to a multitude of marine species and provide crucial services to human society (Costanza *et al.* 1997; Beck *et al.* 2001; Hodgson and Liebeler 2002; Barbier *et al.* 2011). Ecosystem engineers, species that strongly modify their environment, such as reef-building bivalves, seagrasses and corals (Jones *et al.* 1994; 1997), play an important role in structuring coastal communities (e.g. Bruno and Bertness 2001; Bouma *et al.* 2009; van der Zee *et al.* 2012). They diversify the landscape by forming complex structures and relieve environmental stress for instance by attenuating currents and waves (Gutierrez *et al.* 2003; Koch *et al.* 2009; Donadi *et al.* 2013). Due to these habitat modifications, ecosystem engineers typically not only facilitate themselves (Rietkerk *et al.* 2004; van de Koppel *et al.* 2005; van der Heide *et al.* 2007), but also provide a key-habitat for a wide variety of species that depend on them for settlement, refuge or food supply (e.g. Nagelkerken *et al.* 2000; Gutierrez *et al.* 2003; van der Zee *et al.* 2012).

Over the last few decades, coastal ecosystems have become severely degraded worldwide (Lotze *et al.* 2006; van Gils *et al.* 2006; Barbier *et al.* 2008; Waycott *et al.* 2009). At the same time, many dominating ecosystem engineering species have been overexploited or destroyed, with potentially dramatic implications for associated species, community structure and overall biodiversity (Hodgson and Liebeler 2002; Lotze 2005; Waycott *et al.* 2009; Eriksson *et al.* 2010). Especially in soft-bottom ecosystems, large-scale losses of seagrass, tubeworm, mussel and oyster beds can have a significant impact on the associated community, since solid substrate and structure are almost exclusively provided by such species in these otherwise sandy and hostile environments. Moreover, natural recovery of engineering species and their associated communities is often slow, unpredictable or absent due to strong internal positive feedbacks, and even active restoration has proven difficult (Jackson *et al.* 2001; van der Heide *et al.* 2007; Schulte *et al.* 2009; Eriksson *et al.* 2010).

In the Dutch part of the Wadden Sea, one of the world's largest intertidal ecosystems (Wolff 1983), intertidal mussels – ecosystem engineers that create hard substrate, reduce hydrodynamic stress, modify sediment conditions and increase the cohesiveness of the substrata (Kröncke 1996; Widdows and Brinsley 2002; Gutierrez *et al.* 2003; Donadi *et al.* 2013) – covered an area of over 4000 ha at the end of the 1970s. In the beginning of the 1990s, however, intertidal mussel beds disappeared completely, largely due to a combination of dramatic overfishing and three years of recruitment failure (Dijkema 1991; Beukema and Cadée 1996). Furthermore, in addition to the direct physical removal of mussels, sand extraction and bottom trawling for shrimps (*Crangon crangon*) and edible cockles (*Cerastoderma edule*) also removed sediment-stabilizing species and resuspended the upper layer of the sediment (e.g. Riesen and Reise 1982; Van der veer *et al.* 1985; Piersma *et al.* 2001; Kraan *et al.* 2007), which decreased the availability of natural structure and stable sediment even further. Despite a ban on mechanical dredging for intertidal mussels (1999) and cockles (2005), it took more than a decade for mussels to start to re-establish in substantial densities and even though they have been slowly recovering, their reestablishment is currently still mainly restricted to the Eastern part of the Dutch Wadden Sea (Ens *et al.* 2009; Goudswaard *et al.* 2009).

In this study, we empirically test the hypothesis that recovery of aboveground structure and stable sediments are both important ecosystem functions provided by ecosystem engineers that facilitate distinctly different intertidal benthic communities by affecting species composition (i.e. species richness and diversity) and trophic structure (i.e. feeding guild richness and diversity). In a large-scale experiment, we applied anti-erosion mats and created adult mussel beds to test for separate effects of sediment stabilisation and habitat modification, respectively. The experiment was carried out at two different sites to investigate if the treatment effects were consistent across space. 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. After three months, we investigated treatment effects on the invertebrate community.

Methods

Study area

Large-scale experimental plots were established on the intertidal mudflats of two barrier Islands in the Dutch Wadden Sea. The first site was located in the western part, south of the island of Terschelling (53°21'39.69"N, 5°18'29.18"E) and the second site was located in the eastern part, south of the island of Schiermonnikoog (53°28′3.43″N, 6°14″13.40″E) (Fig. 5.1). The site at Terschelling has a small tidal range (~0.9 m, based on mean high water levels), is exposed to waves from the southwest, and is typified by relatively clear water and sandy sediment (Table 5.1). The site at Schiermonnikoog has a higher tidal range (~1.2 m, based on mean high water levels), is situated in more sheltered conditions, and is characterized by very turbid water and more silty sediments (Table 5.1). Both sites were located at approximately the same tidal elevation (0.6 to 0.8 m below mean water level), which is similar to the elevation of natural intertidal mussel and oyster beds in the vicinity of the experimental plots (distance: ~1000–2000 m).

Experimental design

At each site, 12 plots of 20×20 m were established in a line parallel to the gully (distance from the gully ~100–150 m) and with a distance of ~20 m between plots. Plots were divided over three blocks. Within each block, we randomly assigned one replicate of each of the following treatments to the plots: (1) control, (2) addition of a

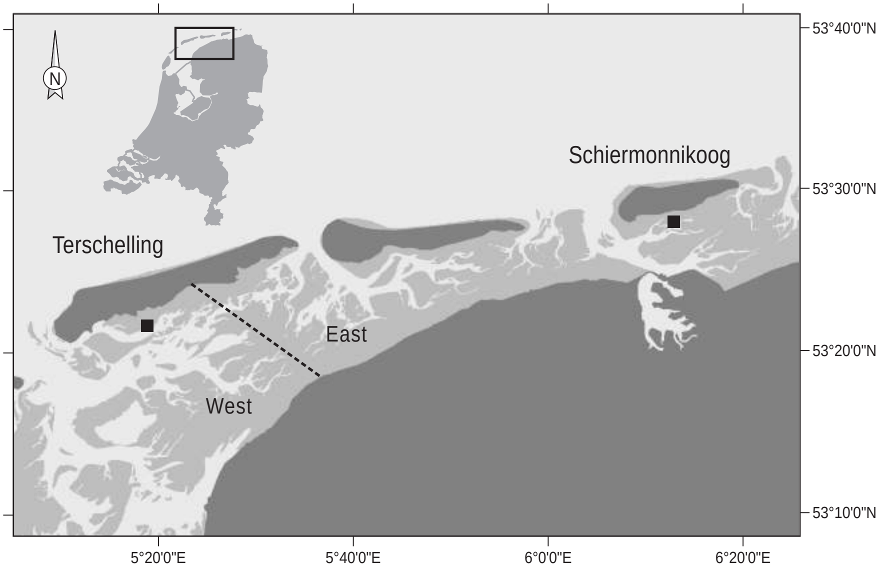

Figure 5.1 Map with locations of the experimental plots in the western Dutch Wadden Sea at Terschelling and in the eastern Dutch Wadden Sea at Schiermonnikoog (black squares). Light grey areas represent water, intermediate gray areas represent tidal flats exposed during low tide and land is represented by dark gray.

Table 5.1 Description of environmental conditions for the site in the western part of the Dutch Wadden Sea (Terschelling) and for the site in the eastern part (Schiermonnikoog). For each site, we obtained sediment silt and organic matter content, tidal elevation and amplitude, diffuse light attenuation, particulate organic carbon and chlorophyll concentration of the water, maximum current velocity, orbital velocity (with NW and W wind direction) and average fetch length. Light attenuation, particulate organic carbon and cholorphyll concentrations were calculated over the monthly composites of May, June and July 2011 from the Modis Ocean satellite.

	West Terschelling	**East Schiermonnikoog**
Silt content (%<63μm)	2.3	3.0
Sediment organic matter content (%)	0.58	0.64
Elevation (m NAP)	-0.8	-0.6
Tidal amplitude (m)	0.9	1.2
Diffuse light attenuation at 490nm (m^{-1})	0.58	1.03
Particulate organic carbon (mg/m^3)	552.33	893.90
Chlorophyll concentration (mg/m^3)	8.76	14.85
Maximum current velocity (ms^{-1})	0.55	0.60
Wave action - Orbital velocity (ms^{-1}) NW	0.21	0.14
Wave action - Orbital velocity (ms^{-1}) W	0.32	0.25
Average fetch length (km)	29.9	9.3

coco-coir mat on the sediment surface to stabilize the sediment, (3) addition of adult mussels, and (4) addition of a coco-coir mat and adult mussels. Coir mats consisted completely out of coconut fibre and are commonly used to prevent erosion of sediment and seeds on bare soil. The mats were applied by hand, fixated along the edges by digging it in to a depth of ~20 cm and in the middle by inserting 15-cm long biodegradable pins into the sediment. To increase sediment stability and deposition on the coir mat plots, we placed 128 knotted burlap balls (diameter ~10 cm) in each plot at regular distances underneath the mat that reduced water flow velocity between elevations of the balls.

Two-year-old alive mussels (shell length: 51.0 ± 1.0 mm; n = 60) 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 ~2.5-m diameter were created by hand at regular distances from each other within each plot, yielding a total cover of around 30% (~2000 kg mussels/plot) – a cover commonly found in natural mussel beds in the Wadden Sea. Shells of the transplanted mussels were relatively clean with very low numbers of sessile epifauna such as barnacles, most likely due to predation by starfish in the subtidal area (Saier 2001). In addition, no macroalgae were present on the mussels. The few crabs and starfishes found after dredging were mostly dead. Therefore, the possibility of co-transplanting relevant numbers of species to the experimental mussel plots was minimal.

The experiment lasted from the beginning of May until the beginning of August 2011. After 3 months, the average density of adult mussels within the patches was on Schiermonnikoog 1251 ± 70 mussels m^{-2} and on Terschelling 999 ± 85 mussels m^{-2}. Furthermore, mussel patches on Schiermonnikoog had a 21% cover of the macroalgae *Fucus vesiculosus*, while patches on Terschelling had a 96% cover of the macroalgae *Ulva lactuca*.

Sediment and benthos sampling

Sediment and benthos samples were collected in the beginning of August 2011. At each control plot, we randomly took sediment and benthos cores. At the coir mat and mussel plots, however, we sampled randomly in between the burlap balls and in the mussel patches, respectively. We pooled three 5-cm deep sediment cores with a PVC corer with an area of 7.1 cm^2. Sediment organic matter content in dried sediment (24 h, 70°C) was estimated as weight Loss On Ignition (LOI; 5 h, 550°C). Sediment samples were freeze-dried for up to 96 hours till dry. Prior to grain-size analysis, organic matter and carbonate were removed using HCl and H_2O_2. The samples were left overnight at 80°C to speed up the reaction. Samples were measured in de-gassed Reversed Orsmosis water. Percentage silt (fraction $< 63\ \mu m$) was determined using a Coulter LS 13 320 particle size analyzer using laser diffraction (780 nm) and PIDS (450 nm, 600 nm and 900 nm) technology. The optical module

'Gray' was used for calculations. Burial depth of the anti-erosion mats was determined with a ruler by 10 random measurements on each coir mat plot in areas without burlap balls. Depth values were averaged per plot afterwards. Two benthos samples were taken within each plot with a stainless steel core with an area of 179 cm^2 down to a depth of 20–25 cm. Samples were sieved over a 1 mm mesh and all fauna was fixed in 4% formalin solution in 2-L bottles for later analyses. In the laboratory, samples were stained with Rose Bengal (CAS 11121-48-5). All fauna were identified to species level and counted. Prior to data analyses, we pooled the two benthos samples and classified all species as either infauna or epifauna species in order to test for treatment effects on the infauna and epifauna community separately (Table S1 & S2).

Data analyses

To get an overview of the differences in the infaunal and epifaunal assemblages among sites and treatments, we first visualized the treatment effects with non-metric multidimensional scaling (nMDS) (Kruskall and Wish 1978) ordination models based on the Bray-Curtis dissimilarity matrix (Clarke and Green 1988). Multivariate analyses were performed on square root transformed data (i.e. for the epifauna data we used $\sqrt{(x+0.1)}$). Differences in the infaunal and epifaunal assemblages among sites and treatments were than analyzed with a distance-based permutational multivariable analysis of variance (PERMANOVA) based on Bray-Curtis dissimilarity measures (Anderson 2001; McArdle and Anderson 2001).

To further test for treatment effects on community structure, we determined species richness (number of species), species diversity (Shannon diversity index H'), feeding guild richness (number of feeding guilds), feeding guild diversity (Shannon diversity index H') for both the infaunal and epifaunal community. Feeding guilds were based on data extracted from online databases for marine invertebrates (MarLIN. 2006; Appeltans *et al.* 2012; see Table S3 and S4 for guild list).

