Summary
Samenvatting
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-exclusion 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.