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 and distribution of network members, ecosystem engineers can also indirectly affect the number and strength of interactions (e.g. Aguiar and Sala 1994; Arkema et al. 2009)(Fig. 1.1.B: orange links). Hence, the interplay of multiple interactions types such as predation, competition and ecosystem engineering are highly important in structuring ecological communities (as emphasized by Berlow 2004; Olff et al. 2009; Fontaine et al. 2011).

In intertidal soft-bottom ecosystems, for example, recruitment failure is an important factor driving bivalve declines and both predation and loss of ecosystem engineering mechanisms have been suggested as potential underlying causes for this failure (Olafsson et al. 1994; Gosselin and 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 engi-
neering. These findings contribute to an increasing amount of evidence that underlines the importance of the interplay of ecosystem engineering and biotic interactions in structuring intertidal soft-bottom ecosystems, like diatom and seagrasses dominated-mudflats (Weerman et al. 2011; van der Heide et al. 2012).

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

The modification of food webs

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

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

**Ecosystem engineering in space and time**

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

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

Long-range engineering by reef-building bivalves, however, did not only affect the distribution of cockles, but also affected hydrodynamic and sediment conditions up to several hundreds of meters away from the reefs (Kröncke 1996; Bergfeld 1999; chapter 2 & 3). Along this spatial gradient, the abundance of microphytobenthos and several macrofauna and shorebird species was enhanced with increasing distance to the reefs (Donadi *et al.* 2013; Chapter 2 & 3). These findings demonstrate that reef-
building bivalves can affect multiple trophic levels far beyond their own physical spatial boundaries (Fig. 8.1. A), and have the potential to affect biotic interactions at large spatial scales.

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

**Implications for conservation**

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

Despite its protected status, the Wadden Sea is ranked among the most degraded systems and is situated in a state far from its historical baseline (Lotze et al. 2006), mostly due to over exploitation and habitat destruction (Wolff 2000; Lotze 2005;
Wolff 2005; Box 1). Coinciding with this overall degradation, structure-providing and sediment-stabilizing ecosystem engineers like reef-building bivalves and seagrasses, have strongly declined in the Wadden Sea (Lotze 2005; Lotze et al. 2006). Although it has been acknowledged that the loss of these ecosystem engineers caused a simplification and homogenization of the Wadden Sea landscape (Lotze 2005; Reise 2005), the consequences of their loss for the (trophic) structure of the intertidal community have remained largely unclear.

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

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

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

* - based on Swart and van Andel (2008) - *

In the 1970s, the exploitation of mussels and cockles intensified by the introduction of mechanized fisheries. In the early 1990s, the decline of both mussel and cockles as a consequence of this intensification was identified, which increased the public and political awareness about the degradation of the Wadden Sea. In response, the Dutch government announced protection measures (LNV 1993). After five years, in 1998, these measures were assessed by an unpublished ecological evaluation study (EVA I). It was concluded that full recovery after fishing had not taken place. However, because of strong fluctuations in cockle densities and because of the short study period, definitive conclusions could not be made (LNV 1998). Furthermore, it was stated that dredging is unlikely to affect the top layer of the sediment and that hydrological processes cause turbidity and deposition of fine material in the top layer of the sediment (Scholten and Kaag 1998). Based on these findings, the Dutch government concluded that there was no need to ban the mechanized cockle fishing. Only after a second inconclusive evaluation study (EVA II; 1999–2003), the
publication of several studies carried out in full independence of the governmental process (Piersma and Koolhaas 1997; Piersma et al. 2001) and an independently organized expert congress at the University of Groningen, the Dutch government finally bought out the destructive cockle dredging industry (for 122 million Euro) in 2004.

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

Findings in this thesis and recent literature now demonstrate that biotic processes also play a major role in the structuring the Wadden Sea ecosystem. Ecosystem engineers like mussels, cockles and seagrass have a much larger ecological impact on the intertidal community than their actual size and lifespan suggests and they can generate strong positive feedbacks (e.g. van de Koppel et al. 2005; Donadi et al. 2013; Donadi et al. submitted; this thesis). Loss of ecosystem engineers can therefore result in 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.