During model selection for the sediment conditions and community diversity, we first selected the best residual error distribution for each model (Gaussian, Poison and negative binomial distributions were tested) and subsequently tested for significance of the random effect 'Block' by analyzing all models with generalized linear mixed-effects models (GLMM) and repeating them with generalized linear models (GLM). The final models were selected based on AIC comparisons. After model fitting, normality of the residual distribution was checked for normality by using a Shapiro-Wilks test ($P = 0.05$). Both sediment organic matter and silt content were log-transformed to obtain normality of the residual distribution and three-way ANOVA models were used based on AIC comparisons. The model selection procedure also selected three-way ANOVA models for species richness, species diversity, feeding guild richness and feeding guild diversity for the infauna community and epifauna community. All statistical analyses were carried out in R (R Development

Core Team 2013). PERMANOVA models and nMDS plots were constructed with the functions *adonis* and *metaMDS*, respectively, in the *vegan* package (Oksanen *et al.* 2013). GLMMs and GLMs were constructed with the *glmmadmb* function in *glmmADMB* package (Fournier *et al.* 2012). Three-way ANOVA models were constructed using the *aov* functions from the *Stats* package.

Results

Sediment conditions

Sediment organic matter content did not differ between the sites (F = 0.05, n = 12, $P = 0.83$, Fig. 5.2A), but silt content was 1.2 times lower at Terschelling than at Schiermonnikoog (F = 5.9, n = 12, $P = 0.03$, Fig. 5.2B). The addition of mussels increased organic matter content by 1.6 times (F = 47.8, n = 12, $P < 0.001$, Fig. 5.2A) and doubled silt content (F = 73.6, n = 12, $P < 0.001$, Fig. 5.2B). The coir mat did not significantly affect either organic matter (F = 0.2, n = 12, $P = 0.69$, Fig. 5.2A) or silt content (F = 0.0, n = 12, $P = 0.97$, Fig. 5.2B). The anti-erosion mat increased suspended sediment deposition, burying the mat under a thin layer of sand (Schiermonnikoog: 33 ± 2 mm; Terschelling: 44 ± 5 mm; mean±SE; n = 6).

Infaunal community

PERMANOVA analyses revealed significant differences in the composition of the infaunal community depending on site, coir mat and mussel additions, which are visualized by nMDS ordination models (Table 5.2, Fig. 5.3A). The infauna species *Capitella capitata*, *Hediste diversicolor* and *Alitta succinea* were abundant in the mussel plots with and without the coir mat (Table S3). *Scoloplos armiger* was abundant in the control plots and in the coir mat plots and *Lanice conchilega* was abundant in the coir mat plots, mussel plots and in the plots with coir mat and

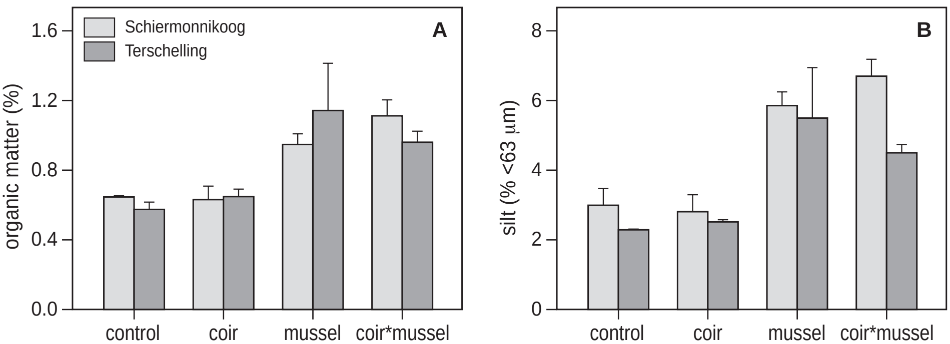

Figure 5.2 Organic matter (**A**) and silt content (**B**) for each treatment (Mean ± SE, n = 3).

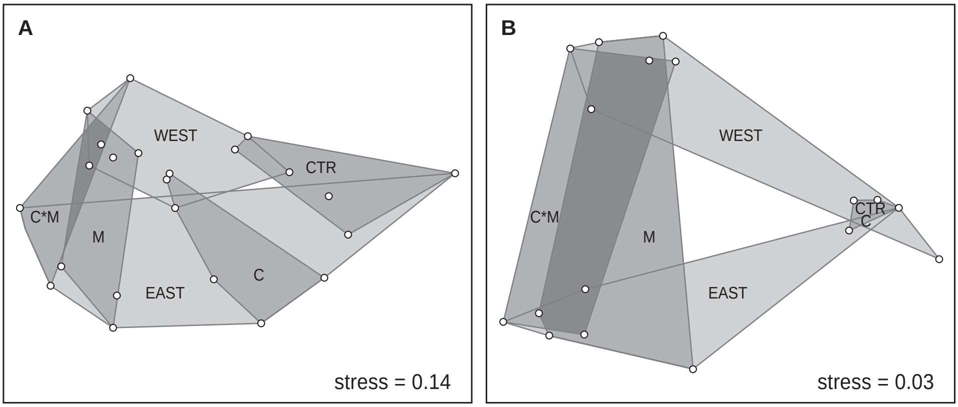

Figure 5.3 Non-metric multi-dimensional scaling (nMDS) for differences among treatments for the infauna (**A**) and epifauna (**B**) community. Coir mat and mussel treatments are represented by the darkgrey polygons, sites by the lightgrey polygons and samples by the white circles (CTR=Control, C=Coir, M=Mussel, C*M=Coir*Mussel, WEST=Terschelling, EAST=Schiermonnikoog). A stress value below 0.2 indicates a reliable ordination.

mussels (Table S3). Eleven infaunal species were only found on Terschelling, while six species were exclusive to Schiermonnikoog (Table S3).

Infaunal species richness was significantly affected by coir mat, mussels and site (Fig. 5.4A, table 5.3). Species richness was around 1.6 times higher in the coir mat plots, in the mussel plots and in the plots with both coir mat and mussels compared to the control plots. On Terschelling, the increase in species richness due to the addition of mussels was 1.9 times stronger than on Schiermonnikoog. Infaunal species diversity was significantly affected by coir mat and site (Fig. 5.4B; table 5.3). Diversity was 1.3 times higher in the coir mat plots compared to the plots without coir

Table 5.2 F-values and significance levels of PERMANOVA based on Bray-Curtis dissimilarities for treatment effects on the infauna and epifauna community. Significance levels: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. Degrees of freedom: 24 in total; 16 residual.

Treatments	Infauna	Epifauna
Coir	3.4 (*)	1.4
Mussels	20.1 (***)	85.5 (***)
Site	9.7 (***)	2.3
Coir × Mussels	1.8	1.4
Coir × Site	1.4	2.1
Mussels × Site	1.5	1.9
Coir × Muss. × Site	0.7	1.8

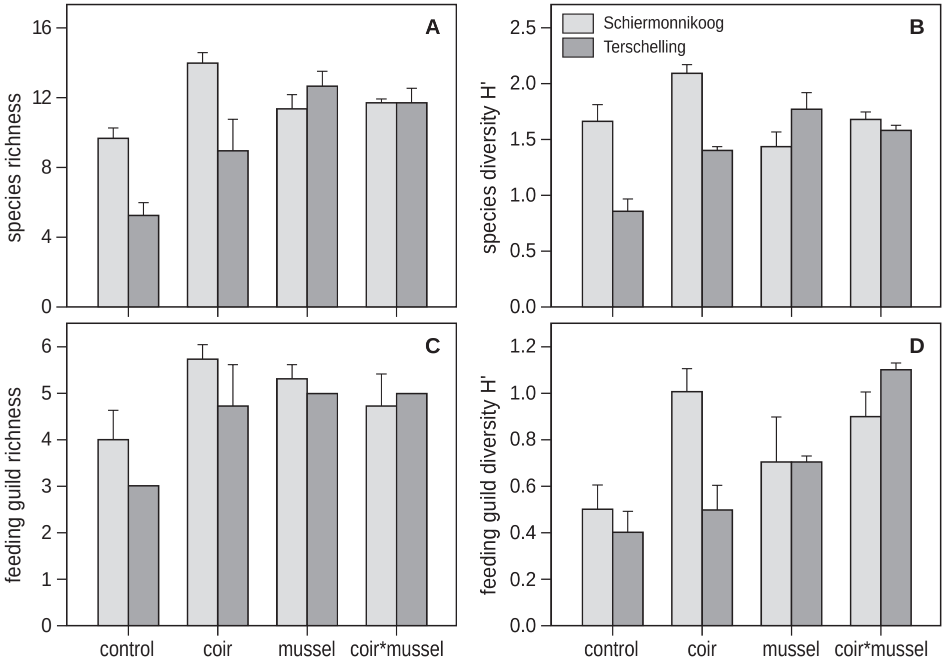

Figure 5.4 Treatment effects on species richness (**A**), species diversity (**B**), feeding guild richness (**C**) and feeding guild diversity (**D**) of the infauna community (Mean ± SE, n = 3).

mats. Furthermore, species diversity was approximately 1.5 times higher on Schiermonnikoog compared to the Terschelling, but only in plots without adult mussels added. Mussel addition on Terschelling, increased species diversity by 1.3 times compared to plots without adult mussels, while on Schiermonnikoog infaunal diversity was unaffected by mussel addition. Feeding guild richness was 1.5 times higher in the coir mat plots and in the mussel plots compared to the control plots (Fig. 5.4C; table 5.3). Feeding guild diversity was significantly affected by coir mat and mussel addition and by the interaction of mussel addition × site (Fig. 5.4D; table 5.3). Feeding guild diversity was around 1.5 times higher in the coir mat plots and in the mussel-addition plots compared to control plots. Guild diversity was 2 times higher in plots where both coir mat and mussels were added compared to control plots. On Terschelling, the increase in feeding guild diversity due to the addition of mussels was 1.7 times stronger than on Schiermonnikoog.

Epifaunal community

PERMANOVA analyses revealed clear differences in the composition of the epifauna community depending on mussel addition, which are visualized by nMDS ordination models (Table 5.2, Fig. 5.3B). The most abundant epifauna species (i.e. *Balanus*

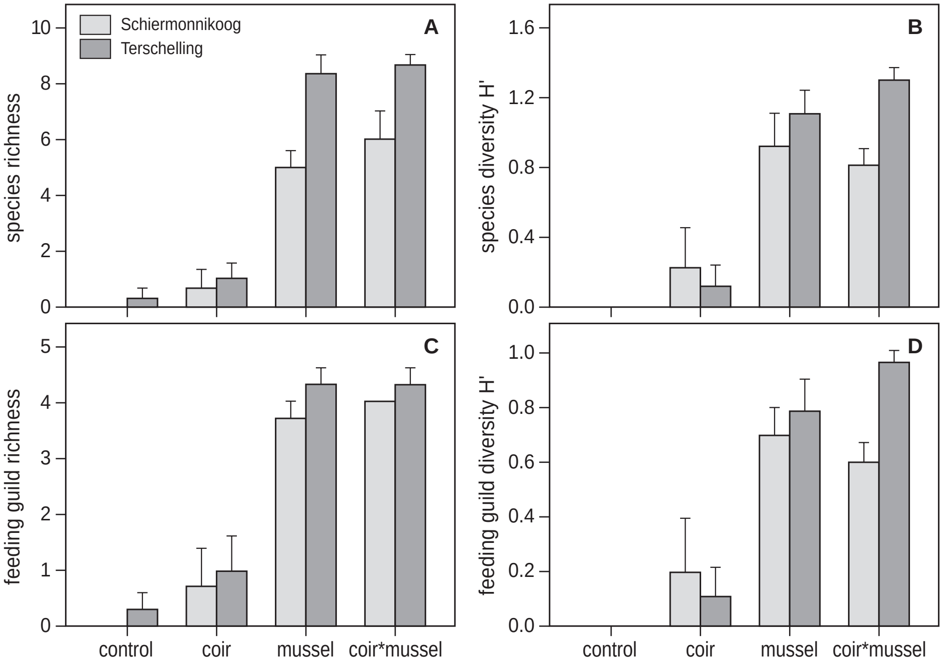

Figure 5.5 Treatment effects on species richness (**A**), species diversity (**B**), feeding guild richness (**C**) and feeding guild diversity (**D**) of the epifauna community (Mean ± SE, n = 3).

Table 5.3 F-values and significance levels of all treatments and their interactions for species richness (S), species diversity (H′), feeding guild richness (F_S) and feeding guild diversity (F_H′) of the infauna and epifauna community. Significance levels: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. Degrees of freedom: 24 in total; 16 residual.

	Infauna				**Epifauna**			
Treatments	**S**	**H′**	**F_S**	**F_H′**	**S**	**H′**	**F_S**	**F_H′**
Coir	8.1(*)	23.4(***)	4.0	18.2(***)	2.6	1.8	2.3	1.7
Mussels	13.1(**)	2.3	4.0	6.0(*)	243.4(***)	43.0(***)	168.1(***)	73.7(***)
Site	9.6(**)	18.8(***)	2.3	2.5	16.0(**)	1.5	2.3	1.9
Coir × Mussels	11.3(**)	4.2	9.0(**)	0.0	0	1.0	0.8	0.9
Coir × Site	0.6	0.1	0.3	0.4	0.2	0.9	0.1	0.4
Mussels × Site	17.1(***)	34.9(***)	2.3	7.3(*)	10.2(**)	9.0(**)	0.1	4.5 (*)
Coir × Muss. × Site	0.1	0.3	0.3	3.1	0.2	3.9(*)	0.1	1.9

crenatus, *Carcinus maenus*, *Gammarus locusta* and *Mytilus edulis* spat) were strongly structured by mussel addition and site (Table S4). Four epifauna species were exclusive to Terschelling, while three species were only found on Schiermonnikoog (Table S4). Further analyses showed that epifauna species richness was significantly affected by mussels and site (Fig. 5.5A; table 5.3). Species richness was 14 times higher in the plots with mussel addition compared with plots without mussel additions. On Terschelling, the increase in species richness due to the addition of mussels was 1.4 times stronger than on Schiermonnikoog. Epifauna species diversity was also significantly affected by mussels (Fig. 5.5B; table 5.3). Species diversity was 11 times higher in the plots with mussel additions compared with the plots without mussel additions and the increase in species diversity due to the addition of mussels was 1.3 times stronger on Terschelling than on Schiermonnikoog. Furthermore, addition of mussels on top of the coir mats yielded a 1.2 times higher diversity compared to mussel plots on Terschelling, while on Schiermonnikoog, diversity in these plots was 1.1 times lower compared to mussel plots. Feeding guild richness was significantly affected by mussel addition (Fig. 5.5C; table 5.3), with 8 times higher values in the plots with mussels compared to the plots without mussels. Feeding guild diversity was 9.5 times higher in the plots with mussel addition compared to the plots without mussel addition (Fig. 5.5D; table 5.3). On Terschelling, the increase in guild diversity due to the addition of mussels was 2 times stronger then on Schiermonnikoog (Fig. 5.5D; table 5.3).

Discussion

In coastal soft-bottom systems, the direct physical removal of ecosystem engineers in combination with mechanical dredging activity itself can result in a reduced availability of hard substrate and stable sediment with potentially dramatic implications for the associated community (Thrush *et al.* 1996; Ferns *et al.* 2000; Piersma *et al.* 2001; Thrush and Dayton 2002). In this study, we empirically demonstrate that stable sediments and aboveground structure are two important properties of structure-providing organisms that can facilitate distinctly different intertidal benthic communities.

Sediment stabilization through the addition of anti-erosion mats stimulated the development of the infaunal community by increasing species and trophic diversity (i.e. richness and Shannon diversity index). The mats prevented erosion, while we detected no changes in sediment organic matter and silt content. This indicated that sediment stabilization alone can enhance this diversity. Depending on location, the addition of mussels slightly increased or had no effect on infaunal diversity. However, it did cause a shift in infaunal species composition, probably due to deposition of faeces and pseudofaeces (Pearson and Rosenberg 1978; Kautsky and Evans 1987; Ragnarsson and Raffaelli 1999). Furthermore, the addition of adult mussels strongly stimulated the development of the epifaunal community by increasing species and trophic diversity, most likely due to the availability of substrate (Thiel and Dernedde 1994; Gutierrez *et al.* 2003; Norling and Kautsky 2007). The effects of mussel addition on species richness are consistent with previous experimental studies in intertidal soft-bottom systems (Ragnarsson and Raffaelli 1999; Beadman *et al.* 2004; Norling and Kautsky 2007; Kochmann *et al.* 2008). However, by including more functionally-informative metrics of community structure, we show that mussel addition not only influences the benthic community structure by species enrichment, but also by trophic enrichment and diversity. This suggests that by attracting more or different species and feeding guilds, stable sediments and mussel beds have the potential to alter the number and strength of biotic interactions among species such as predation and competition, thereby affecting overall ecosystem functioning.

Despite the environmental background differences between the communities of the western (Terschelling) and eastern (Schiermonnikoog) Dutch Wadden Sea, the overall effects of our treatments were similar. Nevertheless, the positive effect size of the mussel treatments on the infaunal and epifaunal community was significantly larger at Terschelling. These more pronounced positive effects on the more exposed and sandy site of Terschelling corresponds to the idea that facilitation by ecosystem engineers becomes more important when environmental stress increases (Bertness and Callaway 1994; Bruno *et al.* 2003; Crain and Bertness 2006). With regard to the effects of mussels on the infaunal community, mussels can increase the cohesiveness of the substrata and reduce hydrodynamic stress (reviewed by Widdows and Brinsley 2002), which can results in suitable substrate for larval settlement (Commito *et al.* 2005) and this seems relatively more important at the more exposed conditions of Terschelling than at the sheltered conditions of Schiermonnikoog. With regard to the effects of mussels on the epifaunal community, mussel addition provides attachment substrate, and shelter from water movement and desiccation (e.g. Stephens and Bertness 1991; Thiel and Dernedde 1994), which also seems to be more important under the more exposed conditions of Terschelling. This differential site effect to the epifaunal community is probably further enhanced by the much higher coverage of epibenthic macroalgae (*Ulva lactuca*) at Terschelling that profit from the relatively high water clarity at this site. These algae on top of the mussels further increase habitat complexity, but may also serve as an additional food source (e.g. Goecker and Kall 2003).

Although it has been widely acknowledged that the loss of ecosystem engineers caused a loss of associated species and a homogenization of the Wadden Sea landscape (Reise *et al.* 1989; Lotze 2005; Reise 2005), the actual consequences for the trophic structure of the intertidal soft-bottom community remained largely unclear. Our results show that structure-providing and sediment-stabilizing ecosystem engineers such as mussels, and most likely also seagrasses and tube-worms (Orth 1977; Widdows *et al.* 1998; Friedrichs *et al.* 2000; Gutierrez *et al.* 2003; Volkenborn *et al.* 2009) may strongly affect the trophic structure of the intertidal benthic community by increasing the number and diversity of feeding guilds. This suggests that ecosystem engineers can form the foundation for a trophic-divers ecosystem. Moreover, the loss of ecosystem engineers often coincides with the loss of species at higher trophic levels (Jackson *et al.* 2001; Lotze *et al.* 2006), suggesting that the overexploitation of ecosystem engineers might have had a significant share in the overall reduction of trophic diversity in coastal ecosystems.

The loss of top-down processes, however, can also strongly determine the trophic structure of coastal systems (e.g. Pinnegar *et al.* 2000; Steneck and Sala 2005; Eriksson *et al.* 2011). Predation pressure by crustaceans, for instance, is increasing in many marine areas due to overfishing of top-predators, which can result in meso-predator-release (Worm and Myers 2003; Eriksson *et al.* 2011). In the Dutch Wadden Sea, shrimp numbers are over twice as high compared to other European coastal waters and increased strongly in the western part of the Dutch Wadden Sea since 1995 (Campos *et al.* 2010; Tulp *et al.* 2012). In addition, shore crab densities strongly increased since 1995, with numbers still rising (Tulp *et al.* 2012). Although underlying causes for this increase of crustaceans in the Wadden Sea are presently unknown, crustacean do play a very important role in determining bivalve recruitment (van der Veer *et al.* 1998; Strasser 2002; van der Heide *et al.* submitted), and may even explain the low recovery rate of mussels in the western part of the Dutch Wadden Sea. Hence, we propose that, in addition to altered abiotic conditions, the Wadden Sea community is disrupted from two biotic directions: loss of ecosystem engineers affects its foundation by decreasing (trophic) diversity, while loss of top-predators affects its top-down regulation.

Our findings can have implications for ecosystem-based management and large-scale restoration strategies of intertidal soft-bottom ecosystems as they indicate that the loss of stable sediments and substrate, caused by removal of ecosystem engineers or mechanical dredging, can negatively affect the structure of the benthic community throughout the Wadden Sea. In addition, this study contributes to the growing awareness that the use of facilitative interactions is important in conservation efforts and that ecosystem engineers should be considered as one of the first target species for restoration and conservation (Boogert *et al.* 2006; Byers *et al.* 2006; Crain and Bertness 2006).

Acknowledgements

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Supplementary tables

Table S1 Infauna species feeding guilds, based on literature data on macrofauna feeding modes from reference literature and websites for European macrofauna (Fauchald and Jumars 1979; MarLIN. 2006; Appeltans *et al.* 2012).

Infauna species	**Feeding guilds**
Aphelochaeta marioni	Deposit feeder
Arenicola marina	Deposit feeder
Autolytus prolifer	Predator
Capitella capitata	Deposit feeder
Ensis directus	Filter feeder
Cerastoderma edule	Filter feeder
Eteone longa	Predator - Deposit feeder
Eulalia viridis	Predator
Eumida sanguinea	Predator
Harmotheo imbricata	Predator
Harmothoe sarsi sarsi	Predator
Hediste diversicolor	Predator - Opportunist
Heteromastus filiformis	Deposit feeder
Lanice conchilega	Deposit - Filter feeder
Macoma baltica	Deposit - Filter feeder
Malacoceros fuliginosus	Deposit - Filter feeder - Grazer
Malmgreniella lunulata	Predator - Opportunist
Marenzelleria wireni	Deposit - Filter feeder - Grazer
Mya arenaria	Filter feeder
Nephtys hombergii	Predator - Opportunist
Nereis longissima	Predator - Opportunist
Alitta succinea	Predator - Opportunist
Nereis virens	Predator - Opportunist
Oligochaeta sp	Deposit feeder - Grazer
Phyllodoce maculate	Predator - Opportunist
Phyllodoce mucosa	Predator - Opportunist
Polydora cornuta	Deposit - Filter feeder - Grazer
Pygospio elegans	Deposit - Filter feeder
Scoloplos amiger	Deposit feeder
Spio martinesis	Deposit - Filter feeder
Streblospio benedictii	Deposit - Filter feeder - Grazer
Urothoe poseidonis	Deposit feeder

Table S2 Epifauna species feeding guilds, based on literature data on macrofauna feeding modes from reference literature and websites for European macrofauna (Fauchald and Jumars 1979; MarLIN. 2006; Appeltans *et al.* 2012).

Epifauna species	Feeding guilds
Asterias rubens	Predator - Opportunist
Balanus crenatus	Filter feeder
Carcinus maenus	Predator - Opportunist
Corrophium sp	Deposit - Filter feeder - Grazer
Crangon crangon	Predator
Crassostrea gigas spat	Filter feeder
Crepidula fornicata	Filter feeder
Gammarus locusta	Deposit feeder
Idotea sp	Predator - Opportunist
Jaera sp	Deposit feeder - Grazer
Melita palmata	Deposit - Filter feeder - Grazer
Metridium senile	Filter feeder
Mytilus edulis spat	Filter feeder

Table S3 Infauna species abundance (mean ± SE) per treatment (Ctr=Control, C=Coir, M=Mussel, C*M=Coir*Mussel).

	Schiermonnikoog				**Terschelling**			
Infauna species	**Ctr**	**C**	**M**	**C*M**	**Ctr**	**C**	**M**	**C*M**
Aphelochaeta marioni	21.3±13.0	19.0±16.0	36.3±19.0	25.7±17.4				
Arenicola marina	2.0±0.6	2.0±0.6	2.0±0.6	1.7±0.9	1.0±0.6	1.3±0.7	3.0±0.6	1.0±0.6
Autolytus prolifer							0.7±0.7	0.7±0.3
Capitella capitata	10.7±4.1	38.0±9.0	68.0±8.1	50.7±6.8	0.3±0.3	4.3±0.9	58.7±16.8	38.3±6.4
Ensis directus				0.3±0.3		0.3±0.3		
Cerastoderma edule spat							0.3±0.3	
Eteone longa	1.3±0.3	6.0±3.5		0.3±0.3	3.7±1.3	3.7±3.2	0.3±0.3	
Eulalia viridis								0.7±0.7
Eumida sanguinea						0.3±0.3	0.7±0.3	0.7±0.3
Harmotheo imbricata								0.3±0.3
Harmothoe sarsi sarsi	1.0±0.6	1.3±0.7	1.0±0.0			0.3±0.3		
Hediste diversicolor	0.3±0.3	6.0±0.0	6.3±2.9	10.0±2.3		0.3±0.3	7.3±2.7	6.0±1.7
Heteromastus filiformis	0.3±0.3	1.0±0.6	0.7±0.7	0.3±0.3				
Lanice conchilega		15.0±5.3	1.3±0.9	2.0±0.6		9.0±4.0	10.7±2.8	15.0±2.6
Macoma baltica	3.7±0.9	3.3±0.7	2.7±0.9	3.0±1.0	0.3±0.3	0.7±0.7	0.3±0.3	0.6±0.3
Macoma baltica spat								0.7±0.7
Malacoceros fuliginosus						0.3±0.3		
Malmgreniella lunulata							1.3±0.3	1.3±1.3
Marenzelleria wireni		0.7±0.7		0.3±0.3				
Mya arenaria			0.3±0.3					
Nephtys hombergii						0.3±0.3	0.3±0.3	
Nereis longissima							0.7±0.7	0.7±0.7
Alitta succinea		0.3±0.3	3.0±0.6	5.0±1.5			2.7±1.7	5.7±0.3
Nereis virens							0.3±0.3	
Oligochaeta sp		0.3±0.3		0.7±0.7				
Phyllodoce maculate						0.3±0.3	1.7±1.7	
Phyllodoce mucosa		6.0±5.0						0.3±0.3
Polydora cornuta		9.0±2.0	7.0±2.9	5.3±1.3			1.0±0.6	3.0±1.0

Table S3 Continued.

	Schiermonnikoog				Terschelling			
Infauna species	**Ctr**	**C**	**M**	**C*M**	**Ctr**	**C**	**M**	**C*M**
Pygospio elegans	9.0±5.1	14.3±4.9	2.7±1.2	6.3±4.9	7.3±1.3	2.7±0.9		
Scoloplos amiger	22.0±5.5	22.0±5.7	0.3±0.3	0.3±0.3	77.3±23.6	41.7±15.7	14.7±4.2	2.7±1.2
Spio martinesis	1.7±0.9			0.7±0.7	1.0±1.0		0.3±0.3	
Streblospio benedictii			0.7±0.7	0.3±0.3				
Urothoe poseidonis	19.7±8.2	31.3±8.8	18.3±9.3	7.3±4.3	33.3±18.5	33.0±8.5	55.7±11.6	16.0±5.1

Table S4 Epifauna species abundance (mean ± SE) per treatment (Ctr=Control, C=Coir, M=Mussel, C*M=Coir*Mussel).

	Schiermonnikoog				Terschelling			
Epifauna species	**Ctr**	**C**	**M**	**C*M**	**Ctr**	**C**	**M**	**C*M**
Asterias rubens							3.3±1.5	5.7±0.3
Balanus crenatus			129.3±28.8	237.7±59.4			253.0±125.8	117.0±16.5
Carcinus maenus		0.3±0.3	37.3±5.2	39.8±1.2		0.3±0.3	26.3±6.7	30.7±6.4
Corrophium sp							0.7±0.3	1.3±0.9
Crangon crangon				0.7±0.7	0.3±0.3		0.3±0.3	0.3±0.3
Crassostrea gigas spat				0.3±0.3				
Crepidula fornicata							0.3±0.3	1.0±0.6
Gammarus locusta			6.0±3.0	7.0±2.5		3.3±2.4	52.0±18.3	32.3±9.3
Idotea sp				0.3±0.3				
Jaera sp			2.3±1.9	1.3±0.7				
Melita palmata							5.7±3.2	4.3±1.2
Metridium senile			0.3±0.3				6.3±2.0	6.3±2.3
Mytilus edulis spat		0.3±0.3	19.3±12.8	22.2±2.7			18.7±10.4	7.5±3.5
Treatment addition								
Mytilus edulis adults			43.2±2.9	46.5±4.5			35.1±3.2	36.5±6.0

Chapter 6

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.

Submitted to Biological Conservation (in revision)

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 exclosure cages. To test for possible cage effects, we also placed cage controls. After 2½ 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

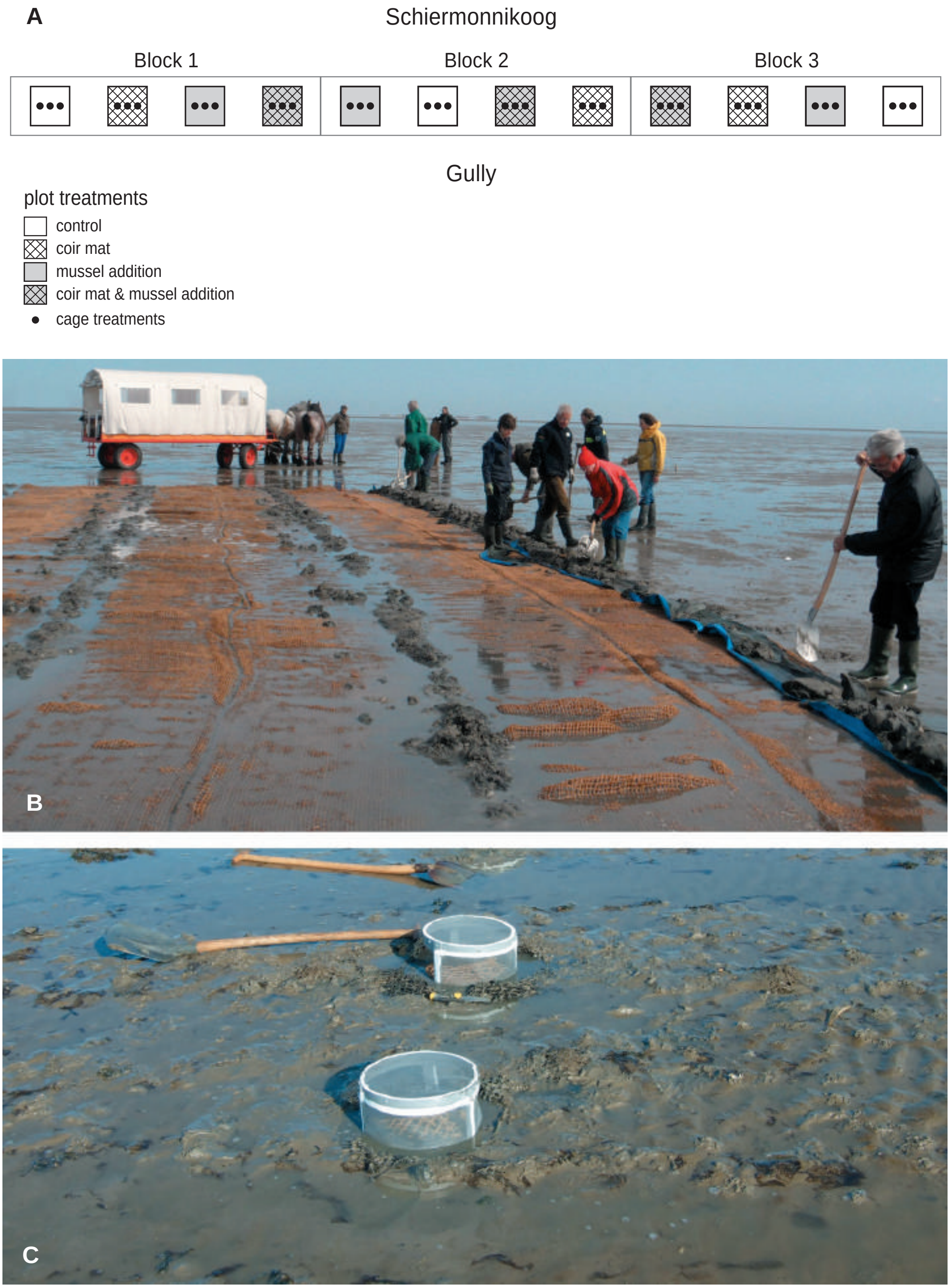

Figure 6.1 (**A**) The experiment was set up in three blocks that included four treatments, with cage treatments (control, cage control and exclosure cage) nested within these treatments. (**B**) Coir mat and adults mussels on the 20×20 m plots were added by hand. (**C**) The 30-cm high cages were pushed 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 ~2 cm. The mats were applied by hand, fixated along the edges by digging it in to a depth of ~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 ~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 ± 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 ~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 exclosure 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 exclosures 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 exclosure 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 5×5 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. 2½ 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 mm) 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 ± 6 (mean ± 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 ± 1.7%; coir: 4.8 ± 2.3%) or organic matter content (control: 0.8 ± 0.2%; coir: 0.9 ± 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 ± 0.8 (mean ± SD; n = 6) to 6.3

Figure 6.2 Top views of a control cage (**A**) and an exclosure 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.

± 0.8 % ($F_{1,6}$ = 44.2, $P < 0.001$), and organic matter increased with a factor 1.6 from 0.6 ± 0.1% to 1.0 ± 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 ± 110 (mean ± SD; n = 6) individuals/m^2, which was lower than in partial cages (564 ± 72 ind./m^2; $\chi^2 = 7.5$, $P = 0.006$). Partial cages, however, did not differ significantly from exclosures (576 ± 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 exclosures and control areas.

Mussel recruits were found almost exclusively attached to either the coir mat or adult mussels and predominately in the predator exclosures (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 exclosures. Cockle densities were highest in sediments of exclosures stabilized by a coir mat (~21000 m^{-2}), but numbers were also high in exclosures on bare sediment

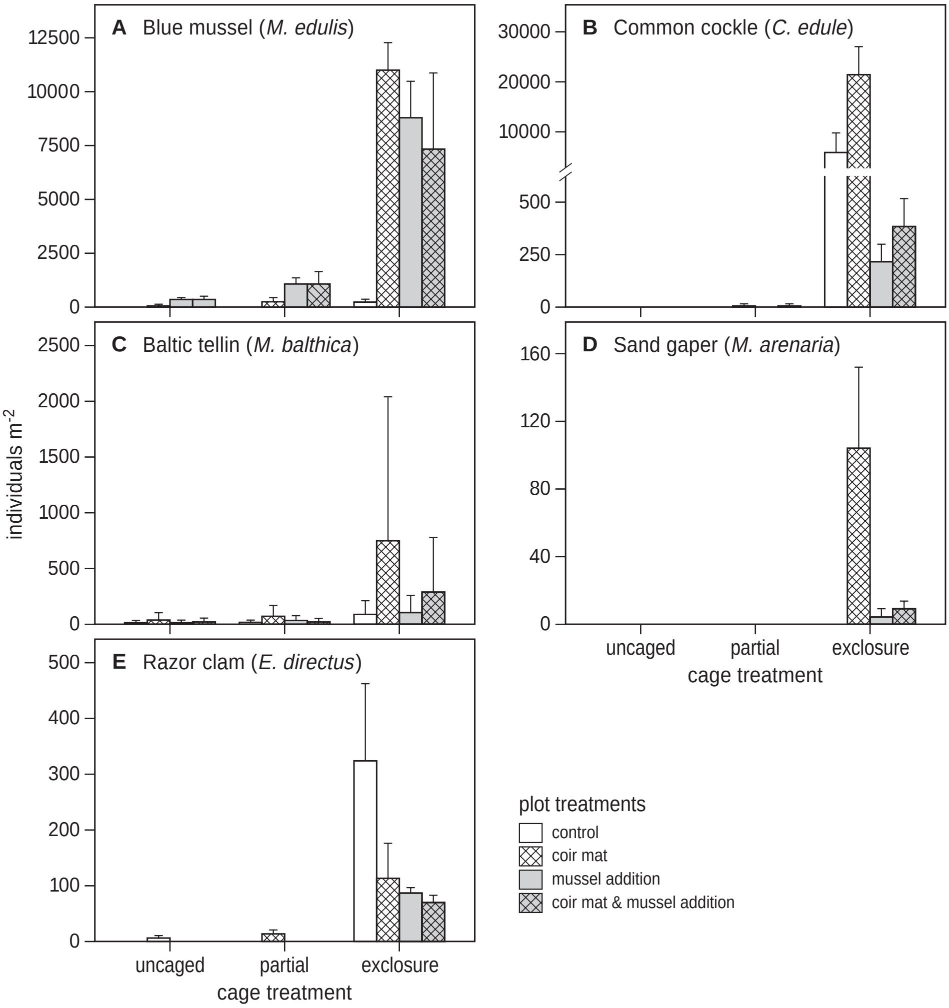

Figure 6.3 Mean number of recruits per treatment for all five bivalve species found at the end of the experimental period. Error bars denote standard errors.

(~6000 m^{-2}), resulting in a ~3-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 exclosure 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/m2 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

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Chapter 7

7

Hierarchical habitat modification shapes food web structure over long timescales

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Abstract

Food webs are often studied in ignorance of non-trophic interactions like mutualism and habitat modification, and their structure is therefore considered as a function of the properties of the trophic network itself. Using a meta-analysis combined with in-depth investigations of a seagrass ecosystem, 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 colonizing seagrass patches, that accumulate silt and form 3D structure, and burrowing crabs, that create large intertidal pools in the accumulated silt layer, dramatically alter food web structure and its temporal development. Our empirical findings show that non-trophic interactions are strongly interwoven with trophic networks, changing network dynamics over time. These outcomes provide grounds for new approaches to ecological network analyses and ecosystem conservation.

In preparation for publication

One of the great challenges in ecology is to elucidate how species interact with each other and their environments, and how these interactions drive the assembly of complex ecological networks. Ever since Darwin (1859) coined the term 'web of life', trophic interactions, the resulting food web structure and its stability have been intensively studied (e. g. May 1973; Pimm 1982; Cohen *et al.* 1990; Neutel *et al.* 2007). However, as Darwin (1859) already noted, trophic relations are only one of many types of interactions through which species can affect each other. Non-trophic interactions, like mutualism and habitat modification can also strongly affect food webs by influencing diversity, community structure or even by facilitating the persistence of entire communities (e.g. Jones *et al.* 1994; Bruno and Bertness 2001; Stachowicz 2001). However, the multi-trophic structure of natural food webs is often studied in ignorance of such non-trophic interactions (as emphasized by Berlow 2004; Ings *et al.* 2009; Olff *et al.* 2009; Fontaine *et al.* 2011) and 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). Additionally, it is increasingly recognized that understanding the assembly of complex ecological networks requires the inclusion of temporal dynamics (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, facilitation through habitat modification also has the potential to affect food web structure over time (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 habitat modification and temporal dynamics in structuring food webs, empirical studies that integrated food web assembly with habitat modification in a temporally explicit manner are lacking to our knowledge. Therefore, even after 150 years the question remains: how (much) do non-trophic interactions affect the development and structure of real food webs over time?

Here, we addressed this question by investigating how non-trophic facilitation by habitat modifying species affects food web structure and biodiversity over a long time scale. As a first indication of how habitat modifiers impact food web structure, we compared the number of species across multiple trophic levels in food webs of unmodified and modified habitats in a 18-study meta-analysis spanning 16 types of marine, freshwater and terrestrial systems (Supp. Mat., table S1). Results revealed consistently higher species numbers in food webs when those feeding networks occurred in habitats generated by habitat modifiers. On average, species richness was over 3.5 times higher in modified habitats compared to unmodified areas (table S1).

Next, we investigated the mechanisms driving food web structure in the seagrass meadows on the intertidal flats of Banc d'Arguin (Mauritania, West-Africa). Seagrasses are important ecological components of coastal zones worldwide that serve as a keystone habitat for thousands of species including large numbers of bivalves, gastropods, shrimp, fish and waterbirds (Beck *et al.* 2001; Larkum *et al.* 2006) and they are habitat modifiers in the sense that they modify their surroundings by providing aboveground structure through their shoots and by trapping suspended sediments and organic particles (Bos *et al.* 2007; van der Heide *et al.* 2007). Here, we present a series of food webs, sampled over a natural gradient of seagrass colonization in the Banc d'Arguin. We identified three distinct stages of colonization, providing us with a unique opportunity to investigate the interplay of habitat modification and food web assembly dynamics over time. Using satellite imagery (U.S. Geological Survey; 1973–2010) combined with ground truthing, we classified (1) bare, (2) colonizing (~3 year-old) seagrass and (3) long-term (>37 year-old) stable seagrass habitats (fig. 7.1. A t/m C, table S2, Supp. Mat.). Next, we selected four replicate sites for each habitat type, with a random spatial distribution and similar environmental characteristics (fig. S1 & table S3).

To examine the effects of seagrasses on their associated community and the abiotic environment (i.e. habitat modification) we determined seagrass properties and sediment conditions in the field (table S4). All four replicates of bare habitat were characterized by coarse, sandy substrate. The sites with 3-year-old, colonizing seagrasses consisted of a mosaic of seagrass patches (*Zostera noltii*) alternating with bare sediment. Average seagrass patch cover at these sites was 46.3 ± 10.3 % (mean ± SE) with a shoot density of 6246 ± 510 shoots per square meter within these patches. Similar to bare habitat, sediments in uncolonized areas consisted of coarse sands. Seagrass patches, however, had accreted a 0.05 ± 0.01 m silt layer during 3 years (fig. 7.1.D). Shoot density in the long-term stable meadows (7167 ± 575 shoots m^{-2}) did not differ much from those measured in patches at the colonizing sites, but overall seagrass cover increased significantly to 87.5 ± 3.2% ($F_{2,9} = 49.2$, $P < 0.001$). The silt layer in the long-term stable meadows had gained a height of 0.9 ± 0.2 m (fig. 7.1D), even though the mean elevation in these habitats did not differ from bare and colonizing sites (table S3).

Apart from a high seagrass cover and a thick silt layer, long-term stable meadows were also typified by a high number of intertidal pools in the silt layer (82.8 ± 9.2 pools ha^{-1}, 0.19 ± 0.01 m depth) that stand for 30 ± 4% subtidal coverage within the intertidal habitat. Using satellite image analysis, we found that these pools were spatially stagnant, but on average increased slowly in size over time (mean $size_{2004} = 37.6 \pm 2.4\ m^2$, mean $size_{2011} = 47.0 \pm 2.7\ m^2$, t = –3.307, n = 60, $P < 0.01$, Supp. Mat.). Because experimental depressions in this area have been shown to quickly disappear (van der Laan and Wolff 2006), these outcomes suggest that the pools represent the outcome of an interaction between sediment accretion by seagrasses and bioturbation by marine animals. Subsequent field surveys revealed high abundances of burrowing crabs (*Callinectes marginatus*) in the long-term stable meadows, as indicated by the number of holes (3300 ± 427 ha^{-1}, fig.

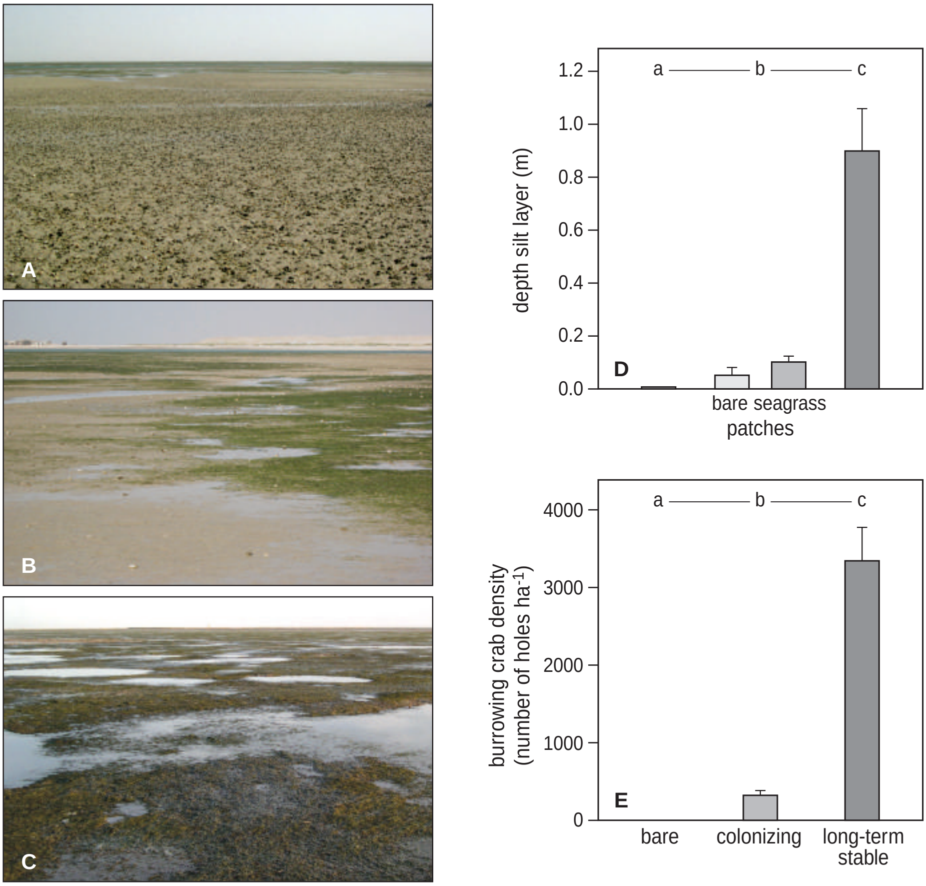

Figure 7.1 Study system. Habitat type: Bare (**A**), Colonizing (**B**) and Long-term stable (>37 years)(**C**). (**D**) Silt accumulation in each habitat. Within colonizing seagrass meadows, the silt layer was measured in seagrass patches and in bare patches, but for statistical analysis bare patches and seagrass patches were averaged. Silt accumulation differed significantly between habitats (One-way ANOVA; $F_{2,9} = 98.3$, $P < 0.001$). (**E**) Burrowing crab densities in each habitat with differing densities for each habitat (Kruskal-Wallis; $\chi^2 = 9.3$, $P = 0.009$).

7.1E), and low densities of other potentially bioturbating animal species, such as fish and birds (supplementary text, tables S5 & S6). Moreover, we found a strong positive correlation between crab hole numbers within the pools and pool size ($R^2 = 0.74$, $t = 17.1$, $P < 0.001$; fig. S2). Finally, an onsite cage experiment (fig. S3) demonstrated that within 24 hours these crabs were able to dig a hole (0.05 ± 0.02 m^2; n = 3) in the silt layer of an undisturbed seagrass meadow. This illustrates that crabs can create pools rather than only colonize them. Overall, these results combined indicate that bioturbation by crabs in the thick silt layer, possibly exacerbated by feeding birds and fish, is the driving mechanism behind the formation of these pools.

We investigated the consequences of this hierarchical organization of habitat modification by seagrasses and burrowing crabs on the food web structure by identifying and collecting all resident (i.e. not migrating with the tides) species at all sites during low tide. Nitrogen and carbon stable isotope values were determined for each species at each site and we constructed trophic interaction matrices based on literature, abundance and isotope data, and mixing models (Supp. Mat. & table S7). Next, we calculated species richness, the number of links per species and connectance (the realized fraction of all possible links) for each site as indicators for food web structure (May 1972; Williams and Martinez 2000; Neutel *et al.* 2007; Gross *et al.* 2009). We found that all three indicators strongly responded to the introduction of habitat modifiers (fig. 7.2 & table S8). Both species richness (S) and the number of links per species (L/S) strongly increased. Species richness and the number of links per species (L/S) increased 1.5 times from bare to colonizing seagrass and was another 2 and 1.5 times enhanced in long-term stable seagrass meadows, respectively (table S8). Connectance (C; defined as L/S2) 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, indicating that habitat modification by seagrasses and burrowing crabs strongly affect food web properties over time (fig. 7.2 & table S8).

To determine how much habitat modifiers impacted food web structure through non-trophic and trophic pathways, we examined the abiotic and dietary requirements of each species (Supp. Mat.). First, we investigated the importance of modification by crabs in long-term stable meadows by removing species from our dataset that depend on the intertidal pools and by comparing the newly calculated values of species richness, number of links per species and connectance to those in colonizing seagrasses and bare habitat. We found that species richness, number of links per species no longer differed between long-term stable and colonizing seagrass habitats (fig. 7.2 & table S8). However, compared to bare habitat, these two indicators were still around 1.5 times enhanced. Connectance no longer differed between all three habitats (fig. 7.2 & table S8). Second, as a test of their trophic effect, we instead removed crabs themselves and their trophic links from the matrix, and as a result also species that were only trophically connected to crabs. Contrastingly, whereas removal of non-trophic effects changed food web indicators by 44% on average, the change in indicators resulting from the removal of the trophic effect of crabs was nearly an order of magnitude lower; 4% on average.

Next, we tested the importance of seagrass modification by also removing species from our dataset that depended on either silt accumulation or aboveground structure provided by the seagrasses. Results show that all three food web indicators in both stable and colonizing habitats converged towards bare, unmodified habitats. In this case, species richness, the number of links per species and connectance no longer differed between any of the habitat types (fig. 7.2 A t/m C &

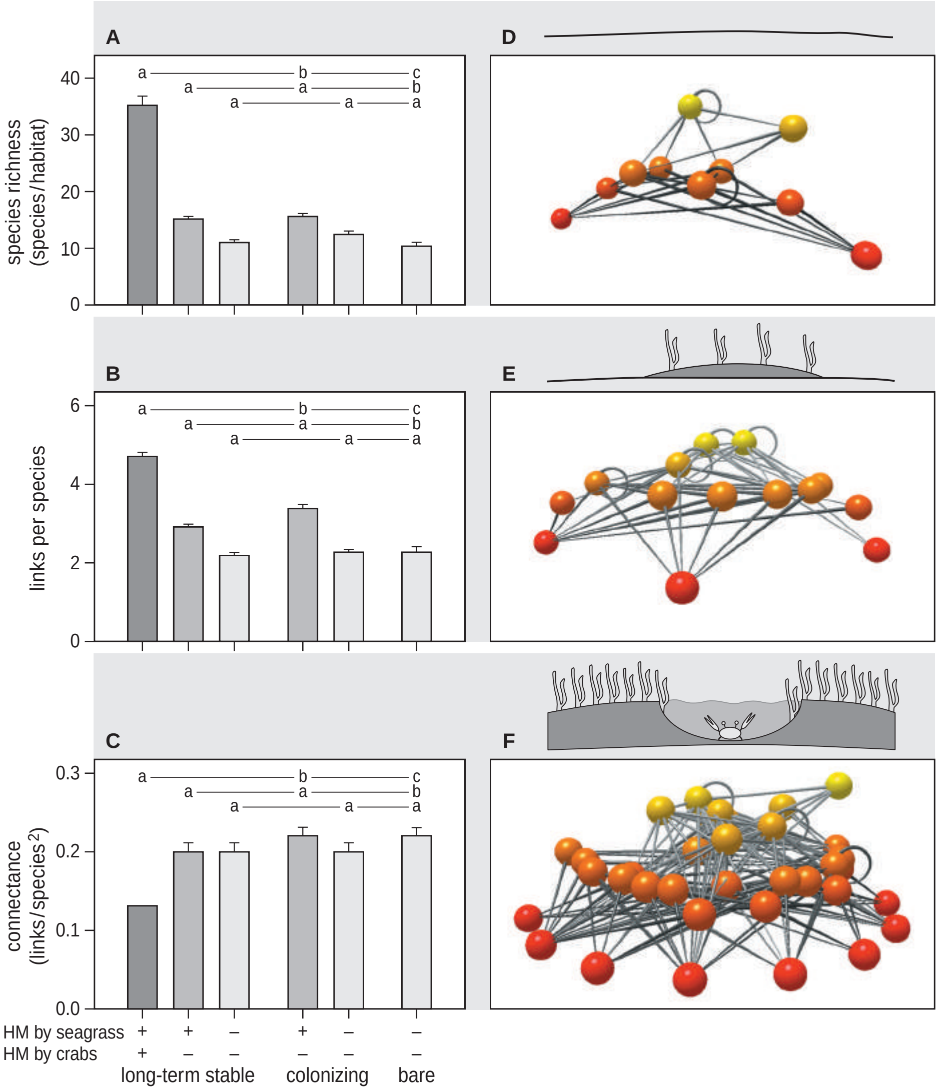

Figure 7.2 (**A**) Species richness, (**B**) links per species and (**C**) connectance for the different habitat types and habitat modification effects (HM). Letters indicate posthoc grouping; Error bars represent SEM. S and L/S are significantly higher in modified habitat, whereas C is lower in long-term stable habitats (see tables S8). Stepwise removal of species from the interaction matrix that are dependent on habitat modification (HM by crabs and HM by seagrass) increased similarity to unmodified, bare habitat. Figures (**D**), (**E**) and (**F**) show a graphical representation of the food webs in bare, colonizing and long-term stable habitat, respectively. Bare sites are typified by a relatively simple food web (**D**). Food webs have higher species richness and link density in habitat colonized by primary habitat modifiers (seagrass, **E**) and these effects are further enhance by secondary habitat modifiers (crabs, **F**) in long-term stable habitat. Node color gradually changes from red (primary producer) to yellow with increasing trophic level. Food web images were made with Network3D (Yoon *et al*. 2004; Williams 2010).

table S8), suggesting that in the absence of habitat modification by seagrass, diversity and complexity do not increase even when trophic relations with seagrass are left intact. Apart from connectance, which appears largely unaffected by both non-trophic and trophic interactions by seagrass, removal of non-trophic effects of seagrass changed food web indicators by 24% on average, whereas removal of trophic effects of primary habitat modifiers changed food web indicators by 4% on average.

Our empirical findings clearly demonstrate that non-trophic facilitation by habitat modification can strongly affect food web structure and its temporal development, not only by enhancing species numbers, but also by changing the linkages and connectance among species. Moreover, we found these non-trophic effects by habitat modifiers to be more important for food web structure than their trophic effects. Still, even though we were able to determine the effect of habitat modification on trophic dynamics, we most likely underestimated the importance of other non-trophic relations since other non-trophic interactions may further complicate the ecological network in our system (van der Heide *et al.* 2012).

Overall, our empirical findings emphasize that food web structure can be strongly controlled by non-trophic interactions and that such interactions can be highly complex in terms of being hierarchical and temporal. Furthermore, since May (1972) mathematically 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.

Due to anthropogenic disturbances many important habitat modifier-dominated systems such as seagrass meadows, rainforests and coral reefs, are currently degrading worldwide at accelerating rates (e.g. Hodgson and Liebeler 2002; Foley *et al.* 2007; Waycott *et al.* 2009). Our study illustrates that the development of such diverse and complex communities can take decades due to the long-term accumulative effects of habitat modification. By showing that multiple species can affect food web dynamics across long timescales by interactively modifying the abiotic conditions, we illustrate that conservation and restoration efforts should not only focus on single species or interaction types. Instead, multiple species should be considered within an integrated network of multiple interaction types in order to adequately determine ecosystem responses to changing conditions.

Supplementary materials

Materials and Methods

Literature survey

To investigate the worldwide importance of habitat-modifying species in structuring food webs, we searched for examples of habitat modification on species distribution across multiple ecosystem types (table S1). Criteria for including a study were: (1) species richness was measured in the presence and absence of habitat modifying species, and (2) habitat modification affected different trophic levels (i.e. either different groups of species or different trophic levels within a group of species. The increase of species richness due to the presence of habitat-modifying species was calculated (%).

Remote sensing and GIS analyses

We used the normalized differences vegetation index (NDVI) obtained from Landsat 5 and 7 images (U.S. Geological Survey, resolution 30 m) to determine if and when seagrass colonized intertidal areas at the Banc d' Arguin. Images were available for the years 1973, 1985, 1994, 1999 to 2003, 2007, 2009 and 2010. Based on these analyses and after ground truthing in the field in 2011, we selected 4 replicates for three types of habitat: (1) bare habitat that was continuously bare from 1973 onwards, (2) colonizing seagrass habitat that was bare until 2007–2009 and was subsequently colonized by seagrass and (3) long-term stable seagrass habitat that had been continuously covered with seagrass from 1973 (table S2). All sites were selected based on a random spatial distribution (fig. S1) and similar environmental characteristics (see below).

To determine the change in intertidal pool size in long-term stable seagrass meadows, we analysed Google Earth images based on Quickbird (October 2004) and Geoeye (March 2011). Using Google Earth Pro, we measured the surface of 60 clearly visible pools at 5 long-term stable areas on the October 2004 image and subsequently, we measured the surface of the same pools again on the March 2011 image. All measured pools had comparable sizes to those observed in the long-term stable meadows during ground truthing (pool surface area < 75 m^2). The number of pools per ha and their relative cover was determined at each long-term stable site during field surveys.

Environmental characteristics

In order to exclude possible abiotic environmental effects in our study system, we tested whether environmental characteristics (e.g. inundation time, hydrodynamic conditions) differed between habitat types. We measured tidal elevation and distance to the gulley and determined an exposure index as a measure for hydro-

Table S1 Meta-analysis of studies investigating effects of habitat modifiers on species richness across multiple trophic levels.

Habitat	HM species	Focal community	Species richness			References
			+HM	-HM	Rel. effect	
Marine						
Kelp forest	Giant kelp	Subtidal	274	176	1.57	Graham 2004
Intertidal mudflats	Blue mussels	Macrofauna and flora	25.6	3	8.53	Norling & Kautsky 2007
Intertidal mudflats	Blue mussels	Macrofauna and flora	10.6	7.1	1.49	Unpublished data Van der Zee *et al.* 2012
Intertidal mudflats	Sand mason worms	Macrofauna	37	22	1.68	Callaway 2006
Rocky shores	Purple mussels	Invertebrates	28.9	2.7	10.7	Silliman *et al.* 2011
Coral reefs	Coral	Fish	17.2	3.4	5.06	Cabaitan *et al.* 2008
Coral reefs	Coral	Fish	~12	~8	1.5	Syms & Jones 2000
Temperate seagrass meadows	Dwarf Eelgrass	Macrofauna	~24	~9	2.73	Do *et al.* 2011
Temperate seagrass meadows	Eelgrass	Macrofauna	30	11	2.67	Böstrom & Bonsdorff 1997
Tropical seagrass meadows	Tasman Grasswrack	Macrofauna	33	15	2.20	Edgar *et al.* 1994
Tropical seagrass meadows	Dwarf eelgrass & marbled swim crabs	Macrofauna	33.3	8.8	3.78	*
Cobble beaches	Smooth cordgrass & ribbed mussels	Macrofauna and flora	~5.5	~2.5	2.20	Altieri *et al.* 2007
Fresh water						
Forest headwater streams	Eastern hemlock	Aquatic invertebrates	47	32	1.47	Snyder *et al.* 2002
Dune slack ponds	Watermilfoil	Macrofauna	16.8	12.3	1.37	**
Terrestrial						
Oak/cypress forest	Spanish moss	Invertebrates	5.9	0.7	8.43	Angelini and Silliman 2014
Tropical forest	Leguminous trees & epiphytes	Insects	113	83.9	1.35	Cruz-Angón *et al.* 2009
Alpine zone	Cushion plants	Plant and arthropods	~7.3	~5.3	1.38	Molenda *et al.* 2012
Cottonwoods	Pale-headed Aspen leafroller moth	Arthropods	~ 11	~2	5.5	Martinsen *et al.* 2000
Mean increase					3.53	

*: this paper; **: unpublished data from our group.

dynamic exposure. We calculated the maximum and modified effective fetch length to calculate the exposure index (Howes et al. 1999). This index varies from 0 (very protected) to 5 (exposed). Results are shown in table S3.

Sediment and benthos field surveys

Field surveys were carried out on the intertidal mudflats near Iwik in the Parc National du Banc d' Arguin (PNBA)(19°52′42″ N, 16°18′50″ W, fig. S1) in January 2011. At each sampling site, a circle with a 50-m diameter was established prior to sampling. Within this circle, 4 sediment and benthos cores were taken and the silt layer height was measured 4 times with a gauge rod. Sediment cores were taken

Table S2 Habitat development over time of each site based on NDVI landsat 5 and 7 images (U.S. Geological Survey, resolution 30 m) for 1973-2010 and field observations in 2011 (B=bare sediment, S=vegetated with seagrass).

	Sites											
	Bare:				Colonizing:				Long-term stable:			
Year	B1	B2	B3	B4	C1	C2	C3	C4	L1	L2	L3	L4
1973	B	B	B	B	B	B	B	B	S	S	S	S
1985	B	B	B	B	B	B	B	B	S	S	S	S
1994	B	B	B	B	B	B	B	B	S	S	S	S
1999	B	B	B	B	B	B	B	B	S	S	S	S
2000	B	B	B	B	B	B	B	B	S	S	S	S
2001	B	B	B	B	B	B	B	B	S	S	S	S
2002	B	B	B	B	B	B	B	B	S	S	S	S
2007	B	B	B	B	S	B	B	S	S	S	S	S
2009	B	B	B	B	S	S	S	S	S	S	S	S
2010	B	B	B	B	S	S	S	S	S	S	S	S
2011	B	B	B	B	S	S	S	S	S	S	S	S

Table S3 Environmental characteristics. A one-way ANOVA was used for tidal elevation, distance to gulley, maximum fetch and modified fetch. A Kruskal Wallis test was used for exposure index.

	Mean values ± SE			Statistics		
	Bare (B)	Colonizing (C)	Long-term stable (L)	df (err.)	F or χ^2	*P*
Tidal elevation (NSI in cm)	-263±11	-247±15	-255±5	2 (9)	0.53	0.609
Distance to gulley (km)	0.09±0.03	0.14±0.04	0.90±0.03	2 (9)	0.66	0.541
Fetchmax (km)	7.77±2.02	8.61±1.20	20.85±10.45	2 (9)	1.69	0.238
Fetchmod (km)	0.76±0.24	0.82±0.18	4.97±3.12	2 (9)	3.35	0.082
Exposure index (class 0-5)	0.5±0.5	0.5±0.5	1.75±0.63	2	3.04	0.219

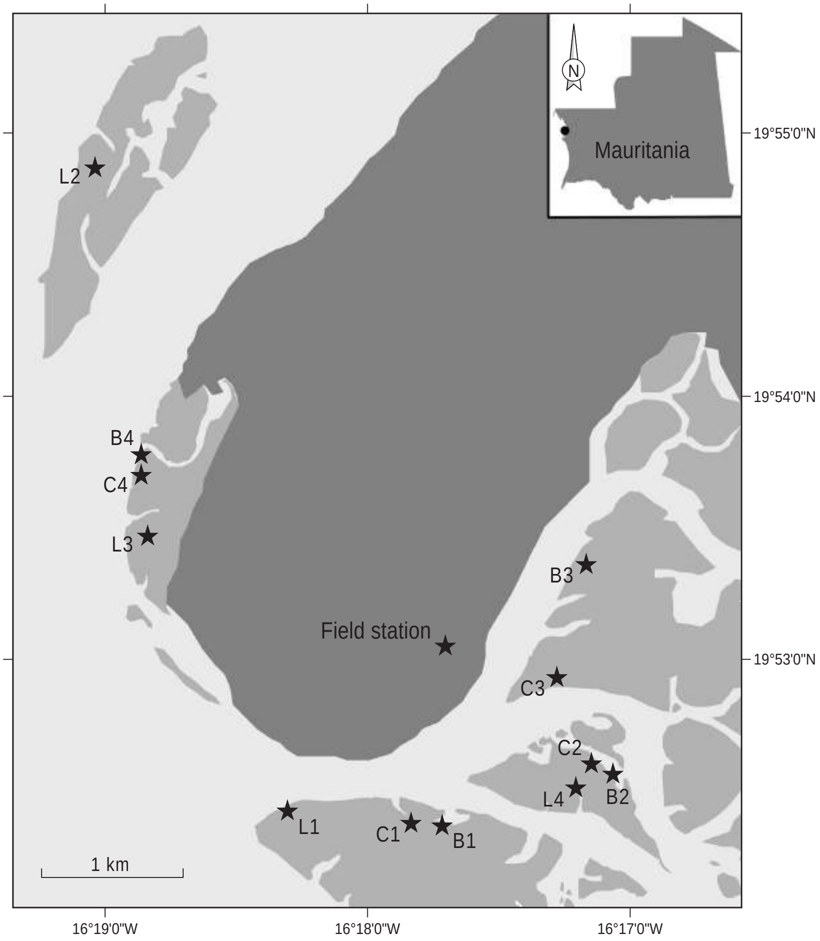

Figure S1 Map of the study area in the Banc d'Arguin, Mauritania. Light grey areas indicate water, intermediate grey areas indicate mudflats exposed during low water and land is represented by dark grey. Black stars represent the positions of the different study sites and the PNBA field station.

with a 12.5-cm^2 PVC corer to a depth of 5 cm. Organic matter content in freeze-dried sediment samples was estimated as weight Loss On Ignition (LOI; 5 h, 550°C). Silt content (% sediment fraction $<63\mu$m) was determined by a Particle size Analyzer (Malvern). Benthos samples were taken with a 179-cm^2 stainless steel core to a depth of 20 cm, after which the samples were sieved over a 1 mm mesh. To determine crustacean densities, four 5-m long hauls were taken with a shrimp net at each site. At the long-term stable sites, the water column of 4 intertidal pools was separately sampled. Crustaceans were sampled by taking 1 haul with a shrimp net from the edge to the centre of a pool, while fish were sampled by pulling a beach seine net through each pool. Additionally, depth and size was measured for each pool. All fauna was identified to species level in the laboratory.

Stable isotope measurements

Apart from the abovementioned species and sediment samples, we separately collected detritus and primary producers (algae, diatoms, seagrasses, epiphytes and detritus) in each area and obtained particulate organic matter samples from the water column (wPOM). wPOM was collected by filtering several litres of seawater over pre-combusted Whatman GF/F glass fibre filters, while sPOM (particulate organic matter from the sediment) was analysed from the sediment samples that were cleared of all living biomass. Benthic diatoms were scraped from the sediment surface. After migration through a mesh (80 Mu) into combusted sand, they were collected in filtered seawater and also filtered over glass fibre filters (Eaton and Moss 1966). We took muscle tissue samples from fish and soft tissue from invertebrates wherever possible, but used the whole animal for smaller samples. All material was rinsed with demineralised water, oven-dried at 50°C for 48 h and ground. We took sub-samples for separate carbon and nitrogen analyses when samples contained inorganic calcified structures. These samples were decalcified for carbon analysis by adding HCl. In total 10 fish species, 46 invertebrate species, 6 primary producers, sPOM, wPOM and zooplankton were analysed for isotopic signature.

Burrowing crabs: abundance and behaviour

At each site, two transects (50 m long and 10 wide) were established and marked with pvc- poles at the corners. The number of crab (*Callinectes marginatus*) holes within these transects was used as a proxy for crab density and activity per site on the emerged tidal flats. At three of our long-term stable sites (L1, L3 and L4), we measured pool size and depth of 18, 31 and 11 intertidal pools, respectively. Within these pools, the number of crab holes was scored to determine the average crab density per pool and the relation between number of crabs per pool and pool size (fig. S2). Both measurements were combined to determine the total amount of crab holes per habitat type (fig. 7.1E & table S4).

In an additional cage-experiment, we determined whether crabs were able to dig holes in the silt layer of a healthy, undisturbed seagrass meadow. A circular cage (50 cm in height with a diameter of 125 cm and mesh size of 1 cm; fig. S3) was pushed into the sediment with full seagrass cover, to a depth of approximately 25 cm. Crabs with an average carapace width of 7.6 ± 0.4 cm were caught in the direct surroundings and released in separate cages ($n = 3$). The length and width of present crab holes were measured after 24 hours.

Fish abundance

Ray abundance on the tidal flats was determined through visual surveys from a boat along random transects, within 10 meters of each side of the front of the boat at a maximum speed of 5 km h^{-1}. Transect lengths were determined using GPS. Fourteen transects (~250–300 m long) were carried out by boat at sites L1, L3 and L4 (42

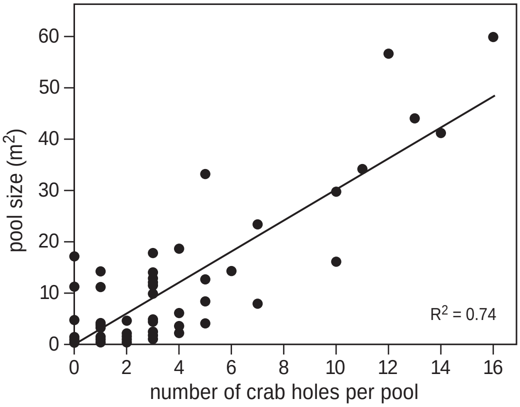

Figure S2 Positive linear relationship ($y = 3.04x$, $t = 17.1$, $R^2 = 0.74$, $P < 0.001$) between number of crabs per pool and pool size (m^2).

transects in total) in October 2012. Rays were identified up to species level whenever possible, but other taxonomic classes (family, order) were occasionally used when identification up to species level was not possible. We used the average number of rays per transect per site as a measure of abundance per hectare on the tidal flats (table S5).

Table S4 Habitat characteristics with ANOVA values and Tukey-Posthoc groups (B=bare, C=colonizing, L=long-term stable habitat) for seagrass cover, organic matter, grain size and depth of the silt layer. To obtain normality of variance of residuals, organic matter was reciprocally transformed ($y = 1/x$) and grain size and depth of the silt layer were both log transformed ($y = \log10(x)$). Shoot density and crab density were not normally distributed, also not after transformation and for these habitat characteristics a Kruskal Wallis test was used in combination with Mann-Whitney U tests. Sediment organic matter, grain size and the silt layer were measured in seagrass patches and in bare patches, but for statistical analysis bare patches and seagrass patches were averaged. Significance levels: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

	Mean values ± SE			**Statistics**			
	Bare (B)	Colonizing (C) bare/seagrass patches	Long-term stable (L)	df (err.)	F or χ^2	P	Posthoc groups (B, C, L)
Seagrass cover (%)	0±0	46.3±10.3	87.5±3.2	2 (9)	49.2	***	a, b, c
Shoot density (# m^{-2})	0±0	6246±510	7167±575	2	8.3	*	a, b, b
Organic matter (%)	1.7±0.2	1.6±0.2/2.1±0.2	8.6±0.4	2 (9)	47.4	***	a, a, b
Grain size (% <63μm)	13.0±2.6	11.6±1.2/16.6±3.1	71.3±4.2	2 (9)	40.4	***	a, a, b
Depth silt layer (m)	0±0	0.05±0.0/0.1±0.0	0.9±0.2	2 (9)	98.3	***	a, b, c
Crab density (# ha^{-1})	0±0	308±54	3300±427	2	9.3	**	a, b, c

Figure S3 A circular crab enclosure (50 cm in height (25 cm belowground) with a diameter of 125 cm and mesh size of 1 cm) was used to test whether crabs were able to create holes in a healthy undisturbed seagrass meadow. (Photo: Marjolijn Christianen).

To determine the abundance of rays and other potentially bioturbating fish species in the intertidal pools, we placed underwater cameras (GoPro HD HERO2, Woodman Labs Inc, USA) in pools at sites L1, L3 and L4. Per site, the size of three pools were measured and subsequently monitored by cameras taking photographs at 10-s intervals across one full high tide period. All fish species that entered the pools were marked as potentially bioturbating species. Each fish was identified to species level whenever possible and other taxonomic classes (family, order) were used when identification up to species level was not possible. Average numbers per pool for each species were used to calculate the abundance per hectare per site in the pools (table S5).

Shorebird abundance

Shorebird abundance was measured in a 60×100 m square (0.6 ha, marked with PVC poles) at sites L1, L3 and L4. During low tide, the number of feeding shore birds was scored every 15 minutes in the square from a distance of ~400 m, using a telescope (zoom ocular 20–60×; ATM 80 HD, Swarovski, Absam, Austria). Counting started when the water had retreated from the marked square until the area was inundated again. Birds were counted during three complete tidal cycles in October 2012. We used the average number of birds as a measure of abundance per hectare on the tidal flats (table S6). When shorebirds were encountered in our marked square, we scored whether they were foraging in or outside the intertidal pools. Average numbers per pool for each species were used to calculate the abundance per hectare in the pools (table S6).

Food web analyses

Based on abundance and size data, literature, the WoRMS (World Register of Marine Species) database and connected online databases, we determined potential trophic relations for each species and constructed a maximized interaction matrix for each site that included all potential trophic links. Next, we used stable isotope biplots and Bayesian mixing models (R-package SIAR) per site for all consumers to estimate of the relative contribution of potential resources to the consumer's diet. Based on these analyses, we removed trophic links where a resource contributed less then 5%

Table S5 Ray and other fish densities (number ha^{-1}) at three long-term stable sites. Densities were determined for the number of rays on the tidal flats and for the number of rays and other fish species present in the pools at the same tidal flat.

	Mean values ± SE			
Ray-Fish species	**Site L1**	**Site L3**	**Site L4**	**Total**
TIDAL FLAT				
Dasyatis marmorata	0.11±0.11	0±0	0.85±0.85	0.32±0.27
Rhinobatos sp	1.09±0.43	0.79±0.37	0.78±0.53	0.89±0.10
Total				0.60±0.28
POOL				
Dasyatis marmorata	0.23± 0.15	0.43±0.43	0.18±0.18	0.28±0.08
Rhinobatos sp	0.31±0.25	0.04±0.04	0.09±0.06	0.15±0.08
Total				0.21±0.07
Arius heudelotii	0.19±0.11	2.88±2.77	7.31±3.99	2.28±1.07
Dicentrarchus punctatus	1.34±1.34	2.88±1.95	0.15±0.15	1.46±0.79
Diplodus sp	4.80±3.80	6.55±6.55	0.03±0.03	3.80±2.00
Ephippion guttiferum	0.27±0.12	0.60±0.60	0.02±0.02	0.30±0.17
Epinephelus aeneus	0.31±0.26	0.94±0.94	7.05±3.55	2.76±2.5
Epinephelus sp	0±0	0±0	1.18±0.54	0.39±0.39
Mugil cephalus	3.51±3.45	33.36±32.38	26.97±19.87	21.28±9.07
Rhyzoprionodon acutus	0.04±0.04	0±0	0±0	0.01±0.01
Sciaena umbra	0.04±0.04	0.04±0.04	1.13±0.88	0.40±0.36
Tilapia guineesis	0±0	28.60±28.40	0±0	9.54±9.54
Umbrina canariensis	0±0	0±0	7.90±6.60	2.63±2.63
Total				4.08±1.90

to the diet of the consumer. Finally, we used the obtained interaction matrix to calculate species number (S), number of links per species (L/S) and connectance (C; defined as L/S^2).

To elucidate the effects of hierarchical habitat modification by seagrass and burrowing crabs on the food web structure we excluded modification by crabs and seagrass in a stepwise manner. Based on the physiological constraints of each species, we first constructed a modification-dependence matrix in which the dependence of each species on modification by seagrass (aboveground structure, silty sediment) and crabs (intertidal pools) was expressed as either 1 (dependent) or zero (not dependent). Based on these data, we then removed all species dependent on intertidal pools from each stable site and reconstructed the trophic-interaction matrix. Next, we re-calculated species-richness, the number of links per speciesa and connectance, based on the reconstructed interaction matrix. Finally, this process was repeated for species dependent on modification by seagrasses.

Table S6 Shorebirds densities (number ha^{-1}) at three long-term stable sites. Densities were determined for the number of shorebirds foraging on the tidal flats and for the number of birds foraging in the pools within the same tidal flat.

	Mean values ± SE			
Shorebird species	**Site L1**	**Site L3**	**Site L4**	**Total**
TIDAL FLAT				
Phoenicopterus roseus	0±0	0±0	0.04±0.04	0.01±0.01
Pelecanus onocrotalus	0.04±0.04	0±0	0±0	0.01±0.01
Egretta gularis	0.59±0.21	0.16±0.16	0.48±0.14	0.36±0.18
Ardea cinerea monicae	0.07±0.04	0±0	0.12±0.06	0.06±0.03
Egretta garzetta	0.09±0.09	0.09±0.06	0.04±0.03	0.07±0.01
Platalea leucorodia (*balsaci*)	0±0	0.03±0.02	0.14±0.09	0.06±0.04
Numenius arquata	0.69±0.11	0.44±0.19	1.27±0.40	0.80±0.24
Limosa lapponica	2.71±0.66	1.09±0.37	7.07±2.67	3.62±1.79
Total				0.63±0.22
POOL				
Phoenicopterus roseus	0±0	0±0	0.04±0.04	0.01±0.01
Pelecanus onocrotalus	0±0	0±0	0±0	0±0
Egretta gularis	0.09±0.06	0±0	0.11±0.04	0.07±0.03
Ardea cinerea monicae	0±0	0±0	0±0	0±0
Egretta garzetta	0±0	0.05±0.03	0±0	0.02±0.02
Platalea leucorodia (*balsaci*)	0±0	0.03±0.02	0.07±0.07	0.03±0.02
Numenius arquata	0.22±0.09	0.13±0.07	0.16±0.09	0.17±0.03
Limosa lapponica	0.18±0.05	0.13±0.05	0.57±0.49	0.29±0.14
Total				0.07±0.02

To elucidate the trophic effects of burrowing crabs and seagrass on the food web structure, we repeated the procedure described above by excluding species from the matrices that were trophically dependent on crabs and seagrass in the same stepwise manner. An overview of the results is shown in table S8.

Statistical analyses

Normality of variance of residuals was checked with the Shapiro-Wilks test ($P = 0.05$) and further confirmed by graphical validation of the final models. If the normality assumption was not met, data were transformed or non-parametric tests were used. All relevant transformations are mentioned in the figures or table legends in the supplementary materials. The difference in pool size over time was analyzed with a paired samples t-test. Environmental and habitat characteristics were analyzed with a one-way ANOVA, followed by a post-hoc Tukey HSD test, or with a Kruskal Wallis test, followed by Mann-Whitney U tests. To correct for the multiple testing problem during the Mann-Whitney U tests, significance levels were adjusted based on the false discovery rate control (Benjamini and Hochberg 1995). An overview of the statistical output from these analyses is provided in tables S3 and S4. The food web analyses were done with a one-way ANOVA, followed by a post-hoc Tukey HSD test (see table S8).

Supplementary text

To investigate whether other animals play a significant role in the formation and maintenance of the intertidal pools, we determined densities of possible bioturbating fish and shore birds species (see Materials and Methods). Based on literature, we suspected rays to be one of the more important bioturbating species (Orth 1975; Townsend and Fonseca 1998). We found an average density of 0.60 ± 0.28 rays ha^{-1} on the intertidal flats and an average density of 0.21 ± 0.07 rays ha^{-1} in the pools (table S5). In addition, observations with underwater cameras in the pools yielded an average of 4.08 ± 1.90 individuals ha^{-1} pool of other potentially bioturbating fish (table S5). Apart from fish, we also investigated the presence of shorebirds as possible bioturbating species. Only bird species that were large enough to walk in the pools or could enter the pools by swimming or diving were counted during our observations (table S6). We found an average density of 0.63 ± 0.22 birds ha^{-1} on the tidal flats and an average density of 0.07 ± 0.02 birds ha^{-1} in the tidal pools (table S6). Overall, these results suggest that both fish and bird numbers were too low to explain the high numbers of intertidal pools (82.8 ± 9.2 pools ha^{-1}), especially in comparison to the high number of burrowing crabs (3151 ± 500 ha^{-1}) present in the area and their strong correlation with pool size (fig. S2).

Table S7 Feeding modes.

Species	Group	Feeding mode	Reference
Algae	Algae	-	Round 1984
Abra tenuis	Bivalve	deposit feeder, sPOM, diatoms, detritus/debris	Hughes 1973
Anadara senilis	Bivalve	suspension feeder	Yoloye 1975
Diplodonta diaphana	Bivalve	suspension feeder, wPOM, plankton, sPOM	Macdonald *et al.* 2010, Arruda *et al.* 2003
Dosinia isocardia	Bivalve	suspension feeder, wPOM, plankton, sPOM	Rodhouse and Roden 1987
Loripes lacteus	Bivalve	symbiose met bacterien, suspension feeder	Johnstone *et al.* 1994
Petricola sp	Gastropods	suspension feeder	Appeltans *et al.* 2009
Tellina sp	Bivalve	deposit feeder, sPOM, diatoms, detritus/debris	Yonge 1949, Compton *et al.*2008
Ampithoe sp	Crustacea	seagrass, detritus, epiphytes, algae	Mukai and Iijima 1995, Robertson and Mann 1980
Callinectes marginatus	Crustacea	omnivore: eats everything from plant material, detritus to fish	Laughlin 1982, Mascaro *et al.* 2007
Carcinus mediterraneus	Crustacea	amphipods, isopods, polychaetes, gastropods, bivalves, seagrass, alge, detritus	Baeta et al 2006, Chen *et al.* 2004
Idotea chelipes	Crustacea	omnivore: algae, animal tissue, other isopods, epiphyton	Naylor 1955, Hootsmans and Vermaat 1985
Palaemon sp	Crustacea	amphipods, isopods, polychaetes, gastropods, bivalves, seagrass, sPOM,	Guerao and Ribera 1996, Berglund 1980
Diatoms	Diatoms	-	Barranguet *et al.* 1997
Epiphyton	Epiphytes	nutrients also from seagrass leaves	Orth and Van Montfrans 1984 and references therein
Conger conger	Fish	osteichthyes, crustacean, cephalopoda, polychaeta	Cau and Manconie 1984, O'Sullivan *et al.* 2004
Atherina presbyter	Fish	small crustacea and fish larvae	Quignard and Pras 1986
Diplodus sargus	Fish	omnivore: algae, sea urchins, polychaetes, gastropods and amphipods	Figueiredo *et al.* 2005
Eucinostomus melanopterus	Fish	amphipods, isopods, crabs, bivalves, gastropods, juvenile fish, detritus, diatoms, algae	Gning *et al.* 2010
Mugil cephalus	Fish	algae, diatoms, crustaceans, polychaetes, bivalves, fish, detritus, zooplankton	Soyinka 2008, Blay 1995, Michaelis 1993
Pomatoschistus microps	Fish	polychaetes, bivalves, amphipods, isopods, shrimps, juvenile fish	Salgado *et al.* 2004, Leitao *et al.* 2005
Solea senegalensis	Fish	polychaetes, bivalves, gastropoda, amphipods, isopods	Kostecki *et al.* 2012, Teixeira and Cabral 2010
Stephanolepis hispidus	Fish	amphipods, bivalves, isopods, decapods, gastropods,algae, detritus, seagrass leaves	Prado and Heck 2011
Syngnathus typhle	Fish	amphipods, isopods, shrimps, polychaetes, bivalves, gastropoda, juvenile fish, algae	Oliveira *et al.* 2007
Tilapia guineensis	Fish	sPOM, juvenile fish, zooplankton, aquatic invertebrates, detritus, bivalves, shrimp	Louca *et al.* 2010
Bittium reticulatum	Gastropods	microalgal grazers, periphyton	Rueda *et al.* 2009
Bulla adansoni	Gastropods	algae, diatoms, seagrass, copepods, foraminiferans, larvae of molluscs, epiphytes	Malaquias *et al.* 2008
Clavatula bimarginata	Gastropods	omnivore	WoRMS 2009
Columbella rustica	Gastropods	herbivore: algae, diatoms, epiphytes, live on seagrass	deMaintenon 1999
Crepidula goreensis	Gastropods	filter feeder: diatom particles, wPOM and sPOM	Rueda *et al.* 2009, Orton 1912
Dendrodoris sp	Gastropods	sponges, epiphyton	Zhukova and Eliseikina 2012

Species	Group	Feeding mode	Reference
Elysia sp	Gastropods	herbivore that feeds on seagrass and algae	Clark 1975, Jensen 1983
Gibbula umbilicalis	Gastropods	herbivores that feeds on epiphytes and algae	Steneck and Watling 1982 and references therein
Nassarius miga	Gastropods	omnivore, scavenger, surface deposit feeder	Morton and Jones 2003
Smaragdia viridis	Gastropods	seagrass	Holzer *et al.* 2011, Rueda *et al.* 2009
Tricola pulla	Gastropods	diatoms, detritus, algae, microalgal or periphyton grazers	Rueda *et al.* 2009
Oligochaeta	Oligochaete	deposit feeders, sPOM, detritus, diatoms	Giere 2006
Aphelocheata sp	Polychaeta	surface deposit feeder, transporting sand, debris and diatoms	Farke 1979
Euclymene sp	Polychaeta	subsurface deposit feeder, detritus, sPOM	Chardy and Dauvin 1992, Martin *et al.* 2000
Euphrosine sp	Polychaeta	carnivore: sponges, foraminiferans	Fauchald and Jumars 1979 and references therein
Glycera alba	Polychaeta	carnivore on other worms	Fauchald and Jumars 1979, Ockelmann & Vahl 1970
Harmothoe sp	Polychaeta	carnivore, small crustaceans(amphipods), gastropods, polychaetes	Fauchald and Jumars 1979, Sarvala 1971
Heteromastus filiformis	Polychaeta	surface deposit feeder, transporting sand, debris and diatoms, algae, detritus	Fauchald and Jumars 1979, Macdonald *et al.* 2010
Lanice sp	Polychaeta	detrivore, detritus, diatoms, sPOM, suspension feeder, wPOM	Fauchald and Jumars 1979, Buhr 1976
Marphysa sanguinea	Polychaeta	omnivore	Fauchald and Jumars 1979
Nephtys sp	Polychaeta	omnivore: molluscs, crustaceans and other polychaetes, diatoms, detritus, sPOM	Fauchald and Jumars 1979, Arndt and Schiedel 1997
Nereis sp	Polychaeta	predator and filter feeder: sPOM, wPOM, algae, diatoms, other worms, small isopods	Fauchald and Jumars 1979 and references therein
Ophelia sp	Polychaeta	deposit feeders, sPOM, detritus, diatoms	Fauchald and Jumars 1979 and references therein
Petaloproctus terricola	Polychaeta	detritus, diatoms, small animals, suspension feeding, wPOM, sPOM, zooplankton	Fauchald and Jumars 1979 and references therein
Polydora antennata	Polychaeta	deposit feeders, sPOM, detritus, diatoms, suspension feeder wPOM, zooplannkton	Fauchald and Jumars 1979, Macdonald *et al.* 2010
Scolelepis squamata	Polychaeta	deposit feeder, suspension feeder, wPOM, sPOM, diatoms, zooplankton	Fauchald and Jumars 1979, Dauer 1983
Scoloplos capensis	Polychaeta	deposit feeder	Fauchald and Jumars 1979, Rice *et al.* 1986
Terebellidae sp	Polychaeta	deposit feeder, sPOM, diatoms, detritus/debris	Fauchald and Jumars 1979 and references therein
Cymodocea nodosa	Seagrass	-	Hemminga *et al.* 1991 and references therein
Halodule wrightii	Seagrass	-	Hemminga *et al.* 1991 and references therein
Zostera noltii	Seagrass	-	Hemminga *et al.* 1991 and references therein
Zooplankton	zooplankton	wPOM, sPOM, zooplankton	Suthers and Rissik 2009

Table S8 Change in food web structure indicators due to stepwise removal of (1) non-trophic facilitation effects (i.e., habitat modification) and (2) trophic effects (i.e., direct removal of the species from the network) of of crabs and seagrass respectively. Table shows ANOVA values and Tukey-Posthoc groups (B=bare, C=colonizing, L=long-term stable habitat). Significance levels: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

	Mean values ± SE			**Statistics**		
	Long-term stable (L)	Colonizing (C)	Bare (B)	F	*P*	Posthoc groups (L, C, B)
All included						
Number of species (S)	35.25±1.65	15.50±0.65	10.25±0.85	134.5	***	a, b, c
Links per species (L/S)	4.71±0.11	3.37±0.12	2.25±0.17	46.35	***	a, b, c
Connectance (L/S^2)	0.13±0	0.22±0.01	0.22±0.01	74.18	***	a, b, b
- Crab facilitation						
Number of species (S)	14.50±0.50	15.50±0.65	10.25±0.85	16.70	***	a, a, b
Links per species (L/S)	2.92±0.05	3.37±0.12	2.25±0.17	20.23	***	a, a, b
Connectance (L/S^2)	0.20±0.01	0.22±0.01	0.22±0.01	2.06	ns	a, a, a
- Seagrass facilitation						
Number of species (S)	11.00±0.58	12.50±0.5	10.25±0.85	3.00	ns	a, a, a
Links per species (L/S)	2.18±0.09	2.46±0.09	2.25±0.17	1.16	ns	a, a, a
Connectance (L/S^2)	0.20±0.01	0.20±0.01	0.22±0.01	1.29	ns	a, a ,a
- Crabs						
Number of species (S)	34.25±1.65	14.50±0.65	10.25±0.85	127.0	***	a, b, b
Links per species (L/S)	4.27±0.23	2.96±0.10	2.25±0.17	35.33	***	a, b, c
Connectance (L/S^2)	0.13±0	0.21±0.01	0.22±0.01	117.4	***	a, b, b
- Seagrass						
Number of species (S)	33.25±1.65	13.50±0.65	10.25±0.85	120.0	***	a, b, b
Links per species (L/S)	4.21±0	3.10±0.09	2.25±0.17	30.88	***	a, b, c
Connectance (L/S^2)	0.13±0	0.23±0.01	0.22±0.01	105.9	***	a, b, b

Chapter 8

8

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 (Olff *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; Olff *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 an 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 Qian 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 engineering. 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 then 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,

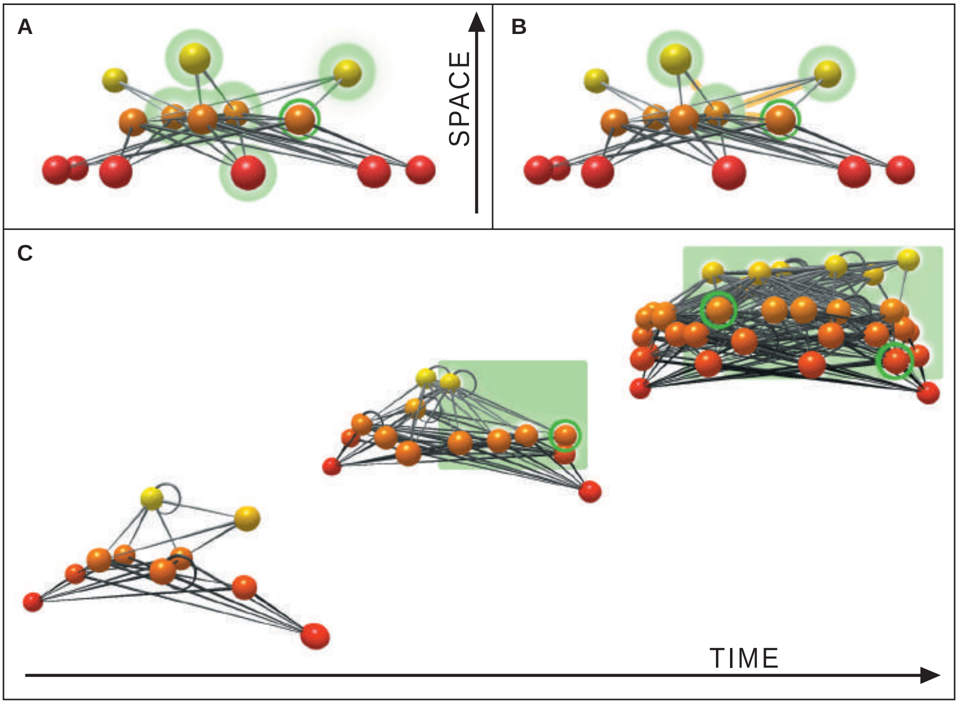

Figure 8.1 Schematic overview of the impacts of ecosystem engineering on the structure and dynamics of interaction webs. The ecosystem engineer in each web is indicated by a green circle and the green shaded areas represent its engineering effect. Ecosystem engineering can affect interactions webs by 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/S2) 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 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 ecologist 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 disproportionally 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 disproportionally 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 restorations 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 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 interactienetwerken sterk te veranderen in ruimte en tijd.

In inter-getijde 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-getijde 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 geleden 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 m2) 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 structuurbiedende 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-getijde 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-getijde gemeenschappen en dat biobouwers een veel groter ecologisch effect hierop hebben dan hun werkelijke grootte en levensduur suggereert. Biobouwers in inter-getijde 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-getijde gebieden te herstellen en te beschermen.

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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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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

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